

EFFECT OF SMALL IMPOUNDMENTS ON LEAF LITTER DECOMPOSITION IN STREAMS

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ABSTRACT

Leaf litter decomposition is an important process providing energy to freshwater biota. Flow regulation and dams can strongly alter freshwater ecosystems, but little is known about the effect of small impoundments on leaf litter decomposition rates in headwater streams. In this study, we examined the effect of small water storage impoundments (80 to 720 m³) on leaf litter decomposition by comparing sites located within 10-m upstream and downstream of nine impoundments (Rhineland Palatinate, Germany) and sites located further upstream and downstream. The impoundments did not have a statistically significant effect on most physico-chemical variables. However, the abundance of shredders and leaf litter decomposition rates decreased in study sites located within 10-m upstream of the area flooded by impoundments. Small impoundments can locally reduce leaf litter decomposition rates in headwater streams. The effect of small impoundments on ecosystem functioning is minor and may require less attention by freshwater managers than other stressors, though this may differ for other ecological aspects such as connectivity. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: shredder; headwater stream; stream ecosystem functioning; damming; leaf litter breakdown; alder tree

Received 5 February 2015; Revised 11 May 2015; Accepted 26 May 2015

INTRODUCTION

Modification of the natural flow of rivers through impoundment is one of the most widespread anthropogenic habitat changes (Nilsson *et al.*, 2005). Impoundments are constructed for purposes such as domestic water supply, irrigation and provision of electricity (Altinbilek, 2002). Increased demand for water has resulted in impoundment of approximately 60% of the world's total river flow (WCD, 2000). Despite the fact that many catchment areas have a high percentage (>85%; Wallace and Eggert, 2009) of low order (first to third) streams that are regulated by small impoundments (i.e. impoundments with reservoir storage capacity less than 3 000 000 m³, WCD, 2000) (e.g. Van Looy *et al.*, 2014), the ecological effects of impoundments have been primarily studied for large dams (Thomson *et al.*, 2005). In addition, most studies focused on the effects of impoundments on river flow, channel structure, water chemistry or benthic invertebrate assemblages (e.g. Petts and Greenwood, 1985; Ligon *et al.*, 1995; Martínez *et al.*, 2013). However, damming may also affect important ecosystem processes such as leaf litter decomposition (e.g. Casas *et al.*, 2000; Mendoza-Lera *et al.*, 2012; González *et al.*, 2013). Decomposition of allochthonous organic matter such as leaf material is an important ecosystem process in small

streams (Webster, 2007) that represents the main source of energy to food webs (Tank *et al.*, 2010; Straka *et al.*, 2012). Hicks (1997) showed that food webs in forest streams were largely supported by terrestrial leaf litter. Thus, any modification in the processing of allochthonous organic matter may affect the trophic structure of streams (Menéndez *et al.*, 2012).

Dams and their associated impoundments can modify the natural flow regime, water temperature, sediment content and water chemistry in the upstream reaches flooded by impoundment and downstream (Baxter, 1977; Greathouse *et al.*, 2006). The stream biota may be modified as a consequence of these physico-chemical changes (Ogbeibu and Oribhabor, 2002; Chaves-Ulloa *et al.*, 2014). Consequently, the leaf litter decomposition process may be affected because stream biota plays a fundamental role in leaf litter decomposition in headwater streams (Gessner *et al.*, 1999).

Small impoundments may increase or decrease leaf litter decomposition in the upstream reaches flooded by impoundment or in downstream reaches depending on their impact on physico-chemistry and biota (e.g. Casas *et al.*, 2000; Muehlbauer *et al.*, 2009; Menéndez *et al.*, 2012). For example, surface release impoundments were reported to decrease leaf litter decomposition rates in the downstream reaches of streams by González *et al.* (2013). The authors suggested that because the impoundments did not have a significant effect on physico-chemical variables, the low abundance of invertebrate shredders at the downstream sites was responsible for the decrease in leaf litter decomposition

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rates. Similarly, a study in Mediterranean streams attributed decreases in leaf litter decomposition rates at the downstream side of small surface release impoundments to the low abundance of invertebrate shredders (i.e. Menéndez *et al.*, 2012). Casas *et al.* (2000) reported that an impoundment releasing deep water had no significant effect on leaf litter decomposition rate. Despite the fact that the high-nutrient concentration at the downstream reach could accelerate leaf litter decomposition rate (Hall and Meyer, 1998), the authors suggested that high-discharge variability at the upstream reach may have caused greater physical abrasion of leaves.

