



Effects of dams and reservoirs on organic matter decomposition in the hyporheic zone in forest mountain streams

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Abstract Decomposition of allochthonous organic matter is an essential process in headwater streams. Damming of streams alters decomposition rates in the benthic zone downstream, but little is known about the effects on hyporheic decomposition. We examined the effects of dams on hyporheic and benthic organic matter decomposition, using the cotton-strip assay over five seasons, in two forest mountain streams in western Japan. The decomposition rates in the hyporheic zone were lower downstream of the dams than at the unregulated reach in spring, rainy season and fall, but they did not differ in winter and summer. Hyporheic decomposition rates were comparable to the benthic rates in one river and were lower in the other river. Decomposition rates did not differ between coarse- and fine-mesh bags in many seasons at all sites, and the densities of macroinvertebrates were low, suggesting that the contribution of

macroinvertebrate to decomposition in the hyporheic zone was small. These results showed that the hyporheic zone is an important zone for decomposition and that presence of dams altered the hyporheic decomposition in some seasons. Thus, it is crucial to examine both the benthic and hyporheic zones when addressing the effects of dams and reservoirs on stream ecosystem processes.

Keywords Benthic decomposition · Cotton-strip assay, Epilimnetic-release · Hyporheic invertebrates · Water temperature

Introduction

Forest mountain streams are often heterotrophic due to limited in-stream photosynthesis, and stream organisms are dependent on organic matter inputs from the riparian zone (Meyer et al., 2000). Leaf litter decomposition are thus pivotal ecosystem functions (Gessner & Chauvet, 2002). Leaf litter decomposition is a complex process, influenced by various biotic and abiotic factors. Microbes and invertebrates play essential roles on leaf litter decomposition in streams (Piscart et al., 2011; Flores et al., 2013), and elevated water temperature and nutrient concentrations affect their activities and stimulate leaf litter decomposition rates (Ferreira et al., 2015). Stream flow affects decomposition rates directly through physical abrasion and indirectly by stimulating microbial activities

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(Ferreira & Graça, 2006; Arroita et al., 2015). Leaf litter decomposition controlled by various environmental factors is considered a useful indicator of stream ecosystem health (Young et al., 2008).

Damming of streams changes water and sediment fluxes and alters many of those environmental factors influencing leaf litter decomposition (Lesnard & Hayes, 2003; Tieman et al., 2004; Poff et al., 2007; Harrison et al., 2009). Previous studies found lower leaf litter decomposition rates in the benthic zone in reaches downstream of dams compared to the upstream reaches (Martínez et al., 2013, 2016). The lower leaf litter decomposition rates were often explained by differences in biotic factors, such as lower abundance and biomass of shredders (González et al., 2013; Mollá et al., 2017) and lower microbial biomass and invertebrate richness (Salomão et al., 2019). Other studies showed no effects or even higher benthic leaf litter decomposition rates downstream of dams because hypolimnetic release tends to increase nutrient concentrations downstream (Casas et al., 2000; Menéndez et al., 2012).

The hyporheic zone is a major site of organic matter storage. A substantial part of leaf litter inputs can be buried in the streambed sediments (Metzler & Smock, 1990; Storey et al., 1999), and the amount of coarse particulate organic matter may be much greater in the streambed sediment than in the benthic zone in headwater streams (Cornut et al., 2012; Wohl et al., 2012). Hyporheic exchange stimulates hyporheic respiration (González-Pinzón et al., 2014), which can account for a large portion of stream ecosystem respiration (Naegeli & Uehlinger, 1997; Corson-Rikert et al., 2016). Despite the potential high rates of organic matter processing in the hyporheic zone, most studies focus only on the benthic zone, and decomposition processes in the hyporheic zone are not well understood.

Still, several studies have compared leaf litter decomposition between the hyporheic zone and the benthic zone. Some studies reported lower decomposition rates in the hyporheic zone (Metzler & Smock, 1990; Cornut et al., 2010; Peralta-Maraver et al., 2019), whereas others reported similar or higher rates in the hyporheic zone (Solagaistua et al., 2015; Burrows et al., 2017). In the benthic zone, macroinvertebrates play a significant role in leaf litter decomposition. In the hyporheic zone, due to the size of pore space, access of macroinvertebrates may be limited,

and microbes may become the primary decomposers (Cornut et al., 2010; Flores et al., 2013). Microbial-driven leaf litter decomposition may also be lower in the hyporheic zone than the benthic zone (Cornut et al., 2010), although some studies reported comparable decomposition rates (Risse-Buhl et al., 2017). Thus, further studies on organic matter decomposition in the hyporheic zone are needed. Furthermore, the effects of dams on subsurface processes are poorly understood (Graham et al., 2019). Flow regulation that alters frequency, duration and magnitude of flow fluctuation impacts hyporheic exchange flow (Graham et al., 2019), and altered stream water temperature and nutrient concentration downstream are also expected to affect hyporheic processes, especially in the downwelling zone (Franken et al., 2001).

Leaf litter decomposition shows seasonality due to the seasonal changes in environmental factors such as water temperature (Ferreira & Canhoto, 2014; Mora-Gómez et al., 2015). The effects of dams on environmental factors may differ depending on season. For example, presence of a dam generally dampens seasonal variation in water temperature downstream, and the effects on water temperature depend on season (Maheu et al., 2016). The existing studies on the effects of dams are often carried out in a single season (González et al., 2013; Mollá et al., 2017; Salomão et al., 2019), and seasonal variability in the effects of dams on leaf litter decomposition remains understudied.

The present study investigated the effects of dams and reservoirs on organic matter decomposition in the hyporheic and benthic zones by comparing decomposition of cotton-strips, enclosed in coarse-mesh bags that allow macroinvertebrates to enter and in fine-mesh bags that exclude macroinvertebrates, in the reaches downstream of dams and in the unregulated reaches that were located upstream and in a tributary in two forest mountain streams, over five seasons. Cotton-strips were used to keep a consistent initial organic matter quality across sites and seasons (Tiegs et al., 2013; Griffiths & Tiegs, 2016; Peralta-Maraver et al., 2019). We examined (1) whether hyporheic decomposition rates downstream of the dams differed from those at the unregulated reaches in all seasons, (2) whether contribution of macroinvertebrates to decomposition was significant in the hyporheic zone and (3) the relative differences in decomposition rates between the hyporheic zone and the benthic zone.

