The Gelså River Restoration Revisited
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Published in:
Ecological Engineering

DOI (link to publication from Publisher):
10.1016/j.ecoleng.2013.09.069

Publication date:
2014

Document Version
Early version, also known as pre-print

Link to publication from Aalborg University

Citation for published version (APA):
The River Gelså restoration revisited: Habitat specific assemblages and persistence of the macroinvertebrate community over an 11-year period

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ARTICLE INFO

Article history:
Received 21 February 2013
Received in revised form 19 September 2013
Accepted 23 September 2013
Available online xxx

Keywords:
River restoration
Macroinvertebrates
Habitat
Diversity
Community persistence

ABSTRACT

The study was undertaken on the River Gelså, Denmark, where a 1.8 km meandering course was established in 1989 to replace a channelized river reach. This restoration project was the first of its kind in Denmark and has the longest time-series of post-intervention data of any restoration project conducted world-wide. Additionally, a 0.5 km upstream (control) reach that remained channelized has been sampled since 1989. In this paper, we examined macroinvertebrate assemblages in distinct habitats in 2008, 19 years after the restoration, and community persistence between two years, 1997 and 2008, to investigate the longer-term effects of restoration on the biota. We found that habitat type influenced macroinvertebrate community composition to some degree, while there were no clear effects on α- and β-diversity of habitat or reach type. Stony substrate habitats introduced as part of the restoration could, however, still be separated from other habitat types and were much more frequent in the restored reach. Furthermore, very little change had occurred over the 11-year period from 1997 to 2008, suggesting a high degree of community persistence. Our results suggest that the local species pool was already close to saturation in 1997 and that only limited immigration of new species occurred in the intervening period until 2008. The lack of long term benefits could be attributed to the simultaneous cessation of weed cutting (which had almost as big a positive impact as restoration), other types of stress on the river (eutrophication) and dispersal limitations. However, it might also reflect that River Gelså is still functionally channelized and is far from exhibiting a dynamic river morphology governed by natural processes that create a range of habitats for the biota and this might explain why there has not been a more pronounced increase in macroinvertebrate diversity in River Gelså.

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1. Introduction

During the last three decades many attempts have been made to improve in-stream habitat conditions through river restoration across Europe and North America (Roni et al., 2008; Palmer et al., 2010; Feld et al., 2011). The dominant paradigm in river restoration has been rehabilitation of physical conditions with primary focus on habitat structure and water flow to enhance habitat heterogeneity and biodiversity. At the intermediate scale restoration schemes aim at restoring degraded river sections to their natural condition through re-meandering of entire sections of the river (e.g. Palmer et al., 2007; Bernhardt and Palmer, 2011; Feld et al., 2011).

A key question in river restoration ecology is if, and how, re-created spatial and temporal physical heterogeneity interacts with the biota to improve ecosystem health compared with pre-intervention levels (Pedersen et al., 2007; Vaughan et al., 2009; Beechie et al., 2010). River morphology is highly dynamic and dependent on catchment-scale controls (hydrology, geology), channel patterns at reach scale and micro-scale variations in, for instance, flow and turbulence structure (Prissell et al., 1986). Very rarely has this fluvial dynamism been taken into consideration in the design of restoration projects and temporal data documenting restoration effects on fluvial processes are missing. Even though the number of river restorations has increased


http://dx.doi.org/10.1016/j.ecoleng.2013.09.069
over the last several decades in both Europe and North America (Bernhardt et al., 2005; Feld et al., 2011; Lorenz et al., 2012), studies providing conclusive empirical evidence of its effects are lacking (Bernhardt and Palmer, 2011). Several published reviews provide almost no evidence of a long-term (>5 years) positive effect of river restoration on biotic communities (Roni et al., 2008; Miller et al., 2010; Feld et al., 2011), albeit Lorenz et al. (2012) in a recent study found a longer-term positive response of macrophytes to restoration measures. The lack of evidence can be attributed primarily to limited spatial and temporal resolution of data on physical habitats and biota. The very limited evidence of links between restoration activities and improvement in ecological status constitutes a substantial problem for water managers when having to select appropriate measures in that the costs involved can be very high (Kristensen et al., 2012).

