

TECHNICAL REPORT

Rapid colonization of aquatic communities in an urban stream after daylighting

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Restoring aquatic ecosystems is still at an early stage and the outcomes of the remediation techniques used are often not reported, which limit opportunities to learn and further improve these methods. One common remediation technique in urban areas is daylighting, which involves the re-opening of once buried streams with the aim of restoring ecosystem functions and services. In this study, we monitored the colonization of two important aquatic communities, benthic algae and macroinvertebrates, and assessed the nutrient retention capacity of a recently daylighted urban stream in the city of Oslo, Norway. The approach used involved transforming a buried channel into an open stream consisting of interconnected riffles and ponds seeded with aquatic and terrestrial plants. Benthic algal and macroinvertebrate communities began to colonize the restored stretch within a relatively short time, 9 months following daylighting. The dynamics of the two aquatic communities differed, indicating that spatial processes are influential in determining the establishment of benthic algae, whereas time is more important for macroinvertebrate communities. The observed net nutrient retention from the daylighted stretch for phosphate, total nitrogen, total phosphorus, and calcium were 226, 128, 38 and 14%, respectively. However, the efficiency of the daylighted stretch to sequester nutrients was limited by the lack of controlling nutrient inputs from diffuse sources. This highlights the importance of addressing the influence of broader-scale processes, extending beyond the boundaries of the restored reach, which can otherwise demise the success of daylighting.

Key words: aquatic communities, benthic algae, daylighting, macroinvertebrates, nutrient retention, stream restoration

Implications for Practice

- Restoration efforts designed to re-open a buried stream in an urban area, which mimicked natural features of streams with respect to habitat heterogeneity (series of riffles and ponds) and re-establishing stream–riparian interaction (mediated by the translocated riparian plants) have the potential to facilitate the (re)colonization of aquatic communities and improve water quality.
- In our study, benthic algal and macroinvertebrate communities were shown to colonize the restored stretch within a relatively short time, 9 months following daylighting. The restored stretch retained nutrients; however, substantial improvement in water quality was not observed probably due uncontrolled nutrient inputs that occurred between the reference site and the restored stretch. Thereby, highlighting the need to account for catchment dynamics when restoring urban streams.

through completely enclosed man-made channels built from impermeable material, and these culverts were then buried to gain land (Elmore & Kaushal 2008; Wild et al. 2011). Such practices substantially impact streams (Elmore & Kaushal 2008; Beaulieu et al. 2014) and lead to alterations in hydrology (Walsh et al. 2005), decreased nutrient retention (Hope et al. 2014), impaired biodiversity (Neale & Moffett 2016), and reduced cross-habitat interactions between land and water due to loss of riparian vegetation (Paul & Meyer 2001; Roy et al. 2003).

Growing awareness of the environmental issues associated with urban streams has in recent years led to an increase in efforts to re-open these streams. Such initiatives were supported

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Introduction

Streams and rivers were previously considered as obstacles for urban development and were subsequently culverted (Paul & Meyer 2001). Culverting entails the redirection of waterbodies

by policies such as the Habitats Directive (92/43/EEC) and the Water Framework Directive (2000/60/EC), which encouraged the use of various rehabilitation techniques (Clarke et al. 2003; Smith et al. 2014). The primary objectives of these restoration and rehabilitation measures were to improve in-stream habitats and reestablish desired ecosystem functions, such as reducing the amount of nutrients moving downstream (Bernhardt et al. 2005; Bernhardt & Palmer 2007; Schwartz et al. 2015; Friberg et al. 2017). It has, for example, been shown that measures that increased streams' surface-area to volume ratios and water residence time improved nutrient uptake and retention by enhancing interactions with benthic communities within the stream corridor (Craig et al. 2008; Kaushal et al. 2008; Bernhardt & Palmer 2011). However, the success of restoration and rehabilitation measures varied. Some studies have, for example, shown negligible effects on biodiversity (Feld et al. 2011; Haase et al. 2013; Friberg et al. 2014), whereas others demonstrated encouraging results (Hering et al. 2015; Kail et al. 2015; Neale & Moffett 2016). A lack of success can generally be attributed to four factors: (1) limited spatial extent of the restored areas; (2) insufficient recolonization opportunities from species pools; (3) disproportionate influence of complex large-scale processes occurring at the catchment level; and/or (4) time-lag responses where positive effects only became apparent after a relatively long time (Craig et al. 2008; Schmutz et al. 2016; Lorenz et al. 2018). However, empirical evaluations of daylighting (i.e. de-culverting; (Wild et al. 2011) of urban streams are still scarce, in particular during the early (re)colonization of aquatic communities (Neale & Moffett 2016; Lorenz et al. 2018).

The present case study addresses the early colonization of aquatic communities and evaluates the nutrient retention capacity after daylighting an urban stream reach of Hovinbekken in Oslo, Norway. The previously culverted channel was transformed into an open stream with low flow velocities and interconnected riffles and ponds, each seeded with aquatic and terrestrial plants. Such morphological transformations have previously been shown to increase heterogeneity, reestablish terrestrial and aquatic interactions mediated by the riparian vegetation, and stimulate in-stream productivity and nutrient retention (Pinkham 2000; Neale & Moffett 2016).

We monitored the responses of two key aquatic communities, benthic algae and macroinvertebrates, to daylighting along different sections within the restored stream reach during the ice-free season. Due to the lack of monitoring data prior to daylighting we used a space-for-time substitution approach, a commonly used technique to evaluate ecosystem responses to environmental changes (Layer et al. 2010; Rawcliffe et al. 2010), where benthic algal and macroinvertebrate communities from the daylighted stretch were compared to an upstream (not culverted) reference site. We hypothesized that:

- (1) Colonization should result in similar benthic algal and macroinvertebrate communities in the daylighted sections as those present at the upstream reference site.
- (2) The implemented morphological changes—slow flow, increased habitat heterogeneity, and re-establishment of riparian-benthic interactions—should increase nutrient retention.

Methods

The Daylighted Stream Reach

A reach of approximately 650 m in the Hovinbekken stream, located within the city of Oslo, Norway, was de-culverted in 2015. The restored stretch (hereafter referred as “daylighted reach”) consists of a flow-controlled channeling system, where water passes through a series of ponds connected by riffles (Fig. 1). The daylighted reach receives water from an 800-m, still-existing culvert, with a maximum discharge of 0.15 m³/s (measured continuously at the inlet by the Agency for Water and Sewage in Oslo; Oslo VAV). The excess water is diverted to the original culvert to avoid overflow of the opened stream reach. Aquatic plants originating from other waterbodies around the city were translocated and placed in (ca. 45% *Phragmites australis*, 45% *Typha latifolia*, and 10% *Iris pseudacorus*) and around (a mix, but mainly *Carex* species) the daylighted reach, mimicking what is normally encountered in lowland streams in Norway. The substrate used for the daylighted reach bed consisted mainly of a mixture of gravel (2–16 mm) and small stones (16–64 mm; Table S1). The system became operational on 20 August 2015, which corresponds to early autumn in Norway.

