Short-term colonization dynamics of macroinvertebrates in restored channelized streams

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Abstract Macroinvertebrate colonization of restored rivers is a function of dispersal into the restored reach and its suitability for population establishment. To maximize potential for colonization success, spatial considerations such as distance to colonizer source pools and dispersal pathways must be included in restoration planning. Unfortunately, the dispersal abilities of macroinvertebrates and ecological importance of different dispersal modes for colonization are still poorly understood. We used a field experiment that controlled colonization by passive drift and allowed distinction between active upstream aquatic and active/passive aerial dispersal, thus testing their differential importance during colonization of experimentally restored stream reaches. Two agricultural streams emanating below culverts were longitudinally separated along the first 30 m and one stream side each was covered with a fine-mesh net to limit aerial dispersal.

Colonization of manually disturbed background and experimentally introduced cobble substrate was investigated over 6 months. We found that upstream in-stream dispersal, especially in these agricultural streams, can be rapid (days) and play an important role in the short-term colonization of restored streams. We conclude that a landscape perspective, in addition to in-stream measures, must be considered when attempting to restore streams dominated by agricultural and urban land use that constrains available species pools and limits dispersal pathways.

Keywords Disturbance · Stream restoration · Dispersal · Diversity · Water quality

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Introduction

River restoration projects attempt to ameliorate anthropogenic impacts on streams. They are now common practice in the management of running waters, advancing a research field that focuses on restoration methodologies and their effects on river hydromorphology, water quality, and aquatic organisms (Feld et al., 2011; Suding, 2011). Restoration responses by aquatic macroinvertebrates are of great interest as they are important for the functioning of river ecosystems and can be used as bioindicators of restoration success (Hooper et al., 2005; Jähnig et al., 2009; Haase et al., 2013). However, restoration

response from a macroinvertebrate point of view has resulted in as many questions as it has provided answers (Palmer et al., 2010), mainly due to the complex spatiotemporal dimensions inherent in river ecosystems (Wohl et al., 2005). Moreover, the majority of restoration projects are located in streams dominated by agricultural and urban land use, typically affected by various autocorrelating stressors (Allan, 2004; Feld et al., 2011). A hierarchically structured approach towards investigating the factors driving macroinvertebrate colonization after restoration, as spatially inherent in the habitat filter concept (Poff, 1997; Lake et al., 2007), can thus be quite insightful.

Dispersal is a primary obstacle that macroinvertebrates must overcome to initially colonize a restored stream (Lake et al., 2007; Winking et al., 2014). Dispersal success is determined by colonizer source pools within a viable dispersal distance along with the dispersal ability of a species that is dependent on locomotion mode and innate locomotion behavior (Parkyn & Smith, 2011; Winking et al., 2014). The study and understanding of macroinvertebrate dispersal and colonization entails many challenges because traditional ecological methods such as direct observation or capture-mark-recapture studies (Southwood & Henderson, 2000) are usually not feasible (Bilton et al., 2001). Nonetheless, the processes involved in macroinvertebrate dispersal have been investigated repeatedly in observational studies and experiments that attempt to distinguish between active (in-stream swimming/crawling, aerial dispersal of winged adults) and passive (in-stream drift, wind-mediated dispersal of winged adults) dispersal modes (reviewed by Mackay, 1992; Bilton et al., 2001; Parkyn & Smith, 2011). Elaborate mark-recapture studies were performed by MacNeale et al. (2005) and Briers et al. (2004) using stable isotope enrichment of aquatic insect larvae and assessing wind-mediated dispersal of winged adults. Unfortunately, such studies are often not realizable, as they are costly and laborious. Creative study designs are therefore required to investigate macroinvertebrate dispersal. For example, Downes et al. (2005) and Downes & Lancaster (2010) used fences on experimental substrates to distinguish between invertebrate settlement from drift in the water-column or colonization by crawling. Elliott (2003) investigated short-term, short-distance movement using small artificial streams. Lastly, dispersal

directions by winged adults was studied using traps along and perpendicular to streams (Kovats et al., 1996; Petersen et al., 2004) and even at different heights above the ground (Didham et al., 2012). We used a manipulative field experiment in the present study to tease apart potential modes of macroinvertebrate dispersal into experimentally restored stream reaches.