In Denmark, cultivation of farmland during the last century has resulted in extensive straightening and culverting of watercourses, and more than 90% of Denmark’s 35,000 km of natural streams have been physically modified (Iversen et al., 1993). One way to counteract this degradation is to rehabilitate riparian and in-stream habitats. Numerous stream restoration projects have consequently been undertaken in Denmark over the past decades to improve stream physical conditions and thereby increase the rate of ecosystem recovery (e.g. Hansen, 1996; Pedersen et al., 2007; Pedersen, unpublished material). The first stream to be re-meandered in 1989 was the Gelså and a number of studies have documented the effect of this restoration on habitat conditions and biota (Friberg et al., 1994, 1998, 2000; Kronvang et al., 1998). Macroinvertebrate communities recovered rapidly after the restoration intervention and stone-dwelling taxa became more frequent in the restored reach compared to an upstream channelized reach (Friberg et al., 1994). Within the first decade of the post-restoration period the two reaches became more similar in terms of habitat distribution and biota (Friberg et al., 1998, 2000), although a distinct mid-stream, high energy habitat with coarse substrate could still only be found in the restored reach (Kronvang et al., 2000). Likewise, the frequency of stones in the bed material, which was introduced to create rip-rap structures along the banks, was still substantially higher in the restored reach in 1997 compared to the channelized reach (Kronvang et al., 2000).

The link between macroinvertebrates and habitats in Gelså, and its potential succession, has not been investigated since 1997 (Friberg et al., 2000). In this study, we examine the inter-generational, temporal effects of a reach restoration on macroinvertebrate community composition using the Gelså project as a case study. We investigate the link between habitats and macroinvertebrates in the restored and channelized (control) reach in 2008, 19 years after the restoration. In order to investigate community persistence, we compare species turnover between samples taken in all habitats in 1997 and 2008. In 1997, eight years post-restoration, any impact of mechanical perturbations from restoration activities would have ceased and early colonization been stabilized (Friberg et al., 1998). We hypothesize that species immigration/emigration and biotic interactions in concert with environmental filtering have changed macroinvertebrate communities in the period from 1997 to 2008 so that (1) macroinvertebrate assemblages are distinct among prominent habitat types with regard to measures of diversity (α- and β-diversity) and community composition; (2) this difference at habitat scale will also be reflected at reach scale (restored vs. control); and (3) community persistence between 1997 and 2008 will be low, reflecting a substantial turnover of species.

2. Methods

2.1. Study site

In this investigation we used the oldest re-meandering project site in Denmark, River Gelså in Southern Jutland, as our study site, which is furthermore unique as it has the longest monitoring time series of any restoration project of its kind in the world. River Gelså has a catchment area of 11 km² upstream from the restoration and an average annual discharge of 1.5 m³ s⁻¹. The catchment geology is primarily coarse to fine sandy alluvial deposits overlaid by peat horizons and land-use is dominated by arable farmland. Nitrogen concentrations are high as a result of farming activities while other water quality parameters measured routinely by local water managers show little sign of impact (Table S1; extract from the National Monitoring Database). The restoration project was carried out in 1989 to rehabilitate a 1.3 km straightened and channelized course of the River Gelså at the town of Bevtto to a 1.8 km meandering course. Creation of 16 new meanders changed the stream channel morphology, decreasing the channel width by 3–4 m and the discharge capacity by almost 50% (from 6.6 to 3.5 m³ s⁻¹). Prior to restoration of the Bevtto reach, a 0.5 km upstream reach with very similar physical, chemical and biological characteristics was selected for comparison with the restored reach.

2.2. Sampling methods

The macroinvertebrate community was sampled in mid-May 1997 and at the end of June 2008 using a Surber sampling approach, while habitat measurements and stones samples were taken in mid-May 2008. Sampling was undertaken in the restored reach (hereafter denoted “restored”) and in an upstream reach that has remained channelized (hereafter denoted “control”). The restoration project is described in more detail in (Friberg et al., 1994, 1998). The macroinvertebrate community response to habitat composition from the 1997-sampling has been reported in Friberg et al. (2000), whereas the 2008 data has not been published previously. We therefore use the 1997 data in the persistence analysis only, while we also analyze the 2008 data with regard to habitat preference.