Sampling Sites

Water chemistry, benthic algae, and macroinvertebrates were sampled from the first spring season (May 2016), that is approximately 9 months after the system was operational, corresponding to the early colonization phase of the daylighted reach. Benthic algae and macroinvertebrates were sampled at six different locations (L1–L6 in Fig. 1) within the daylighted reach. In addition, a reference site (L0) located about 850 m upstream the daylighted reach was sampled (see Fig. S1). The reference site was separated from the daylighted reach by a culvert of approximately 800 m, which leads the stream underneath an area of dense urban infrastructure. Site L1 was adjacent to the inlet pond (i.e. the culvert's exit) and positioned within the first riffle section, whereas site L2 was located at the lower end of this riffle section, right before the second pond. After the second pond, a pipe of approximately 10 m connected the reach with the next sites. The pipe was installed at the bottom of the pond to reduce the potential transport of oil further downstream. This simple pipe installation targets the fact that oil is less dense than water to sequester and keeps any light oil contaminants floating on the surface of the second pond, thus from spreading downstream. Sites L3, L4, and L5 followed along the downstream riffles and were interconnected by small ponds. These interconnected riffles fed water to the largest pond (Teglverksdammen, max depth 3 m). Site L6 was located at the outlet of the largest pond (Fig. 1).

Sampling Design and Species Identification

Water and aquatic communities were sampled from riffles. Each sampling location (L0–L6) consisted of a 1–2 m long homogeneous stretch with a water depth ranging between 5 and 15 cm. The riffles were chosen to facilitate cross-comparisons between the daylighted reach (L1–L6) and the reference site

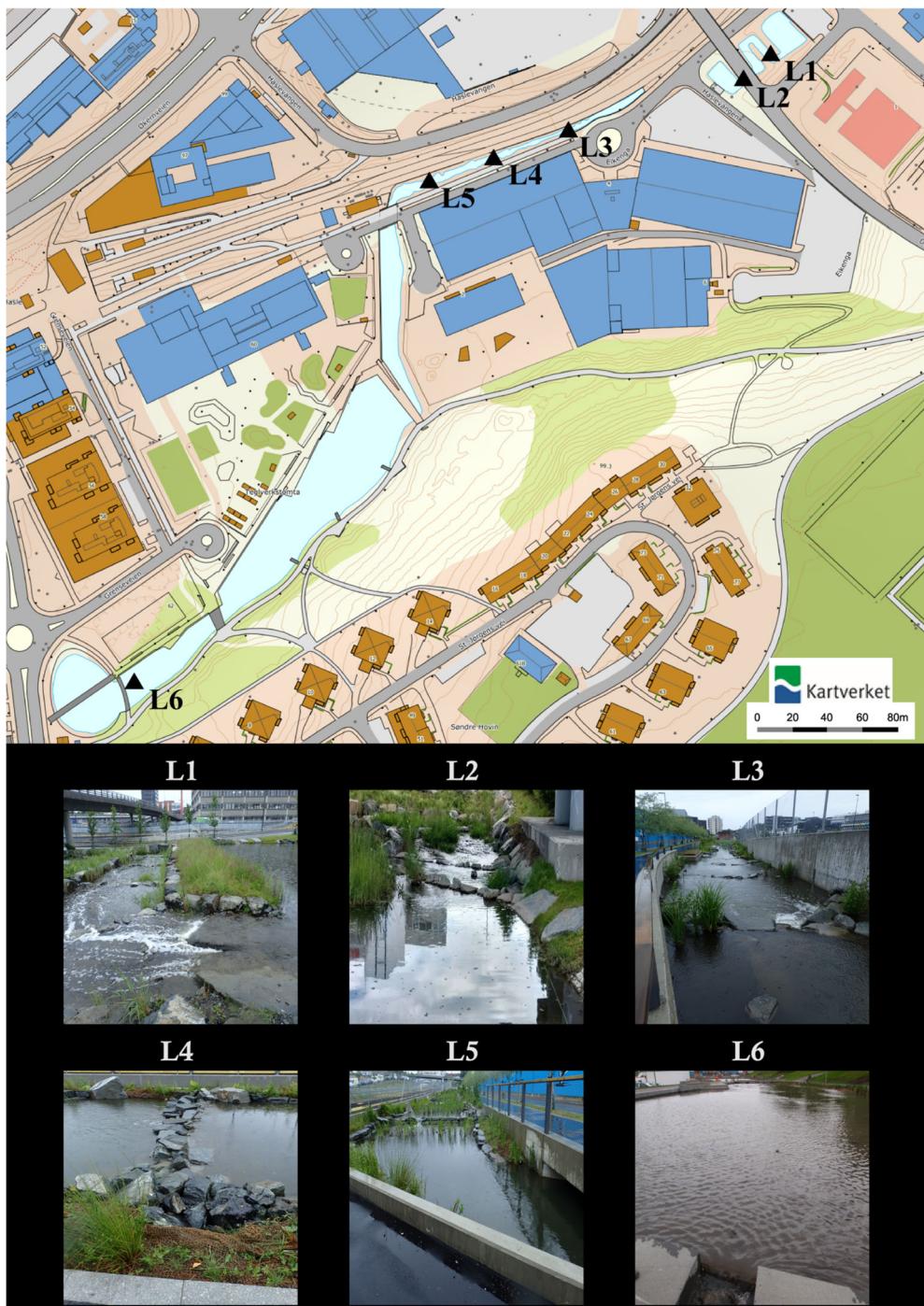


Figure 1. Location and pictures of the sampling sites: L1–L6, from the daylighted reach. The sampling locations in the map (upper panel) are represented by triangles (\blacktriangle). The upstream reference site (L0, not shown on this map) is located about 850 m upstream L1. The respective distance between sites: L1–L2 was ca. 21 m, L2–L3 was ca. 70 m, L3–L4 was ca. 76 m, L4–L5 was ca. 48 m, and L5–L6 was ca. 335 m. The map was downloaded (9 May 2020) from the Norwegian Mapping Authority (<https://www.norgeskart.no>).

(L0), as the latter is a small (1–2 order) and shallow stream without deeper ponds.

Benthic algae were collected in 2016 and 2017, following standard guidelines NS-EN 15708:2009 (2010) (see Supplement S1 for details). During 2016, monthly samples were

collected between May and November. Benthic algae were also collected during May and June 2017 from each site (L0–L6), thereby collectively representing a total of 9 time points over 2 years.

In 2016, macroinvertebrates were sampled at the same intervals (May to November) as the benthic algae, using a Surber sampler and a protocol described by Stark et al. (2001; see Supplement S2 for more details).

Water (1 L) was sampled simultaneously as the aquatic communities, and water quality parameters (total phosphorus, phosphate, total nitrogen, and calcium) were analyzed by the Agency for Water and Sewage in Oslo (Oslo VAV), using standardized procedures (NS-EN ISO 11905-1 1997; NS-EN ISO 6878-1 2004; NS-EN-ISO 15681-1 & 2 2015). Temperature and conductivity were measured in situ using a portable meter (Multi 3420, WTWTM, Germany).

Due to maintenance work in the outlet of the daylighted reach, the water flow was stopped during August and September 2016. This resulted in water stacking up in the ponds, whereas the water flow through the riffles was severely reduced, leading to partially dried-out patches. Consequently, benthic algae from sites L3, L4, and L5 were not sampled in August whereas L6 was not sampled in September. The sampling of macroinvertebrates was similarly discontinued: no samples were taken during August (from all sites L1–L6) and from site L6 in September. However, the sampling of water quality parameters was maintained.

Benthic algae were identified using a light microscope (Leica 2000), adhering to procedures described in NS-EN 15708:2009 (2010). Macroinvertebrates were identified using a stereo microscope (Optika Lab 20) and a quantification method described in Eriksen et al. (2010). Details on the identification procedures are described in Supplement S3.

Statistical Analysis: Determining Nutrient Export and Assessing the Effects of Daylighting on Aquatic Communities

The monthly monitored nutrient concentrations and the flow measurements (when available, i.e. during May–November 2016; Fig. S2) were used to calculate nutrient fluxes. Net nutrient retention (Tot P, Tot N, Ca, and PO₄⁻³) in the daylighted reach was calculated as the difference in nutrient fluxes between the outflow (L6) and the inflow (L1), normalized by the inflow and expressed in percent, and calculated for each month and cumulatively.