Upon reaching a structurally restored stream, dispersers need to establish sustainable populations. Local habitat suitability is determined initially by abiotic physical and chemical characteristics and then by biotic interactions such as competition and predation (Lake et al., 2007). Although the significance of water quality impairment on assemblage composition is repeatedly stated (Jähnig et al., 2010; Sundermann et al., 2011), restoration projects still mostly focus on structural properties (also see Feld et al., 2011 regarding restoration of riparian zones to improve water quality), as they are the most obvious and easiest to modify. For instance, a common practice is the improvement of in-stream habitat by the addition of coarse gravel (Kristensen et al., 2011; Mueller et al., 2014). Although habitat conditions may be improved physically, the establishment of sustainable populations may be limited ultimately by poor water quality (Langford et al., 2009; Robinson et al., 2014). This fact is especially true in agricultural and urban landscapes where not only local habitat conditions are affected, but also regional species source pools are poor due to legacies of historical land-use practices (Allan, 2004; Baumgartner & Robinson, 2015).

Passive drift often plays an important role in macroinvertebrate dispersal (Bilton et al., 2001), but the ecological relevance of other locomotion modes such as active upstream or aerial movement and the respective temporal dimensions remain elusive (but see Winking et al., 2014). Their relevance remains unclear partly because many experimental studies often are unable to distinguish between active and passive colonization pathways and short- versus long-distance dispersal (Downes et al., 2005; see Hughes, 2007 regarding molecular methods for assessing population connectivity). Importantly, this knowledge is required for the spatial prioritization of restoration projects in order to maximize the potential for successful colonization. The current study was designed to address this knowledge gap by controlling the effect of passive drift. Experimental reaches

emanated from culverts with all upstream rivulets flowing underground while draining local agricultural lands, thus eliminating the role of passive drift in colonization. Experimental reaches could only be colonized by upstream in-stream dispersal by swimming and crawling or aerial colonization by winged adult insects. Aerial colonization was further controlled by excluding flying adults from one half of each stream with a fine-mesh net.

Our primary goal was to examine the short-term colonization of experimentally restored reaches over 6 months in the absence of passive drift. A second goal was to examine the colonization potential of invertebrates using upstream in-stream dispersal versus insects that disperse primarily by aerial means. In the absence of passive drift, we hypothesized that macroinvertebrates would initially colonize experimental reaches mostly via upstream in-stream dispersal rather than by active/passive aerial dispersal, mainly because of poor source pools of aquatic winged insects and the relatively long dispersal distances inherent in agricultural landscapes (see, e.g., Sundermann et al., 2011; Winking et al., 2014). Gammarids were dominant at the one site, thus a short-term colonization experiment was conducted to specifically examine how quickly they could colonize upstream study reaches. The results have important implications in the spatial and temporal limitations of restoration projects from a landscape perspective.

Methods

The experiment was conducted in two small streams (Hombrechtikon: 'H,' Volketswil: 'V') situated in agricultural areas near Zurich, Switzerland. Common to agricultural streams in the region, these streams were channelized with hard embankments to facilitate water drainage from agricultural lands. Importance for this study was that the streams emanated from culverts with all upstream rivulets flowing underground while draining local agricultural land. This situation is common in many agricultural stream settings globally. Altitude at the sites was ca. 500 m a.s.l., stream gradients were low at ca. 2%, and average annual precipitation was ca. 1,300 mm (20-year mean, Robinson et al., 2014). The experimental reaches (30 m) had low variation in width (93 ± 4 and 95 ± 4 cm, respectively) and depth (19 ± 3 and

22 ± 3 cm, respectively) based on measures from five equidistant transects. Bottom substrate in each stream consisted of fine gravel (1–2 cm) embedded with silt/sand. During the experiment, water electrical conductivity was 567 ± 37 (H) and 625 ± 26 (V) $\mu\text{S}/\text{cm}$ at 20°C , nitrate-N was 2.2 ± 0.2 (H) and 4.5 ± 1.1 (V) mg N/l, and phosphorous ($\text{PO}_4\text{-P}$) was 42.7 ± 21.7 (H) and 9.2 ± 3.2 (V) $\mu\text{g P/l}$.

