

Article

Substratum Raking Can Restore Interstitial Habitat Quality in Swedish Freshwater Pearl Mussel Streams

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Abstract: Functional and oxygenated stream beds provide crucial habitat for multiple endangered stream taxa, including endangered freshwater mussels, fishes, and insect larvae. Stream bed restoration measures such as substrate raking are often applied to mitigate excess fine sediment introductions and stream bed colmation, yet such measures are controversial. In this study, we conducted a systematic experiment in which sites with stream bed raking and removal of macrophytes were monitored over two years and compared with before-treatment conditions and untreated reference sites in the Swedish Brånsån stream, which still contains a population of the endangered freshwater pearl mussel *Margaritifera margaritifera*. The stream bed restoration resulted in improved habitat quality, as evident from decreased substrate compaction, increased redox potential, and oxygen supply into the stream bed. In contrast to previous studies in Central European catchments with more intensive agricultural catchment uses, the effects of the restoration measure were much longer, extending over two years. Consequently, stream bed raking and macrophyte removal can be considered a useful and more long-lasting restoration measure than currently assumed, especially in streams where excess input of fine sediment has already been mitigated, where catchment land use is rather extensive, and where near-natural flow regimes still prevail.

Keywords: stream restoration; hyporheic zone; salmonid spawning sites; gravel redds; redox potential; stream bed colmation; penetration resistance



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1. Introduction

Freshwater biodiversity is declining globally, with many highly specialized species suffering from severe declines in distribution and population sizes. In particular, species that depend on functional stream beds with high exchange rates between open water and interstitial are most crucially affected by declines, including semi-aquatic insects (e.g., [1–6]), freshwater fishes (e.g., [7–11]), and freshwater mussels such as the endangered freshwater pearl mussel (*Margaritifera margaritifera*), which is considered an important target species of conservation [12]. Freshwater pearl mussels have a complex life cycle that comprises a parasitic phase on a suitable fish host and a post-parasitic phase during which the juvenile mussels burrow within the stream bed for several years, depending on a well-oxygenated and permeable yet stable substrate, which is considered a main bottleneck for recruitment in most European populations [13]. Especially the uppermost 10 cm of the stream bed is considered the most crucial habitat for burrowing juvenile freshwater pearl mussels [13,14]. In light of climatic change, the synergistic interaction of excess amounts of fine sediment, increased temperatures, and low flows can result in reduced hatching success and embryonic development of salmonids, including brown trout (*Salmo trutta*) [15], which is the main host of freshwater pearl mussel in Europe [16,17].

Several measures of stream bed restoration have been proposed to improve interstitial oxygen supply both for gravel-spawning fishes and freshwater pearl mussels. These

include substratum raking, the introduction of sorted gravel of various sizes as well as structural and flow measures affecting the erosion–sedimentation patterns within the stream (e.g., [18–24]). However, most of these measures only improved interstitial habitat quality for very short periods, often less than six months, questioning their applicability in achieving long-term restoration goals [25]. On the other hand, a main limitation in assessing the usefulness of such measures has been that they have only been tested in catchments of rather intensive agricultural land use, known to result in high input of fine sediments into receiving streams [10,26–29]. Consequently, there is an urgent need to test the effects and persistence of substrate restoration measures in areas with more extensive land use, as typical for most parts of Scandinavia.

The core objective of this study was to experimentally test the effectiveness and persistence of a stream substratum restoration measure in relation to habitat quality for the endangered freshwater pearl mussel in a Swedish stream over two years. Specifically, and in contrast to observations from intensively agriculturally used stream catchments in Central Europe, we hypothesized that the effects of raking would result in more long-term improvement in interstitial habitat quality as indicated by decreased stream bed compaction and increased redox potential and oxygen supply.

2. Materials and Methods

2.1. Study Area

The substratum restoration was conducted in August 2019 at the Brånsån stream located in the Brånsån nature reserve in Västernorrland, Sweden. The stream Brånsån is a 3.7 km long stretch of Gådeåns main drainage area flowing from Öjesjön down to Långsjön about 15 km west of Härnösand city in the middle of Sweden (Figure 1A). Agriculture areas and wetlands without rapids dominate the first km downstream of Öjesjön. The last 2.5 km are dominated by spruce forests mixed up with deciduous forests closest to the stream. Stream width is, on average, six meters in this part, and the slope is far more pronounced. Dominating bottom substrates are boulders, stones, gravel, and sand, compared to more fine substrates in the upper part. The lower part of the river holds a decreasing population of freshwater pearl mussels. At the beginning of the 1990s, their number was estimated to be 127,000, and in 2020 it had declined to about 64,000. Brånsån is legally protected by Swedish law as a nature reserve by two decisions (2006 and 2015). Several successful conservation and restoration activities have been carried out in this catchment, like the construction of sediment traps and restrictions on farming, but the stream bed still suffered from earlier siltation and nutrient pollution.