The effects of the daylighting on benthic algal and macroinvertebrate communities were assessed using principal response curves, which is a constrained multivariate technique. The community compositions along the daylighted reach (L1–L6) were systematically compared with the upstream reference site (L0). The analysis is based on redundancy analysis, and effectively disentangles time-dependent effects from the overall treatment effects (i.e. daylighting), where the model significance is tested through permutation (Van den Brink & Ter Braak 1999). In addition, traits lists were derived from the two aquatic communities. The growth form (single celled, branched filamentous, or unbranched filamentous) was assigned to identified taxa of benthic algae. Macroinvertebrates were classified according to their feeding guild (grazers, detritivores, filter feeders, predators, or gatherers) using information compiled in the Freshwater

Ecology database (Schmidt-Kloiber & Hering 2015). These traits matrices were used to calculate two measures of functional diversity in multidimensional space, which is based on principal coordinate analyses (Villéger et al. 2008). Firstly, we assess trait richness, defined as the total area (measured as convex hull volume) occupied by all species' traits in a multidimensional space (Villéger et al. 2008; Mouillot et al. 2013). Secondly, we assess trait evenness, which is a measure of the trait distribution that accounts for the trait abundances within this multidimensional space (Villéger et al. 2008; Mouillot et al. 2013).

The contributions of the environmental dataset (water quality variables), spatial locations (sites), and temporal variations (sampling points) on the benthic algal and macroinvertebrate community structures were assessed using variance partitioning. This technique is based on redundancy analysis and quantifies the proportions of the variation explained by different explanatory variables both individually and combined, which are then expressed as adjusted R² values (Borcard et al. 1992, 2011). Prior to the analysis, the community data were Hellinger-transformed and the environmental (water quality) variables were scaled and centered by subtracting the standard deviation from the mean. Hellinger-transformation is recommended for community data, to account for the high heterogeneity present in such datasets, before using linear ordination techniques to assess the importance of environmental variables for community structuring (Rao 1995; Legendre & Gallagher 2001; Lepš & Šmilauer 2003).

All statistical analyses were performed using R (version 3.4.2) statistical software (R Core Team 2017) using the *vegan* and *FD* packages.

Results

Water Physical and Chemical Parameters: Temperature, Conductivity, and Nutrients

Monthly average water temperatures followed patterns associated with seasonal variations, with maximum (ca. 16°C) and minimum (ca. 4°C) temperatures observed in August and November, respectively (Fig. S3A). Conductivity varied among months and appeared to be slightly lower during May–June 2017 (224–358 µS/cm) compared to May–November 2016 (303–582 µS/cm, Fig. S3B). Most nutrients (total phosphorus [0.01–0.18 mg/L], total nitrogen [0.52–2.3 mg/L], and phosphate [0.003–0.09 mg/L]) were observed to vary by a least a factor of 4.4 over time (Fig. S4A–S4D). The exception was calcium, which was more consistent across time and ranged from 30–48 mg/L. Nutrients levels recurrently increased between the reference site (L0) and the first sampling location (L1) of the daylighted reach (Fig. S4A–S4D), that is within the 800 m culvert (Fig. S1).

Nutrient retention occurred in the daylighted reach (L1–L6) for: total phosphorus and total nitrogen in June, July, August, and October; phosphate in May, June, July, August, and October; and calcium in May, June, August, and November (Table 1, Figs. 2 & 3 and Fig. S5A & S5B). The

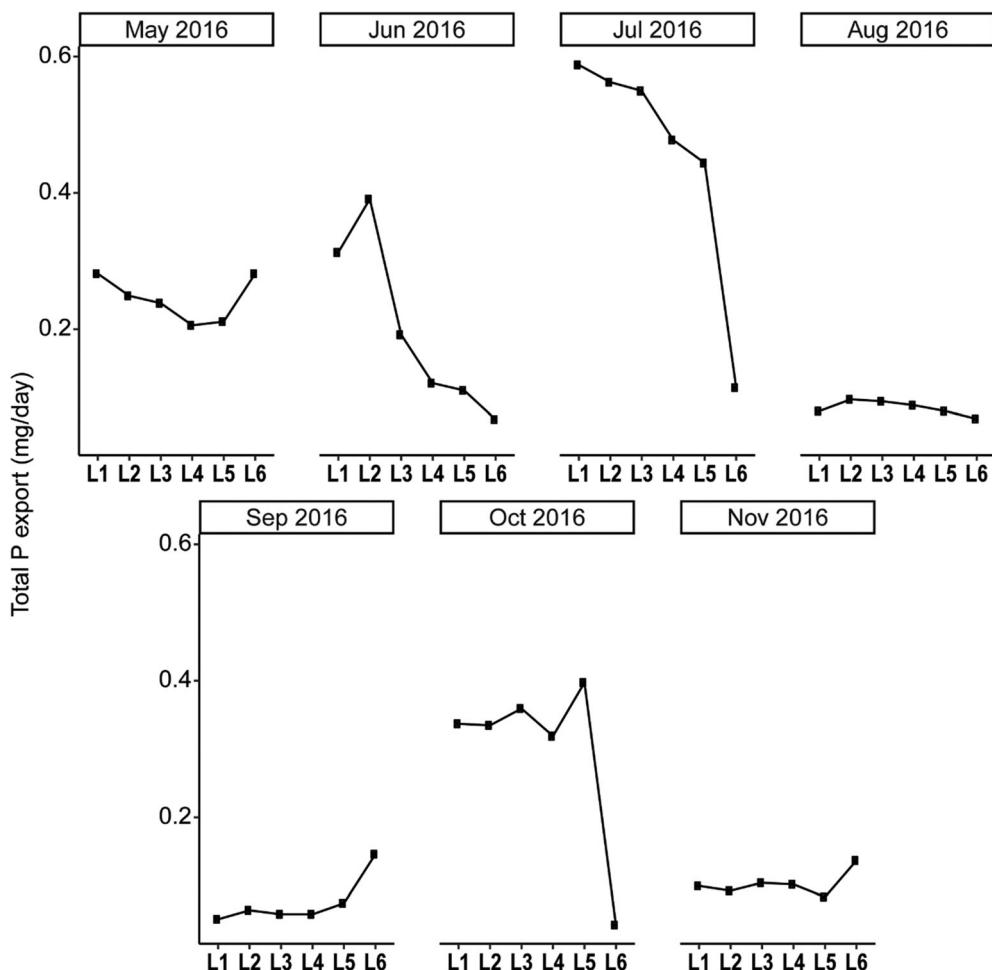
Table 1. Net nutrient retention in the daylighted reach, expressed in percent (%), between the initial inflow (site: L1) and the most downstream site (L6) for May to November 2016 and cumulatively. The absolute retention values measured in mg/day are shown in brackets. The indicated values were calculated from the measured discharge rates. Negative numbers indicate retention and are highlighted in gray.