On 1 February 2012, before installing the experiment, background samples of macroinvertebrates were collected in each stream using standard kick-sampling methods (5 min, 250 μm mesh, $N = 2$ per stream) and preserved with 90% EtOH for analysis in the laboratory. The most upstream 30 m in each stream (experimental reaches) were then strongly disturbed by rigorous raking of the river bed for 30 min each day for 2 weeks to dislodge as much macrozoobenthos as possible (after Matthaei et al., 1996). On 15 February 2012, postdisturbance macroinvertebrate samples were collected in each stream as described above ($N = 2$ per stream to compare with background samples). The experimental reach of each stream was then longitudinally divided by 10 wooden boards ($3.0 \times 0.5 \times 0.025$ m) held in place by iron rods pounded into the stream bed (Fig. 1). The boards were placed in a shallow trench (ca. 10 cm deep) in the stream center to minimize dispersal of invertebrates between the stream sides. One side of each experimental reach was covered with a nylon net (1 mm mesh), which dangled loosely into the stream at both ends and with sides pinned to the adjacent riparian area. The net was intended to limit colonization by flying adult insects.

To improve substrate conditions for macroinvertebrates within each experimental reach, five coarse-mesh metal trays (2.0×0.4 m, 2 cm mesh size, open top) were placed on each side, resulting in a total of 10 experimental substrate units per stream. Trays were distributed equidistant (ca. every 2 m) over the 30-m reach (covering one third of the area, Fig. 1) and filled with sorted alluvial cobble (10 ± 5 cm) from a local quarry. Substrate addition is a common approach in stream restoration to improve habitat conditions for macroinvertebrates and fish (e.g., Friberg et al., 1994; Merz & Chan, 2005). Three large stones of ca. 30 cm diameter, the tops of which were exposed above water, also were added to each tray to facilitate ovipositioning by aerial aquatic insect adults (see Alp et al., 2013). Installation at site H was completed on 20

Fig. 1 **a** Schematic of experimental set-up. The stream originates from a culvert at the *left side* of the figure. *Gray boxes* illustrate metal trays filled with experimental coarse substrate, and *black squares* illustrate natural substrate areas that were sampled. The *hatched area* represents covering with nylon net to limit aerial dispersal by winged adult insects. Abbreviations: *C* control, without net covering, *N* covered by net, *S* experimental substrate, *B* natural substrate. The *number* in the

sampling point name corresponds to approximate distance (m) from the downstream end of the experimental reach. **b** Illustrations of the experimental set-up. *Left* cross section with substrate trays, experimental gravel, stream separation, and net covering. *Right* experimental set-up at site H after installation. The net was readjusted after the picture was taken to loosely dangle into the water

February 2012 and at site V on 25 February 2012. For subsequent sampling, the notation of each sampling point comprised (1) stream name (H: Hombrechtikon, V: Volketswil), (2) net exclusion treatment (N: covered with net, C: control without net covering), (3) substrate treatment (S: experimental substrate, B: natural substrate), and (4) distance from the downstream end of the reach.

The first benthic sample was taken on 29 February 2012 on day 4 (V) and day 9 (H) following the experimental installation. Sampling was conducted every 2 weeks in the first 2 months and then monthly until the beginning of August 2012 (nine sampling events). On each sampling day, one sample per sampling point was obtained, resulting in 20 samples per stream. A sampling point refers to each 2-m-long experimental tray and the 2-m-long area of natural substrate between trays (see Fig. 1). Benthic macroinvertebrates were collected using a modified Surber sampler (0.3×0.3 m, 250 μ m mesh). The sample area was manually disturbed for 10 s with all dislodged material collected in the net. On each sampling date, the actual sampling point was shifted up- or downstream within a 1-m distance within each sample area to allow recovery of previously disturbed sample

points. As adult mayflies were observed at site V (no adults were noticed at site H), the stream at site V was qualitatively sampled (four kick-samples of ca. 0.3×0.3 m each covering different mesohabitats if present) roughly every 300 m downstream on 21 June to identify potential source populations. All collected benthic material from each sample was preserved in 90% EtOH and transported to the laboratory for analysis.