The experimental site where the stream bed restoration was conducted was 50 m long and located in the lower part of Brånsån (Figure 1A, lat 62.615730, long 17.711736). The water velocity in this area varied between 0.2 and 0.4 m/s and the depth between 0.1 and 0.4 m. Average turbidity values measured in 2019 upstream of the experimental stretch were 0.96 FNU, ranging from 0.64 to 1.56 FNU, and they were similar to those below the experimental stretch where average turbidity was 0.93 FNU, ranging between 0.51 and 1.79 FNU. Visual assessment of the stream bed yielded that stones and gravel were the dominating bottom substrate, and about 80% of the site was covered with the water plant *Myriophyllum* before restoration.

To test the effects of substratum restoration at the experimental site, a section of the Brånsån stream was subdivided into two paired treatments at alternating bank sides of the stream, with three replicates each, about 1.5 m apart (Figure 1B,C): within each replicate, one 2.5 × 8.0 m area was left untouched as a reference, while in the adjacent 2.5 × 8.0 m, substratum raking and macrophyte removal were carried out (see below).

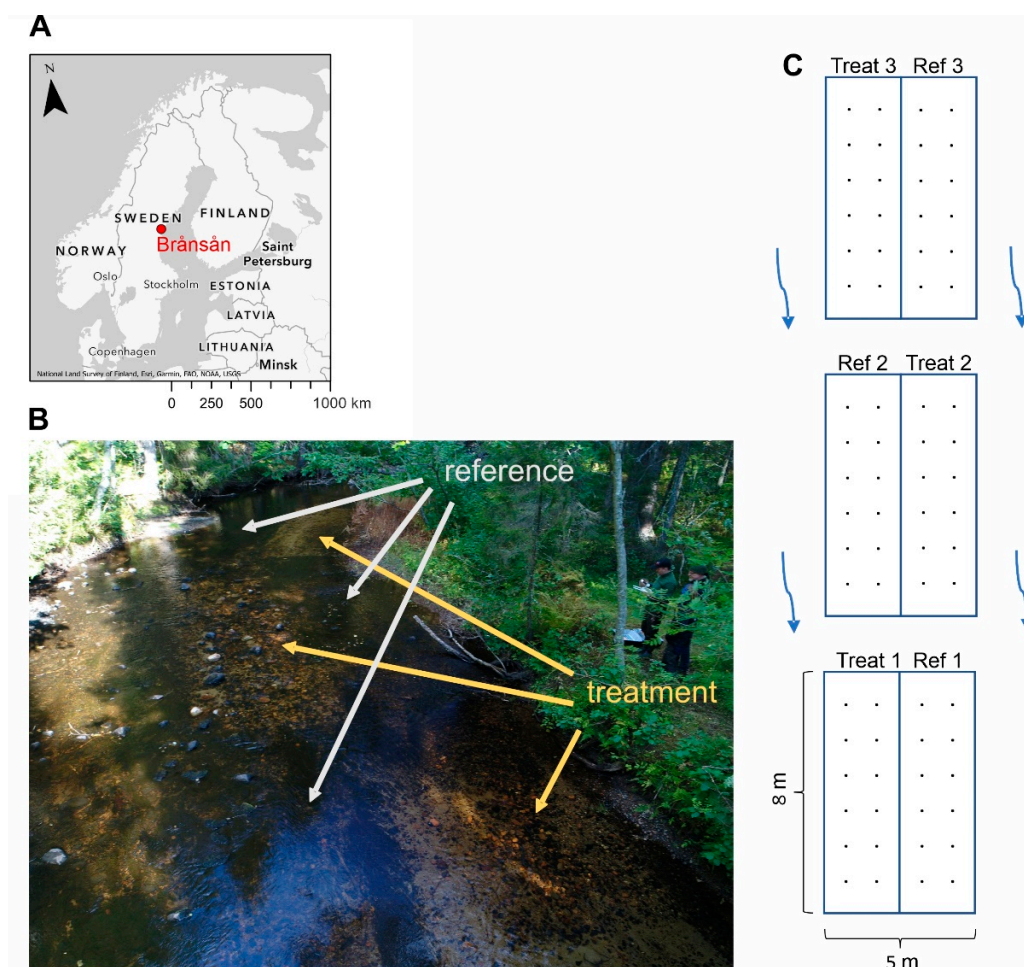


Figure 1. (A) Location of the Brånsån stream in Västernorrland, Sweden; (B) picture of the treated stream segment with treatment sections clearly distinguishable from untreated reference sections by the naked eye; (C) schematic sampling design of the substratum restoration study, boxes indicate treatment type (Treat = section subject to substratum raking, Ref = untreated reference section); dots indicate measurement points of abiotic habitat quality, arrows indicate flow direction.