Month (2016)	Total Phosphorus	Total Nitrogen	Phosphate	Calcium
May	0.00 (0.00)	1.34 (0.11)	-7.14 (-0.01)	-10.00 (-17.88)
June	-78.41 (-0.25)	-59.34 (-4.45)	-86.49 (-0.11)	-14.20 (-24.17)
July	-80.58 (-0.47)	-19.55 (-1.82)	-75.00 (-0.28)	8.44 (13.95)
August	-14.29 (-0.01)	-52.97 (-1.68)	-43.75 (-0.02)	-17.40 (-17.99)
September	185.71 (0.09)	0.00 (0.00)	0.00 (0.00)	3.29 (2.05)
October	-87.33 (-0.29)	-15.39 (-0.33)	-92.54 (-0.14)	15.76 (13.02)
November	37.21(0.04)	18.29 (0.07)	78.57 (0.05)	-0.27 (-0.23)
Cumulative	-37.68 (-0.89)	-127.61 (-7.47)	-226.35 (-0.51)	-14.38 (-31.26)

cumulative decrease was highest for phosphate (226.35%), followed by total nitrogen (127.61%), then total phosphorus (37.68%), and lowest for calcium (14.38%; for May–November 2016 in Table 1 and for May–June 2017 in Table S2). Over the study period from May to November 2016, 0.51 mg PO₄⁻³/day, 7.47 mg Tot N/day, 31.26 mg Ca/day, and 0.89 mg Tot P/day were respectively retained in the daylighted reach (Table 1).

Early Colonization of Benthic Algae and Macroinvertebrates

Benthic algae and macroinvertebrates had begun colonizing the daylighted reach within a relatively short time, approximately 9 months after the flow was initiated (Figs. 4A, 4B, 5A, & 5B). Diatoms (Bacillariophyta) and green algae (Chlorophyta) were the most abundant benthic algal groups, with *Ulothrix zonata* and *Oedogonium* species being the most dominant taxa. For macroinvertebrates, oligochaetes (Oligochaeta) and



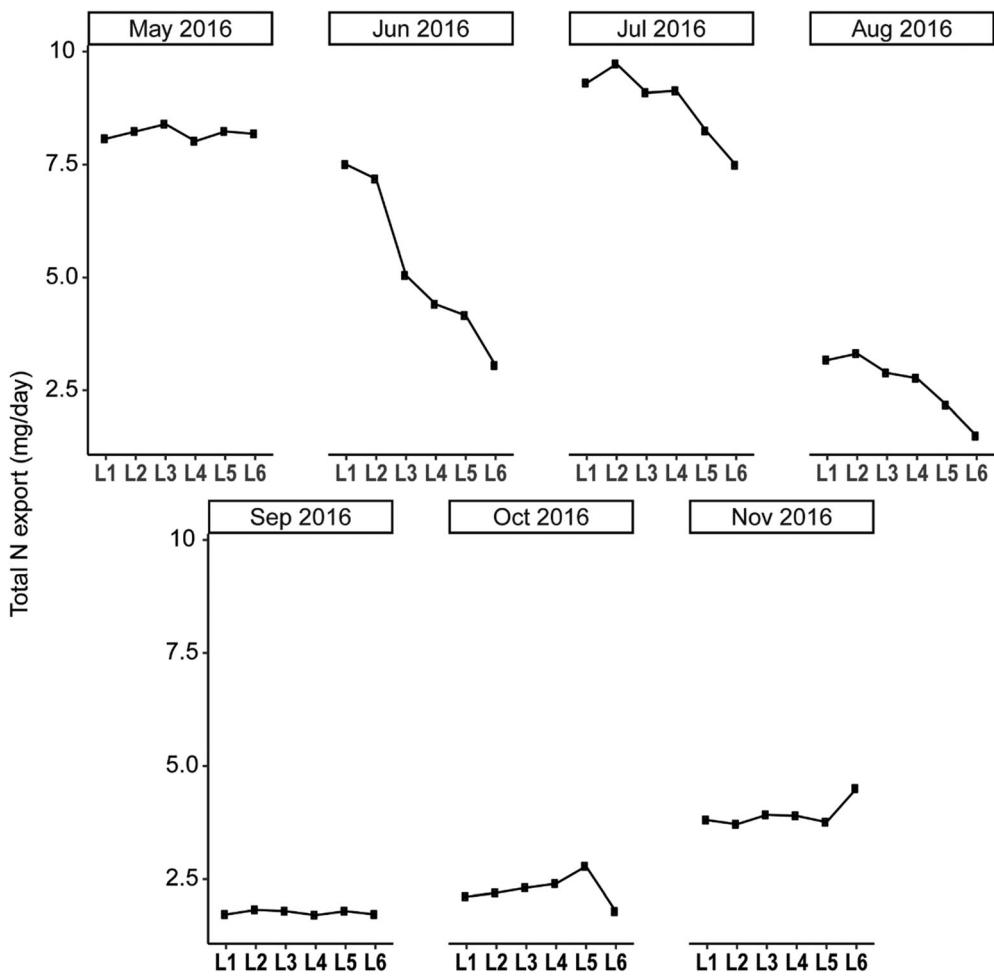


Figure 3. Amount of total nitrogen (mg/day) exported from the different sections of the daylighted reach across time.

Chironomidae larvae (Diptera) were the two most dominant groups. The benthic algal cover and the abundances of macroinvertebrates varied across sites and time, but the most downstream site (L6) resembled the reference site (Figs. 4A & 5A). Species richness of benthic algae and macroinvertebrates decreased along the daylighted reach, with a slight increase after the main pond (L6) (Figs. 4B & 5B). The percent composition of major benthic algal groups at site L6 were more similar to those observed at the upstream reference location (L0) compared to the other daylighted sites (Fig. 4C). Unlike benthic algae, the percent composition of major macroinvertebrate groups along the daylighted reach (L1–L6) differed from the reference site (L0), and these differences increased with distance from the reference site (Fig. 5C). The most dominant taxon from the reference site (L0), Oligochaeta, gradually decreased downstream through the daylighted sites (L1–L6), whereas the proportion of Diptera increased. In addition, the trajectories of the benthic algal communities' temporal development were markedly different from those of the macroinvertebrates (Figs. 4D & 5D and Fig. S6A & S6B). For instance, spatial location was the most important factor determining the establishment of benthic algal communities (Fig. 4D) resembling the reference site

(L0). The temporal benthic algal communities' development showed that site L6 was consistently more similar to the reference site (L0; Fig. 4D) compared with the other daylighted sites (L1–L5). In contrast to benthic algae, time appeared to be more important for macroinvertebrates (Fig. 5D). The macroinvertebrate communities at the daylighted sites (L1–L6) became gradually more similar to the reference site (L0) with time, despite showing relatively major differences at the initial time point (May 2016). Trait richness (Fig. 6A) for benthic algal communities did not follow any temporal patterns, although locations L1, L2, and L6 overall were similar to the reference site (L0). In contrast, trait richness (Fig. 6C) for macroinvertebrates increased over time. Trait evenness (Fig. 6B) for benthic algae seemed to track seasonal dynamics while no distinguishable patterns were observed for macroinvertebrates (Fig. 6D).