In the laboratory, macroinvertebrates were hand-picked, identified to the lowest reasonable level (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, and Crustacea to genus/family level; Diptera to family level, Oligochaeta at order level) using standard keys (Tachet et al., 2010; Waringer & Graf, 2010) and counted using a dissecting microscope at $\times 10$ magnification. The remaining matter was dried at 60°C for 48 h, weighed, combusted at 550°C , and reweighed to quantify benthic organic material as ash-free dry mass. In the course of the experiment, benthic organic matter (BOM) and abundance of a few macroinvertebrate taxa strongly increased. Samples with large amounts of material were scanned at $\times 8$ magnification to pick out rare taxa (EPT taxa and Coleoptera) and afterwards randomly subsampled (down to a 32nd from a

homogenized sample). The subsample was processed as described above and actual values were extrapolated to a full sample. As the colonization of experimental substrata was the focus of this study, natural substrate samples (B) were processed until May for comparison with experimental substrata.

Short-term *Gammarus* colonization experiment

At site V, *Gammarus* was the dominant taxon (>80% of the total invertebrates collected), and occurred at high densities (mean = $3,854 \pm 4,223$ individuals/m²) throughout the experimental period. Due to these high densities, we expected *Gammarus* to quickly colonize upstream into experimental channels, and particularly in trays filled with cobble substrate as these showed large accumulations of organic matter. Following the initial experiment above, we conducted a short-term experiment to examine colonization of the stream channels by *Gammarus*. First, one side of the experimental reach was heavily disturbed by repeated raking of the stream bed for 30 min and the experimental trays then reallocated into three patches along the 30 m to increase the distances in between by 8 m. The other stream side was left undisturbed and the aerial net was removed.

At day 0, background benthic samples were taken using a modified Surber sampler (0.3 × 0.3 m, 500 µm mesh) by manually disturbing the substrate and collecting all dislodged material in the net. On each experimental side, one sample per sampling point was taken as above, resulting in 12 samples. Sampling points were located at 1, 10, 20 (experimental trays) and 3, 13, 23 (natural substrate) meters distance from the downstream end of the study reach. The number of collected gammarids was counted in the field. Two and five days after the disturbance, benthic samples were taken at different sampling points as those above so as to sample nondisturbed locations. Samples were preserved in 90% EtOH and transported to the laboratory for counting of gammarids and quantifying BOM as ash-free dry mass.

Data analysis

All statistical analyses were performed using the open-source program R 3.0.1 (R Core Team, 2012). Illustrative differences in macroinvertebrate community composition at sites by substrate and net

treatments were examined by detrended correspondence analysis (DCA, R-package ‘vegan,’ Oksanen et al., 2013) using square-root transformed abundance data (Legendre & Legendre, 2012). The predicted upstream colonization pattern was tested by analyzing the effects of distance from the downstream end of the experimental reach and colonization time using the Kruskal–Wallis test. Pairwise tests using log-transformed density data were calculated for each substrate type and site (HB, HS, VB, and VS) with distance * colonization time as the dependent factor. Pairwise Wilcoxon rank-sum test with Bonferroni correction was performed as post hoc tests. Because the net treatment was found to have no effect, C and N data were pooled for each distance, substrate, and site to increase statistical power.

No good linear or generalized mixed model (with date as random factor to account for repeated measurements) could be fit to the data. Substrate and net treatment effects were therefore investigated by a Mann–Whitney *U* test for each site comparing density data averaged over the sampling dates. For this analysis, samples with different distances from the downstream end of the experimental reach were pooled within substrate for each net treatment and site. To analyze the effects of substrate, only the first six sampling dates were included, for which S and B data were available. As the net was expected only to have an effect on taxa with winged adults, only these taxa were included in the analysis of the net treatment effect on aerial colonization.

Data analysis for the *Gammarus* colonization experiment

A Kruskal–Wallis test was used to analyze the upstream colonization pattern as described above. Substrate effects were dependent of colonization time (2 or 5 days) in the disturbance treatment and therefore not analyzed with a Mann–Whitney *U* test of time-averaged data as described above. Instead, the dependent factor of substrate and colonization time ($B_0, B_2, B_5, S_0, S_2, S_5$) was introduced and its effect on *Gammarus* abundance analyzed using a Kruskal–Wallis test. Post hoc multicomparisons tests with Bonferroni correction were performed using the R-package ‘multcomp.’ The same analysis was performed to investigate substrate effects on BOM

accumulation. Lastly, linear regression of $\log(x + 1)$ transformed *Gammarus* abundance and BOM concentration was calculated.