2.2. Substratum Restoration

Within the treatment sections, the substratum was loosened manually with a pitchfork, and remobilized fine sediments were sent downstream with the flow current. Substrate loosening was conducted using a fork with 40 cm long teeth. The fork was dug 4–5 times until the substrate was loosened up and then moved to a new place for a similar raking effort until the whole section was covered. The restoration measure started at the most upstream section to avoid impact on the downstream sections. During raking, a plume of fine sediment appeared downstream of the treatment areas. The time spent for the substratum raking was, in total, 25 h, approximately 8 h per section. For easy detectability, the sections were marked with iron poles. The sampling sections were characterized in mid–late August 2019 before and after the substratum raking, then once in August 2020 (i.e., after one year) and once in August 2021 (i.e., two years after the restoration). During the course of the substratum raking, macrophytes were removed.

Additionally, a test of how different raking efforts affect redox potential was performed in August 2020. Initial redox potentials were measured 5 and 10 cm deep in the substrate at 12 measuring points within a square meter delimited by a metal frame directly connected to the experimental site. After that, two raking efforts in each place covering the whole square meter were conducted. The fork penetrated ca. 5 cm, and changes in the redox potential were measured. The next effort was four rakings, which resulted in ca. 10 cm fork penetration,

followed by six, eight, and ten raking efforts with redox measurements between. At eight efforts, the whole fork length of 40 cm was penetrating the stream substrate.

2.3. Stream Bed Quality Assessment

Interstitial habitat quality for juvenile freshwater pearl mussels was assessed at 12 measuring points within each replicate before and directly after the restoration and in the following years in both treated and untreated sections, focusing on key variables that explain differences between functional (i.e., with ongoing recruitment of freshwater pearl mussel) and non-functional streams [13] as outlined in a European CEN standard on monitoring freshwater pearl mussel populations and their environment [14,30]. Substrate quality was assessed by measuring the redox potential (Eh, in mV) as an indicator of long-term oxygen supply using a handheld pH 3110 probe (WTW, Weilheim, Germany) together with a platinum electrode and an Ag/AgCl₂ reference electrode according to [13]. Measurements were conducted in the open water (FW) and at 5 and 10 cm substratum depth (INT 5 cm and INT 10 cm, respectively) to evaluate the loss in redox potential within the substrate, expressed as the delta between open water and the respective substrate depth. Higher delta values represent greater differences and, thus, lower habitat quality for burrowed juvenile stages of the pearl mussel. A pocket penetrometer and two different adapters were used to analyze substrate compaction (Pen, in kg/cm²) as described in [13]. In addition, due to the role of plants in governing fine sediment deposition and interstitial habitat quality [31,32], macrophyte cover was determined visually at each time point in 5% steps. *Myriophyllum* sp. found within the treatment sections was harvested during the initial substratum raking, producing 42.2 kg (wet weight) of plant material. Also, the number of freshwater pearl mussels was counted in all six sections. All sections were searched for freshwater pearl mussels before the measure, yielding 388 (8–301 per section) individuals in the reference sections and 962 (50–573 per section) in the treatment sections. The substratum raking and *Myriophyllum* removal revealed another 135 (12–100 per section) individuals in the treatment sections. The mussels from the three treatment sections were picked up, measured for shell length, stored in a wet place during substratum raking, and reintroduced into the spot from which they originated.

2.4. Data Analyses

Multivariate analysis of abiotic factors describing the substrate quality (Eh in 5 and 10 cm depth, their respective difference from the values in the open water and penetration resistance) were conducted in PRIMER 7 + PERMANOVA (Version 7.0.17, Plymouth Marine Laboratory, Plymouth, UK). Data were normalized by subtracting the mean and dividing by the standard deviation to account for different scales prior to analysis. The normalized dataset was then used to perform PCA (principal component analysis) as ordination to represent differences and similarities between samples. Differences between substrate quality of the sections over time were assessed using ANOSIM (ANalysis Of SIMilarity) based on Euclidian distances between samples.

Univariate comparisons between single substrate quality factors were conducted in R (Version 4.1.0, R core team, 2016, www.rproject.org, accessed on 30 January 2023). Data were tested for normality and variance homogeneity using the Shapiro–Wilk and Levene tests, respectively. Since these requirements were not fulfilled for all parameters, the Wilcoxon rank test was chosen for two-group comparison, whereas the Kruskal–Wallis test with post hoc pairwise Mann–Whitney U-test with Bonferroni correction was used for comparing multiple groups. Spearman's rank correlation test was used to test for significant correlations between substrate parameters. A significance level of $\alpha < 0.05$ was applied in all statistical tests.