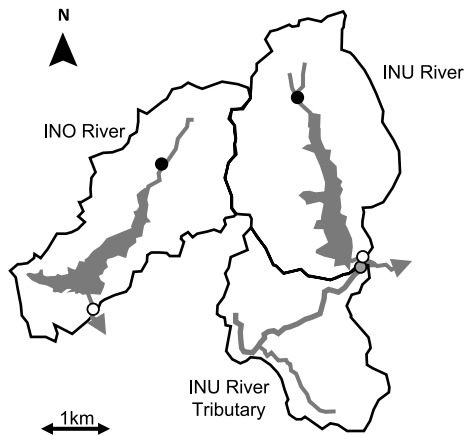


Fig. 1 Location of the study sites within the INO River and INU River watersheds. Open circles indicate where the downstream sites are, and closed circles upstream sites, and grey circle the tributary site

Table 1 Characteristics of the dams and reservoirs constructed in Ino River (INO) and Inunaki River (INU)

	INO	INU
Location	33°41' N, 130°31' E	33°41' N, 130°33' E
Completion year	2000	1994
Height (m)	76.5	79.9
Catchment area (km ²)	5.5	6.1
Active storage capacity (Hm ³)	4.9	4.9
Ave. water retention time (day)	201	204

Materials and methods

Study sites

This study was carried out in the headwater area of two neighboring rivers, the Inunaki (INU) River and the Ino (INO) River, which are both tributaries of the Tataru River that flows into the Hakata Bay in Fukuoka, Japan (Fig. 1). The dams and reservoirs in both rivers were similar in dam height, catchment area, storage capacity, and water retention time (Table 1). Water retention time was calculated as the average volume of water stored in the reservoir divided by the mean annual outflow from the dam. The data of outflow from the dams were provided by Fukuoka Prefecture. Both catchments were covered

by forest, and there were no agricultural fields or industrial facilities in the watershed. The two dams were multi-purpose dams with epilimnetic-release, where water from surface layer of the reservoirs was released downstream.

The study sites were located in a mountain area, where the riparian canopy covered a large portion of the narrow wetted channel, and where the channel gradient was steeper than 0.03 m/m (Table 2). The substrates were dominated by pebbles and cobbles with presence of boulders at all sites. In each river, the downstream site was located about 200 m downstream of the dam. The unregulated sites were located about 200 m upstream from the area flooded by the reservoir in both rivers; for the INU River, an additional unregulated site was set up in a tributary that had similar catchment size and channel size to the downstream site (Fig. 1, Table 2). The downstream sites in the INU River and the INO River were called INU_D and INO_D, respectively, the sites upstream of the reservoirs were called INU_U and INO_U, respectively, and the site in the INU River tributary was called INU_T. All the study sites were set up in the zone of downwelling to examine the effect of altered flow, stream water temperature, and nutrient concentration on hyporheic decomposition rates. Downwelling trend was confirmed by installing piezometers.

The study was carried out in 2016, and annual rainfall that year was 2836 mm, which was higher than the average annual precipitation (2008–2017) of 2099 mm, based on the rainfall data obtained from the nearby Haruda weather station (33°28' N, 130°33' E; 35 m a.s.l.), maintained by the Ministry of Land, Infrastructure, Transport, and Tourism. Rainy season is from June to July, and over 30% of the total annual precipitation fell in these two months in 2016.

Measurement of environmental factors

Several factors that affect organic matter decomposition were measured. A piezometer was installed at each site in November 2015, and water level and vertical head gradient (VHG, m/m) were measured about once a month from February to November 2016. Piezometers were made from PVC pipes by making numerous holes at the bottom 10 cm. The porous portion of the piezometer was inserted to the depth of 20

Table 2 Characteristics of the stream channel, size of the substrate, dissolved oxygen (DO) concentrations, and specific conductance (SC), nitrate concentrations of stream and hyporheic water at each study site in the Ino (INO) River and Inunaki (INU) River. The values in parentheses are a standard deviation.

U indicates upstream site, T indicates tributary site, and D indicates downstream site. D80, D50, and D20 indicate sediment sizes representing the 80%, 50% and 20% cumulative percentile values

		n	INO River		INU River		
			INO_U	INO_D	INU_U	INU_T	INU_D
Altitude (m)			175	103	262	152	148
Ave. channel width (m)			4.8	6.0	3.3	6.7	5.7
Ave. water depth (m)			0.19	0.19	0.10	0.26	0.23
Bed gradient (m/m)			0.08	0.03	0.11	0.09	0.06
D ₈₀ , D ₅₀ , D ₂₀ (mm)			105, 42, 8	152, 94, 1	59, 13, 7	250, 45, 18	180, 60, 14
DO (mg/l)	Stream	8	8.3 (1.2)	7.7 (1.1)	8.2 (0.9)	7.6 (0.9)	7.6 (0.9)
	Hypo	8	5.7 (1.5)	3.3 (1.5)	6.4 (1.3)	2.2 (1.3)	2.2 (1.3)
SC (µS/cm)	stream	8	112.8 (11.0)	110.0 (9.2)	103.9 (18.9)	109.5 (10.4)	96.2 (11.5)
	Hypo	8	108.8 (11.8)	101.0 (17.7)	96.7 (21.2)	105.1 (16.4)	144.2 (38.4)
NO ₃ ⁻ (mg/l)	Stream	6	0.9 (0.2)	0.7 (0.1) *	1.3 (0.1)	1.2 (0.2)	1.1 (0.3) *
	Hypo	6	1.1 (0.3)	0.9 (0.2)	1.4 (0.3)	1.4 (0.4)	0.3 (0.4) * †

* † Downstream site was significantly different from *upstream site and †tributary site (ANOVA, $P < 0.01$)

to 30 cm. The piezometer was also used to sample hyporheic water for analysis of chemical components.

Dissolved oxygen (DO, mg/l), specific conductance (µS/cm) and water temperature (°C) of stream and hyporheic water were measured in-situ at each study site about eight times during February to November 2016, using a portable sensor in the piezometers (YSI Pro2030, OH, USA). Stream water temperature during each incubation was measured at 10 min intervals using the pendant data loggers in stream channel (HOBO, MA, USA). Hyporheic water and stream water were also sampled about six times during February to November 2016, and the samples were brought back to the laboratory on ice and filtered within 24 h using 0.7-µm glass-fiber filters. The filtered samples were stored in the refrigerator until analysis. We run the samples through ion chromatography (DX-120, Dionex, Osaka, Japan) to determine the concentrations of inorganic nitrogen (NO₃⁻, NH₄⁺) after passing the samples through 0.45-µm membrane filter immediately prior to the analyses.

Particle size distribution of streambed sediment was estimated by measuring > 100 particles at each site, covering the area of two riffle-pool sequences. In addition, in the INU River, freeze cores were taken to measure particle size distribution and organic matter content of hyporheic sediment. Freeze cores were taken from the depth of 15 to 30 cm, and three

samples were taken from each INU River site. The cores were taken back to the laboratory, dried at 60°C oven for 72 h and sieved to measure particle size distribution. The fraction of organic matter in the sediment that was < 1 mm in size was measured from the mass loss after putting the samples of sediment in 550°C furnace for 6 h. Because we did not find visible coarse organic matter in the samples, only the sediment samples < 1 mm in size were analyzed.