In years 1997 and 2008, five sub-reaches of the restored reach and two sub-reaches of the control reach were assessed with regard to habitat coverage and three physical attributes: stream width, depth and water velocity. A grid-net of measuring points was established at each sub-reach as described in Kronvang et al. (2000). Water depth, flow velocity at 0.4 times water depth (using a Nautilus 2000 flowmeter), dominant substrate and macrophyte coverage were measured in 300 grid points in both 1997 and 2008. The dominant substrates were visually assessed in four categories: fine organic material (mud; grain size <100 μm); sand (grain size up to 2 mm); gravel (grain size 2–64 mm) and stones (>64 mm) using a standard viewing tube. Substrate coverage was estimated to the nearest 5% at each grid point and aquatic macrophyte coverage was divided into four classes (0: no plants; 1: 1–10% coverage; 2: 10–25% coverage; and 3: >25% coverage). In the following, each substrate type and macrophyte coverage class are considered as “habitats” for the macroinvertebrate community.

In both 1997 and 2008, five to seven Surber samples (0.02 m², mesh size 0.2 mm) were randomly taken in both reaches within the four predefined habitat types to determine macroinvertebrate composition and abundance. Samples were preserved in 70% ethanol in the field and processed later in laboratory. The majority of the macroinvertebrates were identified to species or genus level with the exception of Chironomidae midges, which were only identified to sub-family level, blackflies (Simuliidae) which were identified.
to family level, and worms, other than Eiseniella tetada, which were identified to the Oligochaeta sub-class level. All macroinvertebrates were enumerated.

In addition to Surber samples, ten fist-sized stones were collected randomly at the same water depth (approx. 0.5 m) in the restored and control reaches. The stones were lifted into a small submerged hand-net (0.2 mm mesh) into which loosened material and macroinvertebrates were swept. These samples were treated similarly to the Surber samples (see above). The projected surface area of the stones was measured in the laboratory and the average density of macroinvertebrates was calculated. The methodology was similar to that used in previous samplings of stones in 1993 and 1995 (Friberg et al., 1994, 1998).

2.3. Statistical analyses

Fishers-α and Sørensen’s similarity index (as a measure of β-diversity) were calculated for the habitat-specific Surber samples from 2008 according to the following equations: Fishers-α (Fisher et al., 1943) is implicitly defined by the equation

\[ S = \alpha \cdot \log \left( 1 + \frac{N}{\alpha} \right) \]

where \( S \) is the number of species, \( N \) is the number of individuals, \( \alpha \) is Fishers-α and Sørensen’s similarity index SSI (Sørensen, 1948) by

\[ \text{SSI} = 2 \cdot \frac{c}{S_1 + S_2} \]

where \( S_i \) is the number of species for sample \( i \) and \( c \) is the number of common species for samples 1 and 2. This analysis was undertaken for each habitat type combined with pair-wise comparisons of all habitat type combinations. The calculations were done using the S-Plus software (Tibco Inc., 2010). Differences in Fishers-α were tested by applying two-way ANOVA and differences in Sørensen’s similarity index were tested with a Student’s t-test (Snedecor and Cochran, 1989). With regard to the Sørensen’s similarity index only differences in similarity between the same substrate type in the restored and control reach could be tested statistically, as all other index values are dependent of each other because they are calculated as repeated pair-wise comparisons of all combinations of individual samples. However, pair-wise comparisons of substrate types were analyzed using simple regression analysis (Zar, 1984).

Habitat-specific Surber samples from 2008 were furthermore analyzed using PCA ordination with the program PC-ORD (McCune and Mefford, 2011). Differences between macroinvertebrate taxa on stones were analyzed by a Welch modified two-sample t-test on square-root transformed data (Snedecor and Cochran, 1989). Macroinvertebrate community persistence between 1997 and 2008 was analyzed using two methods and each habitat-specific Surber sample was kept separate in both types of analyses. The first type of analysis is described in Woodward et al. (2002) and is based on the detrended canonical correspondence analysis approach (DCCA). Firstly, a DCCA was undertaken using sampling year as an explanatory variable, secondly, a DCCA with sampling year and with treatment (control/restored) as a covariate was performed. Details are given in Woodward et al. (2002) and the analyses were performed using the software Canoco (Ter Braak and Smilauer, 2003).