Dammed streams are suitable systems for testing ecological theories in the context of running waters, and the decomposition of leaf litter may be an important tool for assessing the effect of disturbance at the ecosystem level (Castela *et al.*, 2008). We examined leaf litter decomposition rates in four sites (i.e. two upstream and two downstream sites with different distances to the impoundment) at each of nine surface-release impoundments in Rhineland Palatinate, south western Germany. We hypothesized that the impoundments would primarily alter leaf litter decomposition rates at sites located within 10-m upstream and downstream from the impoundments by modifying physico-chemical variables, such as fine sediment content and oxygen concentration and the abundance of leaf processing invertebrates.

MATERIALS AND METHODS

Study area and sites

The study was conducted in the Palatinate forest (coordinates: latitude 48°76'–49°53' N and longitude 7°31'–8°13' E), south western Germany, between 18 April and 20 May 2014, the period of the year with the highest diversity of invertebrate shredders (Canton and Chadwick, 1983). The geology of the study area is dominated by sandstone, and the altitude ranges from 100- to 673-m above sea level. The study area has dry climate conditions in summer. Study sites were located along nine first-order and second-order (Strahler, 1957) streams affected by small water storage impoundments (volume, 80 to 720 m³; impoundment volume: daily flow volume, 3.7×10^{-4} to 2.2×10^{-3} days) constructed in the 19th century (Frey *et al.*, 2010). Beside impoundment, there were no other human activities (e.g. farming) in the upstream areas, and most sites had riparian vegetation cover (Table S1 on Supporting Information). The impoundments released surface water, were 1.1 to 2.5 m in height and the water residence time varied from 0.5 to 3 min. The study streams typically flow throughout the year, and the impoundments have a continuous flow at the downstream reaches. We selected four sampling sites at each impoundment. Two sampling sites were located immediately

(i.e. within 10 m of the dam wall and area flooded by impoundment) upstream and downstream [i.e. the flooded impoundment reach and plunge zone; immediate upstream (IU) and immediate downstream (ID)]. A third site potentially affected by impoundment was located 300 m further downstream (FD). A fourth site with equal distance as the FD site was selected further upstream (FU). We judged the FU sites to be appropriate standards for unregulated reaches in the studied streams.

Physico-chemical variables

Electrical conductivity, temperature, dissolved oxygen concentration and pH of stream water were measured *in situ* with a WTW Multi 340i/SET (Wissenschaftlich Werkstätten, Weilheim, Germany). Nitrate and phosphate concentrations in stream water were determined on the same day in the laboratory using Macherey-Nagel viscolor kits (Macherey-Nagel, Düren, Germany). Average water depth was computed from measurements taken on a transect across the river channel, and current velocity was estimated by timing a float over a distance of 2 m (Gordon *et al.*, 1994). Water discharge (Q) was calculated from depth, velocity and width (Gordon *et al.*, 1994). Water residence time (T) was calculated as follows:

$$T = \frac{V}{Q}$$

where V is the volume of water stored in the impoundment (Rueda *et al.*, 2006). At each site, a transect was established, and benthic substrates were assessed visually and categorized as 'boulders': >250 mm, 'cobbles': 60–250 mm, 'gravel': 10–64 mm, 'fine gravel': 2–10 mm, 'clay, sand and silt': <0.06–2 mm and 'coarse organic matter' (e.g. leaves) (Bain and Stevenson, 1999; Mullner *et al.*, 2000). Canopy cover and substrate embeddedness, a measure of the degree to which large particles (e.g. cobbles) are covered by fine sediment, were also assessed visually (Gordon *et al.*, 1994).

Decomposition of leaf litter and invertebrates

Leaves of alder tree [*Alnus glutinosa* (L.) Gaertner], a typical species in the riparian zones of temperate Europe (Hewitt, 1999) and one of the dominant tree species in the study area, were used to evaluate leaf litter decomposition in terms of leaf mass loss at each sampling site. Leaves were collected shortly before abscission in October 2013 from trees growing along the Queich River, near Landau, Germany (49°20' N; 8°14' E) and were preserved in a freezer (–20 °C) before use. Approximately 3.0 (±0.1) g of air-dried leaves were placed into coarse-mesh leaf litter bags (mesh size: 8.0 mm), allowing invertebrates to colonize and feed on the leaves. At every site, three replicate bags were fastened onto rocks and roots using nylon lines