Measurements of cotton strip decomposition

The cotton-strip assay was used to measure organic matter decomposition rates in this study. To evaluate the seasonal variation in decomposition rates, the cotton-strip assay was carried out five times in 2016: in winter (starting on February 2nd), spring (May 2nd), rainy season (June 27th), summer (August 5th), and autumn (November 4th). The cotton strip assay was carried out following the protocol described in Tiegs et al. (2013). Cotton-strips used were approximately 8-cm long and 2.5-cm wide and made from a roll of Fredrix-brand unprimed 12-oz. heavy-weight cotton fabric, Style#548 (Tiegs et al., 2013). Each cotton-strip was inserted to a plastic mesh bag during incubation in the hyporheic zone and the benthic zone. Two different mesh sizes, 5 and 0.1 mm, were used to make the bags for cotton-strips. The 5-mm mesh bags

allowed macroinvertebrate access to cotton-strips, whereas the 0.1-mm mesh bags prevented macroinvertebrate access (Gonçalves et al., 2006; Braatne et al., 2007).

Two cotton-strips, one in a 5-mm mesh bag and another in a 0.1-mm mesh bag, were treated as a set, and five sets each were placed in the hyporheic zone and the benthic zone at each site. Thus, there were total of 20 cotton-strips incubated at each site in each season. The mesh bags, which housed the cotton-strips, were tied to a nylon cord (4 mm in diameter) using banding bands, and the nylon cord was fixed to a rebar hammered into the streambed so that the cotton-strips in the hyporheic zone could be found easily at the time of collection, and the cotton-strips in the benthic zone would not be washed downstream. In the hyporheic zone, cotton-strips were buried in the sediments to a depth of 10–15 cm in the downwelling zone. The effects of stream water in the downwelling zone decrease with depth, and thus relatively shallow depth was selected. Cotton-strips were placed parallel to the streambed, and the sediment was gently placed back to minimize the damage by installation. In the benthic zone, cobbles were placed on the nylon cord and the edges of mesh bags, not on the cotton-strips, so that the cotton-strips remained in the benthic zone.

To determine the length of incubation period, a preliminary trial was carried out to estimate the time to reach 50% tensile strength loss (TSL) in autumn 2015. Twelve cotton-strips in 5-mm mesh bags were placed in the hyporheic zone and in the benthic zone, and three cotton-strips were removed every week for a month. The results suggested that 20 days of incubation was sufficient to reach 50% TSL in both the hyporheic zone and the benthic zone.

The cotton-strips removed from the hyporheic zone and the benthic zone were gently handled to minimize the loss of tensile strength due to handling. Mesh bags that housed cotton-strips were cut open, and the cotton-strips were placed in 80% ethanol for approximately 30 s. Attached sediments were then removed using distilled water and a soft brush. The cotton-strips were oven-dried at 40 °C and stored in a desiccator until tensile strength measurements.

A tensile tester (Shimazu AG 100kNE, Kyoto, Japan) was used to measure tensile strength of the cotton-strips. The grips were placed at approximately 1 cm from the end of the strips and tighten so that grips would not slip during the measurement, or the

strip would not tear at where the grips were placed. The rate the tension on the strip increases was set to 2 cm/min. The maximum tensile strength was recorded, and TSL per day was calculated using the following equation (Griffiths & Tiegs, 2016):

$$\begin{aligned} & \text{Tensile strength loss}(\%/d) \\ & = \left(1 - \frac{\text{Tensile strength}_{\text{incubated}}}{\text{Tensile strength}_{\text{reference}}} \right) / \text{incubation days} \times 100 \end{aligned} \quad (1)$$

where tensile strength_{incubated} is the maximum tensile strength of the cotton-strips removed from the hyporheic zone or the benthic zone after incubation, and tensile strength_{reference} is the mean maximum tensile strength of five strips that were not placed in the stream, but were cleaned with 80% ethanol, oven-dried at 40 °C, and stored in the desiccator.

Water temperature strongly influence TSL (Griffiths & Tiegs, 2016), and to normalize the effects of water temperature, we also calculated TSL per degree-days by substituting the incubation days in the Eq. 1 by degree-days. Degree-days were calculated by summing up the daily mean stream water temperature for the incubation period.

Contribution of macroinvertebrates to cotton strip decomposition

Contribution of macroinvertebrate to decomposition was assessed using cotton-strips in bags with two different mesh sizes. The cotton-strips in 5-mm mesh bags were accessible to macroinvertebrates. In contrast, the cotton-strips in 0.1-mm mesh bags excluded macroinvertebrates. Tiegs et al. (2013) suggested that cotton-strips were not a palatable food resource for invertebrates, and thus the use of cotton-strips might not be suitable to examine decomposition by invertebrates. However, in this study, the cotton-strips after incubation in the benthic zone showed apparent differences in size and shape between the two mesh bags (Fig. 2). All cotton-strips in 0.1-mm mesh bags maintained rectangular shapes, whereas the sizes of the several cotton-strips in 5-mm mesh bags became smaller and jagged after 20 days of incubation, suggesting a contribution of macroinvertebrates to decomposition. The cotton-strips are basically cellulose, and it differs in quality from leaf litter. Thus, contribution of macroinvertebrate to organic matter

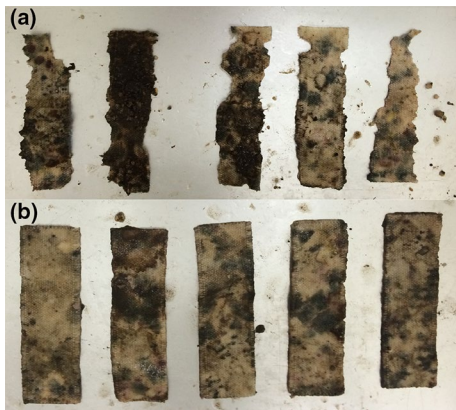


Fig. 2 Examples of cotton-strips incubated in the benthic zone for 20 days. **a** cotton-strips in 5 mm mesh bags, and **b** cotton-strips in 0.1 mm mesh bags

decomposition estimated from this experiment may be lower than the contribution estimated from experiments using leaf litter. However, we considered that this approach could still be used to compare relative contribution of macroinvertebrates among sites.

