

Is fine sediment deposition a main driver for the composition of benthic macroinvertebrate assemblages?

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ABSTRACT

Intensive agriculture causes increased fine sediment and nutrient runoff into running waters. Despite various approaches to quantify the entry of fine sediment into streams, its biological impact is not well understood. In particular, it is unclear whether the potential effects on the biota can be explained by fine sediment loads alone or in combination with other physicochemical and/or hydrological impacts. In this study, we investigated the impact of fine sediment deposition relative to other impacts on the benthic macroinvertebrates in small headwaters in Luxembourg, a region that is sparsely populated and characterised by agricultural land use on the hills and wooded stream valleys. The surficial-deposited fine sediment, content of inorganic sediment, proportions of organic matter, and carbon to nitrogen (C/N) ratio were recorded 1 year. The stream macroinvertebrate assemblages were recorded in the spring and autumn using multi-habitat sampling. A partial canonical correspondence analysis (pCCA) was applied to quantify and verify the impact of individual sediment components and other environmental variables on the community composition, whereas redundancy analysis (RDA) was used to examine the impact of environmental variables on the macroinvertebrate diversity and functional metrics. Oxygen content, C/N ratio as well as fine gravel explained best both the taxa composition and macroinvertebrate metrics, whereas large-scale variables such as land use were less important. The biological response to oxygen deficits and the C/N ratio of the deposited fine sediment indicate the potential effects of fine sediment deposition through oxygen consumption.

Our results show that the chemical composition of the deposited sediment is more important than the amount of sediment, as the C/N ratio alone explained a substantial amount of variance in species composition. Thus, we suggest that future studies on the impact of fine sediment on the macroinvertebrate community should focus on small-scale factors, including the chemical composition of the deposited fine sediment in combination with the physicochemical and hydromorphological stream parameters.

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1. Introduction

High amounts of fine sediment are delivered into aquatic systems, mainly through intensive agriculture (Walling and Fang, 2003; Collins and Anthony, 2008; Collins et al., 2011). Although the problem is widely recognised, little is known about the response of biota to fine sediment deposition (Rowe et al., 2003; Bryce et al., 2008; Collins et al., 2011).

Most of the research on the entry of fine sediment and its effects focused on suspended sediment, which can be determined relatively easily (Rowe et al., 2003; Collins et al., 2011). Several studies have addressed bedded subsurface fine particles,

which were recorded as substrate composition during freeze-core analyses (Carling, 1981; Ricking and Schulze, 2003). The measurement of suspended fine sediment from interstitial spaces was conducted by Soulsby et al. (2001) and Larsen et al. (2009); sediment-disturbing methods, such as shower sampling (e.g., Kaller and Hartman, 2004) or the imbedding of sediment traps into the streambed (e.g., Fox, 2011), have also been performed. Few studies investigated surficial sediment deposition, which is mostly estimated visually as the substrata bed-cover percentage (e.g., Zweig and Rabeni, 2001; Rowe et al., 2003; Bryce et al., 2008) or identified by proxies, such as flow patterns (partially by Extence et al., 2011). However, the amount of deposited fine sediment is difficult to quantify as no standard method yet exists. Moreover, sediment loads exhibit high spatial and temporal variability (Acornley and Sear, 1999; Collins et al., 2011) exacerbating the quantification of the sediment deposition.

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Elevated fine sediment levels in the suspended solids or the streambed sediments are known to have a wide range of effects on the aquatic biota. Sediment transport and movement of particles affect the feeding and attachment mechanisms of benthic macroinvertebrate such as the clogging of filter-feeding molluscs or blackflies, and the destruction of nets of feeding caddisfly larvae (Kurtak, 1978; Gaugler and Molloy, 1980; Armitage and Blackburn, 2001; Jones et al., 2011). The siltation of streambeds can change the behaviour of organisms by hindering their motility and increasing the drift rate (Culp et al., 1986; Molinos and Donohue, 2009; Larsen and Ormerod, 2010; Jones et al., 2011), and can affect the availability of habitats through a lack of substrate diversity, sediment aggregation and clogging of the interstitial spaces between stones with fine sediment (Burton and Johnston, 2010). This situation can affect the availability of food sources, including the supply of organic matter, and a shift of the periphyton quality (Schofield et al., 2004), thereby influencing the community composition with regard to the richness and abundance of certain invertebrate groups (reviewed by Jones et al., 2011). Indirectly, the entry of fine sediment and organic matter can influence the physical and chemical conditions in streams due to the filling of the interstitial spaces with fine particles, resulting in an increase in decomposition. As a result, the oxygen availability can decline, which is lethal for salmonids spawning in gravels beds and young freshwater pearl mussels (Soulsby et al., 2001; Österling et al., 2010).

Both the sediment load in running waters and aquatic biota are a result of the catchment land use, surrounding vegetation, and in-stream conditions characterised by the geomorphology, hydrology, and topography (Allan, 2004). The non-point input of terrestrial sediments due to soil erosion from tillage or livestock trampling is frequently combined with a runoff of fertilisers, and pesticides and thus is correlated to other stressors (Lenat, 1984; Cooper, 1993; Jones et al., 2001; Allan, 2004). The organic pollution directly or indirectly caused by fertilisers can reduce the abundance of sensitive species (Lenat, 1984; Friberg et al., 2010). Conversely, the surrounding riparian vegetation, such as deep-rooted grasses or trees, stabilises stream banks (Lyons et al., 2000; Allan, 2004; Søvik and Syversen, 2008) and traps sediment and nutrients, thereby reducing the input into aquatic systems (Tomer et al., 2008).

Upland streams are characterised by riffle-pool sequences, a high heterogeneity of substrates, and habitats with different hydrological conditions (Montgomery and MacDonald, 2002). The effect of fine sediment deposition might be expected in riffles due to a high supply of sediment or the accumulation of mud on stones and periphyton, whereas pools may act as natural sinks. The deposited inorganic fine sediment is accompanied to a varying degree by particulate nutrients and organic matter (Parkyn, 2004), and the proportion of mineral particles to organic matter is crucial for decomposition processes and for the quality and availability of food for aquatic macroinvertebrates.

In this study, we measured the fine sediment deposition in 29 riffles and 29 pools of headwater streams 1 year; all of the sites were also subject to standardised macroinvertebrate sampling and the recording of additional environmental variables. With this data, we addressed the following research questions: (1) Do benthic macroinvertebrate assemblages on the reach scale respond to the increased amount of fine sediment deposition? If so, which part of the variability in the community composition is explained by fine sediment deposition in comparison to riparian and catchment variables and physicochemical conditions? (2) Which biotic indices best reflect the biotic response to fine sediment deposition? (3) Is there a quantifiable relationship between the deposition components (amount of fine sediment, organic matter or C/N ratio)? Which component of deposited fine sediments affects the aquatic macroinvertebrate community the most?

2. Materials and methods

2.1. Study streams

The study area is situated in the Ardennes mountain range in northern Luxembourg (Europe) at elevations ranging from 286 to 530 m above sea level (Fig. 1). The region is characterised by rock and clay or silt layers, which tend to experience soil erosion due to the dominant agricultural land use of the upper slopes (Colling et al., 1994).

A total of twenty-nine stream reaches, with catchment sizes ranging from 0.4 to 6.4 km² and 1st or 2nd stream orders, were selected in a way that the total study sites covered riparian zones dominated by non-native coniferous forests (mainly *Picea abies*) and deciduous forests (*Fagus sylvatica*, *Carpinus betulus*, and *Quercus petraea/robur*). The stream reaches were 3–7 m wide, with a wetted zone of 0.5–4 m and substrata dominated by boulders and gravel. The stream waters were well-oxygenated with average nitrate concentrations of 10.77 mg NO₃⁻ l⁻¹, average pH values of 7.4, and conductivities ranging between 126 and 253 μS cm⁻¹. The macroinvertebrate communities were diverse and characterised by spring brook species dominated by Ephemeroptera, Plecoptera and Trichoptera.

2.2. Environmental parameters

We recorded 28 environmental variables characterising the catchment, riparian zone, and in-stream features specifying the deposition parameters, cover of bottom substrates, cover of deposited fine sediment, morphometry, and physicochemical parameters.

Data for the catchment area (km²), land use type and their cover were deduced partly from the project Interreg Projekt NATOUR and Occupation Biophysique du Sol (OBS, 1999) and completed for the sampling sites using ArcGIS version 9.2 (Environmental Systems Research Institute, ESRI) (Table 1). The land-use categories were based on Corine Land Cover, third level (Commission of the European Communities (CEC), 1993). The forest area was subdivided into deciduous, mixed and coniferous forests.

The riparian vegetation type (deciduous forest, coniferous forest, and grassland; mean ± standard deviation and range % of the total area) and amount of shadowing (mean ± standard deviation % of the total area) were recorded as a proportion of the total cover for a stretch of 25 m up- and downstream and a width of 5 m from the banks of the sampling sites (Table 1).

The deposited fine sediment (<2 mm in diameter) was collected upstream of the macroinvertebrate sampling sites to avoid the entry of additional sediment through macroinvertebrate sampling from September 2008 to September 2009 at two sections (one riffle and one pool) at each tested reach. Artificial turf mats (10 cm × 15 cm) were used for the sampling. The mats were anchored with cable ties and iron sticks to the streambed; at three-week intervals, the mats were carefully removed and placed into zip-lock plastic bags to avoid the loss of sediment and transferred to the laboratory. After the collection, new mats were placed at the same locations to enable consecutive sediment sampling. In the laboratory, the upside-down mats and associated water were transferred to aluminium dishes. The residue in the zip-lock bags was suspended with as little tap water as possible and washed into the corresponding aluminium dish. Following these preparations, the mats were left to suspend of sediment for a couple of hours. The mats were subsequently washed with additional tap water, and the remaining water from the aluminium dish was rinsed through a sieve (mesh width = 2 mm) to remove coarse inorganic and organic matter. As a result of this procedure, all of the collected sediment from one site was concentrated in one aluminium dish. Next, the

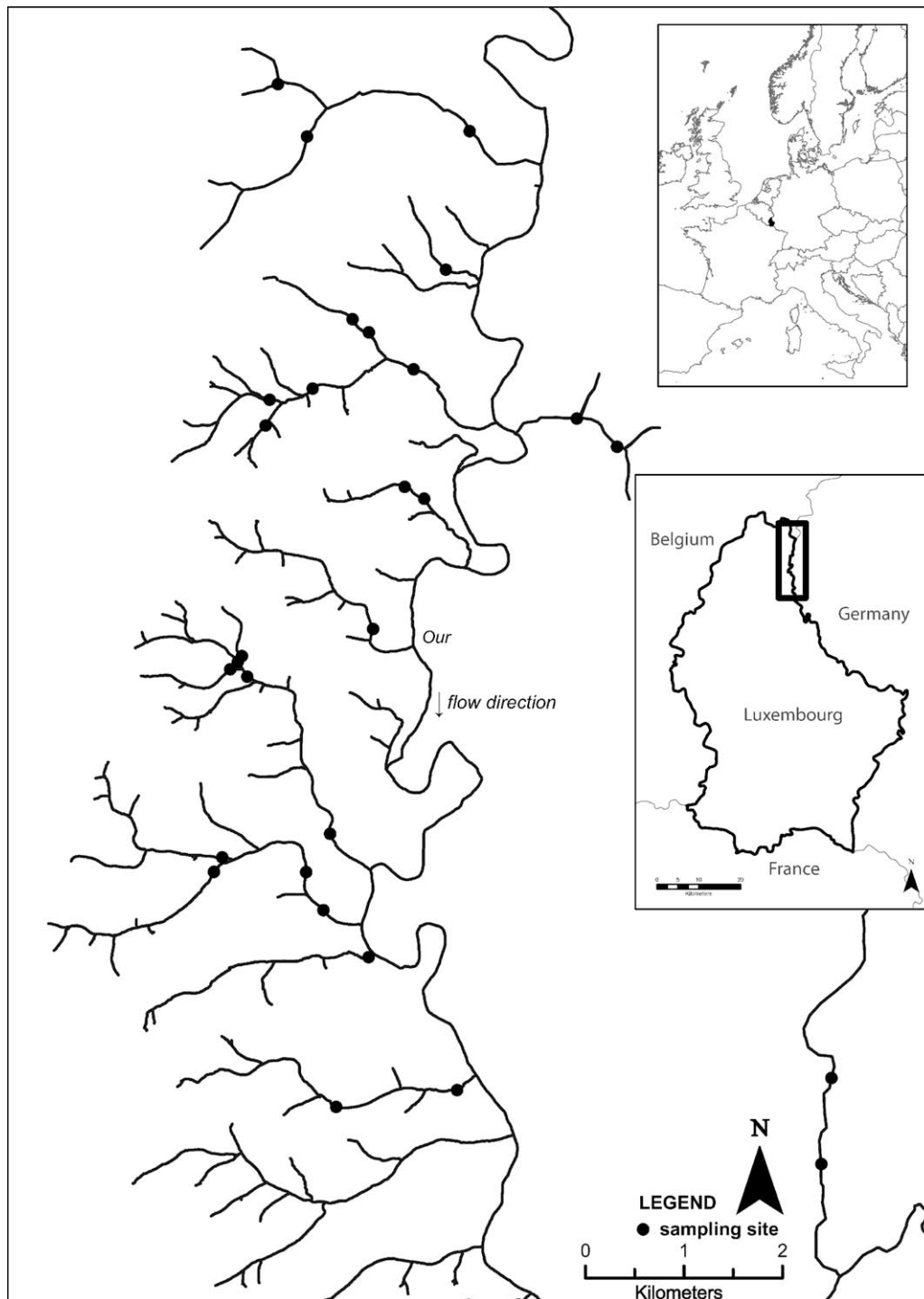


Fig. 1. Sampling sites and streams in the Our catchment (Luxembourg/Germany).

dishes were left undisturbed for at least 2 h to allow the sediment to settle. When the overlaying water was clear, it was removed by suction, leaving only the moist sediment in the dish. The moist sediment was dried in a compartment drier (Memmert, Modell UFE-600) at 100 °C for approximately 5 h. With this procedure, we ensured that the inorganic fraction <2 mm was obtained. All of the samples were weighed using a balance (FAUST FA 1500-2, maximum weight 1.500 g and an accuracy of 0.01 g). The following fine sediment components were obtained. The total carbon (TC) and total nitrogen (TN) were recorded using an Elemental

Analyser (EuroEA, HEKATEch GmbH). The presence of CaCO_3 was evaluated using HCl and was not found in the sediment; hence, the TC equals the organic carbon (OC). The percentage of organic matter was calculated as a multiplication of the OC by 1.724, assuming the soil material contains 58% carbon (Ad-hoc-Arbeitsgruppe Boden, 2005; Rowell, 1994). The C/N ratio was calculated by dividing the organic carbon (OC=OT) by the total nitrogen (TN). The sediment variables were calculated as the arithmetic means for each sampled reach per year. For linking the sediment deposition patterns to the biota, we calculated all of the sediment variables

Table 1
Mean \pm standard deviation (SD) values and range of environmental variables recorded for the 29 sampling sites. CPOM, coarse particulate organic matter. For further explanation, see text.

| Variable | Unit | Mean \pm SD | Range |
|---|--------------------------|------------------|------------|
| Catchment variables | | | |
| Catchment area | km ² | 2.0 \pm 1.6 | 0.3–6.4 |
| Deciduous forest | % | 13.5 \pm 9.3 | 0–30.3 |
| Coniferous forest | % | 19.9 \pm 9.7 | 5.2–45.3 |
| Mixed forest | % | 1.1 \pm 3.2 | 0–15.4 |
| Cropland | % | 26.6 \pm 11.8 | 4.8–57.1 |
| Pasture | % | 30.8 \pm 8.8 | 14.6–47.2 |
| Urban development | % | 3.8 \pm 3.3 | 0–10.8 |
| Riparian zone (R) land use (5 m) | | | |
| Coniferous forest | % | 46.6 \pm 40.4 | 0–100 |
| Deciduous forest | % | 19.1 \pm 32.7 | 0–100 |
| Grassland | % | 7.4 \pm 17.6 | 0–50 |
| Shading | % | 68.4 \pm 29.1 | 0–100 |
| Sediment variables | | | |
| Fine sediment (deposited) | kg m ⁻² | 2.8 \pm 1.2 | 0.9–6.1 |
| Organic matter | % | 11.8 \pm 3.0 | 7.7–18.3 |
| C/N ratio | | 13.1 \pm 1.7 | 10.8–17.3 |
| In-stream variables | | | |
| Fine gravel (0.2–2 cm) | % | 6.7 \pm 8.7 | 0–30 |
| Microolithal (2–6 cm) | % | 21.9 \pm 12.1 | 0–50 |
| Macrolithal (20–40 cm) | % | 8.3 \pm 12.0 | 0–40 |
| CPOM | % | 7.8 \pm 5.1 | 0–20 |
| Dead wood | % | 6.2 \pm 8.7 | 0–40 |
| Cover of deposited fine sediment (<2 mm) (visual estimated) | % | 54 \pm 24.6 | 10–95 |
| Pool | % | 12.4 \pm 10.3 | 2–35 |
| Max. bank height (R/L) | m | 1.07 \pm 0.99 | 0.2–3.5 |
| Physico-chemical parameters (for oxygen mean of two measurements) | | | |
| Oxygen (dissolved) | | 10.2 \pm 0.5 | 9.4–11.6 |
| Oxygen (saturation) | mg l ⁻¹ | 93.4 \pm 4.6 | 85.5–101.2 |
| Conductivity | μ S cm ⁻¹ | 239.5 \pm 48.7 | 146.5–329 |
| NH ₄ ⁺ | mg l ⁻¹ | 0.21 \pm 0.10 | 0.05–0.44 |
| NO ₃ ⁻ | mg l ⁻¹ | 9.13 \pm 1.68 | 4.76–12.60 |
| NO ₂ ⁻ | mg l ⁻¹ | 0.05 \pm 0.02 | 0.01–0.12 |

per season and site (Table 2). The seasons were defined as follows: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

The in-stream parameters of substrate cover, percentage of fine sediments (<2 mm), and morphometry were collected prior to and after each sediment sampling period, the estimates based on a length of 25 m up- and downstream of the sampling site. The percentages of the substrates were estimated prior to the macroinvertebrate sampling; the percentage of fine sediment and the proportion of pool habitats were visually estimated. The maximum value of the bank height was obtained from the right and left bank. The following physicochemical parameters were collected: the pH value; the dissolved oxygen (mg l⁻¹), available oxygen (% of saturation), and conductivity (μ S cm⁻¹) were measured using the Multi350i (Wissenschaftlich-Technische Werkstätten GmbH,

Table 2
Mean \pm SD values and range of fine sediment deposition, organic matter content and C/N ratios for 29 headwater streams sampled in 2008–2009 in the Our catchment Luxembourg (Europe). The organic matter and C/N ratios are proportion of the fine sediment content measured.

| Variable | Season | Unit | Mean \pm SD | Range |
|----------------|--------|--------------------|----------------|------------|
| Fine sediment | Winter | kg m ⁻² | 6.1 \pm 2.4 | 2.0–10.9 |
| Fine sediment | Spring | kg m ⁻² | 2.0 \pm 1.2 | 0.3–4.8 |
| Fine sediment | Summer | kg m ⁻² | 1.3 \pm 1.6 | 0.2–6.6 |
| Fine sediment | Autumn | kg m ⁻² | 1.1 \pm 1.1 | 0.2–5.4 |
| Organic matter | Winter | %/site | 6.6 \pm 2.4 | 3.6–11.6 |
| Organic matter | Spring | %/site | 10.2 \pm 3.4 | 4.9–16.0 |
| Organic matter | Summer | %/site | 15.6 \pm 3.8 | 8.8–24.8 |
| Organic matter | Autumn | %/site | 16.1 \pm 4.7 | 7.4–26.3 |
| C/N | Winter | Ratio/site | 11.7 \pm 1.8 | 9.61–11.2 |
| C/N | Spring | Ratio/site | 13.3 \pm 2.2 | 10.41–18.5 |
| C/N | Summer | Ratio/site | 13.8 \pm 2.0 | 9.6–18.0 |
| C/N | Autumn | Ratio/site | 13.6 \pm 2.1 | 10.5–18.8 |

WTW); and the nitrogen components (NO₃⁻, NO₂⁻, and NH₄⁺) were obtained using a photometric analysis using the 109713 Nitrate Test (Merc Spectroquant® Tests). The conductivity was measured at all of the sediment samplings, and the maximum value per site was used for further analyses. The remaining parameters were measured once per macroinvertebrate sampling season, except for the nitrogen fractions, which were measured in spring of 2009 only.

2.3. Macroinvertebrate sampling

Macroinvertebrate samples were collected using a 25 cm \times 25 cm frame shovel sampler (500 μ m mesh width) in two seasons: 29 samples in the early autumn of 2008 (September/October) and 29 in the spring of 2009 (March/April). The substrate composition was estimated prior to the multi-habitat sampling procedure (Barbour et al., 1999; Hering et al., 2004). Ten samples reflecting the substrate composition were collected in the riffles and pools within a 25 m stretch, preserved (96% ethanol), and transferred to the laboratory for sorting, identification, and counting. When possible, the organisms were identified to the species level with the exception of Oligochaeta (family level) and Diptera (mostly family or tribus level). For further analysis, taxalists resulting from both of the sampling seasons were tallied and used for the calculation of the taxa composition and density for each reach. With the resulting composite taxalists, we calculated the biotic indices and species traits that potentially reflected the influence of fine sediment deposition, such as the diversity and functional metrics (Table 3).

2.4. Biological indices

Twelve biotic indices and species traits were assumed to reflect the impact of sediment on the benthic macroinvertebrates and

Table 3
Mean \pm SD of biological metrics calculated for the 29 sampling sites.

| Biotic indices | Unit | Mean \pm SD | Range |
|---|------|-------------------|-------------|
| Shannon-Wiener-Index | | 3.02 \pm 0.36 | 1.86–3.48 |
| Evenness | | 0.74 \pm 0.08 | 0.47–0.85 |
| Pelal | % | 9.54 \pm 6.44 | 2.59–37.10 |
| Agryllal | % | 0.35 \pm 0.51 | 0.00–1.92 |
| Gatherer/collector | % | 33.20 \pm 7.33 | 17.44–52.62 |
| Grazer | % | 25.71 \pm 6.39 | 10.40–36.04 |
| Active filter | % | 3.87 \pm 2.77 | 0.88–12.49 |
| Passive filter | % | 5.87 \pm 6.50 | 0.76–33.87 |
| Predators | % | 8.00 \pm 2.87 | 2.03–13.75 |
| Burrowing/boring | % | 18.00 \pm 8.02 | 5.72–39.44 |
| EPT richness | % | 57.22 \pm 15.38 | 24.54–79.55 |
| LIFE (Lotic-Invertebrate Index for Flow Evaluation) | | 7.85 \pm 0.22 | 7.31–8.21 |

were calculated using Asterics 3.3 (ASTERICS, 2008) (Table 3). We utilised a metric of the invertebrate richness/diversity using Shannon-Wiener-Index (Shannon and Weaver, 1949) and Evenness. The composition/abundance was addressed by the proportion of Ephemeroptera, Plecoptera, and Trichoptera (EPT). The functional measures, such as the microhabitat preference, feeding types, and locomotion types (Schmidt-Kloiber and Hering, 2012), potentially provide additional information on the response to sediment deposition. We selected a proportion of the species preferring habitats of pelal (mud) and agryllal (clay) because the occurrence of these groups may be increased by a high accumulation of mud and clay. The enhanced load of inorganic and organic particles affects both the food source quality and availability; the effect is assumed to be positive for gatherer/collector and passive filter feeders (excess of food) and negative for grazers (reduction of periphyton composition; Schofield et al., 2004), active filter feeders (clogging of filters), and predators (high turbidity decreasing the visual range). Furthermore, metrics indicating the locomotion type of the invertebrates were chosen, such as the proportion of burrowing/boring organisms, to test whether a disturbance in the streambed due to clogging and the embeddedness of interstitial spaces may affect the biota. Lastly, we selected the Lotic-Invertebrate Index for Flow Evaluation (LIFE, Extence et al., 1999), which provides information on flow preferences of different invertebrate species and is highly correlated to the Index of Proportion of Sediment-Sensitive Invertebrates (PSI; Extence et al., 2011).

2.5. Statistical analysis

Different ordination methods were used to assess and quantify the impact of the 28 environmental variables and deposited sediment components on the macroinvertebrate community composition and biotic indices. First, a detrended correspondence analysis (DCA) was used to determine the gradient lengths of the response variable data sets (i.e., the community composition and diversity and functional indices). As the gradient length of the community composition data was >1.5 standard deviation units, a canonical corresponded analysis (CCA) as a unimodal method was used to analyse the response of the community composition to environmental variables. Forward selection with Bonferroni correction was used (499 Monte Carlo unrestricted permutations) to identify the single environmental variables explaining the variation in the community composition and metrics. Because the catchment area proved to be dominant within the data set, this parameter was run as a co-variable in the CCA to partial out its influence on the explanatory power of the remaining variables. Furthermore, a partial CCA (pCCA; Borcard et al., 1992) was used to separate and quantify the effect of the sediment components (fine sediment, organic matter and C/N ratio) on the community composition.

In pCCA, the variation in the macroinvertebrate community composition was partitioned and the effect of the sediment components was quantified. In the first run, a CCA with all three sediment components was performed to quantify the total variance (explained and unexplained). Then, several partial CCAs (pCCAs) were performed with two sediment components as main explainers and the third component as co-variables and vice versa. For instance, a run consisted of fine sediment and organic matter as two main explainers and the C/N ratio as co-variable. This step was repeated several times with different combinations of all sediment components, resulting in a total of 13 runs. With three sediment components, the total variation of the macroinvertebrate community composition was then partitioned into seven components including covariance terms. The variation explained by these components is then subtracted from the total variation to obtain the unexplained variation. This procedure was repeated for each season (autumn 2008 and spring 2009) separately.

The DCA with the metric data revealed a gradient length <1.5 standard deviation units; thus, the metrics were analysed using redundancy analysis (RDA; Ter Braak and Šmilauer, 2002). Forward selection with Bonferroni correction was also used (499 Monte Carlo unrestricted permutations) to determine the significant variables explaining the variation within the biological metrics.

Linear regression was used to evaluate the relationship between the amount of fine sediment (kg m^{-2}) and percentage of organic matter and C/N ratio and between the percentage of organic matter and the C/N ratio of the sediments (arithmetic means per annum and site).

Prior to the statistical analyses, all of the environmental variables, catchment area, morphometric data, chemistry data, and content of fine sediment were log-transformed ($x+1$). The land-use/vegetation cover and substrate variables and shading and percentage of organic matter were square-root-transformed. The community composition data, biological metrics, and C/N ratio were processed untransformed. All of the ordination methods (CCA, RDA and pCCA) were performed using CANOCO Version 4.5 (Ter Braak and Šmilauer, 2002), and the linear regressions were performed using Statistica 10.0 (Statsoft Inc., 2009).

3. Results

3.1. Relationship between environmental variables and community composition

All of the environmental variables explained 20.8% (cumulative percentage of species data of the first two CCA axes) of the variance in the benthic invertebrate assemblages. The variance in the community composition was best explained by the oxygen saturation, 15% ($F=2.56$; $p=0.002$), followed by the percentage of fine gravel on the streambed (13%; $F=2.38$; $p=0.002$) and C/N ratio (11%; $F=2.04$; $p=0.002$). The catchment variables, such as land-use cover and the amount of deposited fine sediment in the sampling sites are not significant for explaining the community composition (Fig. 2).

Many taxa were correlated with the presence of fine gravel on the streambed, such as *Brachyptera risi* (Morton, 1896), *Nemurella pictetii* Klapalek, 1900, *Nemoura* sp., *Siphonoperla* sp. (Plecoptera), *Simulium* sp., *Tipula* sp. Linnaeus, 1758 (Diptera), and *Gammarus fossarum* Koch in Panzer, 1836 (Crustacea) (Fig. 2). The oxygen saturation is positively related to *Rhithrogena semicolorata*-Gr. (Ephemeroptera) but negatively to *Sialis fuliginosa* Pictet, 1836 (Megaloptera), *Ibisia marginata* (Fabricius, 1781), Psychodidae Gen. sp. (Diptera) and larvae of *Haliplus* sp. A high C/N ratio correlated with *Crunoecia irrorata irrorata* (Curtis, 1834), *Plectrocnemia conspersa* (Curtis, 1834), *Sericostoma personatum* (Kirby and Spencer, 1826), *Wormaldia occipitalis occipitalis* (Pictet, 1834) (Trichoptera)

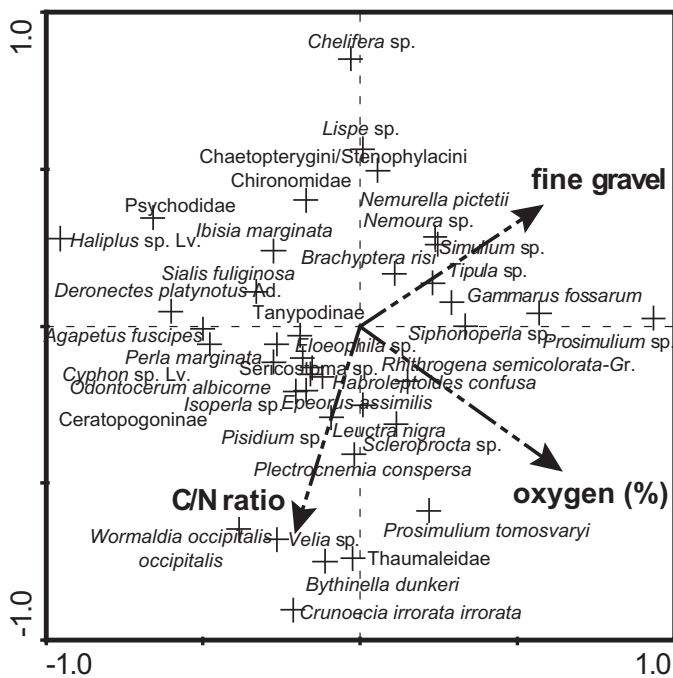


Fig. 2. CCA biplot of significant environmental variables explaining the community composition variation. Taxa with a fit range >10% are also shown. The fit range affords a measure for the variance explained by an individual species (Ter Braak and Šmilauer, 2002). Fine gravel = percentage of fine gravel in the substrate cover; oxygen (%) = oxygen saturation.

Bythinella dunkeri (von Frauenfeld, 1857), *Pisidium* sp. Pfeiffer, 1821 (Bivalvia), *Scleroprocta* sp. Edwards, 1938, Thaumaleidae Gen. sp. (Diptera), *Velia* sp. (Heteroptera), *Leuctra nigra* (Olivier, 1811), *Isoperla* sp. (Plecoptera), *Epeorus sylvicola* (Pictet, 1865), and *Habroleptoides confusa* Sartori and Jacob, 1986 (Ephemeroptera).

3.2. Relationship between environmental variables and biological metrics

Two environmental variables explained 33.6% of the variance in the biotic metrics (cumulative percentage of the metric data of the first two RDA axes): the C/N ratio in the deposited fine sediment explained 18% ($F=6.83$; $p=0.004$) and dissolved oxygen 16% ($F=5.42$; $p=0.016$) of the variance in the biotic metrics. The content of dissolved oxygen was linked to the abundance of passive filter feeders, such as caddisfly larvae (e.g., *Philopotamus ludificatus* and *Hydropsyche instabilis*), but it was negatively correlated to the gatherers and sediment collectors (e.g., worms and certain Ephemeroptera, respectively; Fig. 3). The C/N ratio was connected with taxa richness, such as the evenness, Shannon-Wiener-Index and EPT richness, burrowing/boring biota and LIFE metric, and correlated negatively to the number of active filter feeders (e.g., molluscs) and taxa preferring the pelal. The remaining metrics showed no obvious relationships.

3.3. Relationship between components of the deposited fine sediment to each other and to the taxa composition with regard to the season

The amount of deposited fine sediment was negatively correlated to the organic matter content with high significance ($R^2=0.51$, $p<0.0001$) and the C/N ratio ($R^2=0.46$, $p<0.0001$; Fig. 4A and B). In contrast, the correlation between the organic matter and the C/N ratio is positive but weak ($R^2=0.32$, $p<0.05$; Fig. 4C).

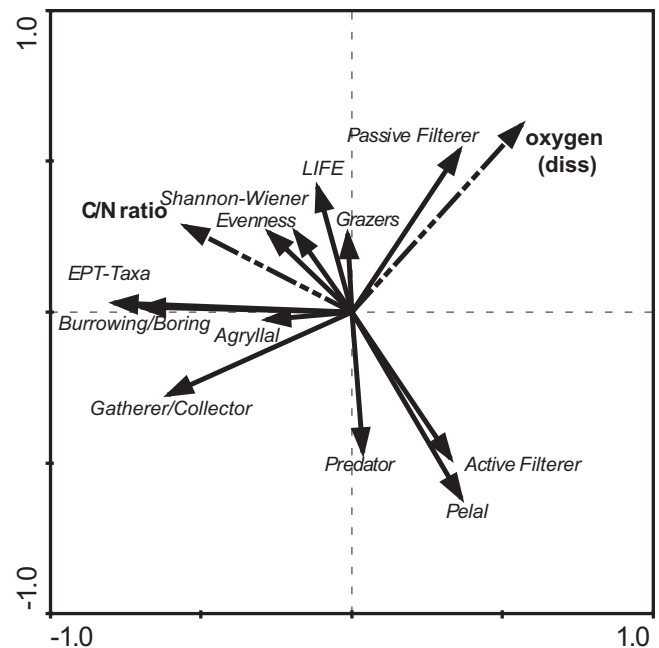


Fig. 3. RDA biplot of the environmental variables in relation to the selected biotic metrics. Only significant variables are shown. LIFE, Lotic-Invertebrate Index for Flow Evaluation; EPT-Taxa, proportion of Ephemeroptera, Plecoptera, and Trichoptera; oxygen (diss), dissolved oxygen.

The amount of deposited fine sediment, proportion of organic matter, and C/N ratio explained 57.1% of the total variance in the taxa for the autumn samples and 52.9% for the spring samples (Fig. 5A and B). For both seasons, the unique effect of the tested variable on the taxa is explained best by the C/N ratio (20.1% autumn; 18.1% spring) and second-best by the organic matter (14.9% autumn; 15.2% spring) followed by the content of fine sediment (14.5% autumn; 15% spring; Fig. 5A and B). In comparison, the high cumulative effect of the C/N ratio, which was recorded as a total of the combined and unique effect, was higher in the autumn and lower in the spring (Fig. 6A and B). The cumulative effect of the fine sediment on the biota was strong in comparison to the unique value for both seasons (Figs. 5 and 6). The cumulative explanation power was higher for the autumn assemblages than the spring assemblages (Fig. 6A and B).