and incubated above the stream bed. An extra set of three bags was immersed into stream water for 24 h, on 18 April 2014, to determine the loss from leaching, which was used to correct the initial dry weight of the other bags. After deployment, leaf litter was thoroughly washed in a 500- μm sieve and individually rinsed with demineralized water to remove macroinvertebrates and attached debris (Dinakaran *et al.*, 2008). The leaves were oven-dried at 60 °C (24 h) and weighed. Leaf litter decomposition was expressed as percentage dry mass remaining per day (% DM d⁻¹) (Danger *et al.*, 2013). Invertebrates were preserved in 70% ethanol before identification in the laboratory. Invertebrates were identified (Brohmer *et al.*, 1964; Ludwig, 1989; Nilsson, 1996; Waringer and Graf, 1997) with a dissecting microscope to the lowest level feasible (mainly genus), counted and classified into feeding groups (Merritt and Cummins, 1996; Tachet *et al.*, 2002).

Data analysis

The effect of site location (i.e. FU, FD, IU and ID) on physico-chemical variables and leaf litter decomposition was tested using Linear Mixed-Effect Models (LMMs), with site location as a fixed factor and stream as a random factor. The effect of site location on the abundance of invertebrate shredders was tested using generalized linear mixed effect models with negative binomial distribution (Pinheiro and Bates, 2000; Zuur *et al.*, 2009). The Holm correction (Holm, 1979) was used to adjust *p*-values for multiple testing, and we report the corrected *p*-values. Model assumptions were checked visually as outlined in Zuur *et al.* (2009). Pairwise comparisons for statistically significant models were made using Tukey contrasts (Hothorn *et al.*, 2008). Relations between leaf litter decomposition, physico-chemical variables and invertebrate shredders were tested using Spearman's rank correlation test (Hauke and Kossowski, 2011). Statistical analyses were performed using R (R Development Core Team, 2014).

RESULTS

Leaf litter decomposition

After 24-h leaching, leaf mass loss was 15.8 ± 1% (mean ± SE). Mean leaf litter decomposition rate was the lowest (1.9 ± 0.5% DM d⁻¹) in the IU sites and differed significantly from the ID, FU and FD sites (*p* = 0.0001 in LMM; all *p* < 0.001 in pairwise comparisons with Tukey contrasts) (Figure 1). Leaf litter decomposition rates in the ID, FU and FD sites ranged from 3.8 to 4.0% DM d⁻¹. Leaf litter decomposition was not significantly correlated with physico-chemical variables, though temperature was close to significance (*p* = 0.06).

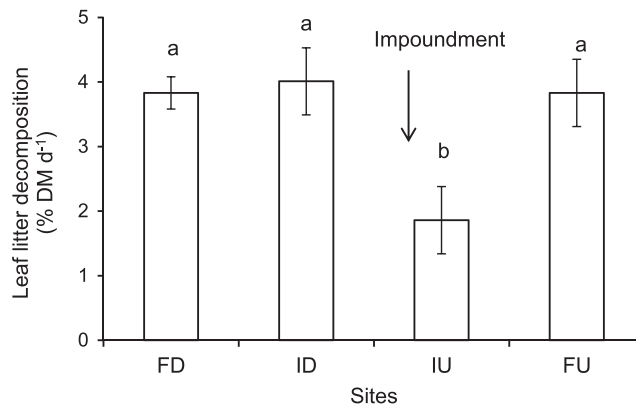


Figure 1. Mean (±SE) leaf litter decomposition rates (% DM d⁻¹) at the further downstream (FD), immediate downstream (ID), immediate upstream (IU) and further upstream (FU) sites. Significant *post hoc* differences are indicated by different letters (Tukey test, *p* < 0.05). The result of linear mixed model is shown. Sites ordered from downstream to upstream

Physico-chemical variables

Most variables did not exhibit statistically significant differences amongst the sites. Only the percentages of pools/riffles and embeddedness were statistically significantly (all *p* < 0.05 in LMM) different, with the percentage of silt/sand and clay marginally non-significant amongst sites (*p* = 0.07). Tukey contrasts showed that the sites IU exhibited higher mean percentages of pools and embeddedness (all *p* < 0.05). Although not statistically significant, the IU sites had higher phosphate concentrations (>40%) and per cent silt/sand and clay, but velocity and per cent gravel were lower (Table I).