Variance Partitioning

A total of 27% of the variance in the benthic algal communities could be explained by spatial location, environmental variables (water quality parameters), and time. The proportions of variance uniquely explained by space, time, and environmental

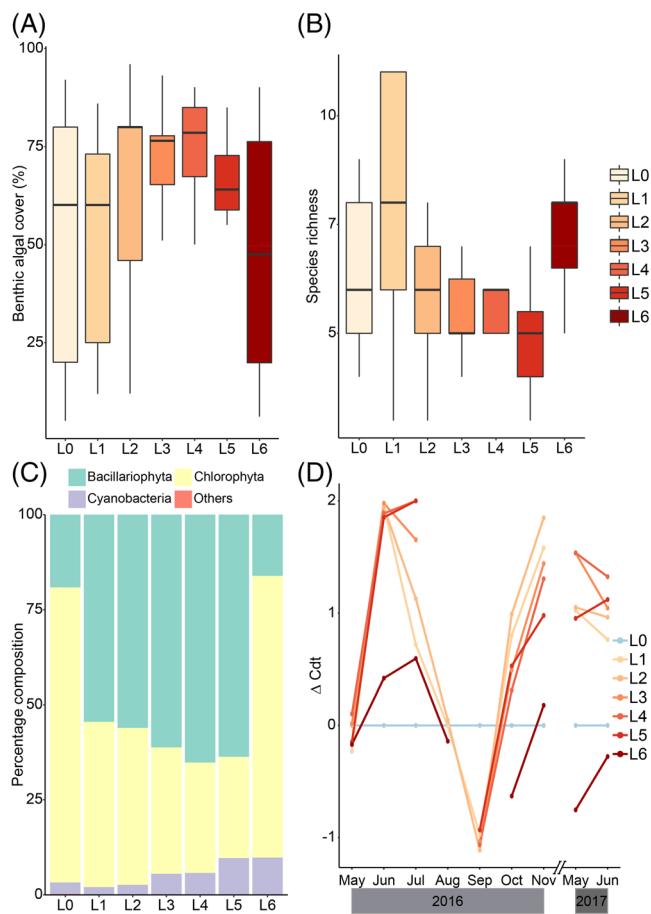


Figure 4. Comparison of benthic algal community assemblages across sites and time. Time integrated percentage algal cover (A) species richness (B) and percentage community composition (C) are shown across sites (L0–L1). The last panel (D) shows the results of the principal response curve analyses from the benthic algal communities across the different sites and sampling points. In this analysis (D), the de-culverted sites (L1–L6) were standardized to the reference site L0 (thereby represented as a straight horizontal line $y = 0$).

variables were 17, 4, and 3%, respectively, whereas the shared (space, time, and environmental parameters) proportion reached a total of 3% (Fig. 7). Total nitrogen and calcium were the two significant environmental variables that were closely related to benthic algal assemblages. For macroinvertebrates, the analysis showed that 20% of the community variance could be explained by time and environmental variables. Time alone explained 12%, environmental variables explained 6% and the shared fraction between time and environmental variables was 2% (Fig. 7). Total phosphorus was the only significant environmental variable that was related to macroinvertebrates.

Discussion

In this daylighting project, major transformations were undertaken to deliberately change a culverted channel into an open stream. Our results indicate that daylighting can promote

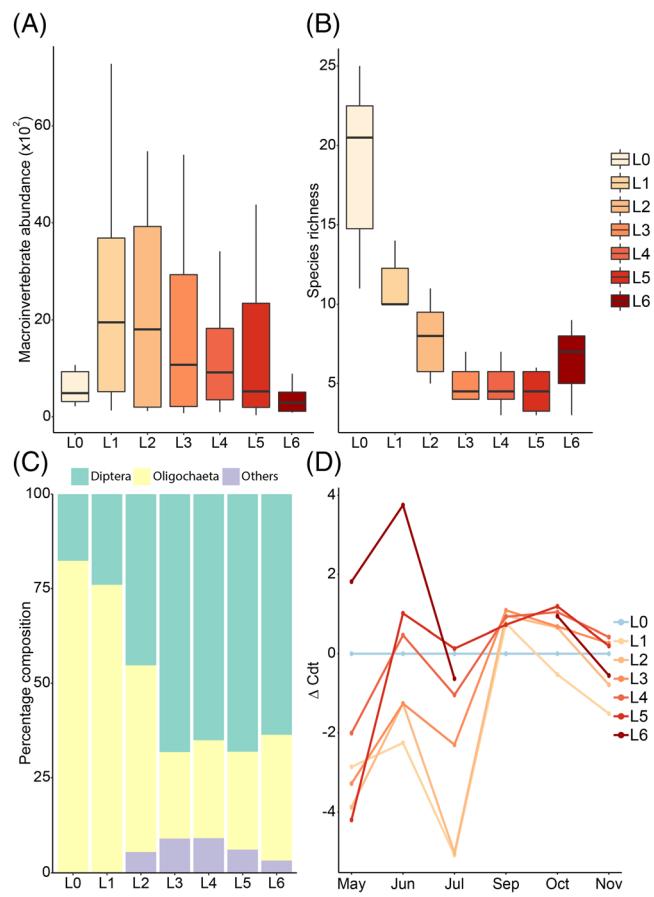


Figure 5. Comparison of macroinvertebrate community assemblages across sites and time. Time integrated total abundance (A) species richness (B) and percentage community composition (C) are shown across sites (L0–L1). The last panel (D) shows the results of the principal response curve analyses from the macroinvertebrate communities across the different sites and sampling points. In this analysis (D), the de-culverted sites (L1–L6) were standardized to the reference site L0 (thereby represented as a straight horizontal line $y = 0$).

nutrient retention and does not hinder the establishment of aquatic communities, although these must be interpreted with some caution due to the sampling design that tracked temporal processes better than spatial variations (not replicated).

Effects on Nutrient Retention

Over the study period from May to November, the daylighted reach overall retained nutrients. A combination of biological activities and sedimentation along the stream reach are the most probable causes for retaining nutrients. Benthic algae and vascular aquatic plants incorporate nutrients into biomass, but some chemical forms can more readily be taken up than others (Whitford & Schumacher 1961; Reynolds & Davies 2001; Wilkie & Mulbry 2002; Ellegaard et al. 2018). This might explain the higher retention of phosphate compared to total phosphorus. Calcium is needed by macroinvertebrates for osmotic balance and building their exoskeleton

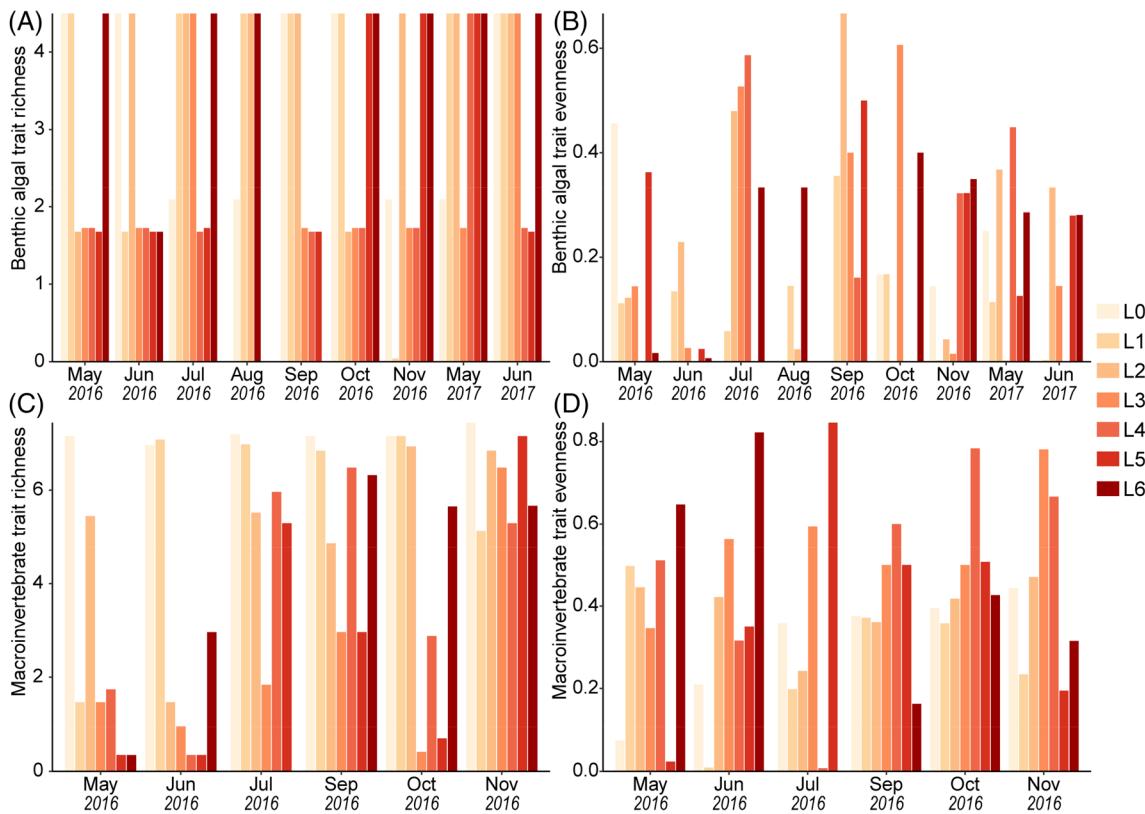


Figure 6. Comparison of trait indices across sites and time. Shown are trait richness and trait evenness for benthic algal (A, B) and macroinvertebrate (C, D) communities.