4. Discussion

4.1. Relationship between environmental variables and taxa composition

As a criterion of microbial decomposition, the in-stream variability, characterised by the oxygen saturation, substrate composition and C/N ratio, explained approximately 20.8% of the variance of the macroinvertebrate composition. Certain taxa, mainly occurring in the lentic sections, e.g., larvae of Psychodidae (Diptera) and larvae of alderflies (*S. fuliginosa*), are tolerant to oxygen limitation. Several taxa preferred the sections of fine gravel, including the larvae of Plecoptera (e.g., *N. pictetii* and *Nemoura* sp.), which are associated with gravel (Graf et al., 2007), whereas the larvae of the crane fly *Tipula* sp. prefer the wet zone along the shoreline. The strong relationship with the substrate can partly be explained by the preference for certain food sources (Lammert and Allan, 1999; Rempel et al., 2000; Usseglio-Polatera et al., 2000; Piscart et al., 2009). Another impairment reflected by the substrate composition is the clogging of the interstitial spaces between the gravel particles by fine sediments, which may

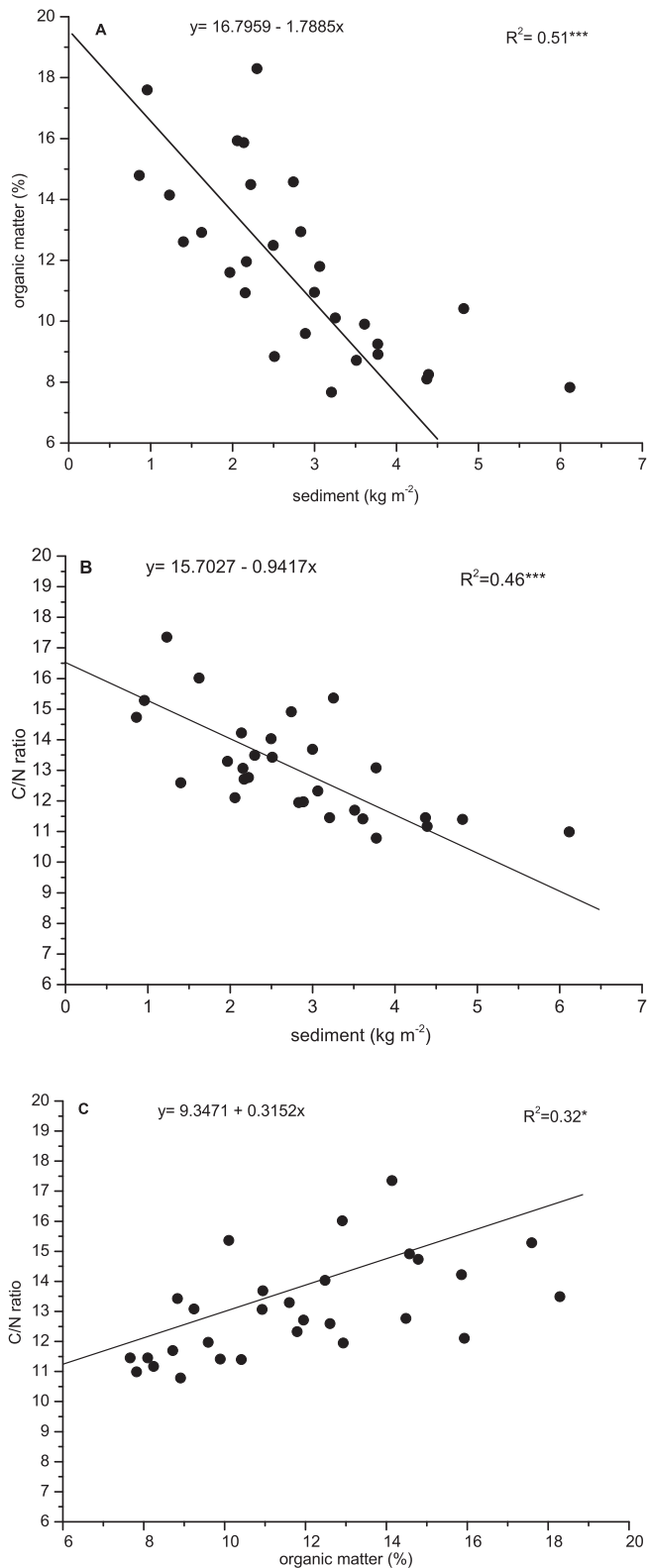


Fig. 4. Linear regression between the components of fine sediment (mean per year at 29 sites showing (A) the amount of fine sediment (kg m^{-2}) and organic matter (%), (B) the amount of fine sediment (kg m^{-2}) and C/N ratio, and (C) the organic matter (%) and C/N ratio. Statistical significance: * $p < 0.05$; ** $p < 0.001$; *** $p < 0.0001$.

particularly affect the early larval instars of several taxa living in the hyporheic zone (Minshall, 1984). Several Trichoptera (e.g., *C. irrorata irrorata*, *P. conspersa*, and *W. occipitalis occipitalis*), molluscs (*B. dunkeri* and *Pisidium* sp.), and Plecoptera (*L. nigra* and

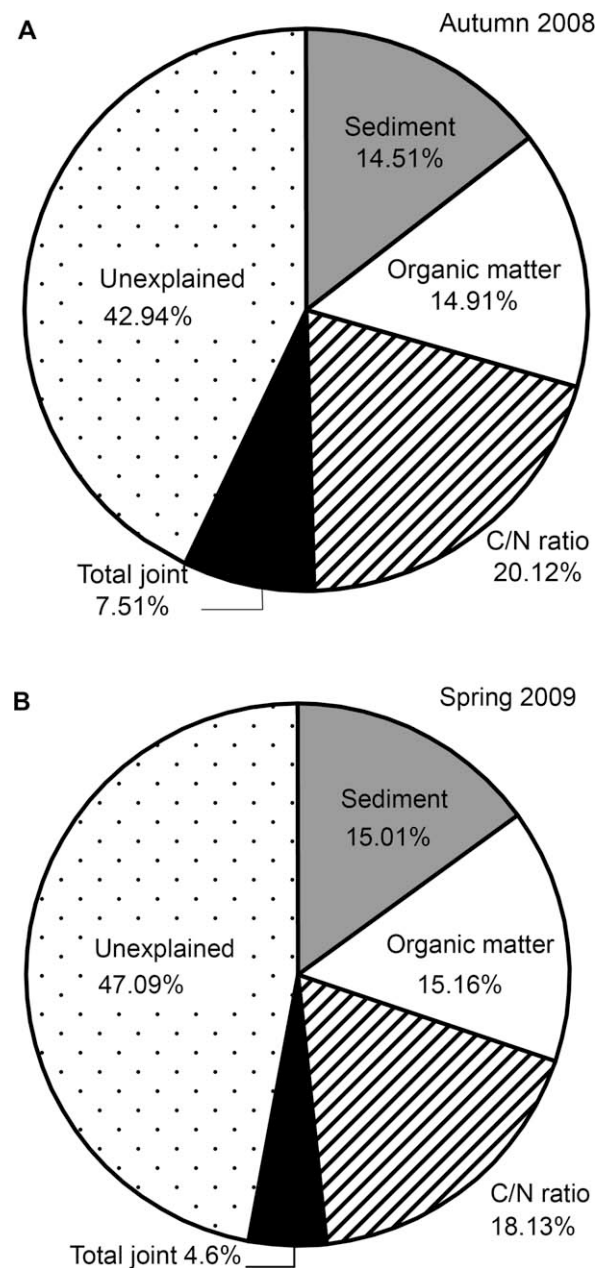


Fig. 5. The sources of variation in the invertebrate composition explained by three components of the fine sediment for autumn 2008 (A) and spring 2009 (B). The percentages of the unique variation for the deposited fine sediment (kg m^{-2}) in grey, percentages of organic matter in white, the C/N ratio (banded), the combined variance of all of the components (in black) and unexplained variance (dotted) of the macroinvertebrate composition are shown.

Isoperla sp.) predominantly occurred in the sites with a high C/N ratio. The abundance of these taxa ranged from sporadic (*W. occipitalis occipitalis* and *C. irrorata irrorata*) to highly dense (*Isoperla* sp. and *L. nigra*). Most of these taxa prefer spring brooks and are sensitive to organic pollution; therefore, they prefer unimpaired sites with high C/N ratios. The C/N ratio has a greater effect on the biota than the remaining physicochemical parameters (except for the oxygen saturation). The long-term effect of nutrients in deposited fine sediment might therefore be a key factor for shaping the macroinvertebrate community by impacting the bioavailability of oxygen and dissolved nutrients at the microhabitat level. However, these results could be not validated by other physicochemical variables, such as the biological oxygen demand consumed in

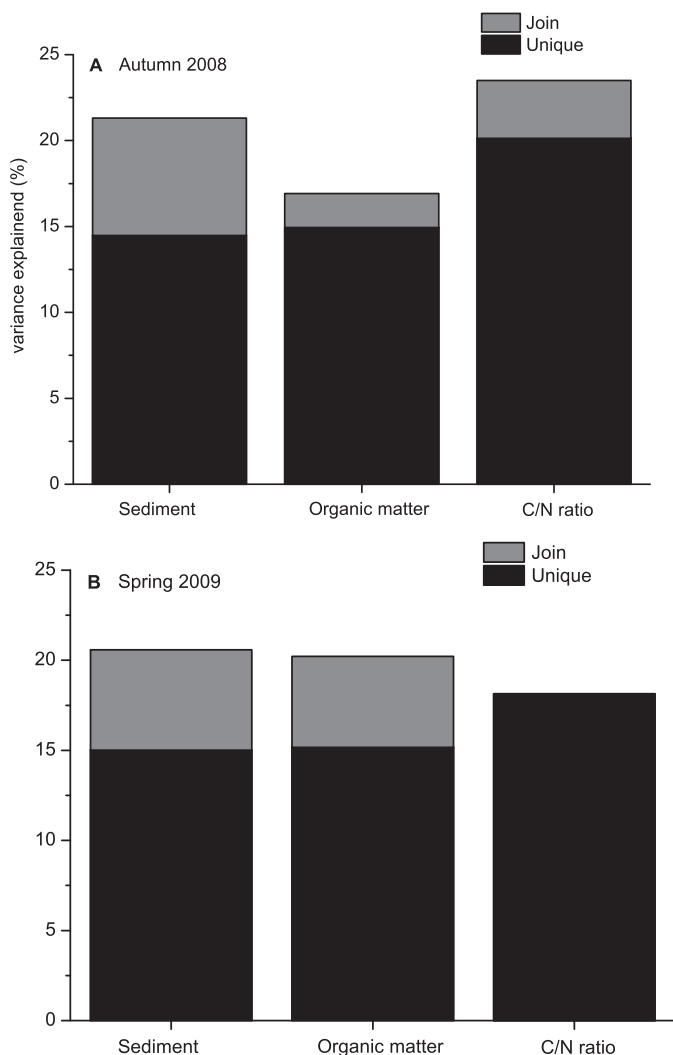


Fig. 6. The cumulative effect of the fine sediment components on the taxa composition in autumn 2008 (A) and spring 2009 (B).

5 days by bacteria (BOD_5) or hardness, because these variables were not recorded. In contrast to the C/N ratio, the amount of fine sediment and the proportion of organic matter have no significant effect on the composition of taxa. The C/N ratio affects the physiological conditions directly, whereas the ecological impact of increased amounts of fine particles on the biota is wide-ranging and more complex. The critical effect of fine particle release might be dependent on the physicochemical and hydrological streams conditions. The response of aquatic insects to the sediment load might also be influenced by their actual life stage, i.e., emergence or juvenile. For instance, Hanquet et al. (2004) found that the larvae of *Ephemera danica* prefer different sections of the substrate, depending on larval stage. The young larvae occur in the sections with a higher frequency of coarse substrates and in medium depth, whereas larger nymphs prefer shallow and sandy sections. Many studies suggested that the land-use cover in the catchment and riparian land can predict the biota diversity (e.g., Lenat, 1984; Fritzpatrick et al., 2001), and this linkage is based on the terrestrial provision of nutrients and the alternation of structures in the surrounding area (Lammert and Allan, 1999; Vondracek et al., 2005; Yates et al., 2007). The relationship between the catchment land cover and riparian vegetation to the biota could not be demonstrated directly by our results. Allan (2004) suggested that the impact of land-use variables on the biota is the highest when the

land-use status in the catchment area ranges from nearly natural to degraded. This co-variation of the anthropogenic and natural gradient in our study is marginal because of the typical topography of low mountain ranges. This rural region is sparsely populated and dominated by agricultural use in the upper hills and wooded downstream areas. However, the impact of the land-use cover was indirectly connected through the physicochemistry in our study.

In conclusion, our results lend support to the conjecture that chemical composition of the deposited substrates plays a major role and small-scale in-stream factors are crucial for the macroinvertebrate community composition of small streams, which is in contrast to what has been described for streams of a higher stream order (Vondracek et al., 2005; Feld and Hering, 2007; Walsh et al., 2007; Wasson et al., 2010). Hence the land use cover such as in particular the proportion of urbanisation or riparian zone is also a strong significant for the taxonomic composition.

4.2. Relationship between environmental variables and biological metrics

Only two in-stream variables, the C/N ratio and oxygen solubility, were related to the metrics; the remaining variables, including the amount of fine sediment in the deposition, were not significantly linked. In several studies regarding the increase of the fine sediment load, a decline of taxa richness (e.g., Cline et al., 1982; Quinn et al., 1992; Jones et al., 2011) and proportion of EPT taxa (Kaller et al., 2001; Matthaei et al., 2006; Pollard and Yuan, 2009) was observed. Those changes in the biota were caused by the modification of the substrate and food sources and by behavioural changes. The C/N ratio is associated with the processes of decomposition and nitrification, which impact the food quality and particularly affect the oxygen concentration. The patches of deposited fine sediment are probably characterised by a reduced oxygen uptake, which alters the diversity of certain sensitive species.

The linkage of the taxa preferring muddy habitats to the physicochemical conditions was obvious, as these taxa tolerate the limitation of oxygen to a greater extent. However, the occurrence of active filterers was negatively correlated to the C/N ratio, and these taxa were generally rare in the spring brooks. In our study, this group was dominated by the mayfly *E. danica* and the mollusc *Pisidium* sp., which occupy muddy substrates that are characterised by a high level of oxygen consumption due to the deposition of fine particles. Passive filterers (for example larvae of the black fly Simuliidae) occurred mainly at the sites with high oxygen saturation, being feeding groups that usually benefit from the supply of particles and an enhanced oxygen availability. This is also shown by the correlation of the LIFE metric for the flow response of the invertebrates and increase of the C/N ratio and amount of oxygen.

4.3. Relationship between components of the deposited fine sediment to each other and to the taxon composition with regard to the season

The amount of deposited material per annum is variable, and the ratio between the inorganic sediment and organic matter within this deposited fine material is also variable: the more total material is deposited, the more the proportion of organic material decreases. Although the entry of sediment is a consequence to episodic runoff events, which translates into a short-term increase of the inorganic content, the terrestrial supply of organic matter is more consistent and strongly linked to the surrounding vegetation, such as the dropping of leaves or branches (e.g., Webster et al., 1990; Nietch et al., 2005). The shift between the proportion of a low and high total deposition is caused by the runoff from the surrounding land

and hydrological events throughout the hydrological year, such as discharge peaks (e.g., Delmas et al., 2011).

The weak relationship between the organic matter and C/N ratio suggests that the nutrient content is not solely derived from the organic matter and decomposition processes but is also enhanced through the runoff of fertiliser or animal faeces (e.g., Jarvie et al., 2010). These fractions ultimately accumulate in streambeds.

The results of the pCCA emphasise the high importance of the C/N ratio in comparison to the organic matter and the amount of fine sediment for the benthic macroinvertebrate community and confirm the results of the CCA and RDA with various environmental variables. Aquatic insects represent a wide variety of life history patterns, such as emergence, which has a temporal pattern (Corbet, 1964). Due to this variety, we expected a seasonal difference in the impact of the chemical composition on the taxa composition. The impairment of fine sediment on the biota is equal for both assemblages. In contrast to the organic matter, the cumulative effect of the C/N ratio was stronger in the autumn compared to the spring. These differences might be due to the increase of the algal biomass and the beginning of decomposition processes in the spring, thereby supplying fresh organic matter during this period.

5. Conclusions

The impact of fine sediment on the macroinvertebrate community in running waters has been discussed intensively. In this study, we mainly addressed the question of whether the fine sediment load has a separate effect on the biota or whether the impairment by sediment entry might be intensified as a result of the synergy with variables, such as the flow pattern, solids or nutrient supply (Lemly, 1982; Matthaei et al., 2010; Ormerod et al., 2010). Furthermore, we were interested in the spatial scale to which communities respond, such as the reach scale or patch/microhabitat scale (cf. Larsen et al., 2009). Our results suggest that the chemical composition of fine sediment is mainly responsible for the alternation of the macroinvertebrate community composition in small headwater streams; whereas the overall amount of fine sediment offered no significant explanation for community composition. Both the C/N ratio of the deposited fine sediment and variables representing the oxygen availability were significantly explanatory for the taxa composition. The oxygen demand probably becomes stronger in patches with deposited fine sediment due to silty fractions with lower proportions of fine sand, which is characteristic of fine sediment grains in this region. These cohesive sediments have an affinity for the absorption of organic or toxic components (e.g., Droppo et al., 1997). Agricultural and forested areas dominated in our study; thus, portions of the sediment contain high amounts of nutrients, which can advance the decomposition processes. The significance of fine gravel stretches for the biota reveals the importance of the local stream conditions, which may have a greater effect on the relative abundance of the benthic communities compared to the catchment land-use variables. According to our results, the proportion of EPT Taxa, diversity (Shannon-Wiener-Index and Evenness) and functional metrics such as the LIFE metric are suitable parameters for assessing responses to fine sediment. Although the chemical composition of the sediment load is more important than the actual amount entering the stream, certain mitigation measurements such as having a natural riparian zone, the maintaining of the patchy structure of the stream bed as well the river course help reducing the sediment load into the stream as well as provide more qualitative food such as leaves, and thus reduce the decomposition and the lack of oxygen. However, further experimental studies are needed to measure the impact of sediment load, nutrient supply and oxygen demand of the different fine sediment fractions as well as the impact on aquatic biota.

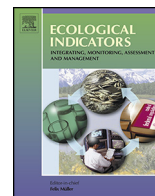
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Short Communication

Developing an improved biomonitoring tool for fine sediment: Combining expert knowledge and empirical data



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Sedimentation

ABSTRACT

The Proportion of Sediment-sensitive Invertebrates (PSI) index is a biomonitoring tool that is designed to identify the degree of sedimentation in rivers and streams. Despite having a sound biological basis, the tool has been shown to have only a moderate correlation with fine sediment, which although comparable to other pressure specific indices, limits confidence in its application. The aim of this study was to investigate if the performance of the PSI index could be enhanced through the use of empirical data to supplement the expert knowledge and literature which were used to determine the original four fine sediment sensitivity ratings. The empirical data used, comprised observations of invertebrate abundance and percentage fine sediment, collected across a wide range of reference condition temperate stream and river ecosystems (model training dataset $n=2252$). Species were assigned sensitivity weights within a range based on their previously determined sensitivity rating. Using a range of weights acknowledges the breadth of ecological niches that invertebrates occupy and also their differing potential as indicators. The optimum species-specific sensitivity weights were identified using non-linear optimisation, as those that resulted in the highest Spearman's rank correlation coefficient between the Empirically-weighted PSI (E-PSI) scores and deposited fine sediment in the model training dataset. The correlation between percentage fine sediment and E-PSI scores in the test dataset ($n=252$) was eight percentage points higher than the correlation between percentage fine sediment and the original PSI scores (E-PSI $r_s = -0.74$, $p < 0.01$ compared to PSI $r_s = -0.66$, $p < 0.01$). This study demonstrates the value of combining a sound biological basis with evidence from large empirical datasets, to test and enhance the performance of biomonitoring tools to increase confidence in their application.

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1. Introduction

Fine sediment (<2 mm) is an essential component of freshwater ecosystems, critical for habitat heterogeneity and ecosystem functioning (Owens et al., 2005). However, when levels deviate from natural conditions, ecological degradation can occur (reviewed in Bilotta and Brazier, 2008). The PSI index is a pressure-specific biomonitoring tool, designed to identify the impacts of deposited fine sediment, using standardised kick-samples of the benthic invertebrate community (Extence et al., 2011). The tool was developed using previous literature and expert knowledge of invertebrate morphological/physiological traits that are associated with either a sensitivity or tolerance to fine

sediment, in order to select and assign species to one of four Fine Sediment Sensitivity Ratings (FSSRs).¹ The tool thus has a sound biological basis and is linked to ecological niche theory (Hirzel and Le Lay, 2008). The sensitivity ratings are used to assign abundance-weighted scores, which are then used to calculate (Eq. (1)) PSI scores ranging from 0 (heavily sedimented) to 100 (unsedimented). Given that rivers vary in their natural sediment conditions/dynamics (Bilotta et al., 2012; Grove et al., 2015), the index is designed to be used alongside a reference-based model (e.g. River Invertebrate Classification Tool), where observed PSI scores

¹ Fine Sediment Sensitivity Ratings (FSSRs): Group A (highly sensitive) and Group D (highly insensitive) – Log abundance scores: 1–9 individuals present = 2; 10–99 = 3; 100–999 = 4; 1000+ = 5; Group B (moderately sensitive) and Group C (moderately insensitive) – Log abundance scores: 1–9 individuals present = 1; 10–99 = 2; 100–999 = 3; 1000+ = 4.

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Table 1
Characteristics of the River InVertebrate Prediction And Classification System sites.

| Site characteristics | |
|--|---|
| Mean annual precipitation (between 1961 and 1990) | 430 mm–2930 mm |
| Mean annual temperature (between 1961 and 1990) | 7.93–11.45 °C |
| Geology | Various – from hard igneous rock to soft sedimentary rock |
| Altitude at river source | 5–1216 m |
| Average river width | 0.4–117 m |
| Average river depth | 0.02–3.00 m |
| Mean annual discharge | <0.31 m ³ s ⁻¹ to >80.00 m ³ s ⁻¹ |
| Slope | 0–150 m km ⁻¹ |
| Substratum percentage cover of fine sediment (<2 mm) | 0–100% |
| Substratum percentage cover of gravels and pebbles | 0–98% |
| Substratum percentage cover of cobbles and boulders | 0–100% |

can be compared to the expected reference-condition PSI scores to determine whether the site is impacted by fine sediment:

$$\text{PSI}(\Psi) = \frac{\sum \text{Scores for Sediment Sensitivity Groups A and B}}{\sum \text{Scores for all Sediment Sensitivity Groups A–D}} \cdot 100 \quad (1)$$

Eq. (1): Formula used to calculate PSI scores using abundance weighted scores.

A recent evaluation of the performance of the index has shown it to have a moderate correlation ($r_s = -0.64$, $p < 0.01$) with fine sediment (Turley et al., 2014). Based on an analysis of 297 biomonitoring tools used throughout Europe (Birk et al., 2012), which found the median correlation coefficient of invertebrate-based indices to be 0.64 in relation to their respective pressure, the correlation between PSI score and percentage cover of fine sediment is comparable to other indices used in the implementation of the EU Water Framework Directive. However, given the implications of incorrect assignment of ecological status of streams for both water and land managers (from unjustified burdens being placed on the users of water resources, to environmental damage going undetected), greater effort is needed to improve the performance of the PSI index and other similar indices. The aim of this study was to investigate if the performance of the PSI index could be enhanced through weighting individual species in each of the FSSRs of the PSI index, based on empirical observations of invertebrate abundance and percentage cover of fine sediment, collected across a wide range of reference condition temperate stream and river ecosystems.

2. Methods

2.1. Data

The main data set used in this study was the RIVPACS IV (May 2011 version) data set (River Invertebrate Prediction and Classification System – NERC [CEH] 2006. Database rights NERC [CEH] 2006 all rights reserved). For a detailed description of the RIVPACS IV data set, see Wright et al. (2000) and Clarke et al. (2003). In summary, the database contains invertebrate, water quality and catchment characteristics data, recorded at each site over at least one year, between 1978 and 2004. The 835 sites, on temperate streams and rivers, were considered to be in reference condition with no, or only very minor anthropogenic disturbances and supporting biota usually associated with such undisturbed or minimally disturbed conditions. The sites comprise a wide range of environments (Table 1), varying in their (i) climate, (ii) catchment geology, (iii) topography and (vi) morphometry.

The invertebrate data within the RIVPACS IV data set were collected from the 835 sites, using a standardised 3 min active kick sample technique with a 900 µm mesh pond net, where all in-stream habitats within the site were sampled in proportion to their occurrence (Environment Agency, 2009). Invertebrate abundance was recorded to species level or to the lowest possible taxonomic unit (Wright et al., 2000). Each site has a season-specific record of community composition²: spring (March–May), summer (June–August) and autumn (September–November).

Fine sediment data were available for all 835 sites within the RIVPACS IV database, including the percentage of the substratum consisting of (i) silt and clay (<0.06 mm), and (ii) sand (≥0.06 and <2.00 mm). The visual assessment method, described in the River Habitat Survey Field Survey Guidance Manual (Environment Agency, 2003) was used to collect these data. This method involves the operator, estimating the substratum composition over a given reach, based on a visual inspection. The values used represent a mean of three seasonal measurements². Whilst this technique does not quantify the volume of deposited fine sediment, which PSI is designed to relate to, it does provide a measure of the percentage cover, which theoretically should be related to the PSI index (Glendell et al., 2013).

2.2. Statistical analyses

2.2.1. Developing the E-PSI index

The relevant data were extracted from the RIVPACS IV database and compiled in Microsoft Excel. Prior to analysis the substratum data <2 mm (sand, silt and clay) were combined and are referred to as percentage fine sediment. The reasons for this were that a recent evaluation of the PSI index found this metric to be the most related to PSI scores (Turley et al., 2014) and further, to acknowledge the difficulties in differentiating between the various fractions using the visual assessment method. Using SPSS statistical software (IBM SPSS Statistics 20), the data were found to be non-normally distributed and show heteroscedasticity and could not be successfully transformed. Therefore, the nonparametric Spearman's rank correlation was used to analyse the relationships. The 835 sites were split using random allocation, to create a training dataset (751 sites, $n = 2252$) and an independent test dataset (84 sites, $n = 252$). This 90:10 split (similar to Kelly et al., 2012) of the dataset was chosen in order to maximise the number of sites used to develop the species weightings, whilst leaving a sufficient amount of data to test these weightings. The PSI formula (Eq. (1)) was re-cast as follows:

$$\text{E-PSI} = \frac{\sum_{j=1}^M w_j \cdot \log A_j}{\sum_{i=1}^N w_i \cdot \log A_i} \cdot 100 \quad (2)$$

Eq. (2): Formula used to calculate E-PSI scores using empirically-derived species sensitivity weights and simplified abundance weighted scores. *Note:* Log abundance categories (log A) in E-PSI were simplified to: 1–9 individuals present = 1; 10–99 = 2; 100–999 = 3; 1000+ = 4.

In this equation, log A_i and w_i are the log-abundance categories and corresponding sensitivity weights for all N species, while log A_j and w_j are the log-abundance categories and sensitivity weights for M sensitive species. Eq. (2) is more flexible than Eq. (1) in varying the sensitivity weightings on a species by species level. In the original PSI index, all species within the same FSSR receive the same log-abundance weights, which were developed through an extensive literature review (Extence et al., 2011) and expert judgements, and were based on invertebrate traits such as physiological and/or morphological adaptations that are associated with either a

² 834 sites have three seasons of data, one site has only two seasons of data.

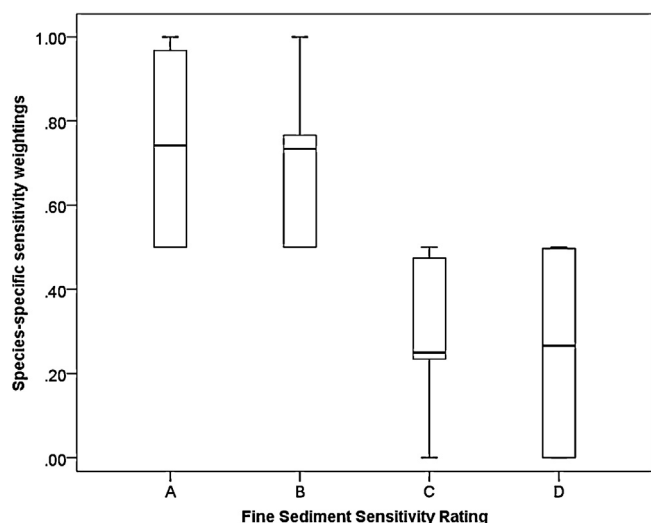


Fig. 1. Distribution of the optimum empirically derived species-specific sensitivity weightings selected for the E-PSI index, within each of the original four Fine Sediment Sensitivity Ratings of the PSI index. Minimum, maximum (shown in the lower and upper whiskers respectively), median (-), interquartile range (boxes).

sensitivity or tolerance to fine sediment. In this study, species weightings were constrained within a range around their original estimates of sensitivity (FSSRs) so as to deviate only slightly, from the expert judgements (Fig. 1) and biological basis. Those species originally identified (FSSRs) as moderately to highly sensitive to fine sediment were assigned a range between 0.5 and 1.0, whilst species identified as moderately to highly insensitive were weighted between 0.0 and <0.5. Sensitive species were assigned this larger weighting as they were deemed to be the most significant species in terms of identifying sediment pressures, whereas those species identified as insensitive, are tolerant of fine sediment but not necessarily directly reliant on it. Using a range of weights acknowledges the breadth of ecological niches that invertebrates occupy and also their differing potential as indicators. The optimum species sensitivity weights were identified using the *fmincon* function (active-set algorithm) of MATLAB (Mathworks, version R2014a). The *fmincon* function is a constrained nonlinear optimisation method (see Mathworks, 2014), which in this study was used to test 100,000 iterations of species sensitivity weightings (within the constraints mentioned above) to find the set of weightings that produced the highest Spearman's rank correlation coefficient between PSI and fine sediment. The set of sensitivity weights that yielded the maximum correlation were used as the Empirically-weighted PSI (E-PSI) for further analysis.

2.2.2. Testing the E-PSI index

In order to evaluate the E-PSI index, the correlation between E-PSI scores and percentage fine sediment was calculated using the test dataset. This correlation was then compared to the benchmark; the correlation between PSI and percentage fine sediment in the same test dataset. In addition, the correlation was compared with those correlations between percentage fine sediment and other non-sediment-specific indices; Average Score Per Taxon (ASPT) (Murray-Bligh, 1999), Lotic-invertebrate Index for Flow Evaluation (LIFE) (Extence et al., 1999), Ephemeroptera, Plecoptera and Trichoptera (EPT) percentage abundance, and EPT percentage richness.

Kruskal–Wallis tests were carried out on both PSI and E-PSI, by grouping the scores into independent groups (0–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90 and 91–100). The Kruskal–Wallis test returns a *p*-value which is used to determine whether any of the groups are significantly different. Groups

Table 2

Spearman's rank correlation coefficients for PSI, E-PSI, LIFE, EPT% abundance, EPT% richness, ASPT, versus percentage fine sediment (<2 mm) for the model training dataset (*n* = 2252) and the model test dataset (*n* = 252).

| Index ^a | Training dataset correlation ^b | Test dataset correlation ^b |
|--------------------|---|---------------------------------------|
| E-PSI | -0.76 | -0.74 |
| PSI | -0.63 | -0.66 |
| LIFE | -0.59 | -0.57 |
| EPT% abundance | -0.59 | -0.56 |
| EPT% richness | -0.55 | -0.52 |
| ASPT | -0.50 | -0.43 |

^a Proportion of Sediment-sensitive Invertebrates (PSI), Empirically-weighted PSI (E-PSI), Average Score Per Taxon (ASPT), Lotic-invertebrate Index for Flow Evaluation (LIFE), Ephemeroptera, Plecoptera and Trichoptera (EPT) percentage abundance, and EPT percentage richness.

^b All correlations are significant at the 0.01 level (2-tailed).

of this size were selected due to the importance of discriminating between different levels of sedimentation, but also to account for the uncertainties in both the sediment and invertebrate data (smaller groups would need to be based on highly accurate and precise data). Pairwise comparisons were then performed using Dunn's (1964) procedure with a Bonferroni correction for multiple comparisons, to determine which groups were significantly different.

3. Results

Fig. 1 shows the distribution of the optimum species sensitivity weightings which were used to calculate E-PSI scores. The set of weightings that comprise the E-PSI index are available in the online supplementary information.

The Spearman's rank correlation coefficients for E-PSI scores versus percentage fine sediment for the model training dataset and the model test dataset are displayed in Table 2. The Spearman's rank correlation for E-PSI versus percentage fine sediment for the model test dataset ($r_s = -0.74$, $p < 0.01$) was eight percentage points higher than the correlation between percentage fine sediment and the original PSI index for the model test dataset ($r_s = -0.66$, $p < 0.01$) and was also stronger than for the other indices tested. Additionally, the correlations between the indices were analysed (Table 3) with all (except ASPT versus E-PSI) showing strong correlations with each other. The E-PSI had a weaker correlation with LIFE, compared to PSI with LIFE ($r_s = 0.77$, $p < 0.01$ and $r_s = 0.91$, $p < 0.01$, respectively).

Fig. 2 illustrates the relationship between grouped E-PSI and PSI scores and percentage fine sediment across the test dataset. Kruskal–Wallis tests showed that percentage fine sediment values were statistically significantly different between the different groups of both E-PSI and PSI scores (χ^2 (9) = 138.44, $p < 0.01$ and χ^2 (9) = 112.80, $p < 0.01$, respectively). Post hoc analysis (pairwise comparisons) identified the groups whose distributions were statistically significantly different from one another. In total, 21

Table 3

Spearman's rank correlation coefficients for relationships between biological indices for the model test dataset (*n* = 252).

| Index ^a | E-PSI ^b | PSI ^b |
|--------------------|--------------------|------------------|
| PSI | 0.86 | 1.00 |
| LIFE | 0.77 | 0.91 |
| EPT% abundance | 0.73 | 0.76 |
| EPT% richness | 0.68 | 0.73 |
| ASPT | 0.58 | 0.69 |

^a Proportion of Sediment-sensitive Invertebrates (PSI), Empirically-weighted PSI (E-PSI), Average Score Per Taxon (ASPT), Lotic-invertebrate Index for Flow Evaluation (LIFE), Ephemeroptera, Plecoptera and Trichoptera (EPT) % abundance, and EPT % richness.

^b All correlations are significant at the 0.01 level (2-tailed).

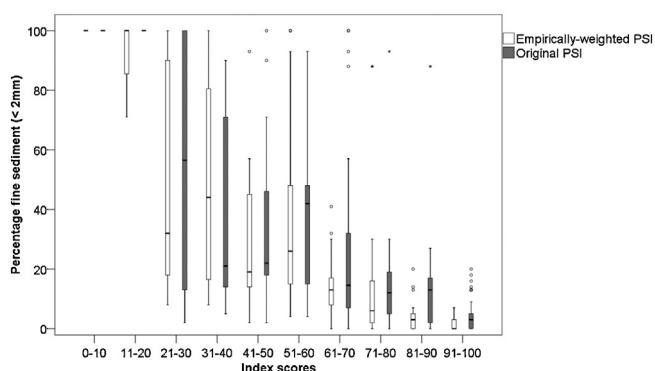


Fig. 2. Boxplot showing the relationship between percentage fine sediment (based on visual assessment) and grouped E-PSI and PSI scores for the test dataset. Note: Minimum, Maximum (shown in the lower and upper whiskers respectively), Median (-), interquartile range (boxes). SPSS identifies potential outliers as >1.5 times (○) or >3 times (*) the interquartile range above the 75th percentile.

significant differences were shown between grouped E-PSI scores, compared to 13 significant differences for grouped PSI scores. These extra group differences were largely between groups with low E-PSI and high E-PSI scores.

4. Discussion

The results of this study show that modelling using an extensive empirical sediment-invertebrate dataset in order to find optimum species-specific sensitivity weightings, has increased the sediment specificity of the E-PSI index in comparison to the PSI index (relationship with percentage fine sediment in test dataset: $r_s = -0.74$ $p < 0.01$, compared to $r_s = -0.66$ $p < 0.01$). By constraining these sensitivity weightings around the original FSSRs, the sound biological basis and mechanistic linkage within the original PSI index has been retained. An increased specificity is also shown by the results of the Kruskal–Wallis test which demonstrated an increase in the number of significant differences between fine sediment values in grouped E-PSI scores, compared to grouped PSI scores.

The E-PSI index has a strong correlation with fine sediment, which is higher than the median correlation coefficient (0.64) of invertebrate-based indices (in relation to their respective pressures) that have been reviewed in Europe (Birk et al., 2012). The correlation between percentage fine sediment and E-PSI scores in the test dataset is also stronger than for the other indices tested. Although those indices are not sediment-specific, EPT indices in particular, are often used to identify sediment pressures, and have been shown to respond to fine sediment to varying degrees (Larsen et al., 2009; Wagenhoff et al., 2012; Zweig and Rabeni, 2001). The LIFE index has been shown to be moderately correlated with fine sediment and highly correlated with PSI (Glendell et al., 2013; Turley et al., 2014) which is likely to be due to the relationship between flow regime and fine sediment dynamics (Matthaei et al., 2010). The Spearman's rank correlation between E-PSI and LIFE is weaker than for PSI and LIFE in the test dataset. Although both are still strongly correlated ($r_s = 0.77$, $p < 0.01$ and $r_s = 0.91$, $p < 0.01$, respectively), this reduced correlation between E-PSI and LIFE may indicate a greater independence of E-PSI from LIFE in comparison to the original index.