In the second type of analysis, which was carried out in the R environment (R Development Core Team, 2011), differences in benthic macroinvertebrate community composition between 1997 and 2008 were tested among binary groups using the adonis routine in the vegan package (Oksanen et al., 2011) by calculating a multivariate analysis of variance using distance matrices (Anderson, 2001; in this case using the Bray-Curtis distance matrix). With adonis we compared if community composition of benthic macroinvertebrates differed between the two years.

Finally, the betadisper routine in vegan (Oksanen et al., 2011) was used to perform the PERMDISP2 routine (Anderson, 2006) where analysis of multivariate homogeneity of group dispersions (variances) is calculated (here using Bray-Curtis distance matrix). Betadisper is a multivariate analog of Levene’s test for homogeneity of variances. The betadisper routine was used to compare variability in benthic macroinvertebrate community composition (potentially a measure of β diversity) between years.

3. Results

3.1. Habitat coverage

Sand and gravel were the two dominant habitat types at both reaches in both years (Table 1). Gravel covered 50% of the stream bed in the control reach in 2008, but only 25% in the restored reach. In both years, coverage of stones was approximately four times greater in the restored reach than in the control reach. In 1997 macrophyte coverage clearly differed between the two reaches, whereas in 2008 it was similar. In both years the two reaches were very similar with regard to width, depth and water velocity (Table 2). The variation in width increased in both reaches from 1997 to 2008, most markedly in the control reach.

3.2. Habitat preferences

Species diversity expressed by Fishers-α at both habitat and reach scale showed no consistent pattern (Fig. 1). Consequently, there were no significant differences among habitats or between reaches with regard to Fishers-α (p > 0.05; F-test).

In both reaches the coarse substrate habitats, gravel and stone, had higher mean Sørensen similarity index values than did the other habitat types (Fig. 2). This suggests that these stable habitats are more similar in macroinvertebrate composition between individual samples than the less stable, fine grained habitats and that macrophytes encompass a range of different morphologies. The Sørensen similarity index value was significantly higher for stones (p < 0.001; t-test), gravel (p = 0.032; t-test) and macrophytes (p < 0.01, t-test) in the control reach than in the restored reach, while there were no significant differences between reaches with...
regard to sand and mud. This implies that coarse substrate habitats (including plants) in the restored reach have a higher species turn-over than in the control reach. The pair-wise comparison of habitat types showed a linear relationship between Sørensen’s similarity index and differences in substrate size and macrophyte presence (Fig. 3). The highest species turn-over was found when comparing mud and stone habitats in both the restored and the control reach. Conversely, the highest similarity between habitats in both reaches was found in the comparison between gravel and stone. Both linear relationships were significant (restored, $r^2 = 0.72, p < 0.001$; control, $r^2 = 0.69, p < 0.001$); however, the slope was higher in the restored reach indicating a higher species turn-over between habitats.

The ordination analysis revealed three distinct clusters, two of which reflected habitat types dominated by either fine substrate or coarse substrate and plants. The last cluster was specific for a subset of coarse substrates in the restored reach (Fig. 4). The analysis indicates that in most samples habitat type is the primary determinant of macroinvertebrate composition and that the reach from which the samples are taken is less important. In contrast, all stone habitat samples from the restored reach were found in the last

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**Table 1**

Coverage of habitats in the restored and control reach of Gelså in years 1997 and 2008 based on substrate types visually assessed as described in Section 2.

<table>
<thead>
<tr>
<th>Reach and year</th>
<th>Mud (%)</th>
<th>Sand (%)</th>
<th>Gravel (%)</th>
<th>Stone (%)</th>
<th>Macrophyte (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Restored 1997</td>
<td>16</td>
<td>41</td>
<td>24</td>
<td>19</td>
<td>10</td>
</tr>
<tr>
<td>Control 1997</td>
<td>20</td>
<td>41</td>
<td>39</td>
<td>&lt;5</td>
<td>35</td>
</tr>
<tr>
<td>Restored 2008</td>
<td>10</td>
<td>52</td>
<td>25</td>
<td>13</td>
<td>21</td>
</tr>
<tr>
<td>Control 2008</td>
<td>12</td>
<td>30</td>
<td>55</td>
<td>3</td>
<td>21</td>
</tr>
</tbody>
</table>

**Table 2**

Mean values and coefficients of variance (in parentheses) of width, depth and water velocity measured in the restored and control reach of Gelså in 1997 and 2008.