Results

Repeated disturbance by raking before installing the experiment reduced macroinvertebrate abundances by 85% (H) and 91% (V). At site H, Oligochaeta were reduced by 90% (from 977 ± 142 to 98 ± 24 individuals/kick sample), Chironomidae by 76% (from $1,259 \pm 502$ to 300 ± 87 individuals/kick sample), *Gammarus* by 97% (from 115 ± 40 to 4 ± 4 individuals/kick sample), and *Baetis* (78 ± 20 individuals/kick sample) by 100%. Several less common taxa (<20 individuals/kick sample before disturbance) such as *Ecdyonurus* and *Serratella* (order Ephemeroptera), *Chaetopteryx*, *Halesus*, *Rhyacophila*, and Limnephilidae (order Trichoptera), Simuliidae and Stratiomyidae (order Diptera) were reduced by 100%. Some taxa with only 2–4 individuals/kick sample (Hirudinea, Psychodidae, Tabanidae, and Tipulidae), on the other hand, persisted. At site V, *Gammarus* abundance decreased from 906 ± 56 to 24 ± 16 individuals/kick sample (97% reduction). Oligochaeta were reduced by 69% (from 118 ± 36 to 38 ± 11 individuals/kick sample), Chironomidae by 30% (from 49 ± 7 to 36 ± 33 individuals/kick sample), and Turbellaria by 67% (from 18 ± 13 to 7 ± 2 individuals/kick sample). Rare taxa with <2 individuals/kick sample each were usually reduced by 100% (*Asellus*, *Baetis*, Ceratopogonidae, Limnephilidae), except Tipulidae, which again persisted. Supplement Table S1 shows a list of taxa found at the two sites.

Macroinvertebrate community composition analysis showed clear separation of sites H and V on DCA1 axis (Fig. 2). Site H not only had high densities of Oligochaeta ($14,617 \pm 28,855$ individuals/m²; DCA1: -1.12) but also harbored few individuals of the EPT taxa *Habrophlebia* (5 ± 13 individuals/m²; DCA1: -1.86), *Serratella* (<1 individual/m²; DCA1: -2.09), and *Halesus* (<1 individual/m²; DCA1: -2.17). Site V was characterized by the dominance of *Gammarus* ($3,854 \pm 4,223$ individuals/m²; DCA1: 1.34), comparably high abundances of Turbellaria (287 ± 441 individuals/m²; DCA1: 2.01), and some Elmidae (11 ± 26 individuals/m²; DCA1: 1.50). Community composition did not change under

substrate or net treatments at either site and no new taxa colonized the sites during the study period. Aerial aquatic insects represented 44% (mostly chironomids) of the assemblage at H, but only 5% of the assemblage at V (also dominated by chironomids) (*data not shown*).

At site V, where up to 27,000 *Gammarus*/m² were found, relatively few *Baetis* larvae (7 ± 33 individuals/m²) were present. As several flying adult Baetidae were observed in the field, dispersal from downstream populations was expected. The qualitative samples of baetids (see methods) at site V revealed few larvae (ca. 15–30 individuals/m²) up to 900 m downstream of the culvert outlet, a few more at 1,200 m (73 individuals/m²), and >150 individuals/m² at 1,500 m downstream of the experimental site.

There was no significant effect of distance from the downstream end of the experimental reach or the interaction of distance and colonization time on macroinvertebrate abundances. There were significantly higher abundances of macroinvertebrates in April and May (after 50, 65, and 95 days of colonization) at site H (mean abundances $1,005 \pm 8,188$ individuals/m² on 11 April, $1,549 \pm 10,487$ individuals/m² on 26 April, and $2,600 \pm 14,784$ individuals/m² on 25 May) and in May (after 91 days of colonization time) at site V (mean abundance = $597 \pm 2,015$ individuals/m² on 25 May) than on the other sampling dates (mean abundance at site H = 121 ± 726 individuals/m², mean abundance at site V = 123 ± 863 individuals/m²; pairwise Wilcoxon rank-sum tests: $P < 0.05$; Fig. 3). These increases in abundance were mostly related to higher numbers of Oligochaeta and chironomids at site H and gammarids at site V (*data not shown*).