Whilst there are limitations to opportunistic data analysis (Vaughan and Ormerod, 2010), it is shown to be useful in the present study to improve the specificity of the PSI index over a wide range of reference condition temperate river and stream ecosystems. The E-PSI index appears more able to identify deposited fine sediment conditions, but as previously discussed, sediment is a natural component of rivers and streams and therefore, any

interpretation of E-PSI scores in terms of impact, should consider observed versus expected scores taken from a reference-based model. Given the uncertainties associated with methods of measuring deposited fine sediment, including the visual assessment method utilised here, any further improvements to the E-PSI index are likely to necessitate higher quality (more accurate and precise) sediment data, which also incorporates the sediment dynamics preceding the invertebrate sampling.

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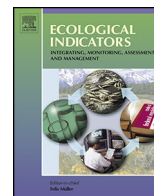
Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2015.02.011>.

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A sediment-specific family-level biomonitoring tool to identify the impacts of fine sediment in temperate rivers and streams



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ABSTRACT

Anthropogenic modifications of sediment load can cause ecological degradation in stream and river ecosystems. However, in practice, identifying when and where sediment is the primary cause of ecological degradation is a challenging task. Biological communities undergo natural cycles and variation over time, and respond to a range of physical, chemical and biological pressures. Furthermore, fine sediments are commonly associated with numerous other pressures that are likely to influence aquatic biota. The use of conventional, non-biological monitoring to attribute cause and effect would necessitate measurement of multiple parameters, at sufficient temporal resolution, and for a significant period of time. Biomonitoring tools, which use low-frequency measurements of biota to gauge and track changes in the environment, can provide a valuable alternative means to detecting the effects of a given pressure. In this study, we develop and test an improved macroinvertebrate, family-level and mixed-level biomonitoring tool for fine sediment. Biologically-based classifications of sediment sensitivity were supplemented by using empirical data of macroinvertebrate abundance and percentage fine sediment, collected across a wide range of temperate river and stream ecosystems (model training dataset $n = 2252$) to assign detailed individual sensitivity weights to taxa. An optimum set of weights were identified by non-linear optimisation, as those that resulted in the highest Spearman's rank correlation coefficient between the index (called the Empirically-weighted Proportion of Sediment-sensitive Invertebrates index; E-PSI) scores and deposited fine sediment in the model training dataset. The family and mixed-level tools performed similarly, with correlations with percentage fine sediment in the test dataset ($n = 84$) of $r_s = -0.72$ and $r_s = -0.70$ $p < 0.01$. Testing of the best performing family level version, over agriculturally impacted sites ($n = 754$) showed similar correlations to fine sediment ($r_s = -0.68$ $p < 0.01$). The tools developed in this study have retained their biological basis, are easily integrated into contemporary monitoring agency protocols and can be applied retrospectively to historic datasets. Given the challenges of non-biological conventional monitoring of fine sediments and determining the biological relevance of the resulting data, a sediment-specific biomonitoring approach is highly desirable and will be a useful addition to the suite of pressure-specific biomonitoring tools currently used to infer the causes of ecological degradation.

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1. Introduction

Streambed deposited fine sediment (<2 mm) is an important, natural component of freshwater ecosystems and is critical for habitat heterogeneity and ecological functioning (Owens et al., 2005; Wood and Armitage, 1997; Yarnell et al., 2006). However, anthropogenic activities can alter sediment delivery and dynam-

ics contributing to ecological degradation (Vörösmarty et al., 2003; Walling and Fang, 2003). Fine sediment can directly impact on stream biota by subjecting them to abrasion, scour or burial; by clogging gills or feeding appendages; by limiting light penetration; as well as indirectly by introducing toxic contaminants sorbed to the surface of fine sediment particles, and reducing oxygen concentrations in the substrate (reviewed in Bilotta and Brazier, 2008). In practice, identifying when and where sediment is the primary cause of ecological degradation is a challenging task. Biological communities undergo natural cycles and variation over time, and respond to other physical (e.g. changes to flow and temperature),

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chemical (e.g. pH, heavy metals, pesticides, nutrients) and biological pressures (e.g. invasive species), (Clews and Ormerod, 2009; Liess and Schulz, 1999; Moore and Ramamoorthy, 2012; Sousa, 1984; Townsend, 1996). The use of conventional (non-biological) monitoring approaches to attribute cause and effect necessitates measurement of multiple parameters, at sufficient temporal resolution, and for a significant period of time (Grove et al., 2015; Harris and Heathwaite, 2012). Biomonitoring tools, which use changes in the presence, abundance or behaviour of biota to indicate, gauge and track changes in the environment (Friberg et al., 2011; Gerhardt, 2000; Wright et al., 1993), can provide a valuable lower-cost alternative to conventional monitoring. Ideally, for reasons discussed in more detail in the following paragraphs, biomonitoring tools should, where possible: (i) have a biological basis, (ii) be easily integrated into standardised biological sampling and recording methods, (iii) be developed and tested over sites from the full range of river and stream ecosystems to which they are intended to be applied, and (iv) have a strong relationship with the pressure of concern.

1.1. Biological basis

There is an emerging consensus among those involved in developing biomonitoring tools, that more reliable tools have a biological basis, i.e. they use biological and ecological traits that influence the tolerance of organisms to a given pressure, and are linked to ecological niche theory (Bonada et al., 2006; Friberg et al., 2011). One of the reasons for this is that these types of tools are not vulnerable to statistical artefacts that may affect purely statistical models. The biological traits (e.g. respiration, locomotion, dispersal, feeding) of taxa in a community reflect the spatial and temporal variations in the environmental factors of a habitat, that act as “filters”, with successful combinations of traits enabling survival and reproduction (Poff, 1997; Statzner et al., 2001b; Townsend et al., 1997). Certain traits or combinations of traits can result in sensitivities/tolerances to particular environmental pressures and therefore these traits have the potential to be used in biomonitoring to discriminate between types of human disturbance (Statzner et al., 2001a). If taxa are selected for inclusion and their sensitivities weighted based on the biological and ecological traits, which influence their sensitivity to a given pressure, the resultant biomonitoring tool will have a mechanistic linkage (rather than a purely correlative linkage) between the pressure of concern and the biotic response (Friberg, 2014).

1.2. Easily integrated into standardised biological sampling and recording methods

One of the many benefits of biomonitoring as opposed to conventional monitoring of multiple environmental parameters is that the biological data collected from the same biological sample can be interpreted by an array of different biomonitoring tools to identify potential pressures. In order for this efficiency and cost-effectiveness to be realised, the biomonitoring tools must be able to make use of data collected using standardised biological sampling methods and recorded to standardised, minimum taxonomic levels. Monitoring agencies in different countries commonly carry out invertebrate identification and recording at different taxonomic levels. For example, within Europe the level of invertebrate taxonomic knowledge varies between countries, as do resources, resulting in different taxonomic resolutions and a lack of comparability between data (Hering et al., 2010; Schmidt-Kloiber and Hering, 2015). Within the UK, England and Wales recently moved

from family level invertebrate recording to a mixed level,¹ consisting of family-, genus- and species-level identifications, with the majority of taxa being identified to species (Davy-Bowker et al., 2010). However, Scotland and Northern Ireland currently record at family-level.² A family-level tool is not only essential for those countries that record at this taxonomic level, but is also crucial for those countries which have recently switched to a higher taxonomic resolution, as it will allow for retrospective analysis of historic family-level data. This ability to assess the historic conditions at sites is particularly important when attempting to distinguish between natural temporal variations (Resh et al., 2005) and those caused by anthropogenic activities, as this can require numerous years of baseline data. Furthermore, a lower-cost family-level biomonitoring tool is likely to be highly desirable for non-regulatory work (e.g. river restoration projects, aquatic research and citizen science programmes) where budgets and taxonomic expertise may be more limited.

1.3. Developed and tested over the full range of different rivers and streams

There are a number of reasons why biomonitoring tools should be developed and tested using data from sites across the full spectrum of rivers and streams to which they are designed to be applied. Firstly, biological communities and species distributions vary naturally, partly as a result of environmental gradients, biotic interactions (McGill et al., 2006) and their ecological requirements (Schmidt-Kloiber and Hering, 2015). As such, a biomonitoring tool must incorporate a range of taxa to ensure that any sampled site will have the potential to include a sufficient number of taxa with sensitivity weightings. Secondly, it cannot be assumed that biological communities will respond uniformly to the same pressure in different rivers and streams. Not only may the pressure of concern occur alongside other, different pressures (potentially having synergistic or antagonistic effects), (Folt et al., 1999), but differences in environmental characteristics (e.g. habitat complexity) may also affect a biological community's resistance and resilience to a specific pressure (Dunbar et al., 2010a,b; Lake, 2000).

1.4. Strong relationship with pressure of interest

Given the implications of incorrect assignment of ecological status of streams for both water and land managers (from unjustified burdens being placed on the users of water resources, to environmental damage going undetected), it is important that biomonitoring tools have a strong relationship with their pressure, in addition to the previous three criteria. Nevertheless, a strong correlation does not rule out the possibility of the tool indicating other aquatic pressures or variables that may occur in parallel with the pressure of concern. A statistical approach may yield strong correlations to the pressure of concern, but these can be the result of statistical artefacts e.g. an inadvertent relationship with an associated pressure (Table 1). Although a biological basis provides a mechanistic linkage for a correlation, biological traits are not always unique to a particular pressure, and as such the influence of confounding pressures also cannot be ruled out (Schuwirth et al., 2015).

¹ This mixed level identification is referred to as TL5 by the Environment Agency.

² This family level identification is referred to as TL2 by the Environment Agency.

Table 1
Confounding pressures commonly associated with fine sediment in rivers and streams globally, and their effect on macroinvertebrates.

| Associated pressure/contaminant | Details | Country of study | Authors | Effect on macroinvertebrates |
|----------------------------------|--|--|---|---|
| Physical Flow | Discharge, velocity | Austria, France, New Zealand, UK | Lefrançois et al. (2007), Matthaei et al. (2010), Petticrew et al. (2007), Slattery and Burt (1997), Tockner et al. (1999), Wood and Armitage (1999) | Decrease/increase in abundance, dependent on the ecological requirements of macroinvertebrates (Extence et al., 1999). |
| Chemical Nutrients | Nitrogen, phosphorus | China, Korea, New Zealand, UK, USA | Brazier et al. (2007), Carpenter et al. (1998), Jarvie et al. (2006), Kim et al. (2003), Owens et al. (2007), Owens and Walling (2002), Piggott et al. (2015), Sun et al. (2009), Wagenhoff et al. (2011) | Hypoxic conditions following eutropication can reduce the abundance of species with high oxygen requirements. Inputs of nitrogenous compounds, can also lead to ammonia, nitrite and nitrate toxicity (reviewed in Camargo and Alonso, 2006). |
| Pesticides | Polychlorinated biphenyls, pyrethroid, organochlorines, organophosphate | Australia, Brazil, China, India, Italy, Vietnam, UK, USA | Camusso et al. (2002), McKenzie-Smith et al. (1994), Minh et al. (2007), Torres et al. (2002), Warren et al. (2003), Weston et al. (2004), Zhang et al. (2003) | Various pesticides have been linked to declines in both abundance and richness, through direct toxicity (reviewed in Wijngaarden et al., 2005), which is also likely to influence predator/prey interactions. |
| Metals | Aluminium, cadmium, chromium, copper, iron, lead, manganese, mercury, zinc | Italy, Pakistan, Turkey, UK, USA | Abernathy et al. (1984), Akcay et al. (2003), Camusso et al. (2002), Dawson and Macklin (1998), Owens et al. (2001), Tariq et al. (1996), Walling et al. (2003) | Responses to metal pollution are varied, but for intolerant groups (e.g. Ephemeroptera), abundance and richness are typically reduced in impacted streams (reviewed in Clements, 1991). |
| Organic matter | | Austria, Luxemburg, Taiwan, UK | Tockner et al. (1999), Von Bertrab et al. (2013), Yu et al. (2001), Glendell and Brazier. (2014b) | Excessive inputs of organic matter and the subsequent biological decomposition, can lead to reduced oxygen levels, impacting those species with high oxygen requirements (e.g. <i>Leuctra</i> sp.), whilst favouring those with low oxygen requirements (e.g. <i>Chironomus</i> sp.), (Friberg et al., 2010). |
| Other | Polycyclic aromatic hydrocarbons | Canada, China, Malaysia, Taiwan, UK, USA | Ashley and Baker (1999), Doong and Lin (2004), Stevens et al. (2003), Yunker et al. (2002), Zakaria et al. (2002), Zhang et al. (2004) | Polycyclic aromatic hydrocarbons are toxic to many macroinvertebrates, and can lead to reduced richness and abundance (Ankley et al., 1994) |
| Biological Bacteria/pathogens | <i>Escherichia coli</i> , <i>Salmonella</i> , <i>Cryptosporidium</i> | Austria, Canada, New Zealand, USA | Droppo et al. (2009), Jamieson et al. (2005), Kernegger et al. (2009), Mallin (2000), Muirhead et al. (2004) | The effects of the many sediment associated pathogens on macroinvertebrates is unclear. <i>Cryptosporidium</i> and <i>Giardia</i> accumulate within some macroinvertebrates, but with uncertain consequences (Reboredo-Fernandez et al., 2015). |

1.5. The Proportion of Sediment-sensitive Invertebrates (PSI) index

The PSI index is a biomonitoring tool that is designed to identify the degree of sedimentation in rivers and streams (Extence et al., 2011). Invertebrate sensitivity ratings (A-Highly sensitive, B-Moderately sensitive, C-Moderately insensitive, D-Highly insensitive) were assigned following an extensive review of the literature, and using expert knowledge of ecological and biological traits, thus providing the tool with a sound biological basis. Traits that may result in sensitivity to fine sediment include feeding, locomotion and respiratory attributes. For example, scrapers/grazers

and passive filter feeders may experience decreased food availability or damage to feeding appendages as a result of deposited fine sediment (Larsen and Ormerod, 2010; Nerbonne and Vondracek, 2001). The PSI index has both family-level and species-level versions, allowing it to be easily integrated into standardised biological sampling and recording methods. However, an evaluation of these versions of the index across a wide range of temperate river and stream ecosystems (Turley et al., 2014), showed it to have moderate correlations with fine sediment ($r_s = -0.61$, $p < 0.01$ and $r_s = -0.64$, $p < 0.01$ respectively), that although comparable with the average invertebrate-based, pressure-specific tool, used throughout the EU (Birk et al., 2012), limits confidence in its application. Recent work

has demonstrated enhancements to the species-level PSI index through the use of empirical data to supplement the expert knowledge and literature, which were used to determine the original four fine sediment sensitivity ratings (Turley et al., 2015).

The aim of the present study was to investigate if similar empirical-weighting techniques could be used to enhance the performance of family- and mixed-level versions of the PSI index, whilst retaining their biological basis, and ensuring that the tools are compatible with historic and contemporary datasets recorded to family-level and/or mixed-level, and have a strong correlation with fine sediment.

2. Methods

2.1. Data

2.1.1. Minimally-impacted sites

It was important that empirical data from minimally-impacted sites were used in this study, in order to reduce confounding pressures in the process of assigning sensitivity weightings. In this instance, a freely available dataset from the UK was utilised. However, this study can be seen as an exemplar to be used in other countries where such datasets exist. The RIVPACS IV (May 2011 version) dataset (River Invertebrate Prediction and Classification System—NERC [CEH] 2006. Database rights NERC [CEH] 2006 all rights reserved) is described in detail by Wright (2000) and Clarke et al. (2003), but is summarised here. The database contains invertebrate, water quality and catchment characteristics data, recorded at each site over at least one year, between 1978 and 2004. The 835 reference condition sites, on streams and rivers across the United Kingdom (Fig. 1), encompass a wide range of environments, varying in their (i) climate – mean annual precipitation totals between 1961 and 1990 of 430–2930 mm and mean annual temperatures between 1961 and 1990 ranging from 7.93 to 11.45 °C, (ii) geology – varying from catchments dominated by hard igneous rocks to catchments dominated by soft sedimentary rocks and (iii) topography – altitudes at river source varying from 5 to 1216 m above sea level. The stream and river sites also vary in their morphometry with widths ranging from 0.4 to 117 m and average depths ranging from 0.02 to 3.00 m (widths and depths are a mean of three seasonal measurements). All of the sites are considered to be as close to reference condition as it is possible in the United Kingdom, and they have no, or only very minor, anthropogenic alterations to the values of the chemistry and hydromorphology, supporting biota usually associated with such minimally-disturbed conditions.

The 835 sites were sampled for macroinvertebrates using the UK standard method; a standardised three-minute kick sample technique using a 900 µm mesh hand net, followed by a one-minute hand search. All in-stream habitats identified at the site were sampled in proportion to their occurrence (Environment Agency, 2009). The database has abundance records of different macroinvertebrates identified to (i) family level, (ii) mixed level, and (iii) species level (Wright, 2000). Each site has season-specific records of community composition: spring (March–May), summer (June–August) and autumn (September–November). As the technique used for macroinvertebrate sampling was semi-quantitative, model development and testing utilised log abundance data rather than raw abundance data or presence/absence data. This recognises the potential importance of changes in abundance when attempting to identify pressure gradients, without placing spurious confidence in the semi-quantitative sampling technique (Furse et al., 1981).

The fine sediment data within the RIVPACS IV database consisted of visual estimates of the percentage of the substrate cover composed of silt and clay (<0.06 mm) and sand (≥0.06 and <2.00 mm), as an annual average based on three seasonal measure-

ments. The visual estimate method used to collect these data is described in the River Habitat Survey Field Survey Guidance Manual (Environment Agency, 2003). Briefly, it involves the operator carrying out a visual inspection over a given reach, estimating the substrate composition and recording the percentage of bedrock, boulders and cobbles, pebbles and gravel, sand, and silt and clay.

Family and mixed level macroinvertebrate data, and site substrate cover were extracted from the RIVPACS database and compiled in Microsoft Excel. The percentage of the substrate cover consisting of sand, silt and clay, were combined to provide an overall estimate of fine sediment (<2 mm) for each of the 835 minimally-impacted sites. The dataset was then split into a training dataset (751 sites, three seasons, $n=2252$) and test dataset (84 sites, autumn season only, $n=84$) using random allocation, to ensure testing of the indices could be considered independent of the development stages. Similar to Kelly et al. (2012), this 90:10 split was chosen to ensure that the indices were developed using a significant number of sites, whilst leaving a suitable number for independent testing.

2.1.2. Agriculturally impacted sites

The family level indices were also tested across a continuum of agriculturally impacted stream sites (upstream catchment land-use ranging from 0 to 90% arable fields, $n=754$) in England, using part of a dataset described by Pearson et al. (2016). In brief, this dataset included seasonal macroinvertebrate data, seasonal fine sediment data, and water chemistry data (mean of the preceding 12 months) that were collected during routine monitoring by the Environment Agency in 2006. For the present study, more detailed macroinvertebrate abundance data were obtained from the Environment Agency, for samples collected in the autumn, along with fine sediment data based on the mean of spring and autumn visual estimates, and Environmental Quality Ratios (based on the observed and expected scores—calculated using RICT) for an index designed to indicate the effects of organic pollution (WHPT index, Paisley et al., 2014). All 754 sites used in the present study were located on independent water bodies, as detailed by the water body names and grid references provided by the Environment Agency.

2.2. Developing the Empirically-weighted PSI (E-PSI) indices

For both the family level and mixed level E-PSI indices, the *fmincon* function (active-set algorithm), a nonlinear optimisation method of MATLAB (Mathworks, version R2014a), was used to test up to 100,000 iterations of taxon sensitivity weightings, to find an optimum set of weightings that resulted in the strongest Spearman's rank correlation coefficient between index scores and fine sediment in the training dataset. The Spearman's rank correlation was used, as the data were found to be non-normally distributed and show heteroscedasticity, and could not be successfully transformed. In order to maintain the biological basis of the original PSI index, those taxa with PSI ratings of “highly sensitive” and “moderately sensitive” were constrained to sensitivity weights between 0.50 and 1.0, and those rated as “moderately insensitive” and “highly insensitive” between 0 and 0.49. Using a range of weights acknowledges the breadth of ecological niches that macroinvertebrates occupy, as well as their differing potential as indicators. A modified version of the original PSI index's equation was used to calculate E-PSI scores:

$$E-PSI = \frac{\sum (\log A_{sens} \times W)}{\sum (\log A_{all} \times W)} \times 100 \quad (1)$$

Formula used to calculate E-PSI scores. The sum of each sensitive taxon's log abundance ($\log A_{sens}$), multiplied by the corresponding sensitivity weightings (W), is divided by the sum of all taxon log abundances ($\log A_{all}$) multiplied by the corresponding sensitivity

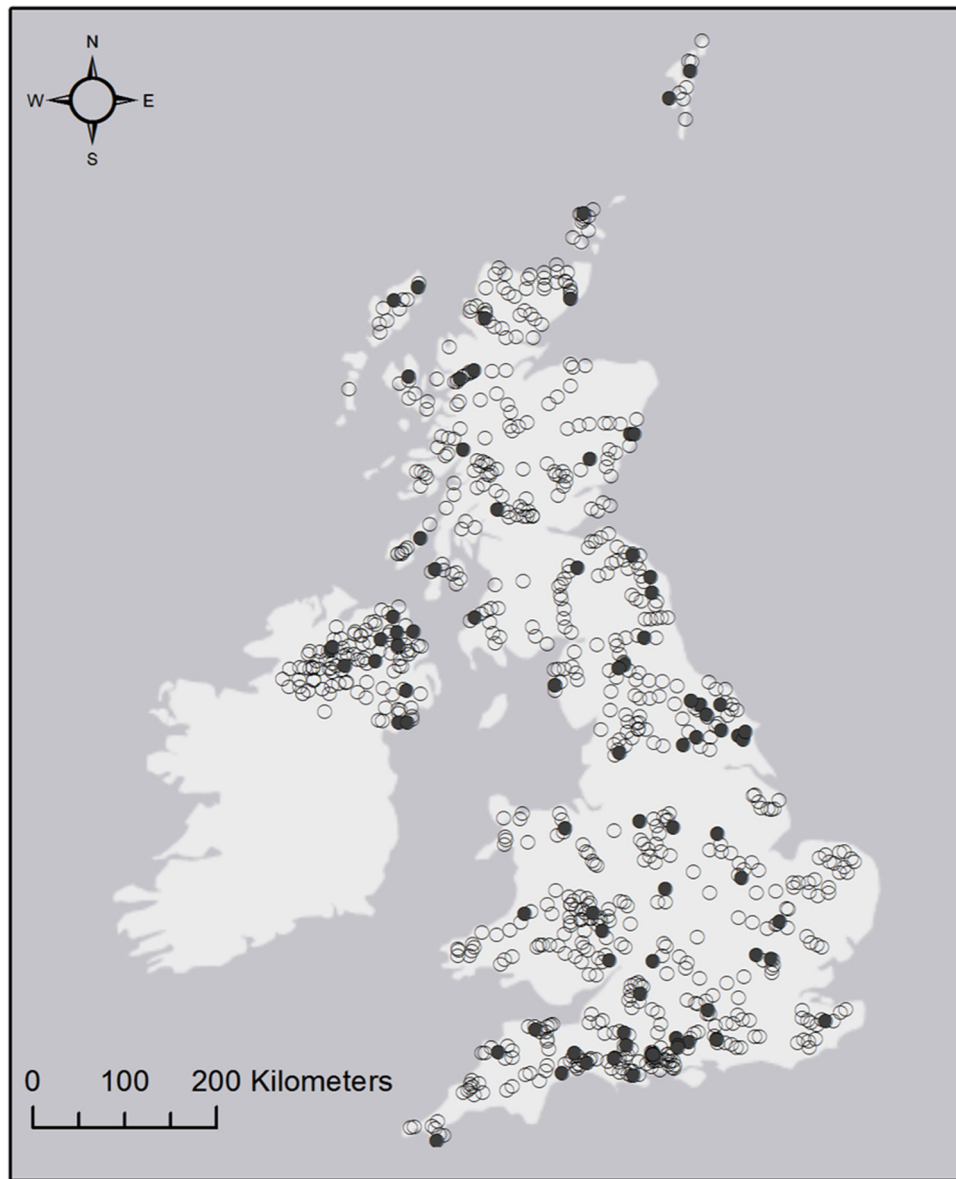


Fig. 1. Distribution of minimally-impacted sites throughout the UK. Light dots are those sites that formed the training dataset ($n = 751$), dark dots are those sites that formed the test dataset ($n = 84$).

weightings (W). This value is then multiplied by 100 to provide the E-PSI score. *Note:* Log abundance categories in E-PSI were simplified to: 1–9 individuals present = 1; 10–99 = 2; 100–999 = 3; 1000+ = 4. E-PSI scores range from 0 to 100; 0 representing a site dominated by fine sediment, 100 representing a site with minimal amounts of fine sediment.

2.2.1. Developing the family level E-PSI index

In total, 79 invertebrate families with PSI sensitivity weightings were present in the family level training dataset. Following the non-linear optimisation procedure, an optimum set of family sensitivity weights formed the E-PSI_{fam} index.

2.2.2. Adjustments for family-level sensitivity variations

In the process of developing the original, family-level PSI index, inevitably some generalisations were made regarding the sensitivities of invertebrate families to fine sediment. Families can comprise numerous genera and species, each with a range of different environmental requirements and sensitivities (Lenat and Resh, 2001), making assignment of sensitivities at family-level a difficult pro-

cess. To determine whether all families identified as sensitive by the original PSI index were correctly identified as useful indicators at this taxonomic level, the empirical data was investigated. Using data from all 835 sites within the RIVPACS dataset, the percentage of fine sediment that corresponded with the 75th percentile of the family's total abundance was calculated for each taxon. This involved using raw abundance invertebrate data, sorting all 2504 samples in order of increasing fine sediment, and calculating the cumulative abundance for each taxon. The 75th percentile of abundance was then calculated for each family, and this value or the next highest value was cross-referenced to obtain the corresponding sediment value for that abundance. This family-specific sediment value, represented the maximum fine sediment percentage at which at least 75% of the families abundance occurred. Similarly to Relyea et al. (2012), this 75% value was used as it recognises the fact that taxa can occur in sub-optimal conditions, often at reduced densities. These family-specific fine sediment values were used to inform the creation of a modified version of the family-level E-PSI index, by excluding taxa whose sediment value was $\geq 33\%$. The families that exceeded this threshold were removed from the index

altogether (instead of being reassigned to the insensitive category) to maintain the biological basis. The removal of these families is not an admission of their tolerance to fine sediment, rather it acknowledges that when considering fine sediment at the reach scale, they are not useful as indicator taxa. The 33% threshold was used as previous research showed that at the patch scale, sediment cover of approximately one third resulted in significant declines in invertebrate richness (Larsen et al., 2009). Once these taxa had been removed from the index, the nonlinear optimisation procedure was performed to return a new set of optimum sensitivity weights based on the new altered community composition/taxon list, forming the E-PSI_{fam69} index

2.2.3. Developing the mixed level E-PSI index

In addition to the family level index, a mixed level version was developed using the same procedures. In total, 355 invertebrate taxa with PSI sensitivity weightings were present in the mixed level training dataset. Following the nonlinear optimisation procedure outlined in Section 2.2, an optimum set of sensitivity weights formed the E-PSI_{mixed} index.

2.3. Testing of the E-PSI indices

The developed E-PSI indices were tested using both the minimally-impacted, independent dataset ($n=84$), as well as the agriculturally impacted dataset ($n=754$), both described in Section 2.1. The performance of these indices were evaluated and compared using their Spearman's rank correlations with fine sediment, due to the non-normally distributed and heteroscedastic data, and the inability to successfully transform. All correlations were interpreted using the Dancy and Reidy (2007) classifications of correlations; 0.1–0.39 = weak, 0.4–0.69 = moderate, 0.7–0.99 = strong.

In order to examine the relationship between E-PSI and fine sediment further, a separate test was conducted on the minimally-impacted (RIVPACS) sites with discharge data ($n=443$). The aim of this exercise was to restrict the potential collinearities between fine sediment and covariates relating to longitudinal gradients, particularly those relating to flow (e.g. discharge, velocity and slope). To achieve this, the sites were grouped by stream power (total stream power per unit stream length, $W m^{-1}$) into five approximately equal groups (see Supplementary material B). The Spearman's rank correlations within each group between the E-PSI indices and fine sediment were then calculated.

Stream power (Ω) was calculated using the following formula:

$$\Omega = \gamma Qs$$

where γ is the specific weight of water ($9810 N m^{-3}$), Q is the average water discharge ($m^3 s^{-1}$), and s is energy slope ($m m^{-1}$, which can be approximated by the river slope), (Knighton, 1999).

2.4. Comparisons with other biomonitoring tools

The Lotic-invertebrate Index for Flow Evaluation (LIFE) (Extence et al., 1999) and the Combined Fine Sediment Index (CoFSI) (Murphy et al., 2015) were calculated and their relationship to both fine sediment, PSI and E-PSI indices were assessed in terms of their Spearman's rank correlation coefficients. LIFE was chosen to determine the influence of known interactions between flow and fine sediment deposition and re-suspension (Dewson et al., 2007). Correlations between LIFE, E-PSI indices and fine sediment were also compared within stream power groups.

The recently developed, predominantly species- and genus-level CoFSI was included in this analysis, as it is a purely statistically based index designed to indicate fine sediment pressures (Murphy

Table 2

Spearman's rank correlation coefficients (2 d.p.) between versions of PSI, E-PSI, LIFE, CoFSI and fine sediment, in the minimally-impacted test dataset, and the agriculturally impacted test dataset.

| Index ^a | No. of sensitive taxa | Minimally-impacted ($n=84$) | Agriculturally impacted ($n=754$) |
|------------------------|-----------------------|-------------------------------|-------------------------------------|
| Family level | | | |
| PSI _{fam} | 36 | −0.59 | −0.66 |
| E-PSI _{fam} | 36 | −0.66 | −0.69 |
| E-PSI _{fam69} | 26 | −0.72 | −0.68 |
| LIFE _{fam} | n/a | −0.57 | −0.62 |
| Mixed level | | | |
| PSI _{mixed} | 139 | −0.60 | n/a |
| E-PSI _{mixed} | 139 | −0.70 | n/a |
| CoFSI | n/a | −0.72 | n/a |
| LIFE _{mixed} | n/a | −0.51 | n/a |

^a The subscripted text identifies the taxonomic level (family or mixed) of the data and the number of taxa used in the calculations of the index. All correlations are significant at the 0.01 level (2-tailed). Mixed level indices could not be tested over the agriculturally impacted sites, as data at this taxonomic level were not recorded.

et al., 2015). All mixed-level indices were calculated using data of the same taxonomic detail, at the level used for Water Framework Directive reporting.

3. Results

3.1. Biological indices and fine sediment

The best performing family-level and mixed-level E-PSI indices were strongly, negatively correlated to fine sediment metrics in the minimally-impacted dataset and similarly, but moderately correlated in the agriculturally impacted test dataset (Table 2). The agriculturally impacted test dataset had WHPT scores of 2.5–8.0 and Environmental Quality Ratios of between 0.4 and 1.3 (see Supplementary material C) indicating that the sites were, at the very least, impacted to varying degrees by organic pollution.

The E-PSI indices with the strongest correlation with fine sediment in the minimally-impacted test dataset were the E-PSI_{fam69} and E-PSI_{mixed} ($r_s = -0.72$ and $r_s = -0.70$, $p < 0.01$, respectively). The optimisation process was responsible for improving the correlations between fine sediment and the E-PSI_{fam} index compared to the PSI_{fam} index, in the minimally-impacted test dataset ($r_s = -0.66$, $p < 0.01$ compared to $r_s = -0.59$, $p < 0.01$). The largest improvement following the optimisation process was for the E-PSI_{mixed} index in the minimally-impacted test dataset, which represented an improvement of 10 percentage points ($r_s = -0.70$, $p < 0.01$ compared to $r_s = -0.60$, $p < 0.01$). LIFE_{fam}, and LIFE_{mixed} had moderate correlations with fine sediment ($r_s = -0.57$ and $r_s = -0.51$, $p < 0.01$, respectively) and CoFSI had a strong correlation with fine sediment ($r_s = -0.72$, $p < 0.01$).

Within the stream power groups (Table 3), the strongest correlation between E-PSI_{fam69} and fine sediment was $r_s = 0.71$, $p < 0.01$ in the group of sites with low stream power, with moderate correlations in all other groups (ranging from $r_s = 0.59$ to $r_s = 0.68$, $p < 0.01$).

3.2. Adjustments for family-level sensitivity variations

By including only those taxa whose corresponding sediment value was $<33\%$, the strength of the correlation between the E-PSI_{fam} index and fine sediment was improved in the unimpacted test dataset, but had essentially the same correlation over the impacted sites. The exclusion process resulted in 10 families being removed entirely from the calculation of index scores. These sensitive families had corresponding sediment values of between 36% and 83% fine sediment. Three of these families had taxa rated as

Table 3

Spearman's rank correlation coefficients between the best performing E-PSI indices, LIFE and fine sediment, in the minimally-impacted dataset, using autumn data, and all sites with discharge data ($n = 443$). Sites are grouped by total stream power per unit length (W m^{-1}).

| Stream power group ^a | E-PSI _{fam69} | E-PSI _{mixed} | LIFE _{fam} | LIFE _{mixed} | E-PSI _{fam69} | E-PSI _{mixed} |
|---|------------------------|------------------------|---------------------|-----------------------|--------------------------|------------------------|
| | Vs fine sediment | | | | Vs LIFE _{mixed} | |
| All sites ($n = 443$) | -0.73 | -0.72 | -0.58 | -0.56 | 0.80 | 0.84 |
| Group 1 ($0.25\text{--}10.59 \text{ W m}^{-1}$) | -0.71 | -0.73 | -0.71 | -0.72 | 0.92 | 0.96 |
| Group 2 ($10.93\text{--}29.34 \text{ W m}^{-1}$) | -0.59 | -0.56 | -0.46 | -0.51 | 0.84 | 0.89 |
| Group 3 ($29.41\text{--}67.01 \text{ W m}^{-1}$) | -0.63 | -0.65 | -0.49 | -0.53 | 0.81 | 0.85 |
| Group 4 ($67.92\text{--}167.95 \text{ W m}^{-1}$) | -0.65 | -0.63 | -0.39 | -0.32 | 0.65 | 0.68 |
| Group 5 ($168.34\text{--}6935.42 \text{ W m}^{-1}$) | -0.68 | -0.65 | -0.44 | -0.19 (ns) | 0.47 | 0.55 |

^a Stream power groups 1 and 5 ($n = 88$), stream power groups 2,3 and 4 ($n = 89$). All correlations are significant at the 0.01 level (2-tailed), unless otherwise indicated, (ns) not statistically significant.

insensitive in the mixed level tool: Limnephilidae, Scirtidae and Gammaridae (for further information see [Appendix A](#)).

3.3. Assigned sediment-sensitivity weightings

The sensitivity weightings that formed the best performing E-PSI indices (E-PSI_{fam69} and E-PSI_{mixed}) in the minimally-impacted test dataset are shown in [Appendix B and C](#). An index calculator is also provided in Supplementary material A.

3.4. Restricting the collinearities between fine sediment and longitudinal gradients

The Spearman's rank correlations between E-PSI and fine sediment within each of the five stream power groups were moderate to strong ($r_s = -0.56$ to $r_s = -0.73$) ([Table 3](#)).