3. Results

3.1. Raking Effort

Redox potential increased both at 5 cm and 10 cm substratum depth with the first two rakings and raised over 300 mV (i.e., to oxic conditions) at 5 cm depth after four rakings. A further, yet not so strong, increase was observed with the continued raking effort. On average, redox potential increased by 26.3 mV at 5 cm depth and 27.6 mV at 10 cm depth (Figure 2) with every two rakings, while the strongest increase of 72.3 and 84.5 mV, respectively, was achieved after four rakings. This corresponded to a 40% increase in redox potential in 5 cm depth compared to the initial conditions and an almost 80% increase in 10 cm depth. Therefore, four to five rakings were applied within the systematic restoration study. After the final 10 raking efforts, the mean redox potential was 131.2 mV higher than before at 5 cm depth and 137.8 mV higher at 10 cm depth. Redox values in the open water were 527 mV over the entire period.

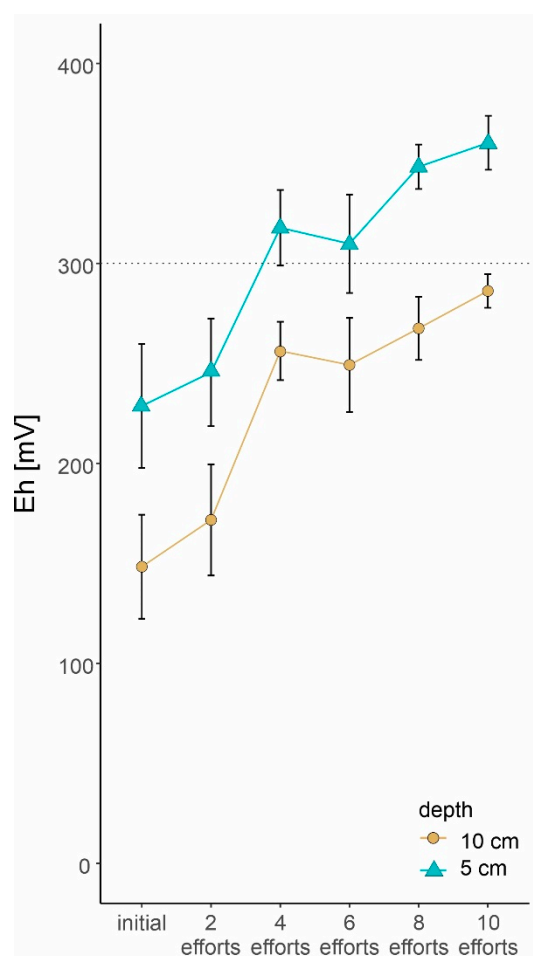


Figure 2. Mean redox potential at 5 cm (blue triangles) and 10 cm (ocher dots) substratum depth measured before (initial) and after the consecutive enhanced raking effort; error bars represent standard errors for the measurements within the six plots (1 × 1 m); the horizontal line represents the threshold of 300 mV, with values < 300 mV indicating anoxic conditions.

3.2. Restoration Effects

3.2.1. Multivariate Analysis

Multivariate analysis, including all parameters describing the substrate quality, yielded significant differences between treatment sections and time points (ANOSIM, Global R = 0.22; $p < 0.001$). While no significant differences could be detected between the reference and treatment sections prior to the restoration and in the reference sections prior

to and directly after the substratum raking (ANOSIM, $p > 0.05$), the substrate quality in the treatment sections directly after the restoration did differ significantly from the initial conditions (ANOSIM, $R = 0.27$, $p < 0.001$). A significant divergence could also be observed one year (ANOSIM, $R = 0.10$, $p < 0.01$) and two years (ANOSIM, $R = 0.06$, $p < 0.05$) after the restoration in the treatment sections. However, the differences became smaller (c.f. R-values). Significant differences in the substrate quality were also observed in the reference sections after one (ANOSIM, $R = 0.13$, $p < 0.001$) and two years (ANOSIM, $R = 0.09$, $p < 0.05$). Substrate conditions in the reference and treatment sections differed significantly directly after the restoration (ANOSIM, $R = 0.40$, $p < 0.001$) and still after both one (ANOSIM, $R = 0.39$, $p < 0.001$) and two years (ANOSIM, $R = 0.32$, $p < 0.001$). In the PCA (Figure 3), treatment sections after the restoration were correlated with increasing values for the redox potential at both 5 and 10 cm depth, while the reference sections seemed more correlated with higher delta redox values. Penetration resistance decreased in the treatment sections after the restoration.