The net covering treatment (C: control without net, N: net covering) had no significant effect on the diversity or abundance of taxa with winged adults, which mainly comprised Chironomidae (mean abundances at site H $852 \pm 7,867$ individuals in C, $668 \pm 6,759$ individuals in N, mean abundances at site V $162 \pm 1,122$ individuals in C, $147 \pm 1,003$ individuals in N; Fig. 4) (Mann–Whitney *U* tests, site H: $P = 0.315$, site V: $P = 0.166$). The substrate (B: natural substrate, S: experimental substrate) had no significant effect on total macroinvertebrate abundance (mean abundances at site H: $774 \pm 6,842$ individuals/m² on B, $750 \pm 7,645$ individuals/m² on S, mean abundances at site V: 146 ± 909 individuals/

Fig. 2 Detrended component analysis (DCA) of macroinvertebrate community composition at the two sites *H* (black) and *V* (gray)

Fig. 3 Colonization of the two substrate types at sites *H* and *V* depending on distance from the downstream end of the experimental reach and colonization time. Color codes for colonization times (in days) are given. For natural substrate (B),

six colonization times were analyzed, for experimental substrate (S), nine colonization durations were analyzed. Error bars indicate standard errors ($N = 2$ as C and N treatments were pooled in the analysis)

Fig. 4 Colonization of net covered (*N*, black lines) and control (*C*, gray lines) stream sides of natural (*B*) and experimental (*S*) substrates at sites *H* and *V* by taxa with winged adults. Error bars indicate standard errors ($N = 5$)

m^2 on *B*, $161 \pm 1,158$ individuals on *S*; Fig. 5) (Mann–Whitney *U* tests, site *H*: $P = 0.193$, site *V*: $P = 0.436$).

Gammarus colonization experiment

No upstream colonization pattern by *Gammarus* was observed, i.e., there was no significant effect of

distance from downstream end of the experimental reach or the factor of distance and colonization time on *Gammarus* abundances (Kruskal–Wallis test, $P > 0.05$ for both). Nevertheless, a trend for an upstream colonization pattern with higher *Gammarus* numbers at more downstream sites, especially at day 2, was observed: a mean abundance of 470 ± 122 individuals/ m^2 was found at the three downstream

Fig. 5 Colonization of experimental (S, black lines) and natural (B, gray lines) substrate at sites H and V for control (C) and net covered (N) stream sides. Error bars indicate standard errors ($N = 5$)

sites, whereas only a mean of 241 ± 28 individuals/ m^2 was counted at the three upstream sites. At day 5, an average abundance of $2,100 \pm 1,976$ individuals/ m^2 was found at the downstream sites, and a mean of $1,144 \pm 1,407$ individuals/ m^2 at the upstream sites.

Experimental cobble substrate (S) had significantly higher *Gammarus* abundances than natural substrate (B) in the disturbance treatment on day 5 (day 2: 289 ± 91 individuals/ m^2 on B, 422 ± 184 individuals/ m^2 on S, day 5: 307 ± 191 individuals/ m^2 on B, $2,937 \pm 1,161$ individuals/ m^2 on S; Kruskal–Wallis test, $P = 0.014$) but not in the control treatment (day

2: $1,270 \pm 616$ individuals/ m^2 on B, $1,792 \pm 633$ individuals/ m^2 on S, day 5: 737 ± 268 individuals/ m^2 on B, 874 ± 141 individuals/ m^2 on S; Kruskal–Wallis test, $P = 0.255$; Fig. 6). The disturbance treatment reduced *Gammarus* abundance (mean abundance before disturbance = $1,363 \pm 689$ individuals/ m^2), which was still observed after 2 days of colonization (356 ± 149 individuals/ m^2). Due to the Bonferroni correction in the post hoc test, this decrease was not significant. After 5 days of colonization, *Gammarus* abundance on experimental substrate was the same as before the disturbance treatment ($2,937 \pm 1,161$

Fig. 6 *Gammarus* abundances before the disturbance treatment (reference state, black), and after 2 (dark gray) and 5 (light gray) days of colonization by substrate type (natural, B, experimental

substrate, S) and distance from the downstream end of the experimental reach ($N = 1$ per distance on each date)

individuals/m²; Fig. 6), whereas abundances on day 5 were still lower than before the disturbance treatment on natural substrate (307 ± 191 individuals/m²).