3.5. Comparisons between biomonitoring tools

In addition to comparing the E-PSI indices to fine sediment, the relationships between indices were considered. The various indices had strong correlations with each other, ranging from $r_s = 0.79$ to $r_s = 0.98$, $p < 0.01$ ([Table 4](#)). All versions of the E-PSI index had weaker correlations with LIFE_{fam} and LIFE_{mixed}, compared to the original versions of the PSI index.

The correlations between E-PSI and LIFE decreased in successively increasing stream power groups ([Table 3](#)), from $r_s = 0.92$ to $r_s = 0.47$, $p < 0.01$ for E-PSI_{fam69} versus LIFE_{mixed}. The correlation between LIFE_{mixed} and fine sediment was strongest ($r_s = 0.72$, $p < 0.01$) in the group of sites with low stream power, and was weakest at sites with high stream power.

4. Discussion

4.1. Identifying fine sediment pressures

The results of this study show that the use of empirical data to assign sensitivity weightings within the PSI index's original biologically-based sensitivity ratings, has improved the performance of the tools, in terms of their correlation with fine sediment. As a result, both the family-level and mixed-level E-PSI indices have correlation coefficients with fine sediment, that are stronger than the average invertebrate-based, pressure-specific biomonitoring tool used throughout Europe in the implementation of the WFD ([Birk et al., 2012](#)). Furthermore, by including only those taxa whose 75th percentile of abundance corresponded with a fine sediment value of $< 33\%$, the E-PSI_{fam69} index has a strong correlation with fine sediment similar to that of the mixed-level E-PSI index (E-PSI_{fam69} versus fine sediment: $r_s = -0.72$, $p < 0.01$). Applying this threshold to the family-level index was intended to acknowledge the likelihood of significant within family variation in terms of sensitivity to fine sediment, and identify any families that were

not useful as indicators at the reach scale. This exercise appears to have had the desired effect, reducing some of the variation in the relationship that may have been caused by varying sensitivities within families. Testing of the E-PSI_{fam69} index also showed similar improvements and correlation ($r_s = -0.68$, $p < 0.01$) over the agriculturally impacted sites, suggesting that the index performs similarly over sites that are impacted by the multitude of pressures associated with agricultural land-use.

Nevertheless, correlations do not prove causality and they should be interpreted with some caution, partly because many in-stream influences are associated with each other in riverine environments ([Allan, 2004](#)). The benefit of biologically-based indices such as the PSI and E-PSI index is that the biological basis provides a mechanistic linkage between index scores and fine sediment conditions. The PSI index utilises existing knowledge on biological and ecological traits and sensitivities to fine sediment, to assign sensitivity ratings, which the E-PSI index combines with empirical data to assign more detailed sensitivity weightings (0–1).

Based on the available data on the ecological preferences of macroinvertebrates from [Schmidt-Kloiber and Hering \(2015\)](#), those families, which have been assigned the highest sensitivity weightings in E-PSI_{fam69} (Heptageniidae, Perlidae, Aphelocheiridae, Chloroperlidae, Lepidostomatidae, Leuctridae, and Perlodidae), are dominated by species with a strong affinity to coarse substrate microhabitats, with the exception of Lepidostomatidae that have some affinity to coarse substrates, but are more often associated with woody debris. Habitat preferences are determined by an invertebrates biological traits or combination of traits. These preferences relate not only to the direct physical properties of the habitat (e.g. the substrate), but also the flow velocities, hydrological and thermal regimes, resource availability and biotic interactions associated with them. These taxa with the greatest E-PSI sensitivity weightings are mainly clingers, with tarsal claws allowing them to “grip” the surface of pebbles, cobbles and boulders in shearing flows ([Pollard and Yuan, 2010](#)). Nevertheless, they depend on the heterogeneity of coarse substrates to provide refugia from these shearing flows, as well as from predators. Previous research has shown reduced densities and richness of clingers, with increasing fine sediment cover ([Pollard and Yuan, 2010](#); [Rabeni et al., 2005](#)). Additionally, the turbulence caused by coarse substrate and the resulting oxygenation is likely to be important for many of these sensitive families. For example, *Aphelocheirus aestivalis* is a plastron-breather and so requires well-oxygenated waters ([Seymour et al., 2015](#)), and fine sediment may also disrupt its respiratory functioning.

4.2. Confounding pressures

A considerable challenge for research carried out over large spatial extents is the occurrence of collinearity between the variable of interest and other environmental variables ([Pearson et al., 2016](#)). Relatively few studies have considered the interactions and co-occurrence of in-stream pressures, which are likely to affect the

Table 4
Spearman's rank correlation coefficients (2 d.p.) between biological indices, in the minimally-impacted, autumn test dataset ($n=84$).

| Index ^a | PSI _{fam} | E-PSI _{fam} | E-PSI _{fam69} | LIFE _{fam} | PSI _{mixed} | E-PSI _{mixed} | CoFSI _{mixed} |
|------------------------|--------------------|----------------------|------------------------|---------------------|----------------------|------------------------|------------------------|
| Family level | | | | | | | |
| PSI _{fam} | | 0.95 | 0.93 | 0.92 | 0.96 | 0.93 | 0.87 |
| E-PSI _{fam} | 0.95 | | 0.98 | 0.85 | 0.94 | 0.96 | 0.93 |
| E-PSI _{fam69} | 0.93 | 0.98 | | 0.85 | 0.91 | 0.96 | 0.94 |
| LIFE _{fam} | 0.92 | 0.85 | 0.85 | | 0.89 | 0.86 | 0.79 |
| Mixed level | | | | | | | |
| PSI _{mixed} | 0.96 | 0.94 | 0.91 | 0.89 | | 0.95 | 0.88 |
| E-PSI _{mixed} | 0.93 | 0.96 | 0.96 | 0.86 | 0.95 | | 0.92 |
| CoFSI _{mixed} | 0.87 | 0.93 | 0.94 | 0.79 | 0.88 | 0.92 | |
| LIFE _{mixed} | 0.88 | 0.83 | 0.79 | 0.85 | 0.91 | 0.85 | 0.80 |

^a The subscripted text identifies the taxonomic level (family or mixed) of the data and the number of taxa used in the calculations of the index. All correlations are significant at the 0.01 level (2-tailed).

performance of biomonitoring tools. A recent study of 9330 sites throughout 14 European countries, found 47% of rivers (90% of lowland rivers) throughout Europe to be subject to multiple pressures relating to hydrology, morphology, water quality and connectivity (Schneegger et al., 2012). This highlights the importance of a mechanistic linkage between indices and sediment conditions, given the potential for these multiple pressures to confound biomonitoring approaches.

In the present study, sites were grouped using site-specific stream power to restrict the collinearities between fine sediment and longitudinal gradients, particularly those relating to flow. Our results show that flow (indicated by LIFE) was related to fine sediment cover, and as such LIFE and E-PSI are strongly correlated. However, this relationship between fine sediment cover and flow weakens as stream power increases, likely because after the critical thresholds for particle entrainment and transport have been exceeded, further increases in stream power cease to result in much further entrainment, transport and removal of fine sediment from the river bed (though the increases in stream power may trigger entrainment and transport of coarser particles as bed load). This is likely to be the reason why the relationship between LIFE scores and E-PSI, and LIFE and fine sediment weaken in successively increasing stream power groups. These results add confidence to our interpretation that although fine sediment cover is related to stream power (for physical reasons), and there will therefore be a moderate to strong relationship between scores derived from sediment-specific and flow-specific biomonitoring tools; these relationships are not fixed, and thus where one pressure (e.g. flow) is stable, whilst the other is variable (e.g. sediment cover), the scores derived from the biomonitoring tools will diverge and provide valuable information on the likely cause of deviation from reference-condition community composition. In the case of LIFE and E-PSI, a similar approach to model development for LIFE could result in even greater decoupling of the two tools.

4.3. Statistically based sediment-specific tools

As noted, other studies have attempted to develop fine sediment-specific indices, using empirical data and statistical methods to select taxa for inclusion and to assign sensitivity weights to these taxa, to achieve a correlation between a tool's score and the pressure of concern. These approaches have achieved moderate-strong correlations with fine sediment but lack a biological basis and mechanistic linkage, which are important for disentangling the multiple pressures in rivers and streams (Friberg, 2014). Murphy et al. (2015) developed CoFSI, an index that endeavours to take account of both the amount and organic content of fine sediment. The authors used partial canonical correspondence analysis to rank taxa in terms of their sensitivity to fine sediment, based on empirical data from 179 stream sites. The re-suspension method of quantifying fine sediment was used, averaging samples from two erosional and two depositional patches to achieve a contemporane-

ous reach-scale average. Despite this technique necessitating some subjective assessment of "erosional" and "depositional" patches, moderate to strong correlations ($r_s = -0.54$ to -0.70 , $p < 0.05$) were observed between the resultant sediment data and CoFSI in their test dataset (Murphy et al., 2015). Due to the difficulties of selecting sites with minimal confounding pressures that at the same time represent a gradient of sediment pressures, their resulting test dataset ($n=83$) is somewhat geographically restricted and is focused on agricultural streams, which may be impacted by an array of different pressures typically associated with agricultural practices (Allan, 2004; Matthaai et al., 2010; Weston et al., 2004). In the present study, CoFSI is shown to have a similar correlation with fine sediment compared to the best performing family and mixed-level E-PSI indices. CoFSI is a mixed-level (predominantly genus- and species-level) biomonitoring tool, and as such cannot be applied to present and historic datasets recorded at family-level.

Most recently, in North America, Hubler et al. (2016) developed a statistically based index for Oregon streams (the Biological Sediment Tolerance Index; BSTI) using weighted averaging to assign tolerance values, and found a moderate correlation ($r^2 = 0.58$) between the index and fine sediment in their independent test dataset ($n=50$). Similarly, Zweig and Rabeni (2001) found a moderate correlation ($r_s = -0.59$, $P < 0.01$) between their Deposited Sediment Biotic Index (DSBI) and visual estimates of fine sediment, using data from four streams in Missouri. The authors used the sediment values that corresponded with each taxon's median abundance, to assign tolerance ratings, and used the same data for testing, therefore lacking an independent test dataset. In addition, the DSBI is currently limited by the small development dataset, which is likely to restrict its spatial applicability. A further example from North America is the Fine Sediment Biotic Index (FSBI), which again used empirical data to assign sensitivity weights to taxa (Relyea et al., 2012). The FSBI showed a large amount of variation, with the data forming a wedge-shaped response that has since been suggested as a typical response to multiple pressures (Friberg 2014); when sediment pressure is low, it has minimal impact on the invertebrate community and other pressures dominate. This wedge-shaped response is also observed in PSI, E-PSI and CoFSI (see Supplementary material D), supporting this generalisation. Some of the variation in these relationships is also inevitably associated with invertebrate sampling and quantifying fine sediment pressures. For example the standardised, three minute kick-sample method has been shown to collect only approximately 50% of the species and 60% of the families present in six replicate samples (Furse et al., 1981). The challenges of quantifying fine sediment pressures in a way that is biologically relevant and accurately represents spatial variation is a further limitation to the development and/or testing of sediment-specific biomonitoring tools. Visual estimates of substrate composition were used in this study due to the data being from an existing database, which had the benefits of a wide geographic coverage. Although the technique is subjective

(Clapcott et al., 2011) it provides a measure of fine sediment surface drupe, which is likely to directly influence macroinvertebrate communities and as such is likely to be a biologically relevant metric (Conroy et al., 2016), relating to niche theory and habitat suitability (Hirzel and Le Lay 2008) over the entire reach.

4.4. Taxonomic resolution

In contrast to previous findings (Relyea et al., 2012; Turley et al., 2014) the taxonomic resolution had little effect on the indices correlations with fine sediment; E-PSI_{fam69} and E-PSI_{mixed} had similar strong correlations with fine sediment. Relyea et al. (2012) found that sensitivities varied within invertebrate families and concluded that family level was insufficient for pressure-specific tools. This within-family variation of sensitivities to fine sediment was expected to result in large differences in terms of the correlation between family and mixed level indices and fine sediment. Despite the similar correlations observed, it is likely that the mixed level tool will provide more diagnostic information, particularly at more impacted sites. The taxonomic sufficiency is a key consideration when developing an invertebrate-based biomonitoring tool, as the taxonomic resolution can affect the accuracy of predictions (Schmidt-Kloiber and Nijboer, 2004) as well as the costs associated with processing biotic samples (Jones, 2008; Marshall et al., 2006). The higher the taxonomic resolution, the more resource intensive biomonitoring becomes (identification requires more time and expertise/training). For macroinvertebrates, some studies have shown that family level is often sufficiently able to detect environmental change (Marshall et al., 2006; Mueller et al., 2013), whilst others conclude that a higher resolution is preferential, particularly for genera-rich families or when attempting to identify subtle environmental changes (Monk et al., 2012; Waite et al., 2004). Furthermore, although our knowledge of species level biology is incomplete, intra-generic environmental requirements have been shown to vary significantly for various families of macroinvertebrates (reviewed in Lenat and Resh, 2001). In terms of a pressure-specific biomonitoring tool, the optimum taxonomic resolution in terms of model predictions is likely to be dependent on the scale or gradient of environmental pressure, but will inevitably be a compromise between the costs associated with high taxonomic resolution and the ecological information lost at lower resolutions. Nevertheless, the development of new pressure-specific tools should ideally align with national/international monitoring agencies, to ensure that they can be applied to existing protocols and historical data.

In addition, as the E-PSI index is not a purely statistically based tool, it is able to include relatively rare taxa (low abundances or small distribution range), which are often removed in the development stages of statistically based indices (Murphy et al., 2015; Relyea et al., 2012). These rare taxa, specifically those with small distribution ranges, may be important indicators of subtle environmental change as they are likely to be more specialised, having a narrower range of optimal conditions, and as such may be the first taxa to indicate the effects of a pressure (Cao et al., 1998; Schmidt-Kloiber and Nijboer, 2004). Whilst these assumptions are intuitive, there is some debate as to the suitability of rare taxa in multivariate analyses particularly relating to their redundancy and their influence on observed versus expected scores (Cao et al., 2001; Marchant 2002; Van Sickle et al., 2007). Furthermore, when conservation issues become a concern for these rare species, their collection should be carefully considered. The E-PSI index only uses taxa that are collected in routine samples by the monitoring agencies, and as such makes the most use of existing data. The River Invertebrate Classification Tool (RICT) used in the UK to derive expected index scores for sites, includes rare species, calculating scores based on their probability of occurrence (Clarke et al., 2003).

4.5. Application of the E-PSI index

In application, most indices should be used within an Ecological Quality Index (EQI) framework, based on observed versus expected invertebrate community composition (Glendell et al., 2014a), particularly when being used for regulatory purposes. This requires a predictive model that is independent of the pressure of concern. At present, in the UK, the predictive model “RICT” (previously RIVPACS IV) is not independent of fine sediment, as substrate composition is a predictor variable (Clarke et al., 2011). Furthermore, it is over-simplistic to assume that deviation of observed from expected community composition (and therefore index score) can be explained by a single measurement at one point in time. Aside from the fact that the structure of macroinvertebrate communities is determined not simply by the contemporaneous fine sediment, but by local sediment dynamics spanning the preceding days, weeks and months, there are multiple reasons for this not being a simple cause-effect relationship. Firstly, fine sediment has numerous direct and indirect effects on invertebrates (reviewed in Bilotta and Brazier, 2008), many of which are poorly understood. Secondly, not only are there often dissociated pressures present, but studies have also shown a number of common sediment-associated physical, chemical and biological pressures (Table 1) that depend on catchment land use, in-stream influences, geomorphology, hydrology and so on. For example, fine sediment pressure is commonly associated with stream flow, due to the influence of stream velocity on the transport, deposition and re-suspension of fine sediment (Wood and Armitage, 1997). Additionally, depending on the sorptive properties of the sediment (i.e. organic carbon content, particle size, clay content and cation exchange capacity) hydrophobic contaminants often become associated via adsorption or absorption, potentially acting as confounding pressures (Warren et al., 2003). Lastly, in disturbed sites, the biological communities have often been subjected to this range of pressures over an extended period of time and therefore the observed biological community composition at any point in time is partly reflective of the legacy of these pressures (Allan, 2004).

The common occurrence of diverse pressures in rivers and streams, places a greater importance on a mechanistic linkage and understanding of biotic response to the pressure of concern. As a result, it is likely that most pressure-specific indices will be limited in terms of their ability to make accurate predictions of the degree of impact across all river and stream ecosystems. Instead, a more achievable and realistic goal is to use a suite of different pressure-specific indices to identify potential areas of ecological degradation and the likely causes of any deviations. The family and mixed level E-PSI indices are two such tools, which could be used alongside other indices to inform more targeted monitoring and mitigation measures.

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Appendix A.

Table A1

Sensitive macroinvertebrate families removed from E-PSI calculations, based on a 33% threshold being applied to their corresponding sediment values.

| Removed sensitive families | Number of sensitive taxa in E-PSI _{mixed} | Number of insensitive taxa in E-PSI _{mixed} | Corresponding sediment value (%) |
|----------------------------|--|--|----------------------------------|
| Sisyridae | 0 | 0 | 83 |
| Piscicolidae | 1 | 0 | 73 |
| Limnephilidae | 5 | 15 | 46 |
| Beraeidae | 3 | 0 | 45 |
| Scirtidae | 1 | 1 | 45 |
| Dixidae | n/a | n/a | 42 |
| Goeridae | 3 | 0 | 38 |
| Gammaridae | 2 | 3 | 37 |
| Polycentropodidae | 7 | 0 | 37 |
| Psychomyiidae | 5 | 0 | 36 |

Appendix B.

Table B1

Sensitivity weights (*W*) for the family-level, Empirically-weighted Proportion of Sediment-sensitive Invertebrates (E-PSI) index.

| Sensitive taxa | <i>W</i> |
|--|----------|
| Heptageniidae | 1 |
| Perlidae | 1 |
| Aphelocheiridae | 0.99 |
| Chloroperlidae | 0.99 |
| Lepidostomatidae | 0.99 |
| Leuctridae | 0.99 |
| Perlodidae | 0.99 |
| Baetidae | 0.75 |
| Brachycentridae | 0.75 |
| Capniidae | 0.75 |
| Hydraenidae | 0.75 |
| Hydropsychidae | 0.75 |
| Taeniopterygidae | 0.75 |
| Planorbidae (genus <i>Ancylus</i> only) | 0.51 |
| Glossosomatidae | 0.51 |
| Leptophlebiidae | 0.51 |
| Rhyacophilidae | 0.51 |
| Elmidae | 0.5 |
| Ephemerellidae | 0.5 |
| Niphargidae | 0.5 |
| Odontoceridae | 0.5 |
| Philopotamidae | 0.5 |
| Potamanthidae | 0.5 |
| Sericostomatidae | 0.5 |
| Simuliidae | 0.5 |
| Tipulidae, Limoniidae, Cylindrotomidae and Pediciidae | 0.5 |
| Insensitive taxa | <i>W</i> |
| Aeshnidae | 0.49 |
| Bithyniidae | 0.49 |
| Calopterygidae | 0.49 |
| Cordulegastridae | 0.49 |
| Corixidae | 0.49 |
| Ephemeridae | 0.49 |
| Hydrophilidae, Helophoridae, Georissidae and Hydrochidae | 0.49 |
| Libellulidae | 0.49 |
| Noteridae | 0.49 |

Table B1 (Continued)

| Insensitive taxa | <i>W</i> |
|---|----------|
| Stratiomyidae | 0.49 |
| Halplidae | 0.48 |
| Hydrobiidae | 0.48 |
| Nepidae | 0.48 |
| Neritidae | 0.48 |
| Phryganeidae | 0.48 |
| Platycnemididae | 0.48 |
| Ptychopteridae | 0.48 |
| Sialidae | 0.48 |
| Sphaeriidae | 0.48 |
| Syrphidae | 0.48 |
| Tabanidae | 0.48 |
| Unionidae | 0.48 |
| Crangonyctidae | 0.25 |
| Dytiscidae | 0.25 |
| Physidae | 0.25 |
| Planariidae | 0.25 |
| Siphonuridae, Ameletidae | 0.25 |
| Valvatidae | 0.25 |
| Asellidae | 0.24 |
| Glossiphoniidae | 0.24 |
| Viviparidae | 0.24 |
| Dendrocoelidae | 0.01 |
| Dryopidae | 0.01 |
| Erpobdellidae | 0.01 |
| Hirudinidae | 0.01 |
| Lymnaeidae | 0.01 |
| Molannidae | 0.01 |
| Caenidae | 0 |
| Corophiidae | 0 |
| Dugesidae | 0 |
| Nemouridae | 0 |
| Planorbidae (excluding genus <i>Ancylus</i>) | 0 |
| Psychodidae | 0 |

Appendix C.

Table C1

Sensitivity weights (*W*) for the mixed-level, Empirically-weighted Proportion of Sediment-sensitive Invertebrates (E-PSI) index.

| Sensitive taxa | <i>W</i> |
|----------------------------------|-----------------------|
| <i>Amphinemura sulcicollis</i> | (Stephens, 1836) 1 |
| <i>Apatania muliebris</i> | (McLachlan, 1866) 1 |
| <i>Baetis rhodani</i> | (Pictet, 1843–1845) 1 |
| <i>Baetis scambus</i> group | 1 |
| <i>Brachycentrus subnubilus</i> | (Curtis, 1834) 1 |
| <i>Brachyptera putata</i> | (Newman, 1838) 1 |
| <i>Ceraclea albimaculata</i> | (Rambur, 1842) 1 |
| <i>Ceraclea annulicornis</i> | (Stephens, 1836) 1 |
| <i>Cheumatopsyche lepida</i> | (Pictet, 1834) 1 |
| <i>Chimarra marginata</i> | (Linnaeus, 1761) 1 |
| <i>Chloroperla tripunctata</i> | (Scopoli, 1763) 1 |
| <i>Crenobia alpina</i> | (Dana, 1766) 1 |
| <i>Dinocras cephalotes</i> | (Curtis, 1827) 1 |
| <i>Diplectrona felix</i> | (McLachlan, 1878) 1 |
| <i>Ecclisopteryx guttulata</i> | (Pictet, 1834) 1 |
| <i>Ecdyonurus</i> sp. | 1 |
| <i>Electrogena lateralis</i> | (Curtis, 1834) 1 |
| <i>Glossosoma</i> sp. | 1 |
| <i>Hydraena gracilis</i> | (Germar, 1824) 1 |
| <i>Hydraena nigrita</i> | (Germar, 1824) 1 |
| <i>Hydroporus ferrugineus</i> | (Stephens, 1829) 1 |
| <i>Hydropsyche contubernalis</i> | (McLachlan, 1865) 1 |
| <i>Hydropsyche pellucidula</i> | (Curtis, 1834) 1 |
| <i>Isoperla grammatica</i> | (Poda, 1761) 1 |
| <i>Lepidostoma hirtum</i> | (Fabricius, 1775) 1 |
| <i>Leuctra fusca</i> | (Linnaeus, 1758) 1 |

Table C1 (Continued)

| Sensitive taxa | | W |
|---------------------------------------|---------------------|------|
| <i>Leuctra hippopus</i> | (Kempny, 1899) | 1 |
| <i>Leuctra inermis</i> | (Kempny, 1899) | 1 |
| <i>Leuctra moselyi</i> | (Morton, 1929) | 1 |
| <i>Macronychus quadrituberculatus</i> | (Müller, 1806) | 1 |
| <i>Neureclipsis bimaculata</i> | (Linnaeus, 1758) | 1 |
| <i>Nigrobaetis digitatus</i> | (Bengtsson, 1912) | 1 |
| <i>Normandia nitens</i> | (Müller, 1817) | 1 |
| <i>Oecetis notata</i> | (Rambur, 1842) | 1 |
| <i>Oreodytes davisii</i> | (Curtis, 1831) | 1 |
| <i>Oreodytes septentrionalis</i> | (Gyllenhal, 1826) | 1 |
| <i>Perla bipunctata</i> | (Pictet, 1833) | 1 |
| <i>Perlodes microcephalus</i> | (Pictet, 1833) | 1 |
| <i>Plectrocnemia geniculata</i> | (McLachlan, 1871) | 1 |
| <i>Polycentropus flavomaculatus</i> | (Pictet, 1834) | 1 |
| <i>Polycentropus kingi</i> | (McLachlan, 1881) | 1 |
| <i>Protonemura praecox</i> | (Morton, 1894) | 1 |
| <i>Psychomyia pusilla</i> | (Fabricius, 1781) | 1 |
| <i>Rhithrogena</i> sp. | | 1 |
| <i>Siphonoperla torrentium</i> | (Pictet, 1841) | 1 |
| <i>Wormaldia</i> sp. | | 1 |
| <i>Alainites muticus</i> | (Linnaeus, 1758) | 0.88 |
| <i>Heptagenia sulphurea</i> | (Müller, 1776) | 0.88 |
| <i>Hydropsyche siltalai</i> | (Döhler, 1963) | 0.88 |
| <i>Protonemura meyeri</i> | (Pictet, 1841) | 0.88 |
| <i>Rhyacophila dorsalis</i> | (Curtis, 1834) | 0.88 |
| <i>Beraea maurus</i> | (Curtis, 1834) | 0.87 |
| <i>Beraeodes minutus</i> | (Linnaeus, 1761) | 0.87 |
| <i>Ephemerella notata</i> | (Eaton, 1887) | 0.87 |
| <i>Orectochilus villosus</i> | (O.F. Müller, 1776) | 0.87 |
| <i>Procloeon pennulatum</i> | (Eaton, 1870) | 0.87 |
| <i>Ceraclea senilis</i> | (Burmeister, 1839) | 0.75 |
| <i>Leuctra geniculata</i> | (Stephens, 1836) | 0.63 |
| <i>Oecetis testacea</i> | (Curtis, 1834) | 0.63 |
| <i>Paraleptophlebia submarginata</i> | (Stephens, 1835) | 0.63 |
| Tipulidae | | 0.63 |
| <i>Melampophylax mucoreus</i> | (Hagen, 1861) | 0.62 |
| <i>Agabus guttatus</i> | (Paykull, 1798) | 0.5 |
| <i>Agapetus</i> sp. | | 0.5 |
| <i>Allotrichia pallicornis</i> | (Eaton, 1873) | 0.5 |
| <i>Ameletus inopinatus</i> | (Eaton, 1887) | 0.5 |
| <i>Ancyclus fluvialis</i> | (O.F. Müller, 1774) | 0.5 |
| <i>Aphelocheirus aestivalis</i> | (Fabricius, 1794) | 0.5 |
| <i>Athripsodes albifrons</i> | (Linnaeus, 1758) | 0.5 |
| <i>Athripsodes bilineatus</i> | (Linnaeus, 1758) | 0.5 |
| <i>Athripsodes cinereus</i> | (Curtis, 1834) | 0.5 |
| <i>Athripsodes commutatus</i> | (Rostock, 1874) | 0.5 |
| <i>Baetis buceratus</i> | (Eaton, 1870) | 0.5 |
| <i>Baetis vernus</i> | (Curtis, 1834) | 0.5 |
| <i>Beraea pullata</i> | (Curtis, 1834) | 0.5 |
| <i>Brachyptera risi</i> | (Morton, 1896) | 0.5 |
| <i>Calopteryx virgo</i> | (Linnaeus, 1758) | 0.5 |
| <i>Capnia atra</i> | (Morton, 1896) | 0.5 |
| <i>Capnia bifrons</i> | (Newman, 1839) | 0.5 |
| <i>Ceraclea dissimilis</i> | (Stephens, 1836) | 0.5 |
| <i>Ceraclea fulva</i> | (Rambur, 1842) | 0.5 |
| <i>Ceraclea nigronervosa</i> | (Retzius, 1783) | 0.5 |
| <i>Crunoecia irrorata</i> | (Curtis, 1834) | 0.5 |
| <i>Cynurus trimaculatus</i> | (Curtis, 1834) | 0.5 |
| <i>Deronectes latus</i> | (Stephens, 1829) | 0.5 |
| <i>Diura bicaudata</i> | (Linnaeus, 1758) | 0.5 |
| Dixidae | | 0.5 |
| <i>Drusus annulatus</i> | (Stephens, 1837) | 0.5 |
| <i>Elmis aenea</i> | (Müller, 1806) | 0.5 |
| <i>Elodes</i> sp. | | 0.5 |
| <i>Gammarus duebeni</i> | (Liljeborg, 1852) | 0.5 |
| <i>Gammarus pulex</i> | (Linnaeus, 1758) | 0.5 |
| <i>Goera pilosa</i> | (Fabricius, 1775) | 0.5 |
| <i>Hydraena riparia</i> | (Kugelann, 1794) | 0.5 |
| <i>Hydraena rufipes</i> | (Curtis, 1830) | 0.5 |
| <i>Hydropsyche angustipennis</i> | (Curtis, 1834) | 0.5 |

Table C1 (Continued)

| Sensitive taxa | | W |
|--|------------------------------------|------|
| <i>Hydropsyche fulvipes</i> | (Curtis, 1834) | 0.5 |
| <i>Hydropsyche instabilis</i> | (Curtis, 1834) | 0.5 |
| <i>Hydropsyche saxonica</i> | (McLachlan, 1884) | 0.5 |
| <i>Labiobaetis atrebatinus</i> | (Eaton, 1870) | 0.5 |
| <i>Lepidostoma basale</i> | (Kolenati, 1848) | 0.5 |
| <i>Leuctra nigra</i> | (Olivier, 1811) | 0.5 |
| <i>Limnius volckmari</i> | (Panzer, 1793) | 0.5 |
| Limoniidae | | 0.5 |
| <i>Margaritifera margaritifera</i> | (Linnaeus, 1758) | 0.5 |
| <i>Metalype fragilis</i> | (Pictet, 1834) | 0.5 |
| <i>Micronecta</i> sp. | | 0.5 |
| Micropterna group | | 0.5 |
| <i>Nemoura cambrica</i> group | | 0.5 |
| <i>Nigrobaetis niger</i> | (Linnaeus, 1761) | 0.5 |
| <i>Niphargus aquilex</i> | (Schiodte, 1855) | 0.5 |
| <i>Odontocerum albicorne</i> | (Scopoli, 1763) | 0.5 |
| <i>Oreodytes sanmarkii</i> | (C.R. Sahlberg, 1826) | 0.5 |
| <i>Paraleptophlebia cincta</i> | (Retzius, 1835) | 0.5 |
| Pediciidae | | 0.5 |
| <i>Phagocata vitta</i> | (Duges, 1830) | 0.5 |
| <i>Philopotamus montanus</i> | (Donovan, 1813) | 0.5 |
| <i>Piscicola geometra</i> | (Linnaeus, 1761) | 0.5 |
| <i>Platambus maculatus</i> | (Linnaeus, 1758) | 0.5 |
| <i>Plectrocnemia conspersa</i> | (Curtis, 1834) | 0.5 |
| <i>Polycentropus irroratus</i> | (Curtis, 1835) | 0.5 |
| <i>Potamanthus luteus</i> | (Linnaeus, 1767) | 0.5 |
| <i>Potamophylax</i> group | | 0.5 |
| <i>Protonemura montana</i> | (Kimmins, 1941) | 0.5 |
| <i>Rhyacophila fasciata</i> | (Hagen, 1859) | 0.5 |
| <i>Rhyacophila munda</i> | (McLachlan, 1862) | 0.5 |
| <i>Rhyacophila obliterata</i> | (McLachlan, 1863) | 0.5 |
| <i>Riolus cupreus</i> | (Müller, 1806) | 0.5 |
| <i>Riolus subviolaceus</i> | (Müller, 1817) | 0.5 |
| <i>Sericostoma personatum</i> | (Spence in Kirby and Spence, 1826) | 0.5 |
| <i>Serratella ignita</i> | (Poda, 1761) | 0.5 |
| <i>Sialis fuliginosa</i> | (Pictet, 1836) | 0.5 |
| <i>Silo nigricornis</i> | (Pictet, 1834) | 0.5 |
| <i>Silo pallipes</i> | (Fabricius, 1781) | 0.5 |
| Simuliidae | | 0.5 |
| <i>Stictonectes lepidus</i> | (Olivier, 1795) | 0.5 |
| <i>Tinodes dives</i> | (Pictet, 1834) | 0.5 |
| <i>Tinodes unicolor</i> | (Pictet, 1834) | 0.5 |
| <i>Tinodes waeneri</i> | (Linnaeus, 1758) | 0.5 |
| Insensitive taxa | | W |
| <i>Aeshna</i> sp. | | 0.49 |
| <i>Agabus didymus</i> | (Olivier, 1795) | 0.49 |
| <i>Agabus paludosus</i> | (Fabricius, 1801) | 0.49 |
| <i>Alboglossiphonia heteroclita</i> | (Linnaeus, 1761) | 0.49 |
| <i>Anabolia nervosa</i> | (Curtis, 1834) | 0.49 |
| <i>Anacaena globulus</i> | (Paykull, 1829) | 0.49 |
| <i>Anisus (Anisus) leucostoma</i> | (Millet, 1813) | 0.49 |
| <i>Anisus (Disculifer) vortex</i> | (Linnaeus, 1758) | 0.49 |
| <i>Bdellocephala punctata</i> | (Pallas, 1774) | 0.49 |
| <i>Bithynia (Bithynia) tentaculata</i> | (Linnaeus, 1758) | 0.49 |
| <i>Bithynia (Codiella) leachii</i> | (Sheppard, 1823) | 0.49 |
| <i>Brychius elevatus</i> | (Panzer, 1793) | 0.49 |
| <i>Caenis horaria</i> | (Linnaeus, 1758) | 0.49 |
| <i>Caenis robusta</i> | (Eaton, 1884) | 0.49 |
| <i>Callicorixa praeusta</i> | (Fieber, 1848) | 0.49 |
| <i>Calopteryx splendens</i> | (Harris, 1782) | 0.49 |
| <i>Centroptilum luteolum</i> | (Müller, 1776) | 0.49 |
| <i>Cloeon dipterum</i> | (Linnaeus, 1761) | 0.49 |
| <i>Cloeon simile</i> | (Eaton, 1870) | 0.49 |
| <i>Cordulegaster boltonii</i> | (Donovan, 1807) | 0.49 |
| <i>Corixa dentipes</i> | (Thomson, 1869) | 0.49 |
| <i>Corixa punctata</i> | (Illiger, 1807) | 0.49 |
| <i>Corophium</i> sp. | | 0.49 |
| <i>Dytiscus semisulcatus</i> | (O.F. Müller, 1776) | 0.49 |