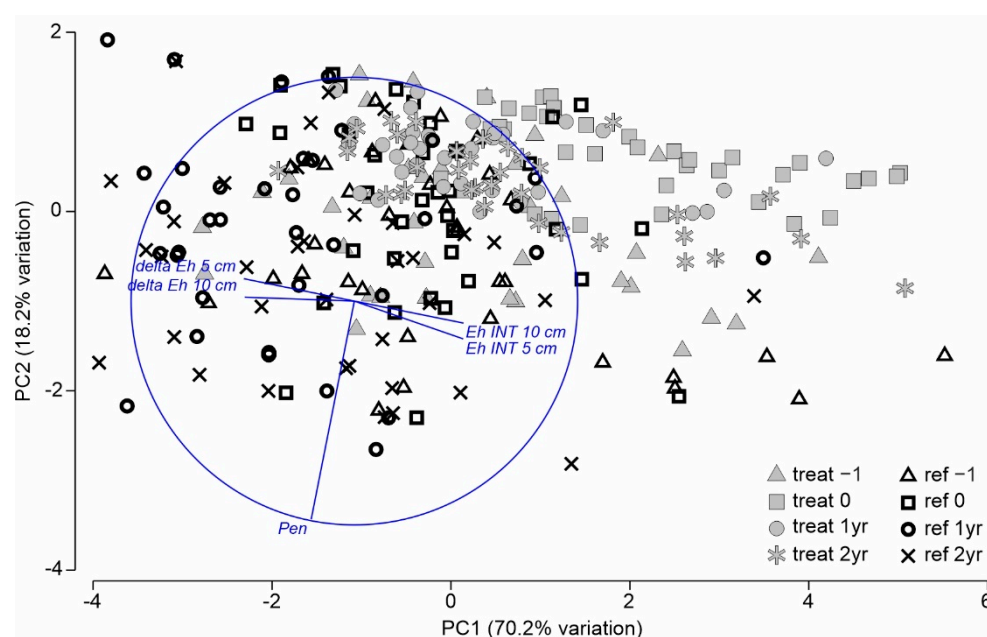


Figure 3. Principal component analysis (PCA) based on normalized values of substratum quality parameters, differentiated between treatment (gray, filled symbols) and reference sections (black, open symbols); triangles represent measurements prior to the restoration, squares represent measurement directly after the restoration, circles represent measurements one year after the restoration and stars/crosses represent measurements two years after the restoration; as indicated in the axis labels, PC1 explained 70.2% of the variation, PC2 explained another 18.2% of the variation; vectors are based on Pearson's correlation indices showing the strength of the correlation of each variable to the first two PC axes (the purple circle represents 100% correlation).

3.2.2. Univariate Analysis

The values measured in the treatment and reference sections at the four time points are summarized in Table 1.

The average redox potential in the open water was 558.5 mV (Figure 4) and did neither vary significantly between the study sections nor among different time points (Kruskal–Wallis test, $p > 0.05$). In contrast, high variability was observed for redox measurements in the interstitial in all measurements. Prior to the restoration, the mean redox potential in the treatment and the reference sections was 388.6 mV at 5 cm substrate depth and 288.9 mV at 10 cm depth, and values at both depths did not differ significantly between the treatment and reference sections (Wilcoxon test, 5 cm: $p > 0.05$; 10 cm: $p > 0.05$). Penetration resistance in both treatment and reference sections ranged from 0.098 to 1.769 kg/cm² and was similar in all sections (Wilcoxon test, $p > 0.05$). After the restoration, redox values in

the interstitial increased substantially in the treatment sections, with the majority of values over the threshold of 300 mV associated with oxidic conditions. In contrast, redox potentials in the interstitial of the reference sections were below 300 mV in more than 50% of the measurements (Figure 4).

Table 1. Mean (\pm sd) values of redox potential (Eh, measured in the open water (FW) and the interstitial at 5 and 10 cm depth (INT 5 cm and INT 10 cm, respectively)) and penetration resistance (Pen) measured in treatment (Treat) and reference (Ref) sections at the four time points prior to ($t = -1$), directly after ($t = 0$), one year after ($t = 1$), and two years after ($t = 2$) the restoration.