More BOM was retained on experimental substrate (S) than on natural substrate (B) in the disturbance treatment (3.5 ± 1.7 g/m² on B, 29.2 ± 7.8 g/m² on S; Kruskal–Wallis test, $P = 0.024$) and the control treatment (9.0 ± 3.0 g/m² on B, 22.1 ± 4.4 g/m² on S; Kruskal–Wallis test, $P = 0.026$; Fig. 7). After 2 days of colonization, there was no significant correlation between *Gammarus* abundance and BOM concentration ($R^2 = 0.47$, $P = 0.14$, Fig. 8). After 5 days of colonization, a positive correlation between

Gammarus abundance and BOM concentration was found ($R^2 = 0.72$, $P = 0.03$).

Discussion

Colonization patterns of macroinvertebrates were examined in two channelized streams draining agricultural lands. Water quality results for both systems were indicative for streams flowing through agricultural landscapes in Switzerland (Robinson et al., 2014). The experimental design (net exclusion) allowed distinction between active upstream in-stream

Fig. 7 Bulk benthic organic matter retained in the two substrate types (natural = B, experimental = S) 2 and 5 days after the disturbance treatment. Boxes indicate median and quartiles, gray points indicate average values, and error bars indicate standard deviations ($N = 3$)

Fig. 8 Correlation of $\log(x + 1)$ transformed *Gammarus* abundance and benthic organic matter

dispersal and active/passive aerial dispersal by winged adult insects. Passive dispersal by drift was controlled by selecting experimental reaches just downstream of drainage culverts. As both study sites drained adjacent agricultural lands, their macroinvertebrate assemblages were dominated mostly by pollution-tolerant generalists. For instance, the assemblage at Hombrechtikon (site H) was dominated by Oligochaeta and

Chironomidae with a few EPT taxa (*Baetis*, *Habrophlebia*, *Serratella*, and *Halesus*) at low abundances, whereas macrozoobenthos at Volketswil (site V) mainly consisted of *Gammarus* (up to 27,000 individuals/m²), oligochaetes and chironomids with few individuals of the mayfly *Baetis*. Notably, chironomids were the dominant winged aquatic insect at both sites. This dominance of generalists is a common feature of streams draining agricultural lands, yet the selected sites represent the types of stream reaches often targeted for restoration. Both sites showed a prevalence of active in-stream dispersal in the short-term colonization of experimental reaches in support of our general hypothesis.

At site V, colonization by the relatively common mayfly *Baetis* was probably obstructed by barriers (abiotic or biotic) to population establishment rather than dispersal. Logan & Brooker (1983) stated that the main driver affecting pollution-sensitive taxa in agricultural landscapes was the correlating loss of appropriate habitats due to degraded riparian zones and increased fine sediment inputs, both present at site V. Although physical habitat was introduced by the experimentally added cobble substrate, e.g., for ovipositioning adults (Alp et al., 2013), other factors also may lead to the exclusion of *Baetis*. Factors further constraining population establishment can include any remaining water quality impairment, such

as found by Masters et al. (2007) in acidified streams following restoration, or exclusion due to competition/predation by the highly abundant *Gammarus*. For instance, Kelly et al. (2002), Kelly & Dick (2005), and Felten et al. (2008) showed the importance of gammarids as predators and in structuring macroinvertebrate community composition in streams. *Gammarus* was highly abundant in both natural fine gravel and experimental cobble areas of the experimental reach. If spatial competition by gammarids posed a barrier to *Baetis* colonization, one disturbance event would not be enough to reduce their population sizes sufficiently. Robinson (2012) conducted a 10-year study investigating the effects of experimental floods on macroinvertebrate community composition in an alpine stream below a reservoir. Although *Gammarus* abundances were reduced by the experimental floods, it still took 8 years for more disturbance-adapted alpine species to colonize the system. The present short-term study precludes speculation on long-term dynamics in these systems following restoration.