Table C1 (Continued)

| Insensitive taxa | | W |
|---|---------------------|------|
| <i>Ephemera danica</i> | (Müller, 1764) | 0.49 |
| <i>Erpobdella testacea</i> | (Savigny, 1812) | 0.49 |
| <i>Galba truncatula</i> | (O.F. Müller, 1774) | 0.49 |
| <i>Glyptotaelius pellucidus</i> | (Retzius, 1783) | 0.49 |
| <i>Gomphus vulgatissimus</i> | (Linnaeus, 1758) | 0.49 |
| <i>Graptodytes pictus</i> | (Fabricius, 1787) | 0.49 |
| <i>Habrophlebia fusca</i> | (Curtis, 1834) | 0.49 |
| <i>Haemopsis sanguisuga</i> | (Linnaeus, 1758) | 0.49 |
| <i>Halesus</i> sp. | | 0.49 |
| <i>Haliplus flavicollis</i> | (Sturm, 1834) | 0.49 |
| <i>Haliplus fluviatilis</i> | (Aubé, 1836) | 0.49 |
| <i>Haliplus ruficollis</i> | (DeGeer, 1774) | 0.49 |
| <i>Haliplus sibericus</i> | (Motschulsky, 1860) | 0.49 |
| <i>Helophorus (Helophorus) minutus</i> | (Fabricius, 1775) | 0.49 |
| <i>Helophorus (Meghelophorus) aequalis</i> | (Thomson, 1868) | 0.49 |
| <i>Helophorus (Meghelophorus) grandis</i> | (Illiger, 1798) | 0.49 |
| <i>Helophorus (Rhopalohelophorus) brevipalpis</i> | (Bedel, 1881) | 0.49 |
| <i>Hesperocorixa linnaei</i> | (Fieber, 1848) | 0.49 |
| <i>Hesperocorixa sahlbergi</i> | (Fieber, 1848) | 0.49 |
| <i>Hydatophylax infumatus</i> | (McLachlan, 1865) | 0.49 |
| <i>Hydraena pulchella</i> | (Germar, 1824) | 0.49 |
| <i>Hydraena testacea</i> | (Curtis, 1831) | 0.49 |
| <i>Hydrobius fuscipes</i> | (Linnaeus, 1758) | 0.49 |
| <i>Hydroporus memnonius</i> | (Nicolai, 1822) | 0.49 |
| <i>Hydroporus pubescens</i> | (Gyllenhal, 1808) | 0.49 |
| <i>Hydroporus tessellatus</i> | (Drapiey, 1819) | 0.49 |
| <i>Hygrotus (Hygrotus) inaequalis</i> | (Fabricius, 1777) | 0.49 |
| <i>Hygrotus (Hygrotus) versicolor</i> | (Schaller, 1783) | 0.49 |
| <i>Hyphyrus ovatus</i> | (Linnaeus, 1761) | 0.49 |
| <i>Ilybius</i> sp. | | 0.49 |
| <i>Kageronia fuscogrisea</i> | (Retzius, 1783) | 0.49 |
| <i>Laccobius (Laccobius) minutus</i> | (Linnaeus, 1758) | 0.49 |
| <i>Limnebius nitidus</i> | (Marsham, 1802) | 0.49 |
| <i>Limnephilus decipiens</i> | (Kolenati, 1848) | 0.49 |
| <i>Limnephilus extricatus</i> | (McLachlan, 1865) | 0.49 |
| <i>Limnephilus flavicornis</i> | (Fabricius, 1787) | 0.49 |
| <i>Limnephilus lunatus</i> | (Curtis, 1834) | 0.49 |
| <i>Limnephilus rhombicus</i> | (Linnaeus, 1758) | 0.49 |
| <i>Lymnaea stagnalis</i> | (Linnaeus, 1758) | 0.49 |
| <i>Molanna angustata</i> | (Curtis, 1834) | 0.49 |
| <i>Mystacides longicornis</i> | (Linnaeus, 1758) | 0.49 |
| <i>Nebrioporus depressus</i> | (Fabricius, 1775) | 0.49 |
| <i>Nemoura cinerea</i> | (Retzius, 1783) | 0.49 |
| <i>Nemurella pictetii</i> | (Klapálek, 1900) | 0.49 |
| <i>Noterus clavicornis</i> | (DeGeer, 1774) | 0.49 |
| <i>Notidobia ciliaris</i> | (Linnaeus, 1761) | 0.49 |
| <i>Ochthebius dilatatus</i> | (Stephens, 1829) | 0.49 |
| <i>Ochthebius minimus</i> | (Fabricius, 1792) | 0.49 |
| <i>Oecetis lacustris</i> | (Pictet, 1834) | 0.49 |
| <i>Oecetis ochracea</i> | (Curtis, 1825) | 0.49 |
| <i>Oulimnius rivularis</i> | (Rosenhauer, 1856) | 0.49 |
| <i>Paraleptophlebia werneri</i> | (Ulmer, 1919) | 0.49 |
| <i>Phryganea</i> sp. | | 0.49 |
| <i>Physa fontinalis</i> | (Linnaeus, 1758) | 0.49 |
| <i>Pisidium</i> sp. | | 0.49 |
| <i>Planorbium corneum</i> | (Linnaeus, 1758) | 0.49 |
| <i>Planorbis (Planorbis) carinatus</i> | (O.F. Müller, 1774) | 0.49 |
| <i>Planorbis (Planorbis) planorbis</i> | (Linnaeus, 1758) | 0.49 |
| <i>Platycnemis pennipes</i> | (Pallas, 1771) | 0.49 |
| <i>Proasellus meridianus</i> | (Racovitza, 1919) | 0.49 |
| <i>Procloeon bifidum</i> | (Bengtsson, 1912) | 0.49 |
| Ptychopteridae | | 0.49 |
| <i>Scarodytes halensis</i> | (Fabricius, 1787) | 0.49 |
| <i>Segmentina nitida</i> | (O.F. Müller, 1774) | 0.49 |
| <i>Sialis lutaria</i> | (Linnaeus, 1758) | 0.49 |
| <i>Sigara (Pseudovermicorixa) nigrolineata</i> | (Fieber, 1848) | 0.49 |
| <i>Sigara (Sigara)</i> sp. | | 0.49 |
| <i>Sigara (Subsigara) falleni</i> | (Fieber, 1848) | 0.49 |
| <i>Sphaerium</i> sp. | | 0.49 |
| <i>Stagnicola palustris</i> | (O.F. Müller, 1774) | 0.49 |
| Stratiomyidae | | 0.49 |

Table C1 (Continued)

| Insensitive taxa | | W |
|--|---------------------------|------|
| Syrphidae | | 0.49 |
| <i>Theodoxus fluviatilis</i> | (Linnaeus, 1758) | 0.49 |
| <i>Unio</i> sp. | | 0.49 |
| <i>Valvata (Valvata) cristata</i> | (O.F. Müller, 1774) | 0.49 |
| <i>Viviparus viviparus</i> | (Linnaeus, 1758) | 0.49 |
| <i>Glossiphonia complanata</i> | (Linnaeus, 1758) | 0.48 |
| <i>Ephemera vulgata</i> | (Linnaeus, 1758) | 0.47 |
| <i>Amphinemura standfussi</i> | (Ris, 1902) | 0.37 |
| <i>Asellus aquaticus</i> | (Linnaeus, 1758) | 0.37 |
| <i>Athripsodes aterrimus</i> | (Stephens, 1836) | 0.37 |
| <i>Callicorixa wollastoni</i> | (Douglas and Scott, 1865) | 0.37 |
| <i>Hydroporus obscurus</i> | (Sturm, 1835) | 0.37 |
| <i>Mystacides azurea</i> | (Linnaeus, 1761) | 0.37 |
| <i>Mystacides nigra</i> | (Linnaeus, 1758) | 0.37 |
| <i>Polycelis felina</i> | (Dalyell, 1814) | 0.37 |
| <i>Potamopyrgus antipodarum</i> | (J.E.Gray, 1843) | 0.37 |
| Psychodidae | | 0.37 |
| Tabanidae | | 0.37 |
| <i>Valvata (Cincinna) piscinalis</i> | (O.F. Müller, 1774) | 0.37 |
| Agrypnia obsoleta group | | 0.25 |
| <i>Anacaena bipustulata</i> | (Marsham, 1802) | 0.25 |
| <i>Aplexa hypnorum</i> | (Linnaeus, 1758) | 0.25 |
| <i>Brachytron pratense</i> | (Müller, 1764) | 0.25 |
| <i>Corixa panzeri</i> | (Fieber, 1848) | 0.25 |
| <i>Dytiscus marginalis</i> | (Linnaeus, 1758) | 0.25 |
| <i>Ecnomus tenellus</i> | (Rambur, 1842) | 0.25 |
| <i>Ephemera lineata</i> | (Eaton, 1870) | 0.25 |
| <i>Haliplus heydeni</i> | (Wehncke, 1875) | 0.25 |
| <i>Haliplus lineolatus</i> | (Mannerheim, 1844) | 0.25 |
| <i>Helophorus (Helophorus) strigifrons</i> | (Thomson, 1868) | 0.25 |
| <i>Laccobius (Laccobius) colon</i> | (Stephens, 1829) | 0.25 |
| <i>Laccobius (Macrolaccobius) sinuatus</i> | (Motschulsky, 1849) | 0.25 |
| <i>Laccobius (Macrolaccobius) striatulus</i> | (Fabricius, 1801) | 0.25 |
| <i>Limnephilus binotatus</i> | (Curtis, 1834) | 0.25 |
| <i>Limnephilus politus</i> | (McLachlan, 1865) | 0.25 |
| <i>Limnephilus vittatus</i> | (Fabricius, 1798) | 0.25 |
| <i>Paracymus scutellaris</i> | (Rosenhauer, 1856) | 0.25 |
| <i>Porhydrus lineatus</i> | (Fabricius, 1775) | 0.25 |
| <i>Enochrus testaceus</i> | (Fabricius, 1801) | 0.24 |
| <i>Nebrioporus assimilis</i> | (Paykull, 1798) | 0.24 |
| <i>Anacaena lutescens</i> | (Stephens, 1829) | 0.12 |
| Anodonta group | | 0.12 |
| <i>Brachycercus harrisellus</i> | (Curtis, 1834) | 0.12 |
| <i>Caenis luctuosa</i> group | | 0.12 |
| <i>Erpobdella octoculata</i> | (Linnaeus, 1758) | 0.12 |
| <i>Gyraulus (Armiger) crista</i> | (Linnaeus, 1758) | 0.12 |
| <i>Gyraulus (Gyraulus) albus</i> | (O.F. Müller, 1774) | 0.12 |
| <i>Haliplus laminatus</i> | (Schaller, 1783) | 0.12 |
| <i>Haliplus lineatocollis</i> | (Marsham, 1802) | 0.12 |
| <i>Helobdella stagnalis</i> | (Linnaeus, 1758) | 0.12 |
| <i>Hemiclepsis marginata</i> | (O.F.Müller, 1774) | 0.12 |
| <i>Hippeutis complanatus</i> | (Linnaeus, 1758) | 0.12 |
| <i>Hydroporus palustris</i> | (Linnaeus, 1761) | 0.12 |
| <i>Ilybius chalconatus</i> | (Panzer, 1796) | 0.12 |
| <i>Leptophlebia marginata</i> | (Linnaeus, 1767) | 0.12 |
| <i>Leptophlebia vespertina</i> | (Linnaeus, 1758) | 0.12 |
| <i>Nemoura avicularis</i> | (Morton, 1894) | 0.12 |
| <i>Oulimnius major</i> | (Rey, 1889) | 0.12 |
| <i>Oulimnius tuberculatus</i> | (Müller, 1806) | 0.12 |
| <i>Sialis nigripes</i> | (Pictet, 1865) | 0.12 |
| <i>Sigara (Subsigara) distincta</i> | (Fieber, 1848) | 0.12 |
| <i>Stictotarsus duodecimpustulatus</i> | (Fabricius, 1792) | 0.12 |
| <i>Laccophilus minutus</i> | (Linnaeus, 1758) | 0.01 |
| <i>Agabus bipustulatus</i> | (Linnaeus, 1767) | 0 |
| <i>Agabus sturmii</i> | (Gyllenhal, 1808) | 0 |
| <i>Anacaena limbata</i> | (Fabricius, 1792) | 0 |
| <i>Bathymphalus contortus</i> | (Linnaeus, 1758) | 0 |
| <i>Caenis pseudorivulorum</i> group | | 0 |
| <i>Caenis pusilla</i> | (Navás, 1913) | 0 |
| <i>Caenis rivulorum</i> | (Eaton, 1884) | 0 |

Table C1 (Continued)

| Insensitive taxa | | W |
|---|-------------------------------|---|
| <i>Corixa affinis</i> | (Leach, 1817) | 0 |
| <i>Crangonyx pseudogracilis</i> | (Bousfield, 1958) | 0 |
| <i>Cyphon</i> sp. | | 0 |
| <i>Dendrocoelum lacteum</i> | (O.F.Müller, 1774) | 0 |
| <i>Dina lineata</i> | (O.F.Müller, 1774) | 0 |
| <i>Dryops</i> sp. | | 0 |
| <i>Dugesia polychroa</i> group | | 0 |
| <i>Dugesia tigrina</i> | (Girard, 1850) | 0 |
| <i>Esolus parallelepipedus</i> | (Müller, 1806) | 0 |
| <i>Gammarus lacustris</i> | (Sars, 1863) | 0 |
| <i>Gammarus tigrinus</i> | (Sexton, 1939) | 0 |
| <i>Gammarus zaddachi</i> | (Sexton, 1912) | 0 |
| <i>Glossiphonia paludosa</i> | (Carena, 1824) | 0 |
| <i>Glossiphonia verrucata</i> | (Fr. Müller, 1844) | 0 |
| <i>Gyraulus (Torquis) laevis</i> | (Alder, 1838) | 0 |
| <i>Halipus confinis</i> | (Stephens, 1828) | 0 |
| <i>Halipus immaculatus</i> | (Gerhardt, 1877) | 0 |
| <i>Helophorus (Helophorus) flavipes</i> | (Fabricius, 1792) | 0 |
| <i>Helophorus (Helophorus) obscurus</i> | (Mulsant, 1884) | 0 |
| <i>Helophorus (Rhopalohelophorus) arvernensis</i> | (Mulsant, 1846) | 0 |
| <i>Hydrochus angustatus</i> | (Germar, 1824) | 0 |
| <i>Hydroporus discretus</i> | (Fairmaire and Brisout, 1859) | 0 |
| <i>Hydroporus nigrita</i> | (Fabricius, 1792) | 0 |
| <i>Hydroporus planus</i> | (Fabricius, 1782) | 0 |
| <i>Laccobius (Macrolaccobius) atratus</i> | (Rottenburg, 1874) | 0 |
| <i>Laccobius (Macrolaccobius) ytenensis</i> | (Sharp, 1910) | 0 |
| <i>Laccophilus hyalinus</i> | (DeGeer, 1774) | 0 |
| <i>Limnebius truncatellus</i> | (Thunberg, 1794) | 0 |
| <i>Limnephilus bipunctatus</i> | (Curtis, 1834) | 0 |
| <i>Limnephilus fuscicornis</i> | (Rambur, 1842) | 0 |
| <i>Limnephilus marmoratus</i> | (Curtis, 1834) | 0 |
| <i>Nepa cinerea</i> | (Linnaeus, 1758) | 0 |
| <i>Ochthebius bicolon</i> | (Germar, 1824) | 0 |
| <i>Ochthebius exsculptus</i> | (Germar, 1824) | 0 |
| <i>Orthetrum</i> sp. | | 0 |
| <i>Oulimnius troglodytes</i> | (Gyllenhal, 1827) | 0 |
| <i>Physella (Costatella) acuta</i> | (Draparnaud, 1805) | 0 |
| <i>Planaria torva</i> | (Müller, 1774) | 0 |
| <i>Polycelis nigra</i> group | | 0 |
| <i>Radix auricularia</i> | (Linnaeus, 1758) | 0 |
| <i>Radix balthica</i> | (Linnaeus, 1758) | 0 |
| <i>Sigara (Retrocorixa) semistriata</i> | (Fieber, 1848) | 0 |
| <i>Sigara (Retrocorixa) venusta</i> | (Douglas and Scott, 1869) | 0 |
| <i>Sigara (Subsigara) fossarum</i> | (Leach, 1817) | 0 |
| <i>Sigara (Vermicorixa) lateralis</i> | (Leach, 1817) | 0 |
| <i>Siphonurus lacustris</i> | (Eaton, 1870) | 0 |
| <i>Taeniopteryx nebulosa</i> | (Linnaeus, 1758) | 0 |
| <i>Theromyzon tessellatum</i> | (O.F.Müller, 1774) | 0 |
| <i>Trocheta bykowski</i> | (Gedroyc, 1913) | 0 |
| <i>Trocheta subviridis</i> | (Dutrochet, 1817) | 0 |
| <i>Valvata (Tropidina) macrostoma</i> | (Morch, 1864) | 0 |

Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.05.040>.

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Does fine sediment source as well as quantity affect salmonid embryo mortality and development?



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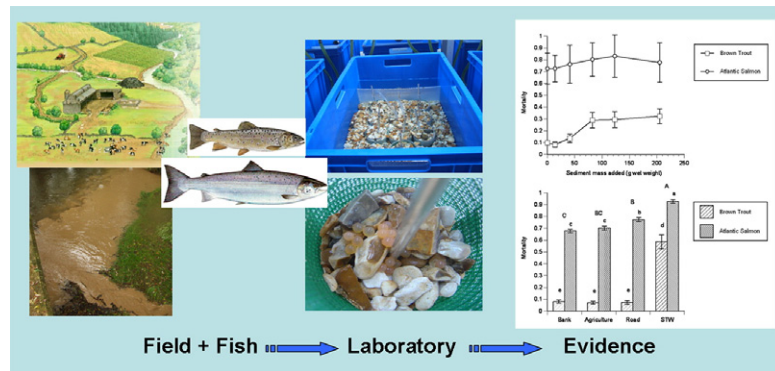
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HIGHLIGHTS

- We expose two salmonid fish species to different sediment loads and sources.
- We examine egg mortality and alevin fitness in response to sediment mass and source.
- We find that sediment source as well as mass effects spawning habitat quality.
- Brown trout are less sensitive to sediment compared to Atlantic salmon.
- Organic matter is the main factor determining the impact of a sediment source.

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Organic matter

ABSTRACT

Fine sediments are known to be an important cause of increased mortality in benthic spawning fish. To date, most of the research has focussed on the relationship between embryo mortality and the quantity of fine sediment accumulated in the egg pocket. However, recent evidence suggests a) that the source of fine sediment might also be important, and b) that fitness of surviving embryos post-hatch might also be impacted by the accumulation of fine sediments. In this paper, we report an experiment designed to simulate the incubation environment of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). During the experiment, the incubating embryos were exposed to different quantities of fine (<63 µm) sediment derived from four different sources; agricultural topsoils, damaged road verges, eroding river channel banks and tertiary level treated sewage. Results showed that mass and source are independently important for determining the mortality and fitness of alevin. Differences between species were observed, such that brown trout are less sensitive to mass and source of accumulated sediment. We demonstrate for the first time that sediment source is an additional control on the impact of fine sediment, and that this is primarily controlled by the organic matter content and oxygen consumption of the catchment source material.

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1. Introduction

Excess fine sediment in watercourses (defined in this paper as $<63 \mu\text{m}$) above natural background levels, is recognised as a pollutant, with important consequences for aquatic ecology and ecosystem function (Jones et al., 2011a & 2011b, Kemp et al., 2011; Collins et al., 2011). Wilkinson and McElroy (2007) report that agricultural river basin sediment delivery ratios have increased by 10–20% relative to the pre-agricultural landscape, which raises concerns over the environmental and socioeconomic consequences of sediment transfer from agricultural land to downstream aquatic ecosystems (Evans, 2010), adding to threats to food and water security from projected climate change (European Union, 2009). Similarly, evidence from lake and floodplain sediments support concerns over offsite impacts of human activity on the land surface (Foster et al., 2011; Macklin et al., 2010; Collins et al., 2012a). This is further supported by studies of the provenance of contemporary fine sediment deposits in river beds (Collins et al. 2010a, 2010b, 2012b, 2012c, 2014) that tend to show the importance of catchment surface sources; the latter often including topsoil eroded from agricultural land. There is also a growing concern over the impact that different sources of sediment have on the aquatic ecosystem, driven in part by legislation set up to protect and enhance the aquatic environment (Collins et al., 2009, 2011). As a result, there is a growing recognition that management of sediment at source is the most sustainable option for achieving the targets set by the legislation (Collins and McGonigle, 2008; Collins et al., 2009, 2011).

In fisheries science, impacts of fine sediment have tended to focus on its accumulation within the spawning gravels of salmonids and specifically, the links between the level of fine sediment (usually expressed as a percentage by weight below a given size) and egg mortality (Sear et al. 2008). Other research has sought to explain the link between the physical impact of fine sediment and the biological response in embryos; highlighting the reduction in the supply of oxygen (Chapman, 1988; Greig et al., 2005a, 2007) or the physical occlusion of micropores on the surface of the egg (Greig et al., 2005b).

Further research has explored the physical characteristics of the fine sediment, seeking to understand which grain size is most closely linked to the mortality of embryos (e.g. summary in Collins et al. (2011)). Thus, Levasseur et al. (2006) concluded that, although very fine sediment ($<63 \mu\text{m} = 0.063 \text{ mm}$) was highly detrimental to embryo survival, larger sediment (up to 2.0 mm) had no corresponding effect. Support for this was observed by Greig et al. (2007) in field studies that showed good survival in spawning gravels with high levels of sand accumulation, citing the permeability of sand compared to other sites where silt/clay occluded the flow of oxygenated water to the embryo. Lapointe et al. (2005) have shown in laboratory experiments, how the lethal effects of silt–clay sediments occur when combined with sand-sized fractions. The sand traps the finer particles that would otherwise have moved through the larger interstices between the gravel framework and reduces permeability, and thus oxygen supply rate, to incubating progeny.

Organic matter content is an important characteristic of fine sediment accumulation in spawning gravels (Collins et al., 2009, 2013, 2014), with two main effects; first, the presence of biological activity driven by organic matter can generate the formation of biofilms, that block the interstitial pores of gravels (Petticrew and Arocena, 2003) and, secondly, decomposition of the organic matter creates an oxygen demand which competes with the demands made by the incubating embryo (Greig et al., 2005a). For Pacific salmon species, Bjornn and Reiser (1991) hypothesized that organic matter accumulation may have deleterious effects on incubating salmon, whilst Petticrew and Rex (2006) report an 18% reduction in intergravel DO following organic matter loading from dying spent salmon.

Collectively, these observations suggest that sediments with different physical attributes might be expected to have different impacts on incubating embryos. The science of sediment fingerprinting is based

on the principle that sediment derived from different sources will be characterised by differing physical or geochemical characteristics (Collins and Walling, 2004; Collins et al., 2010a), thus there is reason to hypothesize that differing sources of sediment will have differing levels of impact on benthic spawning fish.

Recent research has started to develop an evidence base for sub-lethal effects of sedimentation on subsequent life stages (Rousset, 2007; Burke, 2011; Louhi et al., 2011). While studies of incubating salmonids typically estimate survival to emergence, this measure fails to account for the possibility that marginal hyporheic conditions may allow for survival to emergence, but with reduced probability of survival to maturity (Silver et al., 1963; Chapman, 1988). Even at sub-lethal levels of DO, studies have demonstrated smaller and lighter embryos (Youngson et al., 2005; Malcolm et al., 2008), deformity, and delayed hatch and emergence (Alderdice et al., 1958; Silver et al., 1963; Shumway et al., 1964). Against this background of potential complexity, laboratory studies have also demonstrated that embryos can endure short periods (7 days) of very low DO ($<2 \text{ mg L}^{-1}$) without noticeable effects, depending on temperature and stage of development (Alderdice et al., 1958; Geist et al., 2006; Ciuhandu et al., 2008).

Despite these emerging lines of evidence, there is still comparatively little evidence for the effects of sediment load on sub-lethality in salmonids. There is no evidence to date to support the importance of different sediment sources on embryo mortality and fitness. This latter research is required in order to link the growing evidence of source specific sediment loads (e.g. associated with specific risky crops in farming, e.g. maize or winter wheat cropping) to benthic spawning fish (see review by Kemp et al. (2011)). Therefore, in this paper, we seek to test for the first time; (1) the effects of different sediment source and/or loading on embryo mortality; (2) the effects of different sediment source and/or loading on the development of surviving embryos, and; (3) the differing response of two economically important, benthic spawning salmonid species – brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). The experimental work was undertaken as a component of a large multi-partner research project examining the impacts of fine sediment on fluvial aquatic ecology.

2. Methods

2.1. Experimental facility and design

We conducted experiments at the University of Southampton Chilworth hydraulics laboratory Fish Research Facility from 17th November 2010 to 25th January 2011. The facility is a continuous recirculating system, in which water is fed via two main pipes from a biofiltration system to each of 48 separate tanks (Fig. 1). The return water from each tank is collected in a return pipe and passed back into the biofiltration system. The return water is then treated to remove any sediment using fine fabric filters and a sand bed filter, before being passed through a UV and biofiltration system which removes any bacteria or biological material. The water is then recirculated via a chiller unit to control temperature, back through the feeder pipes to each tank. Water is fed into each tank through two inflow pipes, located at the bottom and one close to the top of the tank (Fig. 1) with a single outlet pipe located near the surface. The design is similar to that reported by Louhi et al. (2011). Dissolved material, including nutrients, was not removed by the system but their levels were monitored in the feeder tank prior to distribution through the system. Thus, all 48 tanks received the same amount and quality of water throughout the experiments.

To determine whether alevin growth and mortality were affected by fine sediment load and (or) sediment source, we applied sediment from four different sources (river bank, damaged road verge, agricultural topsoils and treated sewage sludge) at five loads (1% (14 g), 3% (41 g), 6% (82 g), 9% (123 g), 15% (205 g) by wet weight) plus an independent zero sediment control for each source treatment. We applied the same

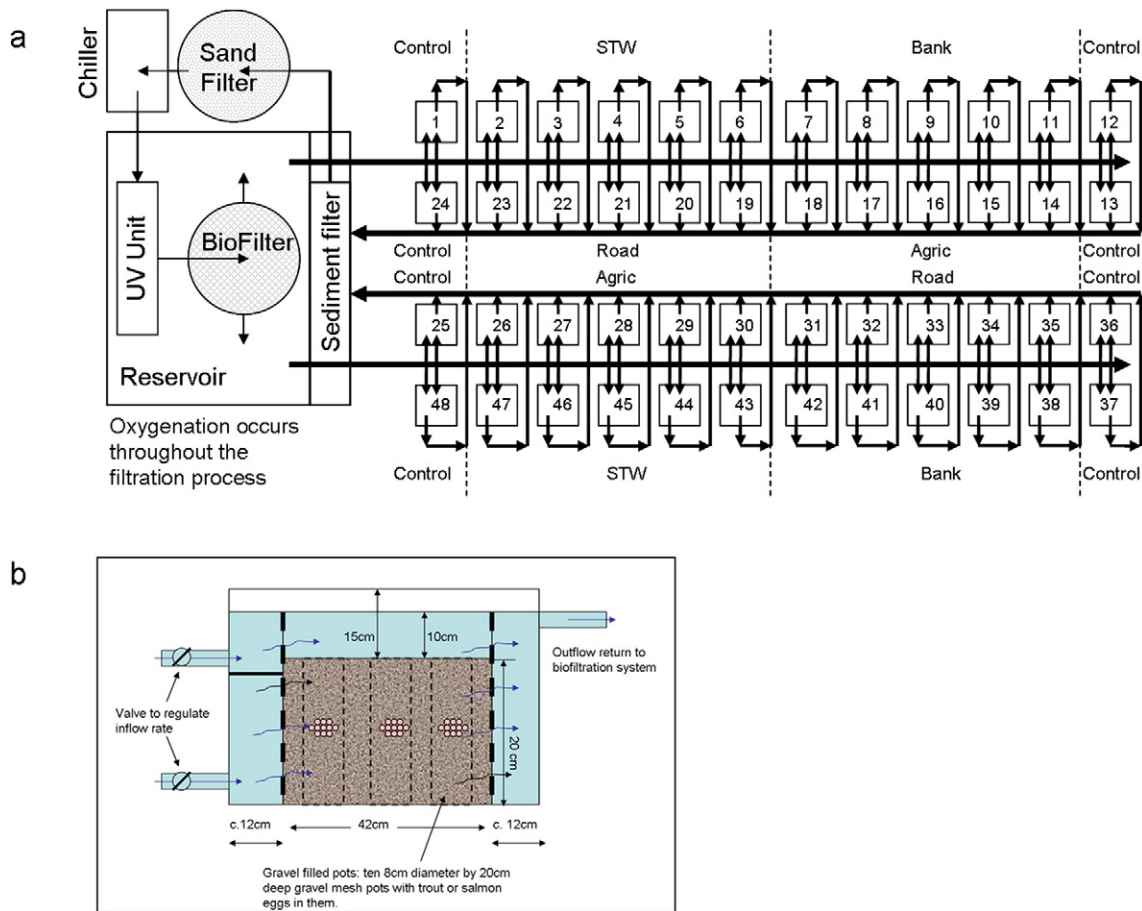


Fig. 1. Chilworth Experimental Spawning facility showing the recirculation system and water quality controls. Diagram also shows details of the individual tanks used to incubate Atlantic salmon and Brown trout eggs.

treatment (source \times load) to each of 10 separate baskets within a single tank (Fig. 1).

The four different sediment sources were collected from the catchment of the River Ithon, Wales, UK, and were selected based on previous sediment fingerprinting studies that had identified the main contributors as (1) agricultural surface soils, (2) eroding river bank material (sampled from below the surface soil level), (3) damaged Road verges, and (4) final treatment sewage sludge (Collins et al., 2012d). All catchment source material samples were collected in October 2009, corresponding with the start of the salmonid spawning season. The sampling strategy was spatially representative of the River Ithon catchment and the distribution of the key sediment source types therein (see Greig et al. (2007) for further catchment details). All accessible watercourses and their surrounding fields and roads were visited to search for suitable sediment sampling sites. 30 sites were sampled for each of the individual sediment sources. A sample of final treatment sewage sludge was collected from a Sewage Treatment works within the River Ithon catchment. This material represents the final stage of solids treatment and can be released into the environment during overflow periods or as a result of accidental release (cf. Collins et al. (2010a, 2010b, 2012a, 2010b)).

All samples from each sediment source type were passed through a $<63 \mu\text{m}$ sieve into buckets. The buckets were then left to stand for 2 days in a dark, temperature controlled environment to allow the sediment to settle. This was to ensure that fine sediment would not be lost during decanting. After this period of settling, excess water was decanted and the remaining slurry was oven dried at 30° for ca. 36 h (or until ready). Higher temperatures were avoided to avert the risk of destroying the organic content of the samples. This process resulted in

a damp cake-like mixture for each of the study catchment sediment sources. Sub-samples of the damp sediment were oven dried to determine differences in water content between source samples. This was used to correct the total wet mass applied to each incubation basket within each experimental tank.

Treatment 2 was defined by the load (mass) of sediment added to the egg zone within each individual incubation basket. The range of quantities of sediment added was based on a national dataset of salmon and trout redd data compiled by the authors. Data from over 83 bulk gravel samples from natural and artificial Atlantic salmon redds were derived from published (Greig et al., 2007, 2005b; Walling et al., 2003, Milan et al., 2000; Crisp & Carling, 1989) and unpublished sources. A cumulative frequency curve for the proportion of silt-clay accumulated in the redd gravels was plotted and values were extracted to represent the full range of silt/clay accumulation found in natural and artificial spawning redds across England and Wales.

Diploid brown trout eggs were obtained from 10 females fertilized with sperm pooled from five males from the same stock. Wild Atlantic salmon eggs were sourced from 3 females fertilised with sperm from 3 males. The unfertilised eggs of both species were transported from the hatchery in ice cooled polystyrene boxes and fertilised at the experimental site. All eggs were water hardened for two hours at $7\text{--}9^\circ\text{C}$. Twenty-five eggs were deposited evenly on washed gravels (replicating freshly cut redd gravels (Crisp & Carling, 1989) in an egg basket in a layer 10 cm (Greig et al., 2007) below the gravel (4–32 mm) surface within 3 h of fertilization. More washed river gravel was carefully added over the top of the eggs along with a short stainless steel tube for injecting sediment into the egg basket at a later date. Each egg basket consisted of a cylinder open at the surface with 1 mm plastic mesh

(diameter 8 cm, height 20 cm). All eggs used in the experiment were of similar initial mass (brown trout mean mass 0.083 ± 0.004 g, $n = 25$; Atlantic salmon mean mass 0.092 ± 0.009 g, $n = 25$).

Ten plastic mesh baskets were placed into each replicated tank and washed gravel carefully placed around them until flush with the surface. This was repeated for all 48 tanks giving a total of 480 individual baskets (Fig. 1). Prior to egg planting, conductometric standpipe (see Greig et al. (2005c)) readings were made in each gravel-filled basket of three tanks to determine the intra-gravel flow velocity (IGFV) through the egg zone and to test for consistency across the baskets and tanks. Using this data, we set the inflow rate at 1.15 L min^{-1} to achieve a clean gravel IGFV of 849 cm h^{-1} , which replicated conditions in good quality spawning habitat measured at UK field sites by Greig et al. (2007). Consistency between tanks was good, with a variation of $\pm 71 \text{ cm h}^{-1}$ (8.76%) between equivalent baskets in each tank. Unfortunately, measurement of IGFV after injection of fine sediments was not possible since the technique requires injection of a saline and alcohol solution which would have affected the survival of the embryos (Greig et al., 2005c). However, measurements of inflow and outflow from each tank after sediment treatment showed no difference between tanks. Thus, any change in IGFV, and hence oxygen supply rate to incubating embryos, was the result of the treatments as planned.

2.2. Physical and chemical parameters

Water quality was monitored throughout the period of incubation to hatch. Manual sampling of the water entering the tanks was conducted every 3 days; whilst dissolved oxygen (Aandera 4175 Optode, accuracy $\pm 5\%$), temperature (Aandera 4175 Optode, accuracy $\pm 0.5\%$), water level (Druck PTX1830 Series, accuracy $\pm 0.06\%$) and turbidity (Analite 9000, accuracy $\pm 1\%$) were sampled every minute within the feeder tank (i.e. after filtration and biological treatment) and the average logged every 10 min on a Delta2 logger. Light levels experienced by each tank/basket were kept constant by covering each tank with a black lid.

Eight small baskets containing 50 eggs but no gravels, were placed on the surface of the substrate in the control tanks and monitored every 3 days for embryo development. Records of the number of live, dead and hatched eggs in these baskets were made. These were used as a check on the predicted time of hatching, to determine the end point of the experiment when the sediment filled baskets could be withdrawn.

After 143 days, each tank was isolated in turn and the same quantity and source of fine sediment was injected into each egg basket within the tank via the stainless steel tube. The injected material consisted of a pre-weighed mass of sediment that was blended with 250 mL of water drawn from the incubation tanks. Half the solution was injected into the egg zone and the other half injected into the gravels above the egg zone. This approach was selected to mimic the process of colmation observed in both flume and field conditions (e.g. Sear et al. 2008). Continuous release of sediment into the recirculating water was not feasible as this would have afforded no control over the sediment mass treatment. Injection into each basket reduced the release of fines into the overlying water column; movement of sediment between baskets within each tank would therefore only result from IGFV. Differences between baskets in each tank were quantified at the end of the experiment by measuring the mass of sediment (inorganic and organic) in each of the 480 separate baskets.

When 50% hatch was reached, each tank was isolated in turn and all ten baskets removed. This occurred after 456 (Brown trout) and 513 (Atlantic salmon) degree days. The sediment from each basket was tipped into counting trays and all live and dead eggs and alevin were identified. A sample of fifteen alevin were taken from baskets 2, 3 and 5 in each tank and where insufficient were available, additionally from baskets 1 and 10. Alevin were preserved in a solution of 4% formaldehyde. The total wet mass and wet yolk sack mass were weighed using

a Mettler Toledo AB204-5 balance accurate to 0.0001 g. Each alevin was also measured for length using a Nikon E100 microscope at 50 \times magnification. Errors in length measurement were checked by repeat measurement and found to be $<0.1 \text{ mm}$.

After removal of the eggs and alevin, the sediment from each basket was wet sieved through a $63 \mu\text{m}$ sieve and dried to constant mass. The mass of fine sediment $<63 \mu\text{m}$ and $>63 \mu\text{m}$ was recorded for each basket. Organic matter content of the $<63 \mu\text{m}$ fraction was determined through loss on ignition (LOI). Samples for LOI were wet sieved to less than $63 \mu\text{m}$ and oven dried. Crucibles and samples were weighed before and after heating in a carbolite furnace for 2 h at 550°C . To determine absolute particle size distributions, a single sample of sediment from each tank was sieved at $63 \mu\text{m}$ using tap water. The $<63 \mu\text{m}$ fraction was retained and dispersed in a 0.05% sodium hexametaphosphate solution. Samples were subsequently ultrasonicated in order to ensure that particles were in suspension. The sediment samples were vigorously shaken and a 30 mL aliquot was used for the grain size measurement. The aliquot was then agitated for 1 h prior to measurement on a shaker bed. Measurements were made in triplicate, using a Malvern Mastersizer 2000.