| | $t = -1$ | | $t = 0$ | | $t = 1$ | | $t = 2$ | |
|---------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | Treat | Ref | Treat | Ref | Treat | Ref | Treat | Ref |
| Eh FW (mV) | 560.1 \pm 14.6 | 555.6 \pm 13.1 | 547.2 \pm 8.7 | 542.8 \pm 9.7 | 544.0 \pm 9.4 | 541.7 \pm 22.2 | 583.5 \pm 13.0 | 592.8 \pm 23.9 |
| Eh INT 5 cm (mV) | 394.8 \pm 59.4 | 382.5 \pm 74.8 | 446.4 \pm 62.0 | 368.5 \pm 50.5 | 382.1 \pm 56.9 | 318.8 \pm 68.9 | 419.8 \pm 69.3 | 358.0 \pm 67.1 |
| Eh INT 10 cm (mV) | 293.6 \pm 62.1 | 284.1 \pm 68.1 | 347.6 \pm 51.2 | 268.4 \pm 39.9 | 284.9 \pm 10.5 | 224.9 \pm 40.5 | 318.1 \pm 45.9 | 268.1 \pm 52.2 |
| Pen (kg/cm ²) | 0.732 \pm 0.358 | 0.912 \pm 0.400 | 0.235 \pm 0.176 | 0.694 \pm 0.451 | 0.395 \pm 0.163 | 0.947 \pm 0.510 | 0.470 \pm 0.148 | 1.114 \pm 0.477 |

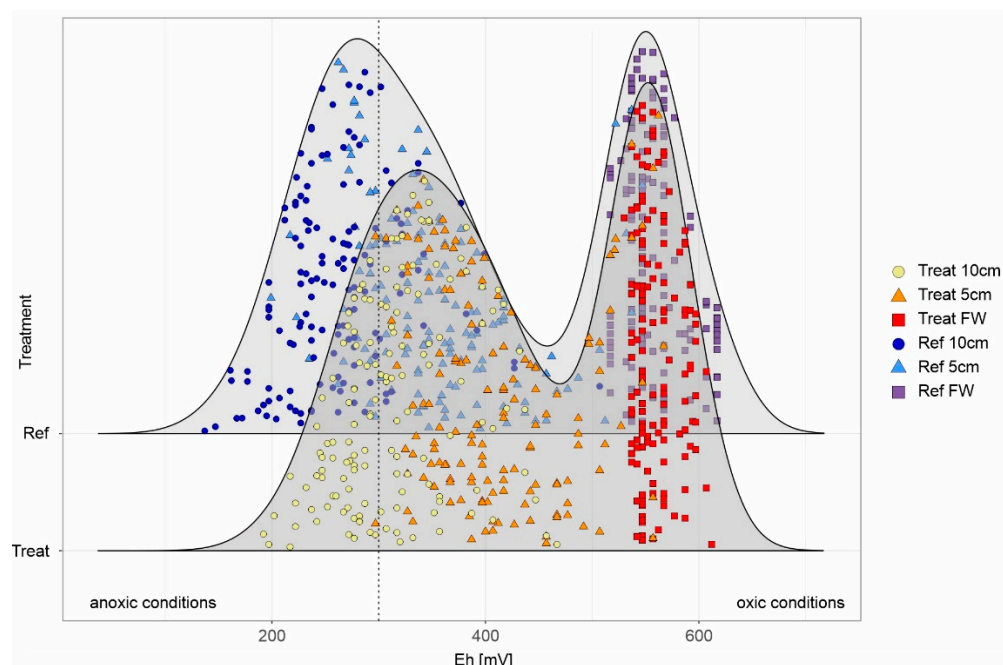


Figure 4. Density plots (grey colors) of redox potential in the open water (FW) (violet squares for reference sections, red squares for treatment sections) at 5 cm substrate depth (light blue triangles for reference sections, orange triangles for treatment sections) and at 10 cm substrate depth (dark blue dots for reference sections, yellow dots for treatment sections) for all measurements in reference (Ref) and treatment (Treat) sections; dots represent original data points with the color indicating the measuring depth; the vertical line represents a threshold of 300 mV, with values <300 mV indicating anoxic conditions.

Directly after restoration, redox potential at 5 cm depth significantly increased by 13% in the treatment sections from an average of 394.8 mV to 446.4 mV (pairwise Mann–Whitney U-test, $p < 0.05$, Figure 5A), which represented a decrease in the mean percentage deviation from the open water from 30% to only 18%. In contrast, the values remained similar in the reference sections (pairwise Mann–Whitney U-test, $p > 0.05$, Figure 5B), indicating no shifting baseline in untreated sections. The same pattern was also observed at 10 cm depth: in the treatment sections, redox values significantly increased by 18% from an average of 293.6 mV to 347.6 mV (pairwise Mann–Whitney U-test, $p < 0.05$), decreasing the mean divergence from the open water from 48 to 37%, while the average in the reference sections remained below 300 mV indicating anoxic and thus unsuitable conditions for

juvenile pearl mussels (pairwise Mann–Whitney U-test, $p > 0.05$). Penetration resistance was significantly decreased by 70% directly after substratum raking in the reference sections (pairwise Mann–Whitney U-test, $p < 0.001$). It did not change in the reference sections (pairwise Mann–Whitney U-test, $p > 0.05$, Figure 5C).