Macroinvertebrates

A total of 11 950 invertebrates belonging to 78 taxa were found in the 107 litterbags analysed. Only 11 taxa had abundances greater than 1% of the total invertebrate abundance (Table II). These taxa constituted 92.4% of all invertebrates analysed, and *Gammarus* sp. (58.0%) was the most abundant taxa. Other major taxa included Simuliidae (8.5%), Chironominae (6.8%), *Hydropsyche* sp. (4.8%) and Limnephilidae (3.0%) (Table II). With regard to the macroinvertebrate feeding groups, shredders were the most (56.2%) abundant. Other major feeding groups included the filterers (25.2%) and the gathering collectors (12.0%). Mean shredder abundance was the lowest (10.1 ± 5.7 individuals bag⁻¹) in the IU sites (Table II) and the related generalized linear mixed effect model indicated statistical significance between sites, with the IU sites differing significantly from the ID sites (Tukey contrasts, *p* = 0.05). Shredders abundance was significantly correlated (*r* = 0.53) with leaf litter decomposition rates.

Table I. Means (\pm SE) of physico-chemical variables measured across site categories. Sites ordered from downstream to upstream

Variable	Sites			
	FD	ID	IU	FU
Width (cm)	149.7 (22.6)	138.6 (16.4)	166.2 (37.9)	120.2 (14.6)
Depth (cm)	12.1 (2.6)	10.9 (3.0)	13.9 (3.7)	10.9 (2.4)
Water temperature ($^{\circ}$ C)	10.1 (0.8)	10.2 (0.8)	9.6 (0.5)	9.7 (0.6)
Velocity (m s^{-1})	0.5 (0.1)	0.4 (0.05)	0.2 (0.06)	0.5 (0.1)
pH	7.5 (0.2)	7.3 (0.2)	7.3 (0.1)	7.4 (0.2)
Nitrates (mg L^{-1})	2.4 (0.4)	2.2 (0.4)	2.1 (0.6)	1.5 (0.4)
Phosphates (mg L^{-1})	0.04 (0.01)	0.07 (0.01)	0.1 (0.03)	0.06 (0.01)
Conductivity ($\mu\text{S cm}^{-1}$)	179.4 (51.9)	178.3 (51.4)	194.0 (56.3)	194.3 (57.1)
Oxygen (mg L^{-1})	10.7 (0.3)	10.6 (0.3)	10.6 (0.2)	10.4 (0.3)
Embeddedness (%)	22.2 (7.5)	40.0 (9.5)	72.8 (4.8)	36.1 (9.5)
Substrate composition				
Boulders (%)	7.2 (5.4)	1.8 (0.9)	1.4 (1.1)	3.3 (1.4)
Bedrock (%)	2.0 (1.0)	0.9 (0.6)	1.7 (1.1)	2.7 (2.2)
Cobbles (%)	8.7 (2.9)	8.4 (3.1)	1.0 (0.6)	8.1 (2.5)
Gravel (%)	19.7 (3.7)	18.7 (4.7)	4.9 (1.4)	17.2 (5.0)
Fine gravel (%)	20.9 (4.7)	20.7 (5.0)	17.3 (5.4)	14.4 (3.3)
Clay/silt/sand (%)	29.7 (6.2)	33.3 (6.6)	56.1 (4.6)	35.5 (5.8)
Organic matter (%)	11.9 (8.8)	21.2 (5.0)	17.6 (4.9)	18.7 (9.2)
Canopy cover (%)	31.4 (8.4)	40.6 (8.7)	35.6 (9.4)	37.2 (9.9)
Riffle (%)	84.4 (6.9)	54.8 (9.4)	28.3 (7.1)	76.7 (7.8)
Pool (%)	15.6 (6.9)	36.1 (8.0)	71.7 (7.1)	23.3 (7.8)

FD, further downstream; ID, immediate downstream; IU, immediate upstream; FU, further upstream; SE, standard error.

DISCUSSION

Effects on leaf litter decomposition

The leaf litter decomposition rate was decreased by twofold in the IU sites when compared with the FU sites. This

finding is in agreement with our hypothesis. However, it contrasts with several studies (e.g. Nelson and Roline, 2000; González *et al.*, 2013) that reported decreases in leaf litter decomposition rates at the downstream sides of impoundments, whereas we did not find significant effects at

Table II. Mean (\pm SE) abundances and the percentages of the total abundances of the major macroinvertebrate taxa and feeding groups per litter bag across site categories. Sites ordered from downstream to upstream