The differences in TSL of the strips between the two types of bags were used to calculate the effects of macroinvertebrates on decomposition rates following Eq. 2 (Mora-Gomez et al., 2016):

$$\begin{aligned} & \text{Effects of macroinvertebrates(\%)} \\ & = \left(1 - \left(\frac{\text{Tensile strength loss}_{0.1\text{mm}}}{\text{Tensile strength loss}_{5\text{mm}}} \right) \right) \times 100 \end{aligned} \quad (2)$$

To support the estimated contribution of macroinvertebrates to decomposition calculated from TSL, sampling of hyporheic invertebrate was carried out at INU_D and INU_T sites in March 2016. Abundances of hyporheic invertebrates and its community composition were compared between the two sites. Three replicate samples were collected at each sampling site from a depth of 15 to 30 cm using the freeze core method (Stocker & Williams, 1972). The collected freeze cores were gently removed from the pipe, brought back to the laboratory while keeping the temperature low, and stored temporarily in a quick freezer (-30°C). Each core taken out from the freezer was returned to room temperature, and the sample volume was measured by Archimedes' principle. The samples were separated into invertebrates, organic matter and

sediment by the floating sorting method. The invertebrates and organic matter were transferred to sample bottles and fixed with 70% ethanol. The invertebrates sorted by sieves (0.063 and 0.125 mm) were examined under a stereomicroscope with a magnification of 10–80 \times (Nikon, SMZ800N). Testacean amoebae (Protozoa: Sarcomastigophora) were identified and counted at a stereomicroscope, and used for analysis together with hyporheic invertebrates. Hyporheic invertebrates were identified to the most precise taxonomic level using keys provided in Kawai & Tanida, (2005) and Mizuno & Takahashi (1991). Each taxon was assigned to a functional feeding group (FFG; collector-filterers, collector-gatherers, grasping feeders, predators, scrapers, shredders), according to Takemon (2005), Kobayashi (2019), Thorp & Covich (2010), and Merritt et al. (2008). Some taxa are known to have different FFG among the subordinate taxa, and all applicable FFG were assigned to those taxa.

Data analysis

All values were reported as mean \pm standard deviation. The differences among sites in mean TSL, daily mean temperature, and nitrate concentration was tested using a one-way analysis of variance (ANOVA). ANOVA was also used to compare TSL between 5-mm and 0.1-mm mesh bags, and between hyporheic zone and benthic zone. Effects of water temperature on TSL was tested using analysis of co-variance. The effect of study site and seasons, and their interaction was tested using the two-way ANOVA. The density of hyporheic invertebrate assemblage between INU_T and INU_D were compared using Kruskal–Wallis test.

Results

Environmental factors

Inflow into the reservoir and release from the dam showed that the flow fluctuation patterns were similar because both dams had epilimnetic release (Fig. 3). The exceptions were during the low flow period over the winter, when inflow peaks did not propagate to the dam release, and in August, when the release was artificially increased to prepare for the typhoon season in September and October. During

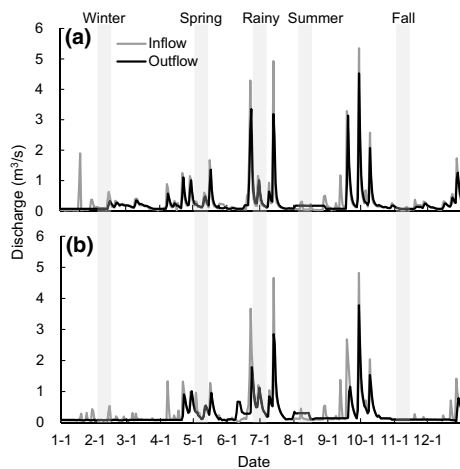


Fig. 3 Inflow to the reservoir (grey lines), and release from the dam (black lines) in **a** the INO River and **b** the INU River. Shaded areas indicate the periods that the cotton-strips were incubated

incubation experiments in spring and rainy season, the study sites experienced several high peak flows, whereas during winter, summer and fall incubation, the flow was relatively stable (Fig. 3). Vertical head gradients (VHG) showed that all the incubation sites maintained downwelling trend throughout the year (Fig. 4ab). In the INU River, the downwelling trend was weaker compared to the INO River, and during the rainy season, the site shifted slightly to upwelling trend (Fig. 4b). In the INO river, downwelling trend was often stronger at INO_D than INO_U (Fig. 4a).

The lowest mean daily stream water temperature (less than 10 °C) was observed in winter, and it gradually increased in spring and rainy season (Fig. 5ad, Table 4). The highest mean water temperature was observed in summer (exceeding 20°C at all sites) and then it decreased in fall. The differences between the two rivers were small when water temperature at upstream sites was compared (Table 4). Sites downstream of the dams had significantly warmer water temperature than upstream sites in both rivers, except for spring in the INO River and winter in the INU River (Table 4). INU_T showed significantly lower water temperature than INU_D in all seasons (Table 4).

Concentrations of dissolved oxygen in the hyporheic zone showed seasonal trend at all sites, except for INU_D site (Fig. 4cd). Concentrations were high during spring, gradually decreased to a minimum in

summer and increased again during autumn. Concentrations of dissolved oxygen in the hyporheic zone were lower at downstream sites than at unregulated sites in both rivers throughout the year (Fig. 4cd).

Concentrations of nitrate-N in the hyporheic zone fluctuated and did not show apparent seasonality, except for INU_D where slightly higher values were observed from July to October (Fig. 4ef). In the INO River, the mean concentrations of nitrate-N did not significantly differ between INO_U and INO_D (Fig. 4e, Table 2), but INO_D had lower nitrate-N concentration than INO_U at all sampling date, except for June. In the INU River, the mean concentrations were significantly lower at INU_D compared to INU_U and INU_T (Fig. 4f, Table 2).

Streambed substrate was dominated by pebbles and cobbles at all sites, where D50 ranged from 13 to 94 mm across sites (Table 2). D50 of the hyporheic sediment, measured from freeze cores, was 14 mm at INU_U and INU_T, and 26 mm at INU_D. Fractions of organic matter in < 1 mm sediment size were similar among sites, 5.5 (±0.4) % at INU_U, 3.4 (±1.0) % at INU_T, and 5.5 (±0.7) % at INU_D.

Tensile strength loss (TSL) in the hyporheic zone

For cotton-strips in 5-mm mesh bags, TSL in the hyporheic zone (TSL_{hypo}) was significantly lower by 0.7 to 1.7%/d downstream of the dams than at unregulated sites in all seasons, except on summer in both rivers and on winter in the INU River (Fig. 5b, e, Table 3). For cotton-strips in 0.1-mm mesh bags, TSL_{hypo} was significantly lower by 0.7 to 1.5%/d downstream of the dams than at unregulated sites in spring and fall in both rivers, and in winter in the INU River (Fig. 6b, e). Thus, the trend of lower TSL_{hypo} at the downstream sites was observed in both rivers but it was not maintained in all seasons.

TSL_{hypo} showed seasonality in both rivers, where the lowest values were found in winter and the highest values in the rainy season and summer (Figs. 5be, 6be). This seasonal variation in TSL_{hypo} was similar to the seasonal variation in stream water temperature. When degree-days were used in TSL_{hypo} calculation to remove the effects of water temperature, seasonality of TSL_{hypo} disappeared at all sites (Figs. 5cf, 6cf), suggesting that water temperature was the primary factor resulting in seasonal variation in TSL_{hypo} .