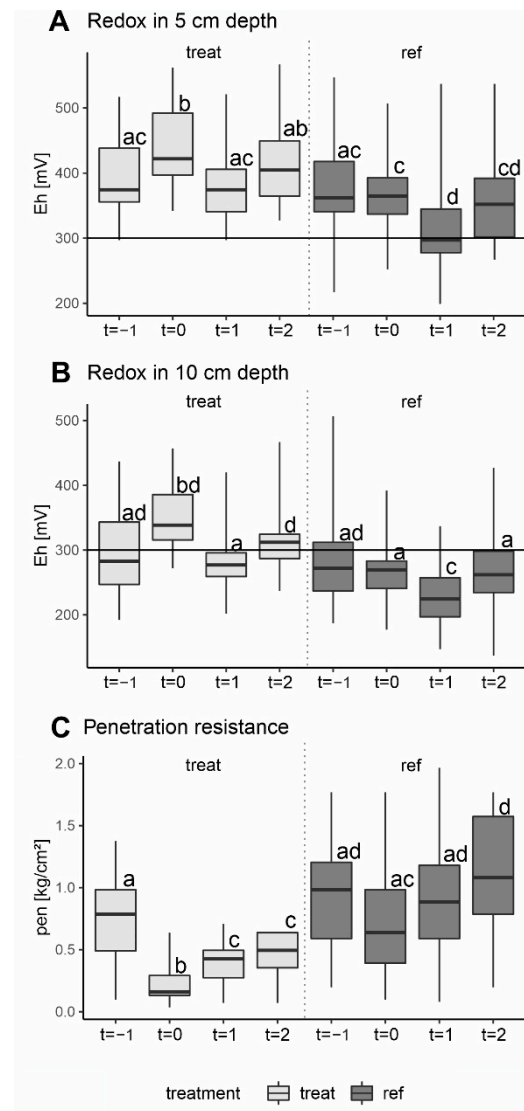


Figure 5. Box-and-whisker plots of (A) the redox potential at 5 cm interstitial depth, (B) the redox potential at 10 cm depth, and (C) the penetration resistance of the substrate in the treated sections (light grey boxes) and the untreated reference sections (dark grey boxes) at the four time points before ($t = -1$), directly after ($t = 0$), one year after ($t = 1$), and two years after ($t = 2$) the restoration action; different letters at the boxes indicate significant differences between sections and time points; the horizontal line indicated the 300 mV threshold for redox potential, with values < 300 mV indicating anoxic conditions.

One year after the restoration, the mean redox potential in the interstitial decreased in all sections. However, while the redox values at 5 cm depth were similar to the starting conditions in the treatment sections (pairwise Mann–Whitney U-test, $p > 0.05$), they were significantly lower in the reference sections, where the average values dropped to 318.8 mV (pairwise Mann–Whitney U-test, $p < 0.01$). These values were more than 41% lower than in the open water, while the mean divergence had been only 31% in the initial measurements. Similar effects were observed at 10 cm interstitial depth. In the treatment sections, penetration resistance increased significantly compared to the conditions directly

after the restoration (pairwise Mann–Whitney U-test, $p < 0.01$) but was still 45% lower than before the restoration. In the reference sections, penetration resistance did not change significantly compared to the starting conditions (pairwise Mann–Whitney U-test, $p > 0.05$).

Two years after the restoration, the mean redox potential in the interstitial in the treatment sections was slightly higher than before the restoration at both depths. They were neither different from the conditions directly after restoration (pairwise Mann–Whitney U-test, 5 cm: $p > 0.05$; 10 cm: $p > 0.05$) nor from the initial values (pairwise Mann–Whitney U-test, $p > 0.05$) but intermediate. Mean values at 5 cm depth of 419.8 mV represented a mean divergence from the open water of 28%, while they were 40% lower than in the open water in the reference sections. At 10 cm substratum depth, the mean redox potential in the treatment sections of 318.1 mV was even above the 300 mV threshold, while it was as low as 268.1 mV in the reference sections. The penetration resistance remained significantly lower than prior to the restoration in the treatment sections (pairwise Mann–Whitney U-test, $p < 0.05$), while it remained similar to the initial measurements in the reference sections (pairwise Mann–Whitney U-test, $p > 0.05$).

Weak but significant negative correlations were observed between the penetration resistance and both the redox potential at 5 cm (Spearman's rank correlation, $\rho = -0.22$, $p < 0.001$) and at 10 cm substratum depth (Spearman's rank correlation, $\rho = -0.24$, $p < 0.001$).