Taxa	Sites				%
	FD	ID	IU	FU	
<i>Gammarus</i> sp.	75.7 (13.4)	104.7 (27.9)	32.0 (6.9)	44.2 (6.4)	58.0
Simuliidae	9.9 (2.8)	9.1 (2.6)	7.1 (3.3)	11.5 (3.8)	8.5
Chironominae	6.6 (0.9)	16.6 (3.9)	3.2 (0.4)	4.0 (1.0)	6.8
<i>Hydropsyche</i> sp.	0.37 (0.1)	20.6 (10.2)	0.5 (0.2)	0.11 (0.02)	4.8
Limnephilidae	2.5 (0.5)	6.3 (1.5)	2.2 (0.3)	2.5 (0.4)	3.0
Orthocladiinae	2.8 (0.7)	2.3 (1.5)	1.4 (0.3)	4.9 (1.0)	2.6
Oligochaeta	0.3 (0.1)	0.5 (0.1)	10.1 (3.6)	0.6 (0.1)	2.6
<i>Perla</i> sp.	1.9 (0.4)	2.3 (0.5)	1.1 (0.3)	4.5 (1.6)	2.2
Tanypodinae	1.4 (0.3)	1.8 (0.4)	1.3 (0.4)	2.4 (0.9)	1.3
<i>Baetis</i> sp.	2.2 (0.3)	1.2 (0.2)	0.4 (0.1)	2.0 (0.5)	1.3
<i>Protonemoura</i> sp.	0.1 (0.04)	2.8 (0.7)	0.1 (0.03)	1.6 (0.3)	1.0
Shredders	20.9 (9.3)	38.5 (23.9)	10.1 (5.7)	13.6 (5.9)	56.2
Filterers	9.0 (7.6)	13.2 (7.3)	5.2 (4.4)	9.8 (7.7)	25.2
Gathering collectors	2.9 (0.9)	6.1 (2.9)	4.7 (1.9)	4.0 (1.6)	12.0
Scrapers	1.0 (0.4)	1.3 (0.4)	0.6 (0.2)	1.5 (0.6)	3.0
Predators	0.9 (0.5)	1.4 (0.9)	0.8 (0.4)	1.8 (1.2)	3.4
Piercers	0.07 (0.12)	0.04 (0.06)	0.07 (0.08)	0.07 (0.08)	0.2

FD, further downstream; ID, immediate downstream; IU, immediate upstream; FU, further upstream; SE, standard error.

the ID sites. This discrepancy may be attributed to differences in the size of impoundments and location of study sites. For example, the IU sites in our study represented the upstream impounded reaches and were located within 10 m from the area flooded by impoundments. By contrast, in the aforementioned studies, the upstream sites were between 300 and 700 m above the impoundments. When comparing the upstream sites with our sites FU, the results are similar in that we also did not detect significant effects FU. Moreover, the impoundments investigated in the other studies were bigger (90 000 to 700 000 m³) compared with the ones from our study (80 to 720 m³). The size of impoundments determines the effect on river habitats and biota (Poff and Hart, 2002), which in turn will affect leaf litter decomposition rates.

The magnitude of the impact of impoundment on leaf litter decomposition rates in our study is similar to the range (twofold to threefold decrease) reported for other small impoundments (100 000 to 2 000 000 m³) (e.g. Menéndez *et al.*, 2012; Mendoza-Lera *et al.*, 2012). However, the impact in the other studies was recorded FD (80 to 700 m) from the impoundments, suggesting that the impacts may exceed those of our study in the direct vicinity of the impoundments. When comparing the effect of small impoundment with other stressors, the impact on leaf litter decomposition can be considered small (e.g. small impoundment: up to twofold; nutrients: onefold to eightfold; logging: onefold to fivefold; metals: threefold to fivefold; acidification: up to ninefold) (Gessner and Chauvet, 2002). However, depending on the environmental context, the effects from impoundment may interact with other stressors. In our study, additional stressors were largely absent because the upstream catchments were largely free from anthropogenic impacts through logging, farming or mining.

Effects on physico-chemical variables

Decomposition of leaf litter in streams is influenced by physico-chemical variables and biotic communities such as invertebrate shredders (Suberkropp and Chauvet, 1995; Belančič *et al.* 2009; Martínez *et al.*, 2015). However, the studied impoundments did not have a significant effect on most physico-chemical variables, including temperature, nutrients and oxygen concentration, though phosphates and velocity were considerably increased and decreased, respectively, in the sites IU. However, the physical habitat structure of the IU sites differed statistically from the other sites. The higher embeddedness and per cent of fine sediment in terms of silt, sand and clay may be attributed to higher sediment retention and is in agreement with our hypothesis, but no effect on the oxygen concentration was found. Previous studies of Santucci *et al.* (2005) and Principe (2010) also reported no significant effect of small impoundments on