2.3. Statistical analyses

Although treatments were applied to each basket independently and data from each basket handled separately in the statistical analysis, each set of 10 baskets was nested within a single tank making it potentially difficult to separate any effect of the tank from that of the treatment. This design was chosen as there was a significant concern that we would not be able to apply different levels of sediment treatment to individual baskets randomly within tanks without the treatment applied to one basket potentially affecting neighbouring baskets in some way (particularly where large amounts of organic sediments were added), which would tend to homogenize the treatments. Therefore, we opted for a less statistically robust design (i.e. all baskets within a tank received the same treatment) which gave us more confidence that the baskets would experience the desired treatment. To determine if the tanks had any effect, eight control tanks, to which no sediment was added, were included in the range of treatments tested (see above). These were located at the start and end of each line of tanks to capture any variation based on distance along the line of replicated tanks (Fig. 1).

General Linear Models (GLM) were used to perform ANCOVAs to test for the effects of sediment source and quantity, and interactions between these effects on specific response variables of the two fish species using SAS 9.1. Sediment source (d.f. 3) and fish species (d.f. 1) were included as fixed main factors, whereas mass of sediment added (d.f. 1) and mass of sediment recovered (d.f. 1) were included as continuous variables (d.f. 1). The ANCOVA model was species|source|mass. If effects were significant, pairwise comparisons were performed for the class effects species and source using post hoc tests (Tukey's HSD). Significance was set at 0.05 in all tests. An initial test was undertaken using both the mass of sediment and mass of organic matter recovered from the baskets as response variables (model = species|source|mass added), to verify that the experimental addition of sediment had been successful. Where sub-lethal measures of alevin performance were used, individuals were nested within the baskets they were incubated in, and basket (d.f. 9) and individual treated as random variables (model = species|source|mass basket individual(basket)). Type III (orthogonal) sums of squares used throughout as these are more appropriate for unbalanced designs and for the assessment of interactions among variables. All data were either arcsine (e.g. % survival) or log transformed to ensure homoscedasticity when necessary.

It should be noted that in our experimental design, to avoid homogenization of treatments, all the replicates of each sediment source \times mass treatment were contained within an individual tank. Hence, any potential effect of the tanks was confounded with treatment.

To test for any effect of tank, for each response variable a separate GLM analysis was conducted on the control tanks ($n = 4$ for each species) to which no sediment was added. Here, the effect of the tanks was compared to the effects of the baskets and, for sub-lethal effects, individuals. In these analyses tank and species were fixed main effects, and basket a random effect nested within tank \times species (model = species|tank basket(tank)). Where sub-lethal effects were considered, a further level of hierarchical nesting was included, with individual alevins a random effect nested within baskets (model = species|tank basket(tank) individual(basket)). Where these analyses indicated no significant effect of tank it was assumed that tank had no influence and the replicates of each treatment were assumed independent of tank.

Where an effect of sediment source on the fish was detected, a further test was undertaken using mass of organic matter recovered (as a continuous variable, d.f. 1), to determine if any effect was attributable to differences in the organic content of sampled material collected from the different catchment sediment sources. In this case the model was as above, but with organic mass recovered from each basket used rather than the mass of sediment added.

3. Results

3.1. Characterising sediment sources

In this analysis, the characteristics of the source material pertinent to the incubation experiment included absolute particle size, organic matter content and for the first time, sediment oxygen demand (SOD both 5 days (labile) and 20 days (refractory)). SOD has been highlighted by Greig et al. (2005b) as influencing the oxygen supply rate to incubating embryo. Physical differences between the study catchment sediment source materials are shown in Table 2. Sewage Treatment Work (STW) sediment had a significantly higher organic matter and Organic carbon content than the other sources ($p = 0.0192$). In terms of absolute particle size, damaged Road verge had the highest clay content (2%), River Bank had no detectable clay content and Agricultural topsoil had the second highest clay content and was the finest sediment source material overall. STW and Road verge had the highest SOD for both 5 day and 20 day tests. Agricultural topsoils had the lowest SOD of all sources tested in the experiment.

3.2. Physical conditions during incubation and hatch

The physical conditions within the experimental spawning gravels were constant over time. Monitoring of nitrite, nitrate and ammonia showed a sharp and short (<24 h) increase post sediment injection (Table 1), but levels remained below those reported as critical for incubating salmonids (Westin, 1974; Kincheloe et al., 1978; Sonderberg et al., 1983; Timmons et al., 2002;). A decision was taken, one week after injection, to isolate and end the sewage treatment work sediment experiments with >3% (41 g) by mass of sediment introduced, since these were suspected as a potential cause of deterioration in water quality. All eggs recovered from these tanks were found to be dead. Water quality in the recirculation facility continued to remain below critical levels across all replicated tanks for both species.

Table 1

Water quality summary for the experimental period.

| Parameter | Mean | Standard deviation | Range |
|--|-------|--------------------|-------------|
| Temperature (°C) | 7.40 | 0.60 | 5.43–9.37 |
| Dissolved oxygen (mg L ⁻¹) | 10.02 | 0.23 | 9.45–11.01 |
| Water level in reservoir (cm) | 37.27 | 1.72 | 34.88–62.97 |
| pH | 7.98 | 0.17 | 7.6–8.2 |
| NH ₄ ⁺ (mg L ⁻¹) | 0.27 | 0.19 | 0.0–0.5 |
| NO ₃ ⁻ (mg L ⁻¹) | 14.17 | 13.11 | 0.0–40.0 |
| NO ₂ ⁻ (mg L ⁻¹) | 0.23 | 0.31 | 0.0–1.0 |

A short (<12 h) increase in turbidity occurred in tanks when sediment was being injected, replicating the pulse of sediment delivery that occurs during natural flood events in river catchments. During sediment injection all fine sediment was contained within the tank being treated, ensuring that baskets in each tank received the same treatment, but no between-tank physical effects of sediment injection were incurred. Water temperature varied with diurnal fluctuations in air temperature, but within a range that was below critical for salmonids (Crisp 1990).

GLM tests indicated that the sediment injection procedure was successful in producing the target treatment levels within the egg baskets (Table 3, Fig. 2). The mass of sediment recovered from the egg baskets did not differ significantly among treatments with different fish species or sediment sources, but did differ in a highly significant manner with the mass added ($p < 0.0001$). The interaction between sediment source and mass added was not significant at the 5% level. The mass of organic matter recovered from the egg baskets did not differ significantly among treatments with different fish species, but again did differ significantly with the mass of sediment added ($p < 0.0001$). In contrast to the total mass of sediment recovered from the egg baskets, there were highly significant differences in the mass of organic matter recovered among the sediment sources, and with the interaction of sources and mass added (Table 3), reflecting differences in the characteristics of the sediment added (see Table 2). Thus, we are confident that the individual baskets in a tank were replicated (i.e. no significant difference in the mass of organic matter or total mass of sediment between baskets in a given tank) but there was a significant difference between tanks (treatments).

3.3. Sediment, mortality and survival

A GLM test using data from the control tanks indicated a significant difference in survival of the two fish species, but no effect of the tanks or individual egg baskets within the tanks (Table 4A, Fig. 3a). Mean mortality of brown trout in the egg baskets in the absence of any additional fine sediment was 9.9% whereas for Atlantic salmon it was 74%. The cause of the increased mortality in salmon resulted from the process of transfer from the hatchery to the Chilworth hydraulics laboratory since all physical variables within the facility were well within published tolerances of the particular species, and in previous experiments, survival had been good (>89%) and control batches at the hatchery showed 10.2% mortality for Atlantic salmon and 2.1% for the brown trout. This difference in survival between species was controlled for in subsequent GLM modelling by including species as a main factor. The results thus highlight where there is a difference between the species. However, where there is a significant interaction with other factors, the inclusion of species in the model indicates that the species are reacting differently to the other factors.

In addition to the difference in mortality between Atlantic salmon and brown trout, the GLM analysis of the experimental addition of fine sediment indicated significant effects of different sediment sources and of the mass added, together with interactions between mass added and species, mass added and sediment source, and mass added, species and sediment source (Table 4B, Fig. 3a and b). Fig. 3a shows how the response of trout differs from Atlantic salmon; while both species show an increase in mortality with increasing fine sediment load, trout show a rapid increase in mortality between 1% and 6% wet mass. Average mortality of salmon eggs increases almost linearly between 1% and 9% wet mass added but, unaccountably, mortality decreases after 9%.

Tukey's test indicated that mortality was significantly higher with STW sediment compared to all other sources. Furthermore, STW sediment caused an increase in mortality at lower added mass than other sources, whilst damaged road verge material caused the next highest mortality for Atlantic salmon. Complete mortality of both species occurred in the tanks containing >3% by mass STW loadings,

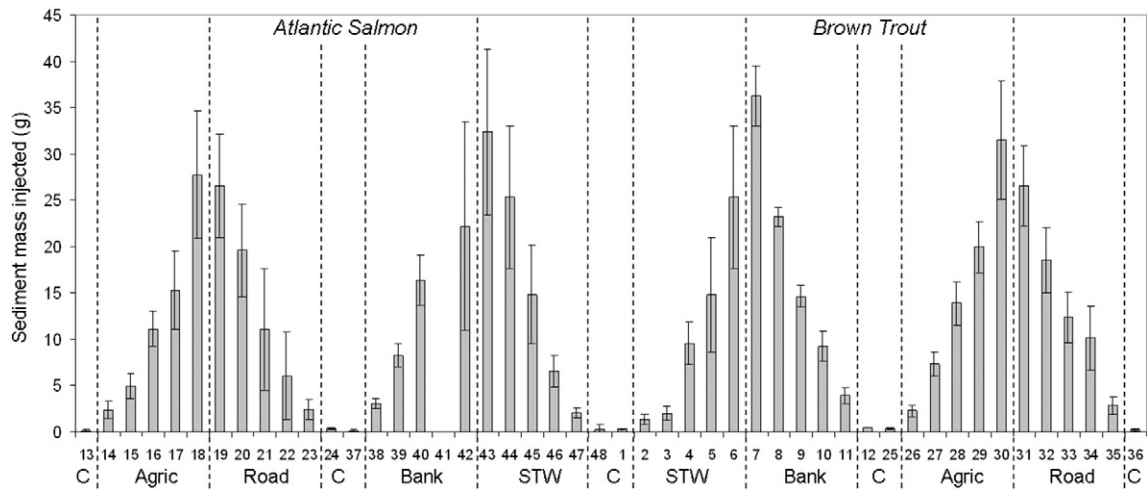


Fig. 2. Sediment mass treatment showing the mean (bars) and standard deviation of the mean (error bars) of sediment mass injected from the egg baskets after hatch. Missing values refer to STW tanks that were isolated and stopped early (see text for details). Missing bank data (tank 41) occurred due to laboratory error.

which were isolated and closed down earlier in the experiment than the remaining treatments. In addition, there was a significant difference in the response of the two fish species to the mass added of different sources (species*source*mass); a lower mass of STW and damaged road verge sediment was required to cause an increase in mortality for Atlantic salmon than for brown trout (Fig. 3b).

When the mass of organic matter recovered was included as a covariable in the GLM analysis (rather than mass added), the effects of species, source and their interaction on mortality remained significant (Table 4C). There was also a highly significant effect of organic matter and a significant interaction between organic matter and species. However, when the mass of organic matter recovered was included with source (i.e. Organic*Source and Organic*Species*Source), the interactions were not significant. In other words, although there were differences in mortality with different sources, the mass of organic matter recovered was sufficient to explain the differences in mortality between the different sediment sources.

3.4. Sub-lethal affects on alevin

The data from the control tanks again indicated that there was no effect of the tanks or individual egg baskets within the tanks on the three indicators of alevin fitness used, namely; wet mass, length and wet yolk sack mass (Table 5A). For all measures of alevin fitness the differences between the egg baskets and between individuals within egg baskets were not statistically significant.

The GLM analysis of the experimental addition of fine sediment mass indicated significant differences between the two fish species (Table 5B), with brown trout overall lighter (0.0922 ± 0.0144 g cf. 0.0949 ± 0.0102 g) and shorter (16.01 ± 0.05 mm cf. 16.97 ± 0.04 mm) and with more yolk sac (0.596 ± 0.0006 g cf. 0.0568 ±

0.0004 g) than Atlantic salmon for the same relative incubation time (defined by degree days to 50% hatch in the surface egg baskets). Accounting for the inter-species difference in alevin mass, there were significant differences in the mass of alevin exposed to different sources and masses of injected sediment (Table 5B, Fig. 4a and d); the more sediment added, the smaller the mass of alevin. The interactions between species and mass of sediment added, and species and source were not significant (Table 5B), indicating that alevin mass of both species reacted similarly to the mass of sediment added (Fig. 4a) and the different sources (Fig. 4d).

The interaction between mass of sediment added and source was significant, with a more pronounced reduction in alevin mass with increasing mass of STW sediment added compared to the other sources. A similar response was seen in the mass of yolk sac, with the exception that the interaction between mass of sediment added and source was not significant (Table 5B).

There were significant differences in alevin length associated with species (as expected trout alevin are shorter), source, mass of sediment added, and the interactions between species and source, mass and species, and mass and source (Table 5B, Fig. 4b, e). The length of alevin decreased with an increasing mass of sediment added.

When the mass of organic matter recovered from the egg baskets was included in the GLM model rather than the mass of sediment added, the differences between sources of sediment were not significant for alevin length, not significant for yolk sac mass, and significant for alevin mass (Table 5C). A significant effect of mass of organic matter recovered was apparent for all three measures of alevin fitness, with all three measures declining with increasing mass of organic matter. However, the interaction between the mass of organic matter recovered from the baskets and sources was not significant (Table 5C), indicating

Table 2 Summary of sediment source characteristics used in the experiments. Note the high levels of organic matter and 5-day sediment oxygen demand associated with the STW and road verge sources.

| Source | % Organic content (LOI) | % Organic carbon | 5 day Sediment oxygen demand mgO ₂ /g/day | 20 day Sediment oxygen demand mgO ₂ /g/day | % Silt | % Clay | D ₁₀ (µm) | D ₅₀ (µm) | D ₉₀ (µm) |
|---|-------------------------|------------------|--|---|--------|--------|----------------------|----------------------|----------------------|
| Sewage treatment works (Tertiary treated waste) | 56.54 (6.62) | 60.0 (5.0) | 12.97 (2.39) | 7.40 (1.92) | 99.85 | 0.15 | 8.36 | 24.19 | 50.05 |
| Road verge | 14.53 (0.94) | 9.0 (8.0) | 10.69 (0.49) | 1.34 (0.84) | 97.93 | 2.07 | 3.53 | 13.19 | 39.67 |
| River bank | 7.66 (0.69) | 3.0 (3.0) | 6.83 (2.10) | 0.97 (0.39) | 100.00 | 0.00 | 37.87 | 49.59 | 63.49 |
| Agriculture (field) | 14.05 (1.01) | 6.0 (7.0) | 3.91 (1.18) | 0.88 (0.56) | 98.08 | 1.92 | 3.43 | 11.92 | 37.52 |

Figures in brackets are 1 standard deviation of mean. For % organic carbon figures in brackets are CV. LOI is Loss on Ignition at 550°C.

Table 3

Statistical results of general linear model of the effect of sediment addition on the total mass and mass of organic matter recovered from the baskets.

| | Species | | Source | | Mass added | | Source* mass added | |
|------------------------|--------------------|-------|--------------------|---------|--------------------|---------|--------------------|---------|
| | F _{1,216} | p | F _{3,216} | p | F _{1,216} | p | F _{3,216} | p |
| Mass recovered | 2.19 | 0.140 | 0.81 | 0.488 | 2685 | <0.0001 | 2.22 | 0.0861 |
| Organic mass recovered | 1.97 | 0.161 | 1093 | <0.0001 | 2820 | <0.0001 | 889 | <0.0001 |

that the mass of organic matter recovered was sufficient to explain the differences among the sediment sources.

4. Discussion

The results provide preliminary evidence for both lethal and sub-lethal effects of silt/clay-sized (<63 µm) fine sediment on pre-emergent salmonid embryos (Lapointe et al., 2005; Sear et al., 2008; Louhi et al., 2011). Increasing the mass of fine sediment resulted in higher mortality in both salmonid species. However, we were unable to find a significant linear relationship between specific size fraction (silt or clay) and mortality. In this respect our findings are similar to those of Louhi et al. (2011) who reported that percentage survival was not related to any specific inorganic absolute grain size. Unlike Louhi et al. (2011), we did find a significant effect of sediment mass on mortality. The absence of an absolute particle size (specifically clay) based effect is counter to the findings of Greig et al. (2005a, 2005b, 2005c) who identified a physically-based rationale for the additional effectiveness of clay via blockage of the micropores on the surface of salmon eggs. The mass of clay reported for all these experiments are similar, but the experimental conditions differ; Greig et al. (2005a, 2005b, 2005c) measured oxygen uptake in a small container with only 3 eggs directly exposed to clay, whilst Lapointe et al. (2011) and more recently Franssen et al. (2012) demonstrate the importance of a coarser sand sized component that amplifies the effects of silt/clay sized particles by reducing pore sizes and leading to enhanced blocking by fines. It is possible that within the egg baskets used by Louhi et al. (2011) and in this experiment, local concentrations of clay were much lower, resulting in a lower probability of encountering an egg, or a micropore on the egg surface. We demonstrate that in the absence of sand sized particles, concentrations of silt/clay of only 3% by mass result in deleterious effects on both egg mortality and alevin fitness, and that the effect is non-linear in both salmonid fish species.

Higher sediment load was shown to affect alevin fitness in both brown trout and Atlantic salmon. As sediment mass increased, salmon

and trout alevin were lighter, shorter and, in salmon, had a smaller yolk sack mass, whilst in trout, after 6% wet mass of sediment was added, the reduction in yolk sac mass was smaller. Whilst this partly agrees with previous studies of salmonid species, our observation of reduced egg yolk mass runs counter to previous research. Hamor and Garside (1976), Argent and Flebbe (1999) and Youngson et al. (2005), found smaller, lighter alevin with larger residual yolk sacs in conditions of low dissolved oxygen saturation, whilst Louhi et al. (2011) found that yolk sacs in alevin exposed to sedimentation were larger compared to non-sediment controls. Roussel (2007) explained this in terms of a delay in yolk sac absorption under hypoxic conditions – reduced oxygen leads to reduced growth and hence less demand on yolk. Our observations for brown trout and Atlantic salmon differ from these and might be explained by a higher metabolic rate as the alevin attempt to move into more oxygen rich water (Kamler, 2002). Thus, whilst growth is reduced due to longer development time, increased metabolism increases the rate of yolk depletion. Alternatively, with a decrease in oxygen supply, metabolic processes can be partly shifted towards less efficient anaerobic processes, less efficient use of resources and therefore greater use of the yolk sac (Kamler, 2008). At this stage, we do not know the reason for the observed differences in existing experimental outcomes. Differences in body size and amount of yolk at emergence are reported to have fitness consequences (Miller et al., 1988; Andesen, 1988; Skoglund et al., 2011). However, two strategies exist: one which maximises mobility whereby the fry are larger with a small yolk mass and are more effective at predator avoidance, and a second in which smaller fry emerge with a larger yolk sack, and are able to avoid risk of starvation (Skoglund et al., 2011). The effects of fine sediment on brown trout and Atlantic salmon in this experiment are counter to either of these strategies, and their fitness is therefore sub-optimal compared to those incubated in the control treatments.

The results permit for the first time, comparison between the response of two common salmonid species. The results show that response to sediment load and sediment source is broadly similar between species but with some species specificity; brown trout show

Table 4

Statistical results of general linear model of effects of sediment addition on mortality. A) Comparison among the control tanks (0 g sediment added) to determine the influence of tanks and basket (nested within tanks). B) Comparison among experimental treatments to determine the influence of species (i.e. trout or salmon), source of sediment added (i.e. Road verge, agricultural, river bank or sewage works), mass of sediment added and basket. Basket was regarded as a random factor and mass of sediment added as a continuous variable. C) Comparison among experimental treatments to determine the influence of species (i.e. trout or salmon), source of sediment added (i.e. Road verge, agricultural, river bank or sewage works), and mass of organic sediment recovered from the basket. Mass of organic sediment recovered was regarded as a continuous variable.

| A) | | | | | | | | | | | | | | | |
|-----------|-------------------|---------|-------------------|-------|--------------------|-------|--|--|--|--|--|--|--|--|--|
| | Species | | Tank | | Basket | | | | | | | | | | |
| | F _{1,39} | p | F _{3,39} | p | F _{36,39} | p | | | | | | | | | |
| Mortality | 368.7 | <0.0001 | 0.64 | 0.595 | 0.87 | 0.667 | | | | | | | | | |

| B) | | | | | | | | | | | | | | | | |
|-----------|--------------------|---------|--------------------|---------|--------------------|-------|--------------------|---------|--------------------|--------|--------------------|---------|---------------------|---------|--------------------|-------|
| | Species | | Source | | Species*Source | | Mass | | Mass*Species | | Mass*Source | | Mass*Species*Source | | Basket | |
| | F _{1,451} | p | F _{3,451} | p | F _{3,451} | p | F _{1,451} | p | F _{1,451} | p | F _{3,451} | p | F _{3,451} | p | F _{9,451} | p |
| Mortality | 645.9 | <0.0001 | 14.28 | <0.0001 | 2.57 | 0.054 | 115.5 | <0.0001 | 13.91 | 0.0002 | 99.27 | <0.0001 | 28.12 | <0.0001 | 0.69 | 0.722 |

| C) | | | | | | | | | | | | | | | |
|-----------|--------------------|---------|--------------------|---------|--------------------|--------|--------------------|---------|--------------------|---------|--------------------|-------|------------------------|-------|--|
| | Species | | Source | | Species*Source | | Organic | | Organic*Species | | Organic*Source | | Organic*Species*Source | | |
| | F _{1,211} | p | F _{3,211} | p | F _{3,211} | p | F _{1,211} | p | F _{1,211} | p | F _{3,211} | p | F _{3,211} | p | |
| Mortality | 250.1 | <0.0001 | 138.3 | <0.0001 | 7.28 | 0.0001 | 288.06 | <0.0001 | 50.83 | <0.0001 | 0.56 | 0.647 | 0.51 | 0.668 | |

Table 5
Statistical results of general linear model of effects of sediment addition on the mass, length and mass of yolk sac of surviving alevins. A) Comparison among the control tanks (0 g sediment added) to determine the influence of tanks, basket (nested within tanks), and individual fish (nested within baskets). B) Comparison among experimental treatments to determine the influence of species (i.e. trout or salmon), source of sediment added (i.e. road verge, agricultural, river bank or sewage works), mass of sediment added, basket, and individual fish (nested within baskets). Both basket and individual fish were regarded as random factors and mass of sediment added as a continuous variable. C) Comparison among experimental treatments to determine the influence of species (i.e. trout or salmon), source of sediment added (i.e. road verge, agricultural, river bank or sewage works), and mass of organic sediment recovered from the basket. Mass of organic sediment recovered was regarded as a continuous variable.

| A) | | | | | | | | | | | | | | | | |
|----------|-------------------|-------|-------------------|-------|--------------------|-------|--------------------|-------|--|--|--|--|--|--|--|--|
| | Tank | | Basket | | Tank*basket | | Individual | | | | | | | | | |
| | F _{3,89} | p | F _{9,89} | p | F _{12,89} | p | F _{35,89} | p | | | | | | | | |
| Mass | 1.60 | 0.195 | 1.39 | 0.202 | 0.75 | 0.628 | 0.99 | 0.502 | | | | | | | | |
| Length | 0.68 | 0.564 | 1.13 | 0.350 | 0.38 | 0.911 | 0.78 | 0.799 | | | | | | | | |
| Yolk sac | 1.34 | 0.267 | 1.08 | 0.387 | 1.66 | 0.129 | 0.88 | 0.651 | | | | | | | | |

| B) | | | | | | | | | | | | | | | | |
|----------|--------------------|---------|--------------------|-------|--------------------|---------|--------------------|---------|--------------------|--------|--------------------|-------|--------------------|-------|---------------------|-------|
| | Species | | Source | | Species*source | | Mass | | Mass*species | | Mass*source | | Basket | | Individual | |
| | F _{1,588} | p | F _{3,588} | p | F _{3,588} | p | F _{1,588} | p | F _{1,588} | p | F _{3,588} | p | F _{9,588} | p | F _{35,588} | p |
| Mass | 7.89 | 0.005 | 3.04 | 0.029 | 0.47 | 0.702 | 15.33 | <0.0001 | 2.38 | 0.123 | 2.47 | 0.043 | 1.36 | 0.204 | 0.96 | 0.536 |
| Length | 120.0 | <0.0001 | 2.82 | 0.038 | 16.73 | <0.0001 | 12.1 | 0.0005 | 2.38 | 0.035 | 3.35 | 0.019 | 1.43 | 0.172 | 0.29 | 1.000 |
| Yolk sac | 10.73 | 0.001 | 4.44 | 0.004 | 1.56 | 0.199 | 6.58 | 0.0105 | 0.00 | 0.9998 | 1.51 | 0.211 | 1.52 | 0.135 | 1.29 | 0.128 |

| C) | | | | | | | | | | | | | | | | |
|----------|--------------------|---------|--------------------|-------|--------------------|---------|--------------------|--------|--------------------|-------|--------------------|-------|--------------------|-------|---------------------|-------|
| | Species | | Source | | Species*source | | Organic | | Organic*species | | Organic*Source | | Basket | | Individual | |
| | F _{1,536} | p | F _{3,536} | p | F _{3,536} | p | F _{1,536} | p | F _{1,536} | p | F _{3,536} | p | F _{9,536} | p | F _{33,536} | p |
| Mass | 8.25 | 0.004 | 2.65 | 0.048 | 1.16 | 0.325 | 14.19 | 0.0002 | 2.74 | 0.099 | 0.22 | 0.883 | 1.25 | 0.262 | 0.58 | 0.972 |
| Length | 84.91 | <0.0001 | 2.13 | 0.948 | 17.14 | <0.0001 | 11.09 | 0.0009 | 2.71 | 0.100 | 1.15 | 0.328 | 1.50 | 0.144 | 0.47 | 0.996 |
| Yolk sac | 8.00 | 0.048 | 2.21 | 0.086 | 0.96 | 0.412 | 5.52 | 0.019 | 0.01 | 0.937 | 0.22 | 0.882 | 0.49 | 0.882 | 1.29 | 0.130 |

a change in response to fine sediment mass at around 6% per sediment wet weight. After 6%, rates of mortality, alevin and yolk sac mass loss all decrease, whilst rate of shortening decreases. For Atlantic salmon, such trends are less obvious, but at 9% by wet mass of fines in spawning gravels, rate of mortality decreases and loss of alevin mass increases, whilst rates of change in length and yolk sac mass remain constant. The results show that Atlantic salmon are more sensitive to catchment sediment sources with higher organic matter content than brown trout. The physiological reason for this remains uncertain but may relate to the larger mass of Salmon eggs relative to trout that has been shown to influence oxygen consumption (Einum et al., 2002) and therefore the demand for oxygen from the surrounding spawning habitat.

For the first time, we report that the source of the fine sediment is a control on embryo mortality and the development of pre-emergence alevin. Of the sediment sources used, STW final treated solids and damaged road verge sediments showed the strongest effects on survival and measures of alevin fitness. The organic matter content of both of these sediment sources sampled in the River Ithon study catchment is high and the resulting oxygen demands (SOD 5 day) exerted by the decomposition of the organics are also the highest of all the sediment sources. We found that the difference in embryo survival and Alevin characteristics between catchment sediment sources was explained by the mass of organic matter recovered. Greig et al. (2005a) highlight how the sediment oxygen demand competes with the egg oxygen demand to lower the oxygen supply rate to embryo, whilst Louhi et al. (2011) found that survival of brown trout was correlated to the mass of fine organic matter. Since organic matter content has been shown in these experiments to have a significant effect on alevin fitness, we hypothesize that this is the main mechanism controlling the effects observed for both species of salmonids incubated in STW and damaged road verge sediment. Here, using a preliminary experiment, we have demonstrated an effect of STW sediment at levels as low as 1% by mass of spawning gravels. Thus, highly organic matter from STWs will be deleterious to benthic spawning salmonids, even at low levels of accumulation in spawning gravels, though less so for brown trout. The implications are that organic matter type (since organic matter is found in all sediment sources) as well as quantity will be an important

control on the SOD of infiltrated sediments within salmon redds or the spawning substrate used by other lithophilous species. Indeed, Collins et al. (2013, 2014) have recently reported the presence of sewage derived organic matter sources in salmon spawning redds within some rural catchments. The same work has also traced the contributions of sediment-associated organic matter ingressing salmonid redds from other important catchment sources including farm yards or steadings and domestic septic tanks.

Lapointe et al. (2005) and Levasseur et al. (2006) have highlighted the importance of sand in trapping silt and clay within the egg zone. The experiments reported in this paper lend support to this observation since without the presence of sand, over 84.0% ± 6.8 of injected silt/clay (based on the difference between injected mass and recovered mass) was transported out of the egg zone by interstitial flow and into the gravels at the bottom of the experimental incubation tanks. This would have increased mortality and reduced alevin fitness due to the higher mass of silt/clay organic matter retained in the egg zone. Thus, catchments producing both sand and silt/clay sized fractions, potentially from different sources (e.g. coarser sands are derived from river banks in the River Ithon study catchment (Burke, 2011)), are likely to have a higher risk of deleterious effects on salmonids. Field experiments by Greig et al. (2007) support this hypothesis, observing that the highest accumulation rates of sand supported high rates of egg survival in the absence of silt/clay sized particles in the wash load. Thus, management of different sediment sources may be necessary in order to reduce cumulative impacts of different sediment sizes and organic matter content on salmonid spawning habitats.

5. Conclusion

The principal findings of the present study may be summarized as follows. (1) The effect of fine sediment load is different between sediment sources; final treatment sewage and damaged road verge sediments were found to be significantly more deleterious to mortality and alevin fitness than other sources relative to fine sediment free controls. (2) Organic matter is highlighted as a major characteristic controlling the effectiveness of spawning habitat, principally through

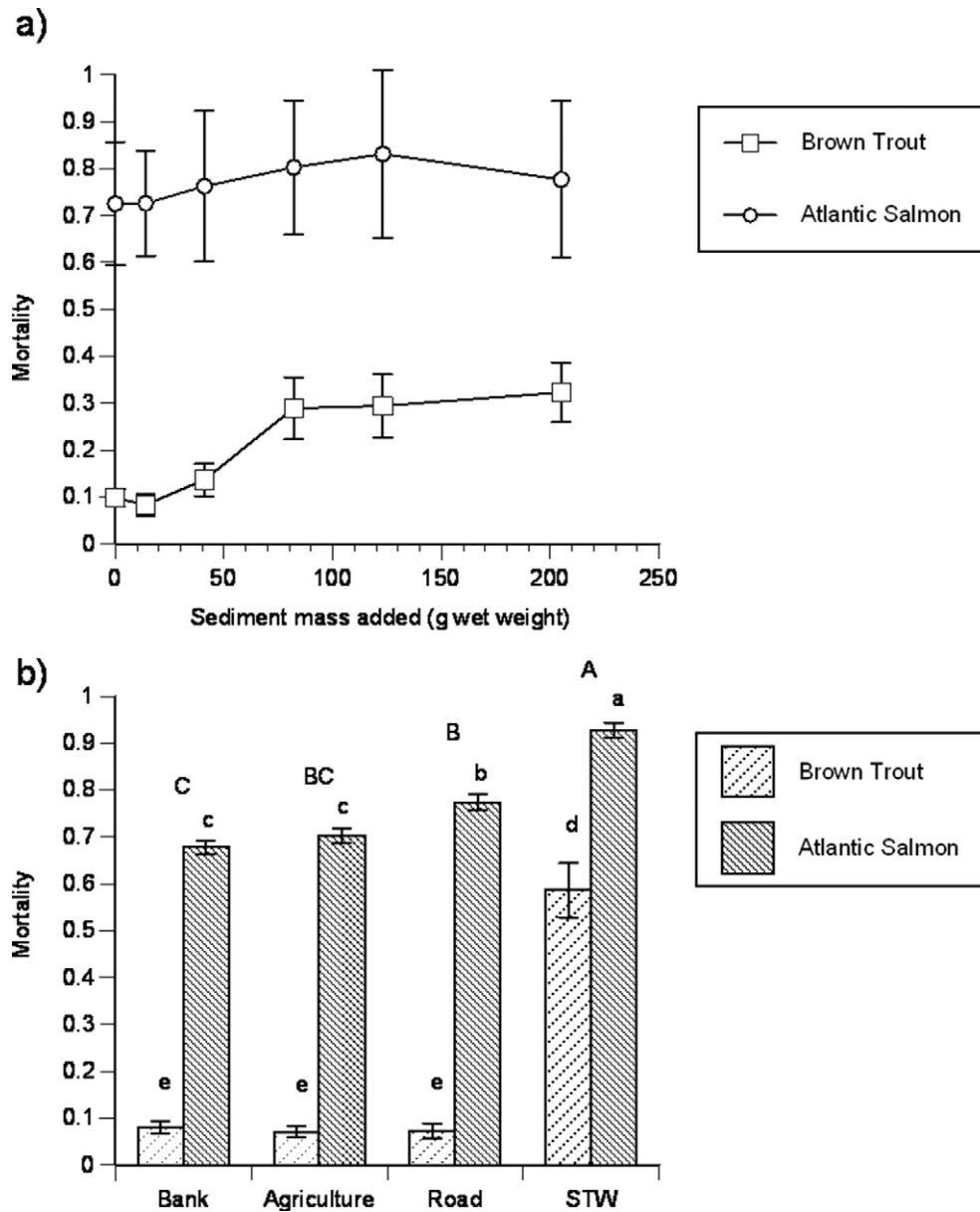


Fig. 3. Variation in mean mortality (\pm SE) of brown trout and Atlantic salmon with a) mass of sediment added to the egg baskets and b) source of sediment added to the egg baskets. Letters above means indicate significant differences between sources, upper case for both species, lower case within species.

its effect on oxygen concentration via SOD (5 days), and possibly through its effectiveness in blocking pores. (3) The effect of fine sediment load is different between species, although the overall effect is increased mortality and reduced alevin fitness. (4) Fine sediment ($<63 \mu\text{m}$) has been shown to effect the mortality and fitness of both brown trout and Atlantic salmon embryos. (5) The experiment confirmed the deleterious effects of increasing fine sediment load on both brown trout and Atlantic salmon. This effect is apparent in surviving alevin via reductions in mass, length and yolk sack mass relative to experimental controls.

The research has two key implications; first, experiments (both laboratory and field) as well as spawning gravel characterisation, should quantify more carefully the physical characteristics of the sediment treatments used; these should include organic matter content, SOD, grain size and mass. Secondly, further research is needed to better understand the processes by which organic matter influences the supply of oxygen in spawning gravels. Recent organic sediment fingerprinting and apportionment techniques have shown site specificity with different organic matter sources dominating in different

catchments (Collins et al., 2013, 2014) reflecting the mix of land use and farming types present.

The identification of multiple effects of fine sediment also highlights the inadequacy of current metrics and sediment targets which are based on quantity of sediment of a given grain size, or total daily maximum loads (cf. Collins and Anthony (2008); Collins et al. (2009, 2011)). These are based on the assumption that all fine sediments are of equal impact on aquatic ecology. Our research points to specific sediment and species effects. High sediment inorganic sediment loads with low SOD, are likely to be less damaging to trout and salmon, and less damaging than materials derived from high SOD organic sources, although impacts will still occur (e.g. entombing of alevin – Greig et al., 2005a). Resource managers now have evidence to support the development of sediment screening techniques that would enable them to target particular sediment source control strategies in the landscape. Critically, these strategies must not focus solely on the proportion of different sources of fine sediment, but also on the characteristics of the mobilised sediment delivered to rivers from individual sources.