<table>
<thead>
<tr>
<th>Reach and year</th>
<th>Width (m)</th>
<th>Depth (m)</th>
<th>Water velocity (m s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Restored 1997</td>
<td>5.48 (0.07)</td>
<td>0.51 (0.35)</td>
<td>0.35 (0.51)</td>
</tr>
<tr>
<td>Control 1997</td>
<td>6.36 (0.09)</td>
<td>0.55 (0.28)</td>
<td>0.25 (0.68)</td>
</tr>
<tr>
<td>Restored 2008</td>
<td>5.68 (0.14)</td>
<td>0.63 (0.39)</td>
<td>0.30 (0.65)</td>
</tr>
<tr>
<td>Control 2008</td>
<td>6.43 (0.22)</td>
<td>0.50 (0.39)</td>
<td>0.31 (0.60)</td>
</tr>
</tbody>
</table>

---

**Fig. 2.** Mean Sørensen similarity index calculated from individual Surber samples collected in five different habitats in 2008 ($n = 5–7$) in the restored reach of River Gelså and the up-stream control reach.

**Fig. 3.** Relationship between mean Sørensen similarity index and pair-wise combinations of habitat types in 2008 from the restored reach (upper panel) and the control reach (lower panel).

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Please cite this article in press as: Friberg, N., et al., The River Gelså restoration revisited: Habitat specific assemblages and persistence of the macroinvertebrate community over an 11-year period. Ecol. Eng. (2013), [http://dx.doi.org/10.1016/j.ecoleng.2013.09.069](http://dx.doi.org/10.1016/j.ecoleng.2013.09.069)
cluster together with three gravel samples and a macrophyte sample, all exclusively belonging to the restored reach. This suggests that the restored reach contains a distinct set of habitat conditions.

The freshwater limpet Ancylus fluviatilis, the mayfly Heptagenia sulphurea, the stonefly Leuctra fusca, the riffle beetle Elmis aenea and the caddis Rhycaophila nubila were more abundant on coarse substrates compared with finer grained substrates. Furthermore, H. sulphurea and L. fusca were more abundant in the restored reach than in the control reach. Fine grained substrate habitats were dominated by Oligochaeta indet. and sediment dwelling taxa belonging to the diptera family Chironomidae. Blackflies Simuliidae indet. were almost exclusively found on macrophytes.

The individual stone samples showed a similar overall picture as the Surber samples (Fig. 5). However, different species dominated the two reaches. A. fluviatilis and the mayfly Baetis rhodani were significantly more abundant on stones sampled in the restored reach ($p = 0.01$ and $p < 0.001$, respectively; $t$-test), while the freshwater shrimp Gammarus pulex ($p = 0.006$), the dysticid beetle Oredytes sanmarkii ($p = 0.023$) and R. nubila ($p = 0.010$) were significantly more abundant on stones in the control reach.

![PCA ordination of the macroinvertebrate community sampled in 2008 in both reaches (restored and control).](image1)

**Fig. 4.** PCA ordination of the macroinvertebrate community sampled in 2008 in both reaches (restored and control).

![Comparison of the abundance of selected macroinvertebrate taxa collected from stones in 2008 in the restored reach and the upstream control reach.](image2)

**Fig. 5.** Comparison of the abundance of selected macroinvertebrate taxa collected from stones in 2008 in the restored reach and the upstream control reach. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.
Fig. 6. Macroinvertebrate community composition groups (based on PCA ordination) divided by year: 1997 (open triangles) and 2008 (open circles). Surber samples from both reaches (restored and control) are included in the analysis.

3.3. Community persistence 1997 to 2008

The DCCA gradient length was 0.922 for axis 1 and the cumulative percentage variance of species data was 6.8%, indicating a high degree of community persistence. After removing the effect of reach type (restored and control) the percentage variance of species data between years was only slightly increased to 7.4%. This indicates that community persistence was not influenced by reach history, i.e. if it had been restored or not. The overlap in species composition between years was also evident in the ordination of the Bray–Curtis distance matrix, with no significant difference occurring between groups ($p > 0.5$; Fig. 6). However, the groups are not completely overlapping, indicating that some species turnover has occurred, which agrees with the DCCA analysis. The distance to centroid between years did not differ significantly between years ($p > 0.05$; Fig. 7), reflecting that samples were equally dispersed in both 1997 and 2008. Hence, there is no indication that differences between samples, and consequently habitats, have changed with regard to macroinvertebrate composition between 1997 and 2008.