Myriophyllum cover did not recover after the restoration and was still below 5% in the treatment sections after two years.

4. Discussion

The findings of this study provide novel insights into the effect strength and persistence of stream bed restoration measures targeting gravel-spawning fishes and freshwater mussels. The described restoration action restored interstitial conditions suitable for the target species for at least two years. The results from the raking effort experiment indicate that the restoration action itself directly increased the stream bed permeability and the inflow of oxygen-rich surface water into the interstitial by loosening fine particles and breaking open the substrate surface. Similar effects have also been demonstrated for bioturbation by aquatic invertebrates [33] and various studies on restoration (e.g., [18,21–24]). Any further raking effort only led to a lower increase and was, on the contrary, potentially harmful to the overall substrate stability. A systematic study on the needed raking effort is rarely applied prior to stream restoration, where substratum raking is often carried out by excavators with standard, blunt shovels. Such technical aid might not offer a precise application of the raking effort as in the manual application chosen in this study. Therefore, a detailed evaluation of the effects of a particular restoration method should be included in restoration schemes.

In contrast to previous findings in Central European streams (e.g., [21,24]), where substrate loosening only resulted in an improvement in interstitial habitat quality for less than six months, the effects of the substrate raking in the Swedish stream extended over more than two years, suggesting it may be more efficient than currently assumed. This different development can be explained by various factors: first and probably most important, the catchment use strongly differs between the Brånsån and the Central European streams, with less erosion-prone agriculture and thus lower input of fine sediment in the Scandinavian stream. In catchments with intensive agricultural land use, fine sediment deposition in a range of several kg per m² and month has been described, realistically filling up the pore volume from any substrate restoration within a short time [34,35]. If fine sediment delivery from the catchment is not addressed, stream restoration approaches are likely to fail since particularly the input of fines is considered a critical problem for stream bed clogging and resulting ecological effects [36]. Several restoration measures to reduce fine sediment and nutrient inputs had already been carried out in the Brånsån before the stream bed restoration, which has likely improved its effects. Moreover, the main source of fine sediments in most Scandinavian streams is occasional forest clearcutting, which might cause high fine sediment inputs during these events, which is different from the

continuous inputs delivered from intensive agricultural land use. Single event-based fine sediment deposition might be more easily addressed with substratum raking shortly after the clearcutting. The results presented in this paper demonstrate that a combination of catchment-wide measures together with in-stream restoration to flush out legacy sediments from before measures were taken can indeed sustainably improve substrate quality. This holds particularly true when internal flow regime processes [20,37,38] are still near natural, as in the Brånsån compared to most Central European streams. Despite the observed improvements in stream bed quality, the increasing penetration resistance and decreasing redox potential over the time course of two years illustrate that these in-stream measures still should not be considered long-term solutions of stream bed restoration but rather as a complementary measure to catchment restoration.

While the effects of the substratum raking in this experiment were obvious over the different time points, the study design does not explicitly answer the question about the relative importance of the raking itself and the removal of aquatic macrophytes throughout the raking process. Synergistic effects of both measures are most likely. As evident from the initial experimental trials on raking effort and the observed silt plumes generated downstream of the treated sections, the raking itself resulted in the washing out of fines from the treatment sites, increasing exchange between open and interstitial water, which consequently improved oxygen supply and redox potentials down to at least 10 cm within the stream bed. The raking also had a loosening effect, demonstrated by the decrease in penetration resistance. Such loosening increases the available pore space, and it can also remove colmated crusts, which form a barrier for exchange between open and interstitial water at the stream bed surface, e.g., resulting from Fe and Mn oxidation [13]. Macrophyte beds strongly affect stream bed quality [31]: they trap fine particles and nutrients due to reduced current speed, therefore increasing fine sediment deposition and decreasing oxygen concentration in the interstitial both by decreasing connectivity between interstitial and surface water and increasing oxygen consumption by microorganisms. Removal of macrophyte cover, therefore, most likely reduced this trapping effect of fines following the restoration action [31,32,39], probably contributing to the lasting effects of the restoration measure, particularly since no rapid re-growth of the macrophytes occurred over the two-year study period.

In the management of freshwater ecosystems and their biodiversity, there has been a call for making conservation and restoration more evidence-based [25,40–42], requiring a thorough assessment of the usefulness of different measures. As shown by the results of this study, the outcome of such an assessment can differ depending on the regional context, making it necessary to consider such differences in restoration planning. While the assessed stream bed restoration can only be recommended as a successful short-term measure requiring repeated annual action for most streams with intensive land use and altered flow regimes [18,21,22], it appears to be much more sustainable in streams with past problems of fine sediment introduction within more nature-like catchments and flow regimes, such as in the Brånsån stream investigated here.

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