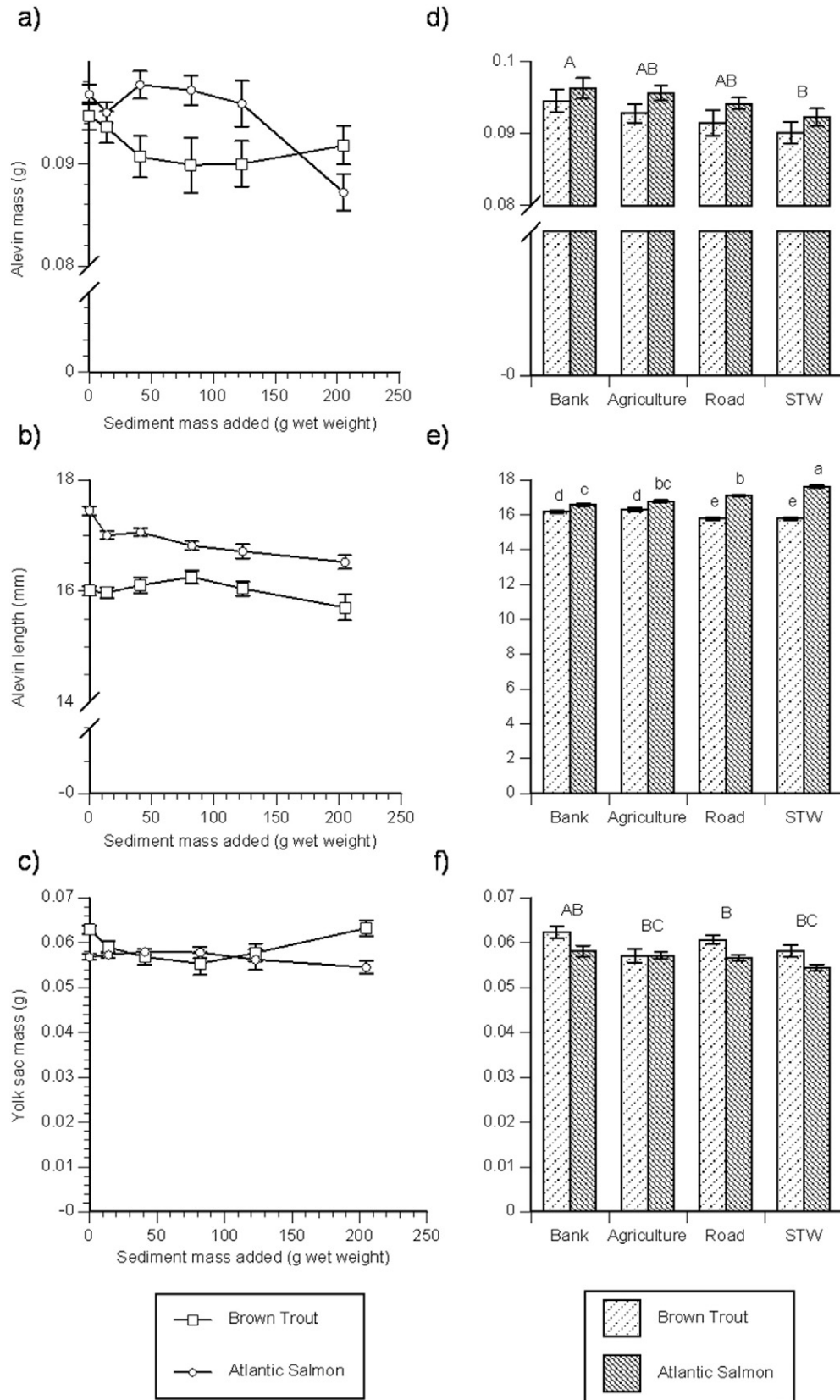


Fig. 4. Variation in mean (\pm SE) alevin mass (a, d), alevin length (b,e) and yolk sac mass (c, f) of brown trout and Atlantic salmon with a, b, c) variation in mass of sediment added to the egg baskets and d, e, f) variation in the source of sediment added to the egg baskets. Letters above means indicate significant differences between sources, upper case for both species, lower case within species.

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Effects of river morphology, hydraulic gradients, and sediment deposition on water exchange and oxygen dynamics in salmonid redds



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HIGHLIGHTS

- Hyporheic exchange and oxygen are crucial for survival in redd and highly variable.
- Oxygen and water exchange are affected by fine sediment, C_{org} and redd morphology.
- Artificial steps in canalized river are positive in high flow section, and negative in low flow section.
- Measurement of crucial parameters in artificial redd was successful.
- Considerable work investment is needed for these measurements.

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ABSTRACT

Fine sediment decreasing gravel permeability and oxygen supply to incubating salmonid embryos, is often considered the main contributing factor for the observed decline of salmonid populations. However, oxygen supply to salmonid embryos also depends on hydraulic conditions driving water flow through the redd. A more generalized perspective is needed to better understand the constraints on successful salmonid incubation in the many heavily modified fluvial ecosystems of the Northern Hemisphere. The effects of hydraulic gradients, riverbed and redd morphology as well as fine sediment deposition on dissolved oxygen (DO) and water exchange was studied in 18 artificial redds at three sites along a modified river. Fifty percent of the redds in the two downstream sites were lost during high flow events, while redd loss at the upstream site was substantially lower (8%). This pattern was likely related to increasing flood heights from up- to downstream. Specific water infiltration rates (q) and DO were highly dynamic and driven on multiple temporal and spatial scales. Temporally, the high permeability of the redd gravel and the typical pit–tail structure of the new built redds, leading to high DO, disappeared within a month, when fine sediment had infiltrated and the redd structure was leveled. On the scale of hours to days, DO concentrations and q increased during high flows, but decreased during the falling limb of the water level, most likely related to exfiltration of oxygen depleted groundwater or hyporheic water. DO concentrations also decreased under prolonged base flow conditions, when increased infiltration of silt and clay particles clogged the riverbed and reduced q . Spatially, artificial log steps affected fine sediment infiltration, q and interstitial DO in the redds. The results demonstrate that multiple factors have to be considered for successful river management in salmonid streams, including riverbed structure and local and regional hydrogeological conditions.

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1. Introduction

Native salmonid populations are declining in numerous countries around the world, including populations of brown trout *Salmo trutta*

in Switzerland (Burkhardt-Holm and Scheurer, 2007), Atlantic salmon *Salmo salar* in the United Kingdom (Youngson et al., 2002) and coho salmon *Oncorhynchus kisutch* in North America (Brown et al., 1994). Habitat degradation is considered a major threat for native salmonids (e.g., Brown et al., 1994; Burkhardt-Holm and Scheurer, 2007; Gilvear et al., 2002; Hicks et al., 1991). In this regard, fine sediment (<2 mm) deposition has been argued as the single contributing factor (e.g., Jensen et al., 2009 and studies cited therein). Deposited fine sediment

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can decrease redd gravel permeability and interstitial flow (e.g., Brunke, 1999; Schälchli, 1995), which, in turn, hinders oxygen supply to incubating salmonid embryos, thereby affecting their survival (S. Greig et al., 2007; Greig et al., 2005; Heywood and Walling, 2007). However, the oxygen supply to incubating salmonids embryos depends on several further factors such as the relative contribution of oxygenated river water infiltration and exfiltration of oxygen depleted groundwater or interstitial water in the redd (Malcolm et al., 2006, 2009) or the oxygen demand of organic material (S.M. Greig et al., 2007). Although these factors vary extensively both temporally and spatially (Brunke and Gonsler, 1997; S.M. Greig et al., 2007; Malcolm et al., 2006), only a few studies have resolved these processes on appropriate temporal and spatial scales.

Modeling approaches on the redd scale indicate that hyporheic velocities and dissolved oxygen (DO) concentrations within the egg pocket are enhanced due to the spawning activity, leading to reduced fine sediment and thus higher hydraulic conductivity (Tonina and Buffington, 2009; Zimmermann and Lapointe, 2005). Redd scale hyporheic exchange, measured on a centimeter to meter scale, can also be induced by the pit–tail structure of salmonid redds (Fig. 1A, Tonina and Buffington, 2009). This initial structure cannot, however, be expected to remain intact during high flow events (Ottaway et al., 1981). Hence hydraulic conditions on the redd scale likely change during the incubation season. Moreover, recent research clearly indicates the need for a multi-scale approach when investigating the dynamics of abiotic conditions in salmonid redds (Baxter and Hauer, 2000; Zimmermann and Lapointe, 2005): the local scale covers a single redd with an applied data grid resolution down to single centimeters (Fig. 1A). The intermediate scale covers the wider redd surrounding area of the riverbed including the relevant neighboring riverbed steps (Fig. 1B). The chosen data grid for this intermediate scale is in the range of meters. The regional scale considers a larger section of the river with a length and width of tenths of meters up to several kilometers (Fig. 1C). Hydraulic processes driven at all these scales can be expected to affect water exchange in a particular redd, and hence oxygen supply to the incubating embryos (Baxter and Hauer, 2000; Malcolm et al., 2008).

In Western Europe and North America many rivers with viable salmonid populations are heavily modified, i.e., channelized and with lateral stabilizations and artificial steps introduced for slope reduction (Brookes, 1988; Gilvear et al., 2002; Wohl, 2006). In channelized rivers, the lack of geomorphic features can substantially reduce hyporheic exchange (Malcolm et al., 2010), whereas hydraulic gradients related to artificial steps can markedly increase hyporheic exchange (Endreny et al., 2011). Artificial steps generate predictable flow-paths, with increased river water downwelling above steps and upwelling of hyporheic water below steps (Fig. 1B, e.g., Gooseff et al., 2006; Huber et al., 2013; Kasahara and Hill, 2006). Accordingly, artificial steps can increase hyporheic exchange in modified rivers (Kasahara and Hill, 2006; Sawyer et al., 2011) and could thereby also affect water exchange and oxygen supply in salmonid redds. Despite this, the effects of artificial steps on abiotic conditions in salmonid redds have, to our knowledge, not been investigated. This knowledge would provide important input for process-based river management in the many heavily modified salmonid streams of the Northern Hemisphere (e.g., Gilvear et al., 2002; Newson et al., 2012).

To this end, the current study evaluates the relative contribution of fine sediment, hydraulic gradients, river morphology, and regional geomorphology to specific water infiltration and oxygen dynamics in artificial brown trout redds in the Enziwigger, a heavily modified headwater river of the Swiss Plateau in the Canton of Lucerne. The Enziwigger also maintains a viable brown trout population (Schager et al., 2007).

The objective of this study was to provide a detailed investigation of the factors affecting the abiotic redd environment in a heavily modified river including I) an investigation of fine sediment deposition, hydraulic conditions (i.e., specific infiltration q , vertical and horizontal hydraulic gradients, and water level) and their effects on oxygen dynamics in the redds, II) an assessment of the morphological change of the riverbed and of the characteristic pit and tail structure of the redds and III) a comparison of the measured data with the results of a groundwater flow model, which was set up for one of the three experimental sites (cf. Huber et al., 2013). This model predicts zones of increased downwelling river water above steps, of hyporheic water upwelling

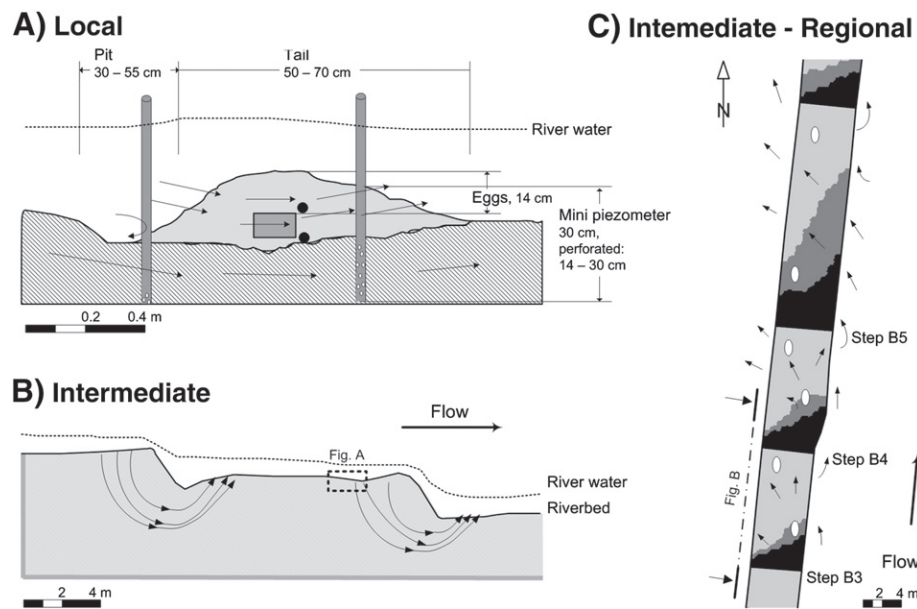


Fig. 1. Schematic view of (A) longitudinal section of an artificial redd (modified after Greig et al., 2007b) including the location of the mini-piezometers, the egg pockets (square) and temperature probes (bullet points) with the local scale flow pattern, (B) the hyporheic flow on an intermediate scale induced by riverbed steps according to the model calculations of Huber et al. (2013), and (C) the intermediate and regional scale water exchange processes (top view). Modeled river–groundwater exchange zones from Huber et al. (2013). Black: only exfiltration, gray: exfiltration and infiltration, light gray: only infiltration. Arrows indicate the main direction of the interstitial and groundwater flow, ovals represent the positions of the redds (for naming see Fig. 2).

below steps and zones with altering upwelling, downwelling and horizontal advection zones between the two steps.

In contrast to most previously published studies, data were collected with high spatial and temporal resolution (i.e., weekly or continuously) to explicitly characterize the temporal and spatial dynamics of the measured parameters. Measured parameters affect brown trout embryo survival in the redds and our results can thus be integrated with studies monitoring survival success of salmonid embryos (Michel et al., in revision), providing a more complete perspective on the factors affecting salmonid incubation success in comparable anthropogenically modified river environments.

2. Materials and methods

2.1. Study site and general setup

The river Enziwigger is a small channelized river located near Willisau, Canton of Lucerne, Switzerland with a total watershed area of about 31 km² (Fig. 2). Mean discharge, measured in Willisau (Fig. 2) by the Cantonal authorities (Nov. 2007–Nov. 2008) was 2.1 m³ s⁻¹, minimum and maximum discharge were 1.1 m³ s⁻¹ and 10.1 m³ s⁻¹, respectively. During the 20th century the Enziwigger was straightened and channelized, and cross-channel log steps were installed as slope breakers to prevent deep channel erosion and bed-scouring during flood events (Fig. 2). Thus, like for most rivers in the Swiss Plateau, its morphology is strongly modified: only 5% is close to natural or natural, 21% is slightly affected and 74% is strongly affected or even artificial (classified with the Swiss modular stepwise procedure for ecomorphology after Huette and Niederhauser, 1998; Stucki, 2010). Despite these extensive modifications, its biological condition, classified with the macrozoobenthos module of the Swiss modular stepwise procedure (Stucki, 2010), is considered good (EBP-WSB-Agrofutura, 2005). The only fish species in the Enziwigger is the brown trout *S. trutta*, which maintains a viable population (EBP-WSB-Agrofutura, 2005; Schager et al., 2007). The flow regime of the Enziwigger is affected

neither by hydro-power facilities nor by effluents from waste water treatment plants.

Measurements were conducted at three experimental sites along the river named A, B and C (from upstream to downstream; Fig. 2) at altitudes from 757 to 583 m a.s.l. The groundwater flow model was set up for site B (Huber et al., 2013). The riverbed at all sites is stabilized with artificial log steps, which strongly affect hyporheic exchange on an intermediate scale with river water infiltration upstream of the steps and exfiltration of hyporheic water downstream of the steps (Fig. 1B). At site A, the bedrock beneath the riverbed lies at a depth of a few decimeters and the hydrogeologic settings are assumed to be dominated by lateral inflow or the exfiltration of groundwater and/or hyporheic water. Piezometer measurements at sites B and C and the groundwater flow modeling at site B indicate on a regional scale a hydraulic gradient from the river to the main valley aquifer on the left side of the river and consequently a domination of river water infiltration (Fig. 1C, Huber et al., 2013). The influence of river flow stage and transient hillside groundwater flow has a minor impact on these intermediate and regional flow patterns (Huber et al., 2013).

Each site was equipped with six artificial salmonid redds in places wherein natural brown trout redds had been mapped in November 2008. The artificial redds were built to create a structure that resembles the structure of natural brown trout redds (Crisp and Carling, 1989). A detailed description of the redd structure and how it was built is given in Michel et al. (in revision). In the Enziwigger, these locations are mostly consistent from year to year (P. Amrein, Fish and Wildlife Service, Canton of Lucerne, pers. comm.). Data were collected during two spawning seasons (season 1 (S1): November 2009 to end of March 2010; season 2 (S2): November 2010 to end of March 2011) in 18 artificial redds per year (n = 36 redds in total). Redds were built in the same location each season (Fig. 2) with the exception of redds A31 and A32, which were covered in ice in January and February, making sampling impossible. Redds are labeled after the site (A, B, C), the terraces between two steps (1–5), the redd location within a terrace (1 and 2) and the season (S1 and S2). For example, redd A41_S1 identifies the first redd in the fourth investigated terrace at site A during

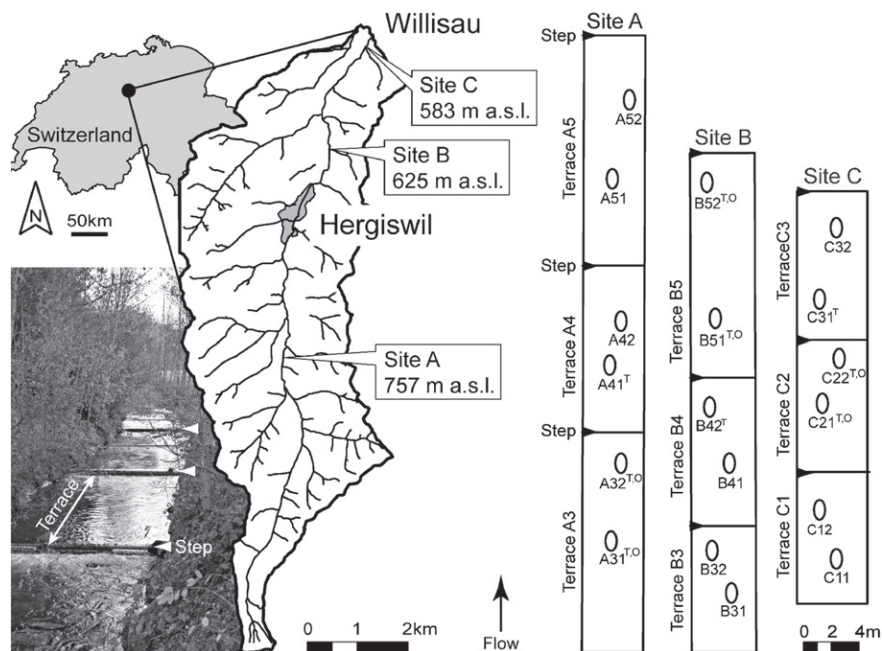


Fig. 2. Location of the Enziwigger watershed in Switzerland. The photograph shows the step and terrace structure at study site B. The watershed map of the river Enziwigger and the towns Willisau and Hergiswil (Canton of Lucerne, Switzerland) shows the locations of the three field sites A, B and C, while the schematic on the right illustrates the location of the redds within each field site. Here, superscripts indicate redds with continuous temperature (T) and oxygen (O) measurements.

the first season (Fig. 2). A detailed description of the river characteristics and field locations is given in Schindler Wildhaber et al. (2012b).

2.2. Sediment collection and analyses

Each redd was equipped with two sediment baskets to assess weekly fine sediment infiltration and net fine sediment accumulation during the entire field season (cf. Acornley and Sear, 1999; Greig et al., 2005; Heywood and Walling, 2007). One of them was emptied at weekly intervals to measure the weekly infiltration rates (= infiltration basket). The second set of sediment baskets was emptied at the end of the incubation season to measure net accumulation of fine sediment during the incubation period (= accumulation basket, Sear et al., 2008). At each site, the sediment basket data were complemented with four to seven freeze core samples to characterize the sediment stratification of the undisturbed river gravel. For a detailed description of the used baskets, the freeze core technique and their handling see Schindler Wildhaber et al. (2012b).

Grain size distribution was measured in a subsample of the fine sediment fraction of the freeze cores' layers 0–10 cm, 10–20 cm and 20–30 cm and in two subsamples of the fine sediment collected in accumulation baskets. Representative subsamples were obtained by a sample divider (Retsch, Haan, Germany). Additionally, grain size distributions of weekly infiltrated fine sediment samples ($n = 80$) were determined. The rest of the infiltrated fine sediment was pooled for each redd and a subsample was analyzed to obtain a mean grain size distribution of the infiltrated fine sediment. Grain size fractions were named according to the German soil taxonomy standard (DIN EN ISO 14688-1): sand: 0.063–2 mm, silt: 0.002–0.063 mm and clay: <0.002 mm (Sponagel et al., 2005).

Porosity (n) was calculated for each site on the basis of sediment grain size distributions from freeze core samples by the formula

$$n = 48.6 \cdot C_u^{-0.2} \quad (1)$$

Where $C_u = d_{60}/d_{10}$ (diameter of grain size at the 60th and 10th percentile of the cumulative sample mass) (Schälchli, 1995).

The Fredle index of the accumulation baskets and of the freeze core samples was calculated by the formula

$$\text{Fredle index} = \frac{d_g}{S_o} \quad (2)$$

where d_g is the geometric mean grain size and S_o is the sorting coefficient derived by taking the square root of the quotient of the grain size at the 75th percentile divided by that at the 25th percentile (Lotspeich and Everest, 1981). The Fredle index is a central tendency quality index of the redd gravel composition, which gets smaller with smaller permeability of the sediment.

2.3. Oxygen

Continuous oxygen measurements were conducted with Aanderaa oxygen optodes 3835 (Aanderaa Data Instruments, Bergen, Norway) buried at the same depth as the incubating brown trout embryos (approx. 14 cm, cf. Michel et al., in revision). Oxygen contents in mg l^{-1} as well as saturation (%) were measured every 10 s and mean values were logged in 10 min intervals. One optode per site was installed during season 1 (redds A32, B51 and C21) and two during season 2 (Fig. 2). Moreover, oxygen concentrations in each redd were measured manually every second week in mini-piezometers located in the pit and tail of each redd (Fig. 1A) with PreSens oxygen dipping probe mini-sensor (PreSens Precision Sensing GmbH, Regensburg, Germany). Each manual oxygen measurement was conducted twice: once in the “old” interstitial water and once in the reflux “new” water approximately 30 min after the “old water” had been extracted.

2.4. Riverbed and redd morphology

Riverbed morphology was mapped at a 0.5 m horizontal resolution in season 1 shortly after redd construction (October 26th 2009) and on December 27th after several high flow events. These data were used to assess morphological changes induced by high flow events on the river segment scale. The water depths above the deepest point of the pit and the highest point of the tail were measured weekly to quantify temporal changes of the typical redd structure.

2.5. Hydraulic investigations

Flow-stage at each site was measured every 15 s with pressure transmitter probes (STS, Sensor Technik Sirnach, Switzerland) and average values were logged at 10 min intervals during both field seasons.

Water levels above the pit and tail of each redd were recorded weekly to assess water level heterogeneity within sites. Vertical hydraulic gradients (VHG) in the redds were measured weekly after Baxter et al. (2003) in mini-piezometers installed in the pit and tail of each redd (Fig. 1; for details see Schindler Wildhaber et al., 2012b). The VHG is a dimensionless parameter calculated by the formula

$$\text{VHG} = \frac{\Delta h}{\Delta l} \quad (3)$$

where Δh is the difference in head between the water level in the piezometer and the level of the stream surface and Δl is the depth from the streambed surface to the first holes in the piezometer (Baxter et al., 2003). Positive values indicate an energy gradient potentially sufficient to produce upwelling and negative values indicate an energy gradient potentially sufficient to produce downwelling. In the following, the VHG values are reported as upwelling or downwelling processes, although they are actually only a measure of upwelling and downwelling potential (Baxter and Hauer, 2000). The differences in VHG between the pit and the tail piezometer of each redd were defined as the horizontal hydraulic gradients (HHGs), which is an indicator for hydraulic gradients driving water flow through the redd.

To obtain the temporal and spatial change of specific infiltration rates (q) in the redds, the one-dimensional heat pulse method was used (e.g., Hatch et al., 2006). For this, stream water temperature and temperatures at two different depths just above and below the incubating brown trout embryos (approx. 12 and 20 cm, respectively) were recorded every minute using thermocouple temperature probes (Campbell Scientific 105 E). Three redds per site were equipped with one or two temperature probes (Fig. 2). In redds equipped with two temperature probes, q could be calculated for the upper part (q_u , 0 to about 12 cm), the bottom part (q_b , about 12 cm to about 20 cm) and the total part (q_t , 0 to about 20 cm). In redds with one temperature probe, q could only be assessed in the upper part. The diurnal amplitude variations in temperature in the different depths and the diurnal phase variations were used to calculate q , but only the results of the former method were incorporated into further interpretations because of their higher stability. The method used allowed the calculation of two specific infiltration rate values per day.

The diurnal sinusoidal alternation was filtered from the temperature data by a discrete bandpass filter (FIR-filter with Hamming-window, 5001 filter coefficients, cut-off frequency $0.8 \cdot f_{\text{Day}}/1.5 \cdot f_{\text{Day}}$). All field temperature data were sampled with a frequency of one measurement per minute. When field sample periods exceeded 1 min, e.g., due to technical problems, linear interpolation was used to fill gaps of up to 10 min. Data gaps exceeding 10 min were marked as missing and not further evaluated. Data-points with time offset between the daily minima or maxima peaks of the corresponding sinusoidal temperature curves at the different depths exceeding 20% of a day period (i.e., 288 min) were also removed from further processing. The resulting temperature amplitude ratio (A_r) was used to estimate q .

The specific infiltration rate q and the vertical flow velocity (v_f) are extracted according to Eq. (4) (Ingebritsen et al., 2006) and Eq. (5) (Hatch et al., 2006, slightly transposed).

$$q = v_f \cdot n \quad (4)$$

$$v_f = \left(\frac{\rho \cdot c}{\rho_f \cdot c_f} \right) \cdot v. \quad (5)$$

For parameter definition and values see Table 1. The vertical fluid velocity (v) can be determined by the amplitude ratio (A_r), identified as v_{Ar} . The values were gained by a numerical solver from the Eqs. (6) and (7) (Hatch et al., 2006)

$$\frac{2\kappa_e}{\Delta z} \ln \left(A_r + \sqrt{\frac{\alpha(v_{Ar}) + v_{Ar}^2}{2}} \right) - v_{Ar} = 0 \quad (6)$$

where

$$\alpha(v) = \sqrt{v^4 + (8\pi \cdot f_{Day} \cdot \kappa_e)^2}. \quad (7)$$

The effective thermal diffusivity (κ_e) is estimated according to Hatch et al. (2006) by the equation

$$\kappa_e = \frac{\sigma}{\rho \cdot c} + \beta \cdot |v_f| \quad (8)$$

where the components of the first term are gained from:

$$\sigma = n \cdot \sigma_f + (1-n) \cdot \sigma_s \quad (9)$$

$$\rho = n \cdot \rho_f + (1-n) \cdot \rho_s \quad (10)$$

$$c = \frac{n\rho_f c_f + (1-n) \rho_s c_s}{n\rho_f + (1-n) \rho_s}. \quad (11)$$

The second term of the Eq. (8) was excluded from the calculations as its contribution to the value of κ_e is negligible with the thermal dispersivity (β) = $1 \cdot 10^{-3}$ as proposed by Hatch et al. (2006) and Keery et al. (2007) but it would strongly increase the complexity of the analysis (Keery et al., 2007).

Heat is mainly transferred through riverbed sediments by advection and conduction. Heat advection describes the heat transfer related to

water flow through the sediment, while heat conduction describes the molecular transport of thermal energy (e.g., Constantz, 2008). The relative contribution of advection and conduction to heat transfer can be quantified with the dimensionless Peclet number (Pe) (Silliman et al., 1995):

$$Pe = \frac{v_f \cdot n \cdot l}{D} \quad (12)$$

where l is the characteristic length, set as 0.01 m due to the range of the setup. The thermal diffusivity D is given by:

$$D = \frac{K_e}{c_s \cdot \rho_s} \quad (13)$$

where K_e is the thermal conductivity of the saturated sediment (Table 1). If Pe is smaller than approximately $2 \cdot 10^{-4}$, the advection component of the solution has little impact for fluxes and conductive heat transport dominates (Silliman et al., 1995).

Median Peclet numbers were between approximately 0.01 and 0.1, indicating that heat is transported not only by molecular transport of thermal energy (conduction) but also by water flow (advection) (Silliman et al., 1995).

2.6. Groundwater flow modeling

Groundwater flow models for site B were setup in GMS (Groundwater Modeling System 7.1, Environmental Modeling Systems, 2002) on the basis of MODFLOW (McDonald and Harbaugh, 1996). Details can be found in Huber et al. (2013). Boundary conditions of a regional scale groundwater model (extension 230 m × 340 m, resolution 2 m × 2 m) were transferred to an intermediate scale groundwater model (extension 110 m × 60 m, resolution 0.5 m × 0.5 m). For the description of the bedrock surface penetration depth of direct-push boreholes were used. For the intermediate scale model the high-resolution measurements of riverbed morphology were considered. Based on continuously measured groundwater heads, the distribution and magnitude of hydraulic conductivities as well as the riverbed conductance were inversely calibrated for a transient data set (220 days, resolution 1d, PEST, Doherty, 1994).

Table 1

Physical parameters used for calculating specific infiltration rates q in alphabetic order (1. Roman letters, 2. Greek letters).

| Symbol | Values | Unit | Parameter |
|--------------|----------------------|---|---|
| A | | °C | Amplitude of thermal oscillation |
| A_r | | – | Temperature (T) amplitude ratio (upper/lower T amplitude) |
| c | | J kg ⁻¹ °C ⁻¹ | Specific heat of sediment–fluid system |
| c_f | 4208 | J kg ⁻¹ °C ⁻¹ | Specific heat of fluid (water at 4 °C) (Lemmon et al., 2012) |
| c_s | 775 | J kg ⁻¹ °C ⁻¹ | Specific heat of sediments, average between values of Schön (1996) (cited by Rau et al., 2010) and Revil (2000) (cited by Keery et al., 2007) |
| f_{Day} | $11.5 \cdot 10^{-6}$ | s ⁻¹ | Frequency of a day period (24 h) |
| K_e | 1 | J m ⁻¹ s ⁻¹ K ⁻¹ | Thermal conductivity of the saturated sediment, Carslaw and Jaeger (1959) (cited by Silliman et al., 1995) |
| n | 0.23 | – | Porosity, assessed from freeze core samples |
| q | | m s ⁻¹ | Specific infiltration rate |
| v | | m s ⁻¹ | Velocity of thermal front |
| v_{Ar} | | m s ⁻¹ | Velocity of thermal front derived from the amplitude ratio A_r |
| v_f | | m s ⁻¹ | Vertical fluid velocity, positive number = down welling (Goto et al., 2005) |
| β | $1 \cdot 10^{-3}$ | m | Thermal dispersivity (cited by Hatch et al., 2006) |
| $\Delta\phi$ | | s | Temperature amplitude phase shift |
| κ_e | | m ² s ⁻¹ | Effective thermal diffusivity |
| ρ | | kg m ⁻³ | Density of saturated sediment |
| ρ_f | 1000 | kg m ⁻³ | Density of fluid (water at 4 °C; Kuchling, 1976) |
| ρ_s | 2650 | kg m ⁻³ | Density of sediment (e.g., Kuntze et al., 1994) |
| σ | 1.50 | W m ⁻¹ K ⁻¹ | Thermal conductivity of saturated sediment (Constantz, 2008) |
| σ_f | 0.60 | W m ⁻¹ K ⁻¹ | Thermal conductivity of fluid (water; Ingebritsen et al., 2006) |

3. Results and discussion

3.1. Spatiotemporal changes in riverbed and redd morphology

The riverbed morphology of the Enziwigger changed substantially during high flow events, despite the steps to prevent deep scouring. This was especially true for the two downstream sites B and C (Fig. 2), where flood events in December 2009 triggered river gravel accumulation or scouring up to 0.9 m (Fig. 3). All redds at site B were strongly affected by scouring, while at site C the gravel bed scoured predominantly in the pools below steps and accumulated towards the right bank of the river. Sediment displacements varied from terrace to terrace within a site. For example, changes of the riverbed morphology below step 3 at site C were much smaller than at the other two examined steps (Fig. 3, right). This was probably due to the slightly wider riverbed

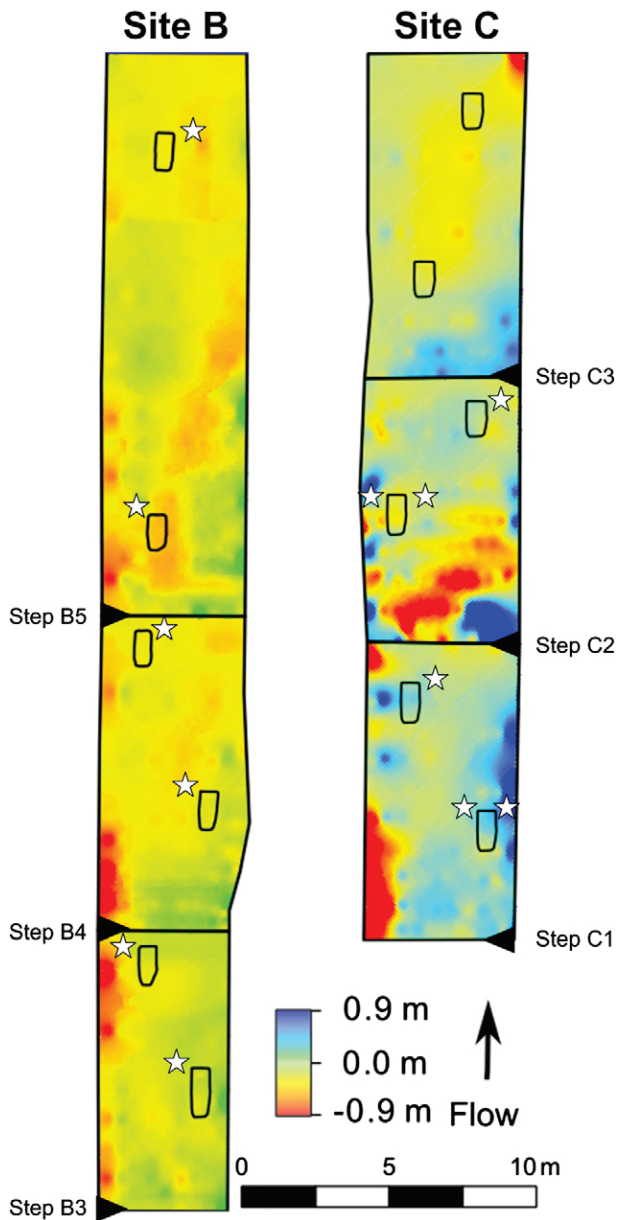


Fig. 3. Differences between the riverbed topography measured in October and December 2009 at the two downstream sites B and C. Negative values indicate gravel bed erosion and positive values indicate sediment deposition. Black ovals are the positions of the artificial redds. Redds lost during season 1 are marked by a star on the left side, while redds lost during season 2 are marked by a star on the right side.

(5.0–5.5 m at step C3, 4.5–5 m at step C2 and 4.5 m at step C1) causing lower water levels and hence less shear stress. These data also agree with the suggestion that sediment transport in rivers is a discontinuous process and sediment often moves in pulses (Klingemann and Emmett, 1982) affected by bed-form and associated sediment sorting (Cudden and Hoey, 2003) or by debris flows (Hoffman and Gabet, 2007). Hence, bed scouring and gravel deposition are not easily predicted, at least on an intermediate scale within individual river sections. Along the entire river (i.e., regional scale) increased gravel displacement was evident at sites B and C as compared to site A (visual interpretation). In total, half of the redds in sites B and C were lost (Fig. 3), while only 8% of the redds were lost at the most upstream site A. This pattern is most likely related to increased bed shear stress in sites B and C caused by higher water levels and only marginally smaller slopes (Schindler Wildhaber et al., 2012b), as also indicated by increasing bedloads and suspended sediment loads from upstream to downstream (Schindler Wildhaber et al., 2012b). In support of this notion the probability of redd excavation increased with the water level above the redd (GLM, $p < 0.05$).