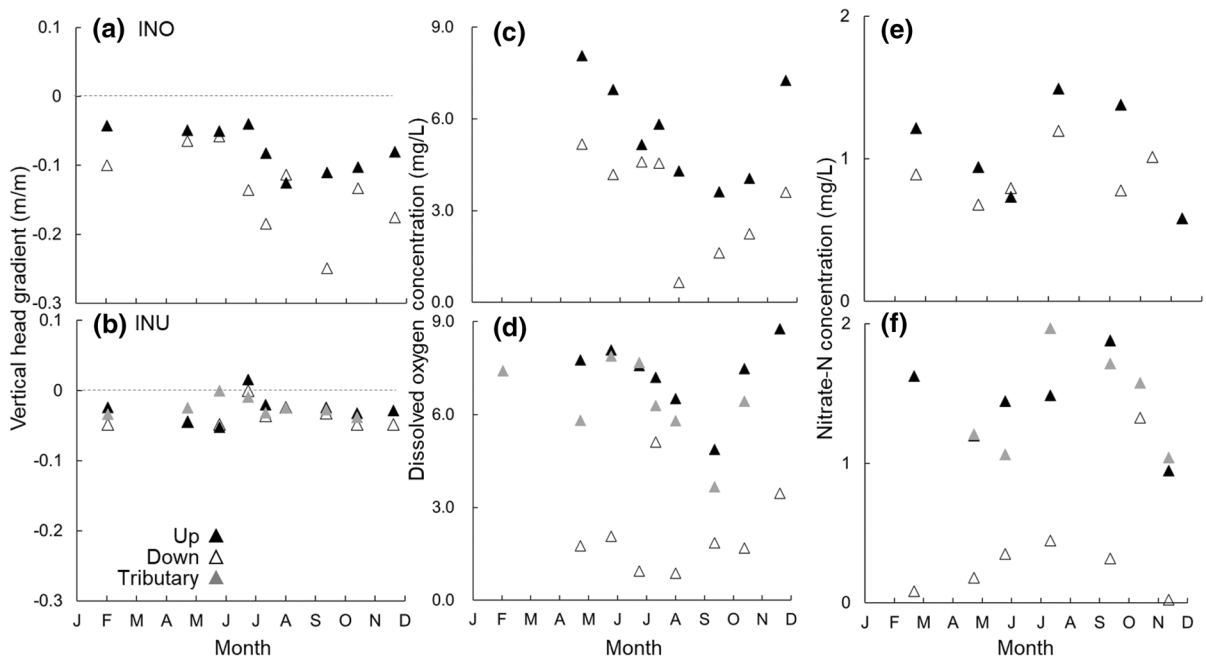


Fig. 4 Vertical head gradients measured at **a** the INO River and **b** the INU River. The negative values indicate downwelling of stream water into the hyporheic zone. Dissolved oxygen concentrations of hyporheic water in **c** the INO River

and **d** the INU River. Nitrate-N concentration of hyporheic water in **e** the INO River and **f** the INU River. Open symbols indicate downstream sites, black symbols upstream sites, and grey symbols tributary site

Comparison of tensile strength loss between the hyporheic and benthic zones

To compare the differences in organic matter decomposition rates between the hyporheic and benthic zones, the TSL from the cotton-strips in 5-mm mesh bags, that allow access of macroinvertebrate, was used. TSL_{hypo} was significantly lower than TSL_{stream} by 0.5 to 1.7%/d in the INO River from spring to fall, and by 0.1 to 1.1%/d in the INU River from spring to summer (Table 3). In winter, mean TSL_{hypo} was higher than TSL_{stream} by 0.5 to 0.8%/d in the INO River and 0.3 to 1.0%/d in the INU River, although the difference was significant only at INU_D.

Contribution of macroinvertebrate to tensile strength loss in the hyporheic zone

Contribution of macroinvertebrates to the decomposition rates were estimated using the differences in TSL_{hypo} between cotton-strips in the two mesh sizes. The mean TSL_{hypo} from 5-mm mesh bags showed higher values compared to TSL_{hypo} from 0.1-mm

mesh bags, but the differences were not significant in many seasons. In the INO River, the significant differences were only observed in winter at INO_U and in rainy season at INO_D (Table 4), and the estimated contribution of macroinvertebrate to decomposition was 50 (± 17) % and 12 (± 7)%, respectively. In the INU River, the significant differences were observed at INU_U in Spring, and at INU_D in winter (Table 4); the estimated contribution of macroinvertebrate was 9 (± 6) % at INU_U in spring and 53 (± 36) % at INU_D in winter. At INU_T, the differences between TSL_{hypo} of 5-mm and 0.1-mm mesh bag were not significant in all seasons. Thus, the seasons with significant contribution by macroinvertebrate was limited and was not consistent among sites.

Hyporheic samples at INU_D and INU_T retrieved 72 invertebrate taxa from six phyla. The dominant taxa in hyporheic invertebrate assemblages 0.063 to 0.125 mm in size were Centropyxis, Diffugia and other Testacealobosia at INU_T, and Diffugia and Centropyxis at INU_D (Table 5). The dominant taxa of hyporheic invertebrate assemblages >0.125 mm in size were Nematoda, Harpacticoida, Centropyxis, and

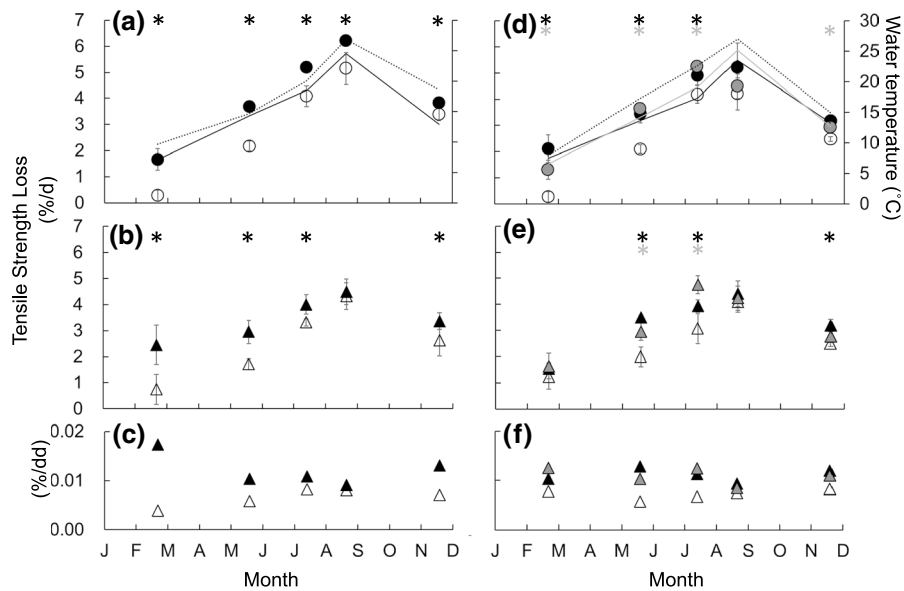


Fig. 5 Tensile strength loss per day calculated from the cotton-strip in 5 mm mesh in the benthic zone in **a** the INO River and **d** the INU River, and in the hyporheic zone in **b** the INO River and **e** the INU River. The error bars show one standard deviation. The black asterisk (*) indicate significant difference between the downstream and upstream sites, and gray asterisk (*) between the downstream and tributary sites (ANOVA,