In total, 42 taxa (65%) were found in both 1997 and 2008. Only seven taxa were found in 1997, while 16 taxa were found in 2008 but not in 1997. However, the majority of these taxa were found in low numbers (1–5 individuals) and in both years constituted less than 1.5% of total abundance. An exception was *L. fusca* that was relatively abundant in 2008 (11th most encountered taxa) but absent in the 1997 samples. Among the ten most abundant taxa in both years, eight were the same, with three taxa belonging to Chironomidae, Oligochaeta induct., *G. pulex*, *B. rhodani* and *Seratella ignita*. The ten most abundant taxa constituted 86% and 95% of total abundance in 1997 and 2008, respectively.

4. Discussion

We found surprisingly little change in macroinvertebrate community composition during our study period. It is evident from our results, however, that habitat type had a certain influence on macroinvertebrate composition and that the coarse substrate habitats introduced as part of the restoration still after 19 years can be separated from other habitat types. It is furthermore clear that very little change has occurred over the 11-year period from 1997 to 2008, suggesting a high degree of community persistence. The initial post-restoration period was characterized by considerable change and an overall improvement in macroinvertebrate diversity compared to the pre-restoration level, which may to some extent be attributed to an increase in macrophyte cover (Friberg et al., 1994, 1998). In this context, our results suggest that the local species pool was already close to saturation in 1997 and that only limited immigration of new species has occurred in the intervening period until 2008. In fact, the differences in species composition between 1997 and 2008 might reflect the slight difference in the timing of sampling between years (mid-May and late-June, respectively). This contention may be true for *L. fusca* occurring in samples from 2008 but not in 1997. *L. fusca* is an autumn flying stonefly with highest nymphal growth during summer and therefore potentially too small to be sampled in early May, although the mesh size of the Surber sampler enabled retention of at least some small nymphs. However, the species is suggested to be a long-distance disperser (Wiberg-Larsen and Norum, 2009), and examination of routine monitoring data from the entire Gelså (unpublished species lists from the national database, WinBio) suggests that *L. fusca* might have been almost absent in 1997, permitting the alternative explanation that the presence of *L. nigra* in 2008 is, in fact, an example of immigration from nearby catchments.

In summary, two of our three hypotheses can be partly accepted, while the hypothesis concerning species turnover must be rejected. The findings in 2008 with a distinctive coarse substrate habitat in the restored reach are remarkably similar to our observations in 1997 (Friberg et al., 2000; Kronvang et al., 2000). This implies that the stony substrate introduced as part of the restoration has not changed, probably because the river does not have sufficient power to move larger stones. The lack of geomorphic development is possibly linked to fixation of the new channel and thereby a limited space for evolution of reach morphological features such as point bars, mid-channel bars, actively eroding banks, etc. (Kronvang et al., 1998). It is evident from the control reach that the extent of gravel has changed quite considerably, which indicates that the river has active sediment transport up to this grain size. Consequently, the longitudinal fluvial processes appear to be functioning, allowing sediment transport processes to redistribute sediment in accordance with changes in local reach hydraulics. The transverse processes allowing sideways migration of meanders are, however, still prevented from interacting naturally with the stream banks; the input of new coarse material from the banks is therefore limited and longitudinal sediment transport dominant, as demonstrated by the fact that the control reach still had less stony substrate in 2008 than did the restored reach.