Winter flood events in some Swiss rivers and also in rivers worldwide have increased over the last decade (Birsan et al., 2005; Scheurer et al., 2009) and are expected to further increase, both, in respect to intensity and frequency, due to climate change (IPPC, 2007; Middelkoop et al., 2001; Thodsen, 2007). In the Enziwigger, high-flow events in early winter are unusual, but it has been suggested that they have increased in recent decades (P. Amrein, Fish and Wildlife Service, Canton of Lucerne, Switzerland, pers. comm.). Accordingly, the high redd loss reported here raises concerns about how the observed and predicted increases of winter floods affect salmonid recruitment in confined rivers like the Enziwigger with small egg-burial depths (0–9 cm; Riedl and Peter, 2013) making salmonid embryos more susceptible to scouring.

High-flow events also strongly affected the morphology of the remaining redds. Initially, the mean difference between the depth of the tail and pit of newly built redds was 9.4 ± 2.8 cm (Fig. 4A). After one month and some high flow events, most redds were basically leveled (Fig. 4A) and a high amount of fine sediment had infiltrated (Schindler Wildhaber et al., 2012b). These observations agree with Ottaway et al. (1981) who documented a flattening of brown trout redds after only the first high water event subsequent to spawning. Both, flattening of the redd and fine sediment content are known to affect the water exchange in redds, either by reducing horizontal pumping flow or by decreasing redd gravel permeability (e.g., Greig et al., 2005; Schälchli, 1995). The concept of enhanced downwelling of oxygenated water due to the redd morphology is still widely discussed (e.g., S.M. Greig et al., 2007; Tonina and Buffington, 2009; Zimmermann and Lapointe, 2005). Our results clearly indicate that redd morphology contributes to local redd scale exchange processes only during the first few weeks after redd building (see below). Once the pit-tail structure has been leveled, exchange processes on intermediate or regional scales gain importance for water-exchange and oxygen supply to developing embryos. In many modified rivers, such processes driven on these scales have to be clearly incorporated into management plans to ensure sufficient salmonid incubation success.

3.2. Hydraulic dynamics in the redds

3.2.1. Spatial patterns of the hydraulic dynamics

Vertical hydraulic gradients (VHG) measured in mini-piezometers did not parallel the expected intermediate scale downwelling and upwelling patterns induced by steps (Gooseff et al., 2006; Huber et al., 2013; Kasahara and Hill, 2006, Fig. 1B). Most redds were located more than one meter before or after a step. Accordingly, they were not located in the main upwelling and downwelling zones predicted by the model, but in areas where downwelling, upwelling and horizontal advection alternate (Fig. 1C). Hence, the applied mini-piezometer approach was

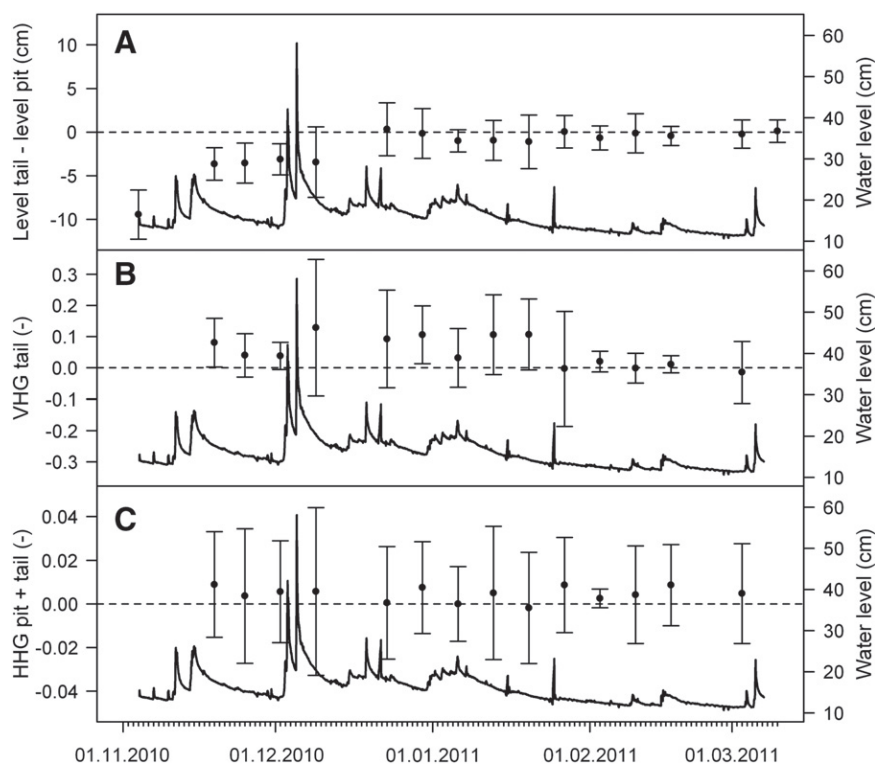


Fig. 4. In each panel, the black graph represents the flow stage at site B. Symbols within panels denote (A) the mean \pm standard deviation (SD) of the riverbed level differences between tail and pit (B) mean \pm SD of the vertical hydraulic gradients (VHGs) in the tail of the redds, and (C) mean \pm SD of the horizontal hydraulic gradients (HHGs) between pit and tail of the redds. Values were calculated from all 18 redds during season 2. A positive hydraulic gradient indicates upwelling and a negative gradient indicates downwelling.

most likely not able to integrate the hydraulic gradients that jointly drove water exchange in redds, i.e., both vertical and horizontal. In redd A32_S1, which provides an exception being located only 0.65 m above a step, considerable downwelling potential was measured (-0.07 ± 0.06). When this redd was located 1.65 m upstream of the step in season 2 (redd A32_S2; Fig. 2), VHGs changed between upwelling and downwelling conditions with a mean close to zero (0.03 ± 0.08). This confirms the model predictions. In general, vertical hydraulic gradients on the redd scale can be expected to show substantial temporal variation related to water level fluctuations and also changes in riverbed morphology (cf. Section 3.2.2).

Specific infiltration rates q , calculated from continuous data, confirmed the predictions from the groundwater flow modeling. Mean q_t increased with smaller distance to the next downstream step and hence confirmed the increased downwelling above steps (Table 2). Similarly, in redds located further upstream smaller and also negative q_t values were found, which again agrees with model predictions (Fig. 1C). Also, weekly fine sediment infiltration increased

with shorter distance to the downstream step (Spearman rank correlation, fine sediment: $\rho = -0.45$, $p < 0.05$, silt: $\rho = -0.52$, $p < 0.05$, clay: $\rho = -0.57$, $p < 0.01$), likely related to increased river water infiltration above steps. Increased weekly fine sediment infiltration had no negative effect on specific water infiltration in redds (Table 2). However, the net fine sediment accumulation did not increase with shorter distance to the step (all $p > 0.12$). Fine sediment accumulation depends not only on fine sediment infiltration, but also on water level, since higher water levels lead to resuspension of fine sediment (see also Schindler Wildhaber et al., 2012b). The specific infiltration rate q decreased significantly in redds with higher fine sediment accumulation and increased with a higher maximal water level above the redd (Table 2).

Hydraulic exchange processes can vary remarkably within a single redd. In most redds q was lower in 12–20 cm depth as compared to the upper 12 cm of redd gravel (t -test, $p < 0.01$; Fig. 5). Freeze core samples of undisturbed gravel in the study area confirmed a significantly lower silt and clay level in the upper part (0–10 cm) compared to the deeper part (i.e., 10–20 cm and 20–30 cm, cf. Schindler Wildhaber et al., 2012b). A comparable increase in fine sediment content paralleled by a decreased hydraulic conductivity was also found in the studies of Brunke (1999) and Sear (1993). Accordingly, the decrease of q with depth reported here suggests higher fine sediment content around our brown trout eggs (i.e., at 12–20 cm depth) compared with the entire redd gravel. A similar distinction between the upper and lower part of the redd gravel was made by Meyer (2003). Our study further documents that this increased fine sediment accumulation around the eggs can decrease water exchange around the eggs, which could hinder oxygen supply to the embryos (see Section 3.3.2) and hence salmonid embryo survival.

At redd A32_S1, the specific infiltration q was higher in the bottom part than the upper part of the redd (Fig. 5, see Fig. 2 for location of the redd), which was probably related to the lower mean water level above this redd (9.8 ± 2.0 cm), triggering high fine sediment deposition and only limited scouring (Schindler Wildhaber et al., 2012b). Redd

Table 2

Spearman rank correlations between median specific infiltration rate q in the upper part (0–12 cm; q_u) and the total part (0–20 cm, q_t) and the total amount of accumulated fine sediment (<2 mm), the accumulated silt and clay fraction, the sum of weekly infiltrated fine sediment, the Fredle index of the accumulation baskets, the maximal water level above the redd and the distance of the redd to the upstream and downstream step. Sample size (n) is given in parentheses.

| | q_u (m s^{-1}) | q_t (m s^{-1}) |
|--------------------------------|-----------------------------|-----------------------------|
| Fine sediment accu. (%) | -0.79 , $p = 0.03$ (8) | -0.89 , $p = 0.03$ (6) |
| Silt and clay accu. (%) | -0.52 , $p = 0.20$ (8) | -0.49 , $p = 0.36$ (6) |
| Fine sediment infiltration (g) | -1.9 , $p = 0.58$ (8) | -0.18 , $p = 0.57$ (6) |
| Fredle index (-) | 0.71 , $p = 0.06$ (8) | 0.77 , $p = 0.09$ (6) |
| Water max. (cm) | 0.60 , $p = 0.03$ (13) | 0.66 , $p = 0.03$ (10) |
| Distance upstream step (cm) | 0.15 , $p = 0.62^a$ (13) | 0.61 , $p = 0.06^a$ (10) |
| Distance downstream step (cm) | -0.17 , $p = 0.58^a$ (13) | -0.68 , $p = 0.03^a$ (10) |

^a Mean q of February and March to get a mean q value of the undisturbed river gravel.

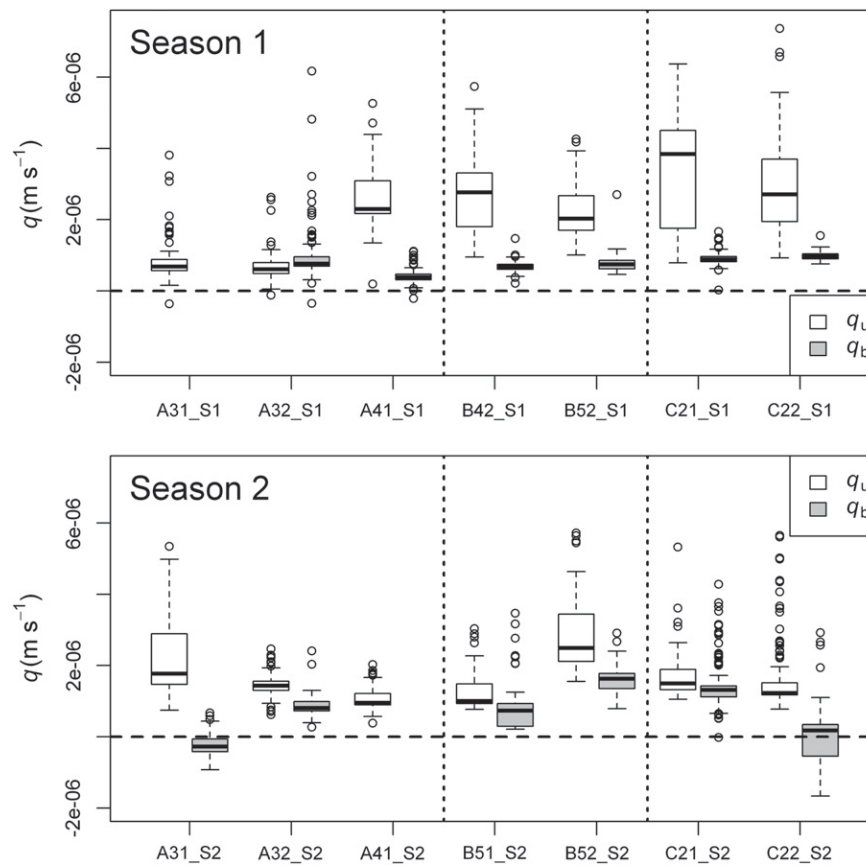


Fig. 5. Specific water infiltration rates in the upper (q_u) and the bottom part (q_b) of the redds during season 1 (top) and season 2 (bottom). Negative values indicate upwelling, positive values indicate downwelling. For each redd the horizontal line indicates the median, the box interquartile range (i.e., center 50% of the data), whiskers mark maximum and minimum values, and points denote values exceeding 1.5 times the interquartile range. Among seasons, redds were built in the same location (Fig. 2) with the exception of redds A31 and A32 (see Section 3.2.1).

A32_S1 was also the only redd equipped with temperature probes that was temporally covered with ice, which could have caused decreased water flow over the redd. In addition, VHG measurements indicated substantial downwelling potential in this redd ($VHG = -0.07 \pm 0.06$, see above). Both factors possibly increased the fine sediment input in the entire gravel column of this redd (Brunke, 1999; Schindler Wildhaber et al., 2012b; Seydell et al., 2009) and hence decreased specific water infiltration q also in the upper part. A low q was also found in the upper part of redd A31_S1 (Fig. 5), which also had a very low mean water level (2.5 ± 1.7 cm). During the second field season, the locations of two redds were changed to locations with deeper mean water levels (A31_S2: 15.1 ± 3.5 cm, A32_S2: 12.4 ± 3.5 cm). This resulted in less fine sediment accumulation (Schindler Wildhaber et al., 2012b) and higher specific infiltration rates q were found (Fig. 5). Further, these patterns of q were closely paralleled by the oxygen dynamics in these redds (see Section 3.3.2).

3.2.2. Temporal pattern of the hydraulic dynamics

Slightly positive VHGs, indicating upwelling processes, were measured in the tail of most redds at the beginning of the incubation period (Fig. 4B). In contrast, horizontal hydraulic gradients (HHGs) between pit and tail did not indicate increased horizontal pumping flows between pit and tail (Fig. 4C). The often suggested redd scale flow pattern, with downwelling in the pit and upwelling in the tail (Tonina and Buffington, 2009), was therefore not confirmed by the HHG measurements. One reason for this might be the influence of the riverbed morphology or the water levels on the vertical and horizontal hydraulic gradients, as indicated by significant correlations between VHGs and the water level ($\rho = 0.4\text{--}0.6$, $p < 0.05$ in 8 of the 18 redds, Fig. 6).

During base flow, VHGs were mostly negative or around zero, indicating downwelling or horizontal advection flow, which agrees with model predictions (Huber et al., 2013). Upwelling or lateral flow dominated for VHG values measured at higher water levels (Fig. 6). On an intermediate scale, upwelling increases below steps (Gooseff et al., 2006; Huber et al., 2013; Kasahara and Hill, 2006). On a regional scale, upwelling can occur when increasing riparian groundwater levels are paralleled by decreasing stream water levels, e.g., during the recession limb of flood events (Geist et al., 2008; Malcolm et al., 2003, 2006; Soulsby et al., 2009). In the Enziwigger, VHG measurements during the rising limb or flood events were not possible because of dangerous physical conditions. Most of the higher water levels in Fig. 6 therefore represent data points measured during the recession limb of flood events. Therefore, the positive hydraulic gradients (Fig. 6) indicate most likely recharge of groundwater on a regional scale and related upwelling in the redds.

Hyporheic flow paths in rivers can be very complex and also change with discharge and morphology (Tonina and Buffington, 2007). In our study, these complex temporal dynamics can best be seen in the specific water infiltration rates. Initially, q values in most redds were consistently high ($6\text{--}7 \cdot 10^{-6} \text{ m s}^{-1}$), and decreased markedly within a month – likely related to fine sediment accumulation and changes in redd morphology – to finally stabilize around $1\text{--}2 \cdot 10^{-6} \text{ m s}^{-1}$ for the rest of the incubation season (Figs. 7, 5). Nonetheless, on the scale of hours and days, q remained responsive to water-level fluctuations, when it increased during high-flow events and returned to baseline levels afterwards (Fig. 7). The most likely explanation for this are local changes in groundwater heads in combination with increased gravel permeability related to remobilization of fine sediment (e.g., Brunke, 1999; Keery et al., 2007; Schälchli, 1995).

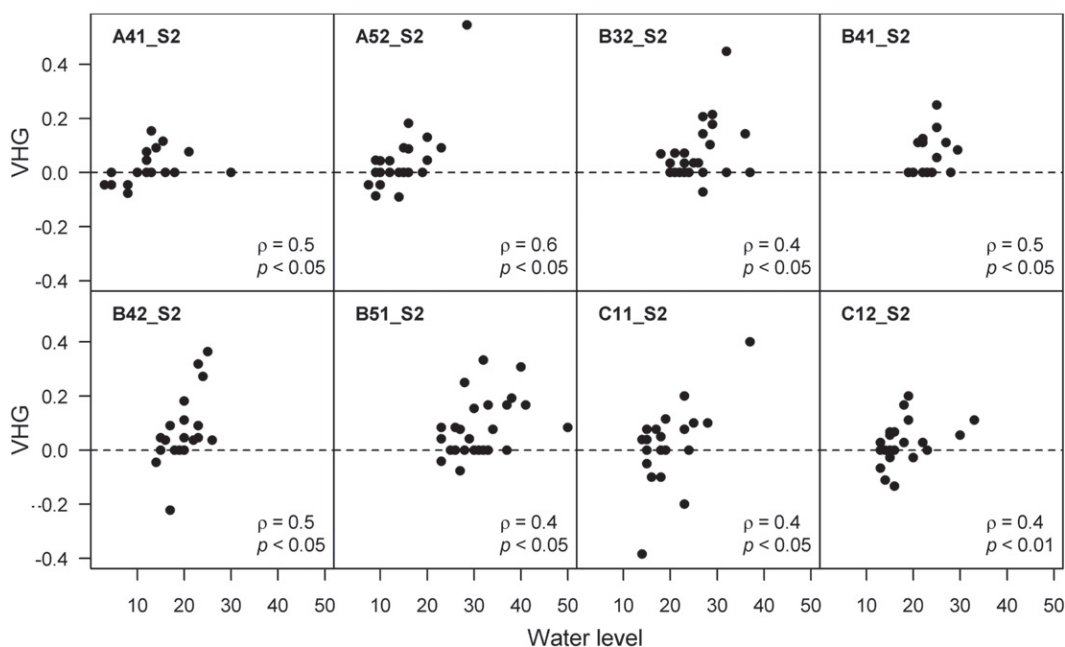


Fig. 6. Relationship between water level and vertical hydraulic gradient (VHG) for individual redds from season 2. Within each panel Spearman correlation coefficient ρ and the p -value are given. Positive VHG indicates upwelling, and negative VHG indicates downwelling. The location of each redd is given in Fig. 2.

Temporally negative q values, and hence upwelling were found in the bottom part (approx. 12–20 cm) of two redds (A31_S2 and C22_S2) where consistent downwelling occurred in the upper part (Fig. 5). Redd C22 (Fig. 8) was located just above a step, where downwelling predominates (Huber et al., 2013). Further, it was located on the right side of the Enziwigger, close to a small tributary river driving exfiltration of groundwater (Fig. 2). Given this specific location, we suspect that river water infiltrated in the upper part of this redd (positive q), while groundwater exfiltrated into the lower part (negative q). As discussed above, this groundwater exfiltration increased during the recession limb of high flow events (Fig. 8). Altogether, these data clearly indicate that exchange processes in salmonid redds are driven on different scales, and that these processes altogether determine water-exchange patterns in the egg pocket, which will then have an influence on the likelihood of embryo survival (Michel et al., in revision).

Specific water infiltration rates q calculated with the intermediate groundwater flow model for specific redd locations in downwelling zones ranged between $8.5 \cdot 10^{-7}$ and $1.5 \cdot 10^{-5} \text{ m s}^{-1}$ (season 1,

Huber et al., 2013). Measured daily q_t values at redd B42_S1 correlated with the modeled values (Pearson's $r=0.3$, $p<0.05$). At redd B52_S1, no significant correlation was found. The groundwater flow model was set up using hydraulic heads of the river and groundwater as well as the local and regional topography. In contrast, the actual q in the redds further depends on the hydraulic conductivity, affected by fine sediment deposition and hydraulic gradients on the redd scale. These differences could have contributed to the lack of correlation in the latter redd, since water exchange rates on the redd scale can vary strongly, either depending on reach scale bedform character and barriers (Baxter and Hauer, 2000) or differences in hydraulic conductivities (Brunke and Gonser, 1997). These results indicate that groundwater flow modeling as applied in Huber et al. (2013) can predict exchange processes on the regional and intermediate scales, but is limited in predicting exchange processes on the redd scale.

Altogether, these findings illustrate that water exchange processes in salmonid redds are complex and driven on multiple scales. Consequently, fine sediment effects on salmonid embryo survival can be expected to differ depending on the redd location relative to river

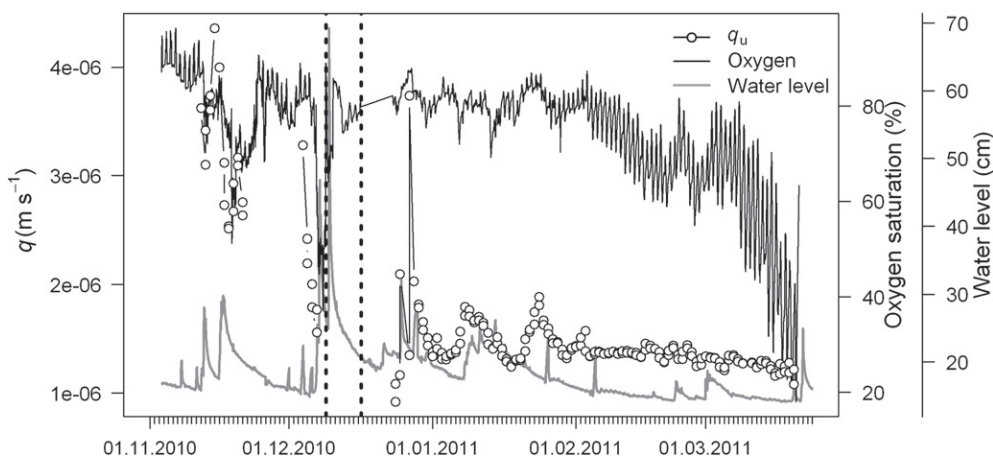


Fig. 7. Example of the temporal dynamics of the specific infiltration q in the upper part of the redd gravel (q_u), the oxygen concentration and the water level. Shown are data from redd C21_S2 (cf. Fig. 2). A period when oxygen and temperature probes were dug out is marked with vertical dashed lines.

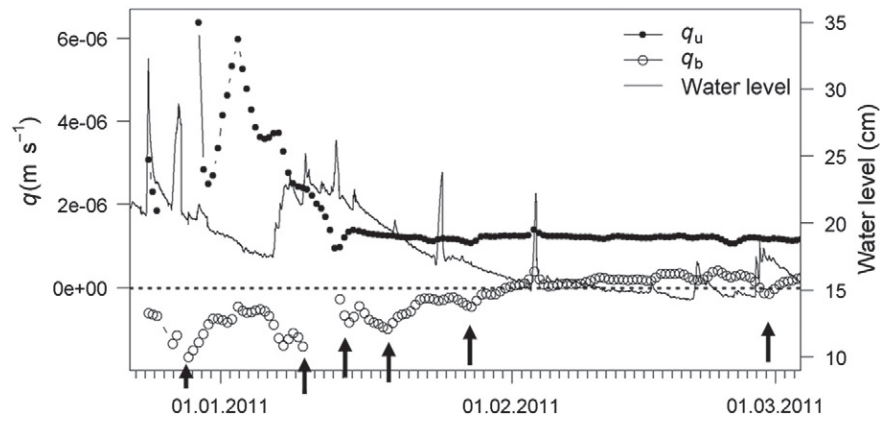


Fig. 8. Temporal changes of the specific infiltration rate q in the upper and the bottom part of the redd C22_S2 (cf. Fig. 2 for location of the redd). Negative values indicate upwelling, positive values indicate downwelling. The arrows point to periods with increased upwelling during the falling limb of high flow events.

morphology and structure and also on regional aspects, such as river interactions with the valley aquifer.

3.3. Oxygen

3.3.1. Manual vs. continuous oxygen measurements

Manual oxygen measurements, conducted on bi-weekly intervals during season 2 in mini-piezometers, indicated a high interstitial dissolved oxygen (DO) concentration in the redds ($10.1 \pm 2.2 \text{ mg l}^{-1} / 75.7 \pm 15.7\%$). However, DO concentrations measured manually did not correlate with DO concentrations from permanent oxygen measurements. Oxygen concentrations in salmonid redds can vary substantially with time (Heywood and Walling, 2007, this study), and hence even weekly or bi-weekly measuring intervals have a high risk of underestimating extreme values (Malcolm et al., 2006). Manual measurements in piezometers could therefore over- or underestimate the amount of oxygen present in salmonid redds, being a poor descriptor for oxygen dynamics during the incubation season. Given these limitations and the methodological bias of the manual DO data, further interpretations are based only on the continuous DO measurements.

3.3.2. Spatial oxygen dynamics

Dissolved oxygen concentrations from continuous measurements in redds documented a high variability on small spatial scales (i.e., between redds), but also a general increase from upstream to downstream (Table 3). Interstitial oxygen concentrations at site A (redd A32_S1) were especially low during season 1 with DO concentrations below 3 mg l^{-1} during 44 of total 135 days of egg incubation time. A DO concentration of 3 mg l^{-1} is considered as a critical threshold for salmonid embryo survival (Michel et al., in revision). The low DO concentrations in this redd could be related to low specific water infiltration q (see Section 3.2.1). This is supported by the observation that, when this redd was moved to a location with a higher water level during season 2, not a single day below 3 mg l^{-1} occurred (redd A32_S2; Table 3). In contrast, redd A31_S2, built about six meters upstream of A32_S2, had 14 days with DO concentrations below

3 mg l^{-1} , likely related to upwelling of DO depleted hyporheic water, as discussed in Section 3.2.2 (Fig. 5). Days below 3 mg l^{-1} were far less frequent at sites B and C (Table 3). These observed low oxygen concentrations at site A could be related to the artificial log steps, breaking down the river slope, inhibiting natural river gravel movements and thus triggering high fine sediment accumulation at sites with low water levels. At the downstream sites, water levels and shear stress were generally higher, leading to a flushing of infiltrated fine sediment, and less accumulation (Schindler Wildhaber et al., 2012b).

Only a small number of accumulation baskets in redds with permanent oxygen measurements survived floods, resulting in a very small data set ($n = 4$) across the two field seasons (Schindler Wildhaber et al., 2012b). However, these four data points were surprisingly evenly spread and showed a perfect linear decrease of the mean DO concentration with increasing fine sediment accumulation (Fig. A1). This has been repeatedly demonstrated before (e.g., Heywood and Walling, 2007), and indicates that also in our study river increased fine sediment accumulation could negatively affect embryo survival by decreasing oxygen supply.

3.3.3. Temporal oxygen dynamics

On the scale of hours and days, DO concentrations decreased during the falling limb of high flow events. This pattern was most pronounced when temporal water exfiltration was measured, e.g., redd A31_S2 (Fig. 9, see also Section 3.2.2), and thus most likely related to intermittent exfiltration of depleted groundwater or hyporheic water through the redd (Section 3.2.2). The same has been reported in other studies (Malcolm et al., 2010, 2006; Soulsby et al., 2009). Nonetheless, decreasing DO concentrations during the falling limb of high flow events were also found in locations where no exfiltration was measured (e.g., redd C21_S2, Fig. 7). Here interstitial DO quickly returned to normal levels after the rising limb of high flow events, also suggesting that this pattern is related to groundwater exfiltration rather than increased fine sediment deposition, which would have likely caused more prolonged effects (Fig. 7).

Table 3

Mean oxygen concentrations calculated from continuous measurement with permanent oxygen probes in one redd per site during season 1 (S1) and two redds per site during season 2 (S2). Given are mean \pm standard deviations, minimum (min) and number of days wherein oxygen concentration was below 3 mg l^{-1} .

| Site | Mean \pm SD O_2 (mg l^{-1}) | | | Min O_2 | | Days $\text{O}_2 < 3 \text{ mg l}^{-1}$ | |
|------|---|----------------|----------------|------------------|-----|---|------|
| | S1 | S2 | Mean (S1 + S2) | S1 | S2 | S1 | S2 |
| A | 4.6 ± 3.3 | 8.4 ± 3.4 | 6.6 ± 3.8 | 0.0 | 0.1 | 44 | 14 0 |
| B | 9.6 ± 2.1 | 10.0 ± 2.3 | 9.8 ± 2.2 | 3.2 | 0.0 | 0 | 4 2 |
| C | 9.6 ± 1.8 | 10.3 ± 1.3 | 10.0 ± 1.6 | 0.6 | 3.8 | 1 | 1 0 |

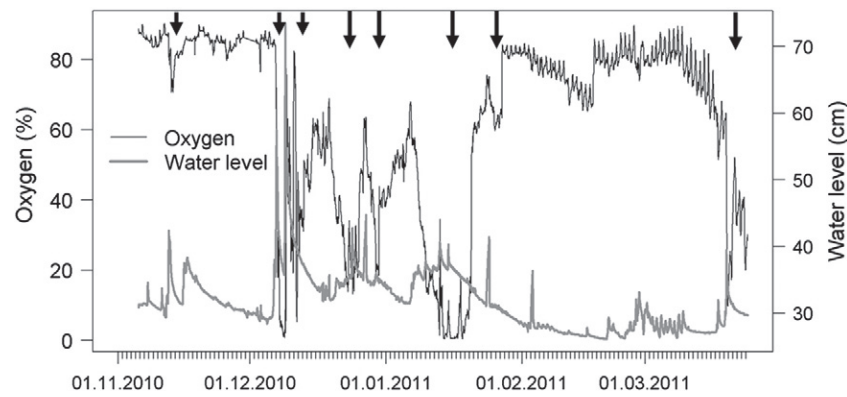


Fig. 9. Example for temporal oxygen concentration and water level dynamics (redd A31_S2, cf. Fig. 2 for location of the redd). Arrows mark the decrease of oxygen concentrations during the falling limb of high flow events.

In addition to these changes in interstitial DO on the scale of hours and days, two general trends over the entire incubation period were evident. The first trend could be observed at the beginning of the incubation season: shortly after redd construction, DO was generally high and paralleled by high specific water infiltration rates q ($10\text{--}12\text{ mg l}^{-1}$, or 80–90% oxygen saturation; for an example see Fig. 7). Within a few weeks, interstitial DO decreased in parallel with q , as also reflected in significant correlations between these two parameters (Fig. 10). The different forms of this relationship among redds (Fig. 10) could be related to local conditions at the redd location that also affect interstitial DO (e.g., organic content, groundwater influence). The second trend could be observed at the end of the incubation season, when several redds

showed a distinct decrease in interstitial oxygen during spring, i.e., just before hatching (Figs. 7, 9). This decrease was usually preceded by prolonged periods of base flow, when smaller sediment particles infiltrated in the redds (Schindler Wildhaber et al., 2012b). These silt and clay sized particles can effectively induce siltation of the riverbed, thereby decreasing hydraulic conductivity (Schälchli, 1995). Moreover, the organic matter concentration of the infiltrated fine sediment increased during base flow conditions (Schindler Wildhaber et al., 2012a). Together with rising water temperatures during spring, the latter likely further decreased the oxygen concentration in the redds (S.M. Greig et al., 2007). This decrease towards the time of hatching, when oxygen demand of the salmonid embryos is at maximum (S.M. Greig et al.,

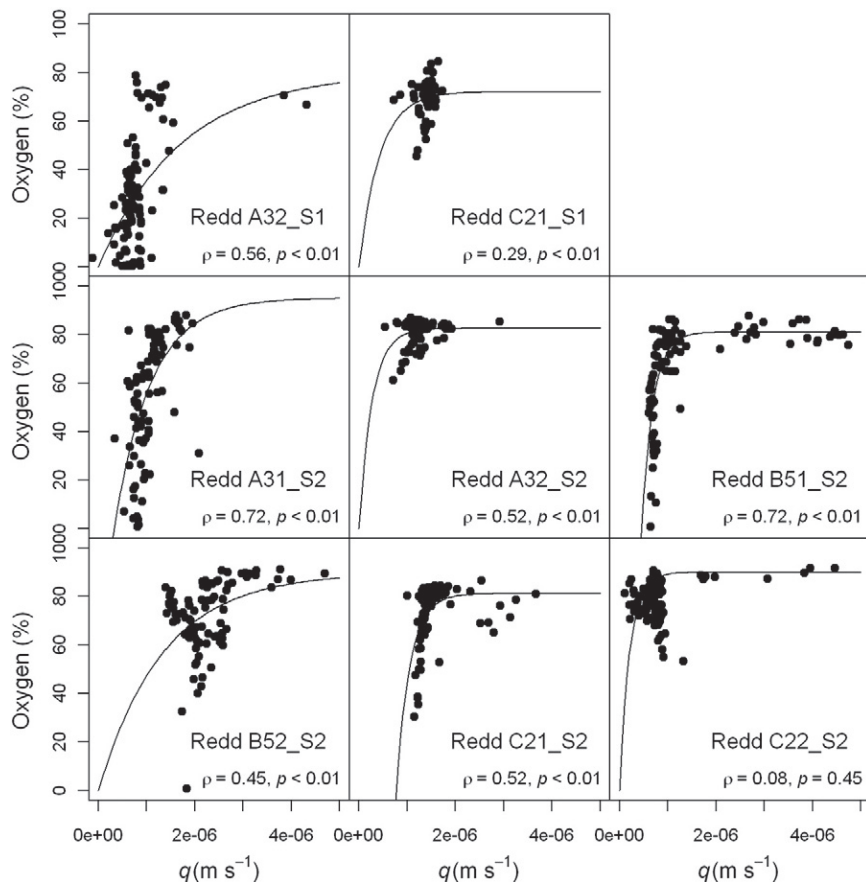


Fig. 10. Relationships between the mean daily oxygen concentrations in redds and the specific infiltration rates q , with non-linear regression lines. Within each panel Spearman correlation coefficient ρ and the p -value are given. See Fig. 2 for location of the redds.

2007), might have also affected embryo survival in some redds (Michel et al., in revision).

4. Conclusion

Artificial steps in channelized rivers can have positive or negative effects on incubating salmonid embryos. In downstream sections, where canalization of the riverbed cause higher water level and an increased slope, resulting in a higher sediment transport capacity, artificial steps decrease river gravel movements and thus scouring of the riverbed. Additionally, artificial steps increase hyporheic exchange processes. Further upstream, in low flow sections, where slopes would naturally be higher, artificial steps inhibit natural river gravel movements due to the decreased riverbed slope. This triggers higher fine sediment infiltration and accumulations, resulting in lower specific water infiltration rates (q) and hyporheic oxygen.

Our data further more demonstrate that q and dissolved oxygen (DO) concentrations in salmonid redds are highly dynamic and driven on multiple scales. Clearly, q and interstitial DO in salmonid redds are affected by conditions at the redd location, such as the amount of accumulated fine sediment, organic content and redd morphology. However, local factors of the magnitude of centimeters to meters are regularly superimposed by processes driven on the intermediate scale (in the range of meters) and regional scale (in the range of tenths of meters to kilometers). On an intermediate scale artificial steps can affect patterns of fine sediment accumulation, water exchange in salmonid redds and hence interstitial DO.

Our results document for the first time an effect of artificial steps on water exchange and oxygen concentrations in salmonid redds. Given the complex interaction of all the processes studied here, multiple factors have to be considered to predict salmonid embryo survival, which is highly time and work intensive. Multiple predictors should include oxygen and fine sediment measurements, riverbed structure such as artificial steps or the channelized riverbed and the hydrological setting of the river in the valley aquifer.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.scitotenv.2013.09.100>.

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