$n=5, P<0.05$). Dashed lines indicate water temperature variation at downstream sites, and solid and grey lines at upstream and tributary sites, respectively. Tensile strength loss per degree day in **c** the INO River and **f** the INU River. Open symbols indicate downstream sites, black symbols upstream sites, and grey symbols the tributary site

Table 3 Tensile strength loss (\pm SD, $n=5$, %/d) in benthic and hyporheic zone in 5 seasons. Values are from the cotton-strips in 5 mm mesh bag. Statistical significance of the comparison between benthic and hyporheic zone is shown using

*($P<0.05$) and **($P<0.01$) based on the results of ANOVA. N.S. indicates no significant differences. U indicates upstream site, T indicates tributary site, and D indicates downstream site

INO River	INO_U			INO_D					
	Benthic	Hyporheic		Benthic	Hyporheic				
Winter	1.66 (0.40)	2.45 (0.75)	N.S	0.28 (0.21)	0.75 (0.57)	N.S			
Spring	3.68 (0.13)	2.95 (0.44)	*	2.17 (0.20)	1.71 (0.21)	**			
Rainy	5.19 (0.17)	4.01 (0.37)	**	4.09 (0.40)	3.32 (0.13)	*			
Summer	6.21 (0.10)	4.49 (0.50)	**	5.15 (0.61)	4.32 (0.51)	*			
Fall	3.82 (0.09)	3.37 (0.31)	*	3.38 (0.24)	2.62 (0.59)	*			
INU River	INU_U		INU_T		INU_D				
	Benthic	Hyporheic	Benthic	Hyporheic	Benthic	Hyporheic			
Winter	2.12 (0.53)	1.55 (0.52)	N.S	1.31 (0.36)	1.64 (0.48)	N.S	0.27 (0.20)	1.23 (0.47)	**
Spring	3.45 (0.33)	3.50 (0.08)	N.S	3.65 (0.17)	2.95 (0.32)	**	2.10 (0.16)	1.99 (0.38)	N.S
Rainy	4.91 (0.37)	4.00 (0.23)	**	5.24 (0.17)	4.75 (0.35) [†]	N.S	4.18 (0.34)	3.07 (0.58)	*
Summer	5.22 (0.93)	4.40 (0.49)	N.S	4.49 (0.46)	4.24 (0.92)	N.S	4.21 (0.61)	4.08 (0.38)	N.S
Fall	2.90 (0.18)	3.18 (0.24)	N.S	2.93 (0.24)	2.77 (0.36)	N.S	2.21 (0.52)	2.48 (0.09)	N.S

[†]Number of samples were reduced to 3 because two were washed out during the incubation

Diffugia in INU_D, and Harpacticoida, Centropyxis, and Nematoda at INU_T. These dominant taxa constituted more than 70% of the average total population density in each size and site (Table 5). The mean density of hyporheic invertebrates, including testate amoeba, 0.063 to 0.125 mm in size was significantly higher at INU_D than at INU_T (Kruskal–Wallis; $P=0.0495$), whereas the mean density of hyporheic invertebrates >0.125 mm in size was not significantly different between the two sites (Table 6, Fig. 7).

Considering hyporheic invertebrates 0.063 to 0.125 mm in size by FFG, the densities of PR and CG/PR were significantly higher at INU_D than at INU_T (Kruskal–Wallis test; respectively $P=0.0495$ and $P=0.0369$, Table 6). Considering hyporheic invertebrates >0.125 mm in size, the density of SC was significantly higher at INU_T than at INU_D (Kruskal–Wallis test; $P=0.0369$, Table 6, Fig. 7b). When comparing the total density of SC and CF/SC, there was no significant difference between sites (Kruskal–Wallis test; $P=0.1266$). The SC contained temporary interstitial organisms such as some Coleoptera (i.e. Elmidae, *Elodes*) and some

Ephemeroptera (i.e. *Ameletus*, *Ecdyonurus*), while the CF/SC contained permanent interstitial organisms such as some Crustacea (i.e. *Alona*, Harpacticoida) and Bdelloidea.

Discussion

Effects of dams and reservoirs on hyporheic decomposition rates

Decomposition rates in the hyporheic zone in two rivers were lower downstream of the dams, compared to the unregulated reach located upstream and in a tributary, in spring, rainy season and fall. In winter and summer, when decomposition rates were lowest and highest respectively, the differences between downstream and unregulated sites were not significant. There are no studies that examined the effects of dams on hyporheic decomposition rates as far as we know, but there are several studies that examined the effects of dams on benthic decomposition rates. The studies in the benthic zone showed lower decomposition rates

based on the results of ANOVA. N.S. indicates no significant differences. U indicates upstream site, T indicates tributary site, and D indicates downstream site

Table 4 Tensile strength loss (\pm SD, n=5, %/d) in two mesh sizes in the hyporheic zone and stream water temperature (\pm SD, n=18) in 5 seasons. Statistical significance of the comparison between 5 mm and 0.1 mm is shown using * ($P<0.05$)

INO River		INU_U				INU_D						
Season	(°C)	5 mm	0.1 mm		(°C)	5 mm	0.1 mm					
Winter	7.1 (1.1)	2.45 (0.75)	1.19 (0.43)	*	9.7 (0.6) [‡]	0.75 (0.57)	0.45 (0.69)	N.S				
Spring	14.3 (0.7)	2.95 (0.44)	2.84 (0.31)	N.S	14.6 (0.9)	1.71 (0.21)	1.64 (0.67)	N.S				
Rainy	18.5 (0.9)	4.01 (0.37)	3.59 (0.46)	N.S	20.0 (1.1) [‡]	3.32 (0.13)	2.92 (0.19)	*				
Summer	24.5 (0.3)	4.49 (0.50)	4.27 (0.74)	N.S	26.8 (0.4) [‡]	4.32 (0.51)	4.10 (0.22)	N.S				
Fall	12.9 (1.1)	3.37 (0.31)	3.05 (0.58)	N.S	18.6 (0.6) [‡]	2.62 (0.59)	1.93 (0.47)	N.S				
INU River		INU_U			INU_T			INU_D				
Season	(°C)	5 mm	0.1 mm		(°C)	5 mm	0.1 mm	(°C)	5 mm	0.1 mm		
Winter	7.5 (0.7)	1.55 (0.22)	1.77 (0.38)	N.S	6.6 (1.0)	1.64 (0.48)	1.13 (0.43)	N.S	7.7 (0.6) [‡]	1.23 (0.47)	0.51 (0.20)	*
Spring	13.7 (0.4)	3.50 (0.08)	3.18 (0.20)	*	14.2 (0.7)	2.95 (0.32)	2.81 (0.22)	N.S	17.3 (1.0) ^{‡‡}	1.99 (0.38)	2.23 (0.39)	N.S
Rainy	17.4 (0.7)	4.00 (0.23)	4.15 (0.18)	N.S	19.2 (1.2)	4.75 (0.35) [†]	4.15 (0.18)	N.S	22.6 (1.5) ^{‡‡}	3.07 (0.58)	2.82 (1.10)	N.S
Summer	23.5 (0.2)	4.40 (0.49)	3.82 (0.58)	N.S	26.8 (0.4)	4.24 (0.92)	3.82 (0.58)	N.S	27.0 (0.4) ^{‡‡}	4.08 (0.38)	3.99 (0.58)	N.S
Fall	13.3 (0.5)	3.18 (0.24)	3.30 (0.54)	N.S	12.6 (1.2)	2.77 (0.36)	2.55 (0.12)	N.S	15.0 (0.6) ^{‡‡}	2.48 (0.09)	2.38 (0.64)	N.S