(Greenaway 1985; Colmer et al. 2011; Raven & Hurd 2012; Poteat & Buchwalter 2014). However, the nutrient retention capacity of the daylighted reach was, in some months, less efficient at counteracting increases in nutrient levels between the reference site (L0) and the first sampling site (L1) of the daylighted reach, which recurrently occurred. Within the short distance (a culvert of approximately 800 m) separating these two locations (reference site L0 and daylighted site L1), substantial increases in nutrient levels occurred. This is probably caused by leakages and faulty connections in the underground sewage system, which is a well-known problem in urban areas, including Oslo, where the sewage system is relatively old.

Nutrient retention can also be influenced by seasonal dynamics, especially in countries experiencing winters with frost and plant die-down. Such seasonality can reduce the importance of primary producers in sequestering nutrients, and instead cause them to act as nutrient sources (Carpenter & Adams 1977; Carpenter 1981). This could explain some of the variations observed in nutrient export and retention in this study. For instance, Choudhury et al. (2018) showed that the maximum nitrogen removal of macrophytes commonly found in boreal regions peaked in August. In our study, at the end of the year (November 2016), the pond acted as a source of nutrients, rather than a sink. This is probably due to breakdown of primary producers occurring during the seasonal transition from autumn to

winter, triggering the release of nutrients that were once sequestered in biomass (Carpenter & Adams 1977; Wetzel 2001).

The addition of a large pond (between sites L5 and L6) contributed in retaining nutrients during the growth season, forcing a small flowing stream into a larger slow flowing water body. This alters the hydrology of the system and increases the water residence time. Increasing water residence time has been shown to increase nutrient removal from the water column by primary producers (Valett et al. 1996; Ensign & Doyle 2005; Sutherland et al. 2014; Newcomer Johnson et al. 2016). This has most probably also occurred in our study, as dense floating algal mats were observed in the pond during summer (Burgess 2018).

Effects on Aquatic Communities' Colonization

The colonization patterns of benthic algae and macroinvertebrates differed. The results from the principal response curve, traits indices, and variance partitioning analyses showed that space (i.e. similarities in local conditions) was the most important factor determining establishment of benthic algal communities that were comparable to the reference site, whereas time was more important for macroinvertebrates.

Compared to macroinvertebrates, the demographic characteristics of benthic algae (small, abundant, and generally short generation time) increase their abilities to disperse passively over

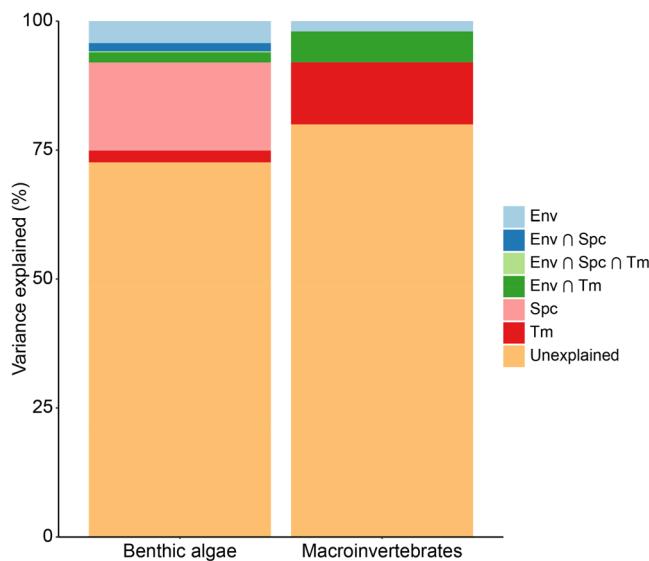


Figure 7. Results of the variance partitioning analysis for benthic algal and macroinvertebrate communities. The figure shows the proportion of variance in community composition explained by the environmental parameters (Env), space (Spc), time (Tm), and the shared fractions.

long distances (Fenchel & Finlay 2004). Though small organisms might overcome dispersal barriers, local environmental conditions are expected to exert a stronger sorting effect (Leibold et al. 2004; Van der Gucht et al. 2007). Thus, successful establishment of benthic algal communities in the daylighted reach was dependent on having similar abiotic conditions as the reference site.

In contrast, the establishment of macroinvertebrates following stream restoration has been shown to be dependent on recruitment from local species pools (Kail et al. 2015; Lorenz et al. 2018). Previous studies have shown that species pools located within a distance of 5 km of the restored site facilitate (re)colonization for macroinvertebrates, and that the first km might be of the utmost importance (Sundermann et al. 2011; Tonkin et al. 2014). The importance of close proximity to local species pools was further supported by the findings of Arnott (2017), who showed that the composition of macroinvertebrates from the daylighted reach was more similar to the upstream reference site (L0) than to the closest neighboring river (Akersselva, approximately 3 km apart). Our results also indicate that macroinvertebrate recolonization depends on time. As time passed, the communities from the daylighted reach became more similar to the reference site. These findings support previous studies (Friberg et al. 1998; Nilsson et al. 2015; Neale & Moffett 2016). Overall, our results suggest a relatively fast colonization of macroinvertebrate communities likely from an upstream species pool (via active dispersal or passive drift from L0) and that the 800-m long culvert separating the reference and the daylighted reach did not act as a dispersal barrier. The culvert (between L0 and L1) could also be a species pool for macroinvertebrates that can survive in low light conditions and could

influence the community composition of the daylighted reach. The pipe installation (between L2 and L3) aimed at reducing the potential transport of oil contaminants further downstream the daylighted reach did not hinder the dispersal of benthic algae and macroinvertebrates, as the communities from these two locations (L2 and L3) had similar temporal patterns. The large proportion of unexplained variance can be attributed to random natural variations (grazing and competition) and other anthropogenic influences (chemical contaminants related to urban areas) that were not measured.

Other Constraining Factors

The restricted spatial scale of the de-culverted reach might not be sufficient to offset the influence of processes occurring at the catchment scale (Sundermann et al. 2015). The high prevalence of macroinvertebrates belonging to Oligochaeta (pollution tolerant group) present at the reference site is indicative of anthropogenic nutrient enrichment (Goodnight 1973; Lauritsen et al. 1985). These obstacles can be overcome by adopting a broader approach based on the entire catchment rather than remediating individual parts of the ecosystem (Schmutz et al. 2016; Friberg et al. 2017). Substantial improvement of water quality can be achieved by combining daylighting with nutrient abatement from multiple sources within the catchment (Sundermann et al. 2013).