The expected upstream in-stream colonization pattern on both experimental sides in each stream and of aerial dispersal by winged adults on the net-free side was not observed. This result likely was because active in-stream dispersal was very rapid in the experimental reaches (i.e., within days by *Gammarus* in the site V short-term experiment). Even though some organisms remained after the raking disturbance (<10%), our results are in accordance with those of Elliott (2003) who studied short-term macroinvertebrate movement in experimental channels. Other studies have suggested the importance of adult dispersal and oviposition for population establishment and recruitment (e.g., Lancaster & Downes, 2014). Lancaster et al. (2010) further stated that reduced egg supply due to oviposition substrate rarity may limit population density (also see Alp et al., 2013). The installed cobbles were intended to facilitate ovipositioning by adult aquatic insects. The lack of a net treatment effect most likely reflects the community composition at each site, as aquatic insects with winged adults were dominated by chironomids (taxa that lay eggs directly in streams) at both sites and most other taxa were rare. Chironomid adults can be quite small and the mesh size of the exclusion net may have been inadequate to fully limit their colonization.

The addition of coarse substrate and water-protruding stones for ovipositioning was expected to provide

favorable habitat for macroinvertebrate colonization as substrate type is an important driver of macroinvertebrate community composition (e.g., Minshall & Minshall, 1977). For instance, Buss et al. (2004) showed that 30% of the species present at a site were associated with one distinct substrate type. Consequently, it is thought that increasing substrate heterogeneity as part of river restoration (i.e., restoration of multiple channels providing many different substrate types) should enhance macroinvertebrate diversity (Jähnig & Lorenz, 2008). For example, it often was observed that coarse substrates harbor more diverse macroinvertebrate assemblages than fine substrates (e.g., Herringshaw et al., 2011). As a result, coarse substrate addition is a common restoration practice (reviewed by Feld et al., 2011), even if it is not appropriate for the focal river type (Kristensen et al., 2011). There are several ways in which coarse substrate provides favorable habitat for biota. First, its interstices offer living space for more kinds of macroinvertebrates, provided they are not clogged by fine sediments (Burdon et al., 2013). Coarse substrate also provides refugia during flood events (Townsend et al., 1997) and increases organic material retention (Milner & Gilvear, 2012). In this study, the added coarse substrate was not favored by macroinvertebrates over the natural substrate at either site. Because only the previously present taxa recolonized the experimental reaches, these taxa clearly can inhabit the fine and highly embedded natural gravel substrate. Further, the low stream slopes at the sites, relatively low discharge, and limited floods are not likely to result in sheer stresses that reduce embeddedness and increase substrate porosity for colonization by less tolerant taxa.

Early colonization dynamics within the first few days, which were missed in the main experiment, were indeed affected by substrate type. In the short-term *Gammarus* colonization experiment at site V, experimental coarse substrate was favored over background substrate 2 and 5 days after the disturbance treatment. On day 5, *Gammarus* abundances were correlated with BOM retained in the experimental substrate patches and potentially was used as a food resource (also see Muotka & Laasonen, 2002). Comparable short-term responses of macroinvertebrates due to artificially increased detritus levels also were found by Pretty & Dobson (2004). The experimental substrate patches initially

may be preferential habitats, but as spatial competition increases, gammarids may quickly colonize the natural substrate areas in the experimental reaches, thereby eliminating the substrate effect on later dates. This short-term experiment clearly confirms that *Gammarus* is an efficient in-stream disperser (Dedecker et al., 2006; Robinson & Uehlinger, 2008).

Conclusions

River restoration often is deemed successful when previously absent taxa colonize the new habitat (Palmer et al., 1997). While this is expected from a theoretical point of view, it is rarely observed in river restoration monitoring (Palmer et al., 2010). For macroinvertebrates to successfully colonize restored habitats, several potential barriers (abiotic and biotic) must be overcome, as inferred in habitat filter theory (Lake et al., 2007). Most importantly, individuals must disperse into the new habitat, but dispersal of macroinvertebrates is still poorly understood. This study nonetheless suggests that upstream in-stream movement can play a more important role than previously stated (Bilton et al., 2001). Furthermore, the results demonstrate the importance of including landscape features towards predicting the colonization potential of restored sites (see Winking et al., 2014). In the current study, experimental sites were situated in an agricultural landscape and relatively isolated from less impacted streams that may act as colonizer source pools. Secondly, dispersing individuals must be able to establish a self-sustaining population. River restoration often focuses on enhancing stream morphology, as it is an obvious aspect of river health and a relatively simple factor to improve. This study shows that other abiotic factors such as water quality or biotic factors such as competition/predation are important drivers of macroinvertebrate community composition and likely drive short-term colonization processes in restored streams.

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