^{‡‡}Downstream site was significantly different from [‡]upstream site and [†]tributary site ($P<0.01$)

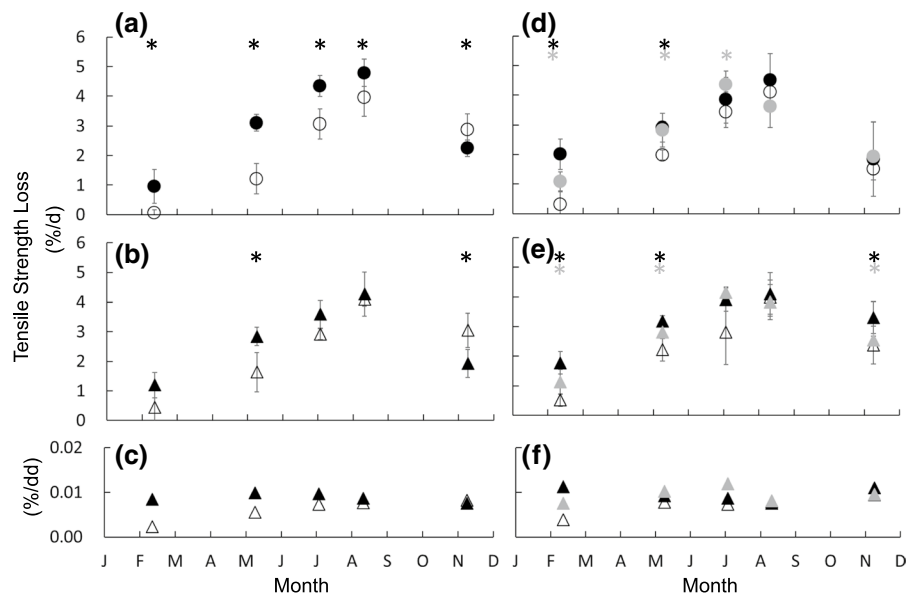


Fig. 6 Tensile strength loss per day calculated from the cotton-strip in 0.1 mm mesh in the benthic zone in **a** the INO River and **d** the INU River, and in the hyporheic zone in **b** the INO River and **e** the INU River. The error bars show one standard deviation. The black asterisk (*) indicate significant difference between the downstream and upstream sites, and gray asterisk (*) between the downstream and tributary sites

(ANOVA, $n=5$, $P<0.05$). Dashed lines indicate water temperature variation at downstream sites, and solid and grey lines at upstream and tributary sites, respectively. Tensile strength loss per degree day in **c** the INO River and **f** the INU River. Open symbols indicate downstream sites, black symbols upstream sites, and grey symbols the tributary site

at downstream of epilimnetic-release dams, and the lower rates were explained by altered water quality and microbial and invertebrate activities (Mendoza-Lera et al., 2012; Menéndez et al., 2012; González et al., 2013). Many of those studies were carried out only in one or two seasons, but Li et al. (2020) studied over five seasons and found lower decomposition rates downstream of the dam in all seasons. Thus, the results of this study and findings from previous studies suggest that the presence of dams and reservoirs results in lower decomposition rates downstream not only in the benthic zone but also in the hyporheic zone. The effects of dam may be consistent throughout the year in the benthic zone (Li et al., 2020), but in the hyporheic zone, the effects may be significant only in some seasons.

Various environmental factors, such as flow, nutrient concentration and water temperature, and biological activities of invertebrates and microbes influence decomposition rates (Young et al., 2008). Inflow to and outflow from the reservoir showed that peak flow magnitudes were dampened at downstream sites in both rivers. Flow fluctuations affect decomposition

rates in the benthic zone through abrasion, but the effects in the hyporheic zone is considered limited (Boulton & Quinn, 2000). Water temperature influenced decomposition rates in the benthic zone (Li et al., 2020). Increase in water temperature stimulates microbial and invertebrate activities, and results in higher decomposition rates (Ferreira & Canhoto, 2014). In this study, when the TSL_{hypo} was normalized by water temperature, seasonality of TSL_{hypo} disappeared (Figs. 5cf, 6cf), and mean TSL_{hypo} showed a positive correlation with surface water temperature in both rivers (Fig. 8). These results suggest that in the shallow hyporheic zone of downwelling, where strong influence of stream water is expected, stream water temperature plays a primary role in the seasonal variations of hyporheic decomposition rates.

When water temperature was compared among sites, the downstream sites were warmer than unregulated sites in almost all seasons, because both dams released water from surface. Temperature differences between the downstream and unregulated sites were more than 3°C from spring to summer in the INU River and in fall in the INO River, but the difference

Table 5 Dominant taxa of hyporheic invertebrates in unregulated tributary site (INU_T) and downstream site (INU_D) in the INU River, ranked in decreasing order of abundance (innumber of individuals/1000 cm.³ and percentage). †Dominant taxa and percentage when excluding testate amoebae