Another limitation was the low diversity of substrates (mainly gravel, 2–16 mm, and small stones, 16–64 mm) and the lack of coarse organic material (e.g. woody debris) might limit the colonization of macroinvertebrate species that depend on dead wood for case building, food sources, and as oviposition surfaces (Winking et al. 2014). The findings of two meta-analyses from published peer-reviewed papers on stream restoration found that increasing substrate heterogeneity through the addition of dead wood increased the diversity of macroinvertebrates (Miller et al. 2010; Kail et al. 2015). The low diversity of macroinvertebrates observed in the daylighted reach could be linked to the lack of dead wood and planting more riparian trees may remediate for this. Another potential obstacle is the influence of the surrounding urban environment; roads, building and bridges, collectively, represent barriers for mature winged stream insects from neighboring streams to reach the daylighted reach (Smith et al. 2009, 2015).

Benthic algae and macroinvertebrates were able to colonize the daylighted reach within a relatively short time. The daylighted reach overall retained nutrients, although we observed seasonal variations. However, substantial improvements in water quality were not observed, probably due to disproportionately large influences of processes occurring at the catchment scale that contributed to nutrient enrichment (leakages and faulty connections). The positive effects of daylighting can become more ecologically meaningful by integrating catchment dynamics to broaden the scope of the restoration efforts (Schmutz et al. 2016; Friberg et al. 2017). Our results show that the use of daylighting as a remediation technique has the potential to bridge urbanization and

environmental protection, while also possibly providing societal and economic benefits.

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LITERATURE CITED

- Arnott DN (2017) Macroinvertebrate colonisation of a recently deculverted urban stream. Norwegian University of Life Sciences, Ås, Norway
- Beaulieu JJ, Mayer PM, Kaushal SS, Pennino MJ, Arango CP, Balz DA, et al. (2014) Effects of urban stream burial on organic matter dynamics and reach scale nitrate retention. *Biogeochemistry* 121:107–126
- Bernhardt ES, Palmer MA (2007) Restoring streams in an urbanizing world. *Freshwater Biology* 52:738–751
- Bernhardt ES, Palmer MA (2011) River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications* 21:1926–1931
- Bernhardt ES, Palmer MA, Allan JD, Alexander G, Barnas K, Brooks S, et al. (2005) Synthesizing U.S. river restoration efforts. *Science* 308:636–637
- Borcard D, Legendre P, Drapeau P (1992) Partitioning out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. New York: Springer
- Burgess SBD (2018) Development in phytoplankton assemblages, ecological status and purification effect in Teglverksdammen: a study of a pond the first two growth seasons following deculverting of an urban stream system in Oslo, Norway. Norwegian University of Life Sciences, Ås, Norway
- Carpenter SR (1981) Submersed vegetation: an internal factor in lake ecosystem succession. *The American Naturalist* 118:372–383
- Carpenter SR, Adams MS (1977) The macrophyte tissue nutrient pool of a hard-water eutrophic lake: implications for macrophyte harvesting. *Aquatic Botany* 3:239–255
- Choudhury MI, McKie BG, Hallin S, Ecke F (2018) Mixtures of macrophyte growth forms promote nitrogen cycling in wetlands. *Science of the Total Environment* 635:1436–1443
- Clarke SJ, Bruce-Burgess L, Wharton G (2003) Linking form and function: towards an eco-hydromorphic approach to sustainable river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13:439–450
- Colmer TD, Winkel A, Pedersen O (2011) A perspective on underwater photosynthesis in submerged terrestrial wetland plants. *AoB Plants* 2011:plr030
- Craig LS, Palmer MA, Richardson DC, Filoso S, Bernhardt ES, Bledsoe BP, et al. (2008) Stream restoration strategies for reducing river nitrogen loads. *Frontiers in Ecology and the Environment* 6:529–538
- Ellegaard M, Godhe A, Ribeiro S (2018) Time capsules in natural sediment archives—tracking phytoplankton population genetic diversity and adaptation over multidecadal timescales in the face of environmental change. *Evolutionary Applications* 11:11–16
- Elmore AJ, Kaushal SS (2008) Disappearing headwaters: patterns of stream burial due to urbanization. *Frontiers in Ecology and the Environment* 6: 308–312
- Ensign SH, Doyle MW (2005) In-channel transient storage and associated nutrient retention: evidence from experimental manipulations. *Limnology and Oceanography* 50:1740–1751
- Eriksen TE, Bækken T, Moe J (2010) Innsamling og bearbeiding av bunnfauna i rennende vann – et metodestudium.
- Feld CK, Birk Sebastian, Bradley David C, Hering Daniel, Kail Jochem, Marzin Anahita, et al. (2011) Chapter three – from natural to degraded rivers and back again: a test of restoration ecology theory and practice. Pages 119–209. In: Woodward G (ed) *Advances in ecological research*. Vol 44. London, England: Academic Press
- Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. *Bioscience* 54:777–784
- Friberg N, Kronvang B, Ole Hansen H, Svendsen LM (1998) Long-term, habitat-specific response of a macroinvertebrate community to river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8:87–99
- Friberg N, Baattrup-Pedersen A, Kristensen EA, Kronvang B, Larsen SE, Pedersen ML, Skriver J, Thodsen H, Wiberg-Larsen P (2014) The river Gelså restoration revisited: habitat specific assemblages and persistence of the macroinvertebrate community over an 11-year period. *Ecological Engineering* 66:150–157
- Friberg N, Buijse T, Carter C, Hering D, M. Spears B, Verdonschot P, Moe TF (2017) Effective restoration of aquatic ecosystems: scaling the barriers. *Wiley Interdisciplinary Reviews: Water* 4:e1190
- Goodnight CJ (1973) The use of aquatic macroinvertebrates as indicators of stream pollution. *Transactions of the American Microscopical Society* 92:1–13
- Greenaway P (1985) Calcium balance and moulting in the Crustacea. *Biological Reviews* 60:425–454
- Haase P, Hering D, Jähnig SC, Lorenz AW, Sundermann A (2013) The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. *Hydrobiologia* 704:475–488
- Hering D, Aroviita J, Baattrup-Pedersen A, Brabec K, Buijse T, Ecke F, et al. (2015) Contrasting the roles of section length and instream habitat enhancement for river restoration success: a field study of 20 European restoration projects. *Journal of Applied Ecology* 52:1518–1527
- Hope AJ, McDowell WH, Wollheim WM (2014) Ecosystem metabolism and nutrient uptake in an urban, piped headwater stream. *Biogeochemistry* 121:167–187
- Kail J, Brabec K, Poppe M, Januschke K (2015) The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: a meta-analysis. *Ecological Indicators* 58:311–321
- Kaushal SS, Groffman PM, Mayer PM, Striz E, Gold AJ (2008) Effects of stream restoration on denitrification in an urbanizing watershed. *Ecological Applications* 18:789–804
- Lauritsen DD, Mozley SC, White DS (1985) Distribution of Oligochaetes in Lake Michigan and comments on their use as indices of pollution. *Journal of Great Lakes Research* 11:67–76
- Layer K, Riede Jens O, Hildrew AG, Woodward G (2010) Chapter 5 – food web structure and stability in 20 streams across a wide pH gradient. Pages 265–299. In: Woodward G (ed) *Advances in ecological research*. Vol 42. London, England: Academic Press
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613
- Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge, UK: Cambridge University Press
- Lorenz AW, Haase Peter, Januschke Kathrin, Sundermann Andrea, Hering Daniel (2018) Revisiting restored river reaches – assessing change of aquatic and riparian communities after five years. *Science of the Total Environment* 613–614:1185–1195