physico-chemical variables. Contrastingly, Camargo *et al.* (2005) reported increased nutrient concentrations below small impoundments. Although not statistically significant, our study found nitrate concentration to increase slightly from upstream to the downstream sites and phosphate concentration to be highest in the IU sites. The impoundments studied by Santucci *et al.* (2005) and Principe (2010), and in our study, released surface water (Csiki and Rhoads, 2010), while those studied by Camargo *et al.* (2005) released deep water. Given that the depth from which water is released to downstream reaches moderates the effect on physico-chemistry (Poff and Hart, 2002), this may explain the differences between the mentioned studies. For example, Menéndez *et al.* (2012) reported that the mean water temperature and dissolved inorganic nitrogen were significantly increased below an impoundment releasing deep water, whereas the two variables were not affected by impoundments releasing surface water. The composition of substrates was not significantly influenced by impoundments. In conclusion, the impoundments in our study did not have a statistically significant effect on most physico-chemical variables, and we suggest that their direct contribution to the differences in leaf litter decomposition was limited.

Effects on macroinvertebrates

Shredders, mainly *Gammarus* sp., were the major macroinvertebrate feeding group, were significantly related to leaf litter decomposition rates and had the lowest mean abundance in the IU sites. The low mean abundance of shredders at the IU sites can be attributed to factors such as reduced flow conditions, increased fine sediment content (i.e. per cent silt, sand and clay) and embeddedness (Table I). The relatively high fine sediment content and embeddedness recorded in the IU sites may have affected the abundances of major shredder groups such as the *Gammarus* sp. negatively, through a covering of leaf material and reduction of interstitial refugia. Both Gee (1982) and Franken *et al.* (2006) reported lower abundances of *Gammarus* sp. in locations where leaf packs were buried by sediment and with fewer interstitial spaces. Accumulation of fine sediment in streams can reduce the availability of detrital food resources for shredders by covering the more retentive coarse substrates (e.g. cobbles) (Koljonen *et al.*, 2012). Consequently, the low content of detritus may lead to increase in predation of shredders because detritus provide them with cover from predators (Rosenfeld, 2000). Reduced flow conditions may also reduce the feeding activity and abundance of shredders (Martínez *et al.*, 2015). The decrease in leaf litter decomposition rates in the IU sites likely resulted from the lower abundance of shredders, given that shredder density influences leaf litter decomposition (Benfield and Webster, 1985). The reduced flow conditions at the IU sites

may also be responsible for reduced leaf litter decomposition rates because flow influences leaf litter decomposition through physical abrasion (Belančić *et al.*, 2009). Differences in the microbial community may also have contributed to the differences between sites, though this remains speculative in the absence of data. For example, Zubrod *et al.* (2015) found fungicide-induced changes in microbial (i.e. fungi) and invertebrate (i.e. shredders) communities composition and abundance to decrease leaf litter decomposition rates. Nevertheless, Nelson and Roline (2000) reported that the decrease in leaf litter decomposition rate below a small impoundment releasing deep water was mainly caused by the low abundance of invertebrate shredders, whereas microbial decomposition did not differ between sites. Another study found small surface release impoundments to decrease leaf litter decomposition rates at the downstream sides (Mendoza-Lera *et al.*, 2012). The authors suggested that because there was no significant difference in physico-chemical variables and fungal abundance; the low abundance of invertebrate shredders was responsible for the decreased leaf litter composition rates. Overall, we suggest that mainly effects on shredder density and in flow caused the reduced leaf decomposition rates in the IU sites of our study.

CONCLUSIONS

The impoundments decreased leaf litter decomposition rates, albeit only directly upstream of the impoundments, presumably caused by the lower abundance of shredders. Thus, small impoundments can have a spatially limited effect on macroinvertebrates and ecosystem functioning. Future studies should include impoundments differing in size as well as with surface and deep water release to examine whether the influence of size and water release type can explain the differences between previous studies. Overall, the effect of small impoundment on ecosystem functioning was minor, both in terms of effect size and the spatial extent of affected stream length, and may require less attention by freshwater managers than other stressors. However, for other ecological aspects such as connectivity and for larger dams as well as multiple stressor interactions, this conclusion may require moderation.

ACKNOWLEDGEMENTS

We thank Daniel Herles and Jan Helmrich Martin von Baumbach for assistance with the field survey and sampling. Diego Fernández González assisted in study site selection. J. G.M. was funded by a scholarship provided by the German Academic Exchange service (DAAD) (grant number: A/12/91652).

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