Individual stone samples also confirm previous findings albeit with some distinct difference in macroinvertebrate composition.
between the two reaches (Friberg et al., 1994, 1998). Since 1993, the scraper Ancylus fluviatilis has been more abundant on stones from the restored reach, whereas most other species over the years have been more or less equally distributed between the two reaches. In 1993, H. sulphurea were only found on stones in the restored reach, but in 2008 we found no significant difference between the two reaches, implying that habitat is more important than reach type in determining species composition. However, the total density of grazing macroinvertebrates such as Ancylus will be much greater at the restored reach due to the larger spatial extent of coarse substrates. Extensive use of coarse materials (gravel and stones), as in the restoration of River Gelså, is a common restoration practice in Danish lowland streams (Kristensen et al., 2011; Pedersen et al., submitted for publication) and may therefore have functional implications for these stream ecosystems. Thus, there is an urgent need to investigate the functional implications of this river restoration practice, not least because large-scale physical restoration projects are expected to be undertaken in the near future in order to fulfill the objectives of the Water Framework Directive (European Commission, 2000).

Our finding that there was almost no long-term effect of river restoration is novel in the sense that no other studies have investigated similarly long time-series. In their study of published literature Feld et al. (2011) found no evidence of longer term (+5 years) positive effects of restoration, which supports our findings. The reasons behind the lack of positive effects of the re-meandering of the River Gelså could be multiple. Firstly, the restored section is small compared to the entire river network and the channel is still confined by the original rip-rap structures that were constructed to avoid flooding and unwanted displacement of the stream itself (this study; Friberg et al., 1998, 2000). Hence, River Gelså is still functionally channelized and is far from exhibiting a dynamic river morphology governed by natural processes (Frisell et al., 1986). It is these natural processes that create a range of habitats for the biota and this might explain why there has not been a more pronounced increase in macroinvertebrate diversity in River Gelså. Pedersen et al. (2005) found significantly more red-list macroinvertebrate species in morphologically intact river reaches than in both restored and channelized reaches.

A second reason for our inability to detect positive effects could be that the control reach having improved considerably during the 19-year period. Ideally, the upstream control reach should have remained as degraded as prior to the restoration of the downstream reach to single out the benefits of the restoration itself. Our results suggest, however, a very limited added value of the active restoration compared with the recovery that can be related to cessation of weed cutting. As reported previously in Kronvang et al. (2000) and Friberg et al. (1998, 2000), the physical and morphological diversity of the control reach has improved after the cessation of weed cutting in 1990 along a stretch of River Gelså including both reaches. Macrophytes are very effective bio-engineers in lowland systems (e.g. Sand-Jensen, 1998) and although the channel planform remained channelized in the control reach, the in-stream habitats became more diverse. This process is still ongoing as shown by our findings that gravel coverage increased substantially between 1997 and 2008 and that the variation in width more than doubled, indicating that the channel is getting more sinuous. In fact, we can only speculate on how great the differences between the reaches would have been if the control reach had remained in its pre-1989 state, but it is likely that the restored reach would have been in a relatively better state in terms of macroinvertebrate community composition and diversity.

The third reason for not finding a more positive effect of the River Gelså restoration is the issue of multiple stressors. Clearly, habitat degradation and channelization are major issues in most lowland systems in an agricultural landscape, but so is eutrophication which also has a negative impact on the biota (e.g. Johnson and Hering, 2009; Friberg, 2010). River Gelså is no exception with its relatively high water concentrations of nitrogen possibly limiting the extent of macroinvertebrate recovery. The fourth and last explanation could be barriers to dispersal from loci in the catchment (Bernhardt and Palmer, 2011) or simply that the regional species pool has been depleted by past human activities (Harding et al., 1998). An extensive survey of species diversity both within the River Gelså catchment as well as in neighboring catchments is required to investigate and test this hypothesis.

The outcome of the restoration in River Gelså has a number of implications beyond the localized effects, or lack of effects, on the macroinvertebrate community. The lessons to be learnt are that careful consideration is needed when planning a restoration project, and ecological benefits are by no means guaranteed. Long-term datasets are essential to obtain an understanding of the effects of river restoration at an ecologically meaningful temporal scale (Kronvang et al., 2008). Streams and rivers in Europe are to reach good ecological status according to the Water Framework Directive (European Commission, 2000) and river restoration could be a key mitigation measure to achieve this. However, good ecological status is to be obtained within a time-frame shorter than that spent on studying the River Gelså restoration, which raises the question of whether water managers are in possession of the necessary tools to make decisions on how to restore rivers successfully.

Acknowledgements

The preparation of this manuscript was partly supported by the EU FP7 project REFORM (contract no. 282656).

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.ecoleng.2013.09.069.

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