- Miller SW, Budy P, Schmidt JC (2010) Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. *Restoration Ecology* 18:8–19
- Mouillet D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28:167–177
- Neale MW, Moffett ER (2016) Re-engineering buried urban streams: daylighting results in rapid changes in stream invertebrate communities. *Ecological Engineering* 87:175–184
- Newcomer Johnson T, Kaushal S, Mayer P, Smith R, Sivirichi G (2016) Nutrient retention in restored streams and rivers: a global review and synthesis. *Water* 8:116
- Nilsson C, Polvi LE, Gardeström J, Hasselquist EM, Lind L, Sarneel JM (2015) Riparian and in-stream restoration of boreal streams and rivers: success or failure? *Ecohydrology* 8:753–764
- NS-EN 15708:2009 (2010) Water quality: guidance standard for the surveying, sampling and laboratory analysis of phytoplankton in shallow running water. Norsk Standard, Standard Norge AS
- NS-EN ISO 11905-1:1997 (1997) Water quality: determination of nitrogen – part 1: method using oxidative digestion with peroxodisulfate (ISO 11905-1: 1997)
- NS-EN ISO 6878-1:2004 (2004) Water quality: determination of phosphorus – ammonium molybdate spectrometric method (ISO 6878:2004)
- NS-EN-ISO 15681-1 & 2: 2015 (2015) Water quality: determination of orthophosphate and total phosphorus contents by flow analysis (FIA and CFA) – part 2: method by continuous flow analysis (CFA) (ISO 15681-2:2015)
- Paul MJ, Meyer JL (2001) Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333–365
- Pinkham R (2000) Daylighting: new life for buried streams. Rocky Mountain Institute, Old Snowmass, Colorado.
- Poteat MD, Buchwalter DB (2014) Calcium uptake in aquatic insects: influences of phylogeny and metals (Cd and Zn). *The Journal of Experimental Biology* 217:1180–1186
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rao CR (1995) A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. *Qüestiió* 19:23–63
- Raven JA, Hurd CL (2012) Ecophysiology of photosynthesis in macroalgae. *Photosynthesis Research* 113:105–125
- Rawcliffe R, Sayer CD, Woodward G, Grey J, Davidson TA, Jones JI (2010) Back to the future: using palaeolimnology to infer long-term changes in shallow lake food webs. *Freshwater Biology* 55:600–613
- Reynolds CS, Davies PS (2001) Sources and bioavailability of phosphorus fractions in freshwaters: a British perspective. *Biological Reviews* 76: 27–64
- Roy AH, Rosemond AD, Paul MJ, Leigh DS, Wallace JB (2003) Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.). *Freshwater Biology* 48:329–346
- Schmidt-Kloiber A, Hering D (2015) www.freshwaterecology.info – an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators* 53:271–282
- Schmutz S, Jurajda P, Kaufmann S, Lorenz AW, Muhar S, Paillex A, Poppe M, Wolter C (2016) Response of fish assemblages to hydromorphological restoration in central and northern European rivers. *Hydrobiologia* 769: 67–78
- Schwartz JS, Neff KJ, Dworak FE, Woockman RR (2015) Restoring riffle-pool structure in an incised, straightened urban stream channel using an ecohydraulic modeling approach. *Ecological Engineering* 78:112–126
- Smith RF, Alexander LC, Lamp WO (2009) Dispersal by terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge. *Journal of the North American Benthological Society* 28:1022–1037
- Smith B, Clifford NJ, Mant J (2014) The changing nature of river restoration. *Wiley Interdisciplinary Reviews: Water* 1:249–261
- Smith RF, Venugopal PD, Baker ME, Lamp WO (2015) Habitat filtering and adult dispersal determine the taxonomic composition of stream insects in an urbanizing landscape. *Freshwater Biology* 60:1740–1754
- Stark JD, Boothroyd IKG, Harding JS, Maxted JR, Scarsbrook MR (2001) Protocols for sampling macroinvertebrates in wadeable streams. New Zealand Macroinvertebrate Working Group Report No. 1. Prepared for the Ministry for the Environment. Page 57. Sustainable Management Fund Project No. 5103
- Sundermann A, Stoll S, Haase P (2011) River restoration success depends on the species pool of the immediate surroundings. *Ecological Applications* 21: 1962–1971
- Sundermann A, Gerhardt M, Kappes H, Haase P (2013) Stressor prioritisation in riverine ecosystems: which environmental factors shape benthic invertebrate assemblage metrics? *Ecological Indicators* 27:83–96
- Sundermann A, Leps M, Leisner S, Haase P (2015) Taxon-specific physicochemical change points for stream benthic invertebrates. *Ecological Indicators* 57:314–323
- Sutherland DL, Turnbull MH, Craggs RJ (2014) Increased pond depth improves algal productivity and nutrient removal in wastewater treatment high rate algal ponds. *Water Research* 53:271–281
- Tonkin JD, Stoll S, Sundermann A, Haase P (2014) Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology* 59: 1843–1855
- Valett HM, Morrice JA, Dahm CN, Campana ME (1996) Parent lithology, surface–groundwater exchange, and nitrate retention in headwater streams. *Limnology and Oceanography* 41:333–345
- Van den Brink PJ, Ter Braak CJF (1999) Principal response curves: analysis of time-dependent multivariate responses of biological community to stress. *Environmental Toxicology and Chemistry* 18:138–148
- Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S, Declerck S, et al. (2007) The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. *Proceedings of the National Academy of Sciences* 104:20404–20409
- Villéger S, Mason NWH, Mouillet D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301
- Walsh CJ, Roy AH, Feminella JW, Cottingham PD, Groffman PM, Morgan RP II (2005) The urban stream syndrome: current knowledge and the search for a cure. *Journal of the North American Benthological Society* 24: 706–723
- Wetzel RG (2001) Limnology: lake and river ecosystems. San Diego, CA: Gulf Professional Publishing
- Whitford LA, Schumacher GJ (1961) Effect of current on mineral uptake and respiration by a fresh-water ALGA1. *Limnology and Oceanography* 6: 423–425
- Wild TC, Bernet JF, Westling EL, Lerner DN (2011) Deculverting: reviewing the evidence on the ‘daylighting’ and restoration of culverted rivers. *Water and Environment Journal* 25:412–421
- Wilkie AC, Mulbry WW (2002) Recovery of dairy manure nutrients by benthic freshwater algae. *Bioresource Technology* 84:81–91
- Winking C, Lorenz AW, Sures B, Hering D (2014) Recolonisation patterns of benthic invertebrates: a field investigation of restored former sewage channels. *Freshwater Biology* 59:1932–1944

Supporting Information

The following information may be found in the online version of this article:

Table S1. Substrate characterization from each sampling site.

Table S2. Net nutrient retention, expressed in percent, between the initial inflow (site: L1) and the most downstream site (L6) for May, June, July 2017 and cumulatively.

Figure S1. Location of the reference site (L0) and the first sampling point (L1) of the daylighted reach.

Figure S2. The volume of water discharged through the restored stream observed during the sampling campaign of 2016.

Figure S3. Temporal variation of total phosphorus (mg/L) across the different sampling sites.

Figure S4. Amount of phosphate (mg/day) exported from the different section of the daylighted stream across time.

Figure S5. Nonmetric multidimensional scaling ordination (Bray-Curtis similarity matrix).

Figure S6. The first panel (a) shows the nonmetric multidimensional scaling plot of the macroinvertebrates' compositions across the reference site (L0) and the closest river; Akerselva (A4, A5, and A6).

Supplement S1. Sampling protocol used for collecting benthic algae.

Supplement S2. Sampling protocol used for collecting macroinvertebrates.

Supplement S3. Method used to identify benthic algae and macroinvertebrates.

Supplement S4. The macroinvertebrate communities of the reference site (L0) compared to the nearest neighboring river "Akerselva."

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