0.063 ~ 0.125 mm							
Dominant taxa	INU_T			Dominant taxa	INU_D		
	Abundance	%			Abundance	%	
<i>Centropyxis</i>	834.0	35.8		<i>Diffugia</i>	15,461.7	63.0	
<i>Diffugia</i>	803.9	34.5		<i>Centropyxis</i>	5790.9	23.6	
Other Testacealobosia	593.5	25.5		Nematoda	1552.8	6.3	
Total 3 taxa		95.8		Total 3 taxa		92.9	
> 0.125 mm							
Dominant taxa	INU_T			Dominant taxa	INU_D		
	Abundance	%	% [†]		Abundance	%	% [†]
Harpacticoida	334.5	31.6	45.9	Nematoda	3959.4	40.2	60.5
<i>Centropyxis</i>	257.3	24.3		Harpacticoida	1676.2	17.0	25.6
Nematoda	179.5	17.0	24.6	<i>Centropyxis</i>	1519.2	15.4	
Other Chironomidae	37.4	3.5	5.1	<i>Diffugia</i>	1115.1	11.3	
<i>Diffugia</i>	37.1	3.5		Other Testacealobosia	661.5	6.7	
Cyclopoida	33.6	3.2	4.6	Oribatida [†]	413.1		6.3
Oribatida	26.6	2.5	3.6	Total 6 and 3 [†] taxa		90.8	92.4
Oligochaeta	23.8	2.2	3.3				
Podocopida	21.3	2.0	2.9				
Other Testacealobosia	16.4	1.6					
Total 10 and 7 [†] taxa		91.4	90.1				

was smaller during winter. Ferreira & Canhoto (2015) showed that warming by about 3°C stimulated litter decomposition but only in cold months. The temperature differences of less than 3°C in winter may be a factor, resulting in no significant differences in hyporheic decomposition rates between downstream and unregulated sites. Besides, the temperature differences between downstream and the unregulated sites were relatively small, compared to seasonal variation. The differences between summer and winter water temperature were larger than 15°C. Therefore, downstream sites had higher water temperature, but the differences were not large enough to affect decomposition processes.

Nutrient concentration is another factor positively influencing decomposition rates (Ferreira et al., 2015). For example, enrichment of nitrate resulted in increased microbial biomass and higher decomposition rates of leaf litter (Ferreira et al., 2006). In this study, nitrate-N and DO concentrations on hyporheic water downstream of the dams

were often lower than the unregulated sites. Pooling of water in reservoirs increases opportunities for denitrification and results in lower nitrate-N concentrations downstream of dams (David et al., 2006; Harrison et al., 2009). The same trend was observed in this study, where the nitrate concentrations at the unregulated site was about 0.2 mg/l higher than at the downstream sites (Li et al., 2020). All the study sites had downwelling trend, and nitrate-N concentrations in the hyporheic zone were influenced by the concentrations of surface water. In addition, DO concentrations in the hyporheic zone downstream of the dams were lower than at the unregulated sites, and sometimes even below 2.0 mg/l, favoring denitrification. Thus, lower nitrate-N and DO concentrations in the hyporheic zone downstream of the dams might have contributed to the lower decomposition rates.

Macroinvertebrates are often considered as primary players in leaf litter decomposition in the benthic zone. Shredders, especially, play an important

Table 6 Density (\pm SD) and dominant ratio of hyporheic invertebrates divided by functional feeding groups (FFG) in unregulated tributary site (INU_T) and downstream site (INU_D) in the INU River, ranked in decreasing order of density (in number of individuals/1000 cm³ and percentage). Abbreviation explanation of FFG; CF: collector-filterers; CG:

collector-gatherers; SH: shredders; SC: Scrapers; PR: predators; GR: grasping feeders; —: a group to which no FFG was assigned. Explanation of connection symbols between two FFG; –: and; /: or. The asterisks (*) indicate that the densities of the FFG were significantly more than that in another site by the Kruskal–Wallis test ($P < 0.05$)

INU_T			INU_D				
FFG	Density (\pm SD)	%	FFG	Density (\pm SD)	%		
0.063~0.125 mm			0.063~0.125 mm				
PR	2306.4	\pm 1241.5	99.0	PR	*22,612.1	\pm 17,766.7	92.1
CF / SC	22.6	\pm 39.1	1.0	CG / PR	*1552.8	\pm 835.7	6.3
				CF	377.0	\pm 327.9	1.5
> 0.125 mm			> 0.125 mm				
PR	398.6	\pm 425.1	37.7	CG / PR	3959.4	\pm 3122.1	40.2
CF / SC	334.5	\pm 422.3	31.6	PR	3295.8	\pm 3893.8	33.5
CG / PR	179.5	\pm 248.3	17.0	CF / SC	1684.6	\pm 1465.0	17.1
CG	54.0	\pm 82.6	5.1	CG	431.3	\pm 553.1	4.4
—	40.0	\pm 48.9	3.8	PR	417.3	\pm 666.8	4.2
GR	33.6	\pm 47.7	3.2	GR	22.0	\pm 8.8	0.22
SC	*7.4	\pm 4.4	0.70	—	15.4	\pm 4.2	0.16
CG / CF	4.7	\pm 4.1	0.44	CF	11.7	\pm 11.5	0.12
SH–CG	2.6	\pm 4.6	0.25	CG / CF	3.3	\pm 2.0	0.034
CF	2.1	\pm 1.8	0.19	SH	0.39	\pm 0.67	0.0039
SH	1.2	\pm 1.3	0.12	SH–CG	0.35	\pm 0.60	0.0035
CG–PR	0.44	\pm 0.76	0.042				

role, and differences in decomposition rates among sites have been explained by differences in the abundance of shredders in several studies (Mendoza-Lera et al., 2012; González et al., 2013; Mbaka & Schafer, 2015). In the hyporheic zone too, shredders were important players (Navel et al., 2009), and grazing activity by hyporheic invertebrates also enhanced microbial activity (Boulton, 2007). In this study, contribution of macroinvertebrates to decomposition was estimated using two mesh sizes, and found that their contribution was often not significant in the hyporheic zone. Each site showed significant contribution of macroinvertebrates in just one season. The benthic zone, on the other hand, showed a significant contribution of macroinvertebrate in many seasons at all sites (Li et al., 2020). In the INU River, densities of hyporheic invertebrate > 0.125 mm in size was much lower than those of ≤ 0.125 mm in size, and limited access of macroinvertebrate to the hyporheic zone due to small pore sizes may have resulted in lower contribution of macroinvertebrates to decomposition (Cornut et al., 2010; Flores et al., 2013). In addition,

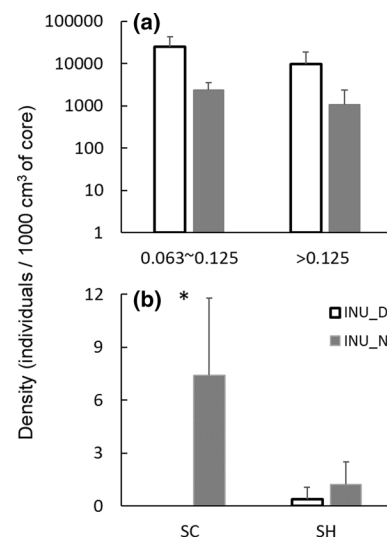


Fig. 7 **a** Density of hyporheic invertebrate (individuals/1000 cm³ of core) in two size groups (0.063~0.125 mm and > 0.125 mm), **b** density of scraper (SC) and shredder (SH) at INO_D and INO_N sites. The error bars indicate 1 standard deviation. The asterisk (*) indicates significant difference between INO_D and INO_N ($P < 0.05$)

densities of shredders and scraper were low at both INU_D and INU_T. Thus, both the results of TSL and sampling of hyporheic invertebrates suggested lower contribution of macroinvertebrates in the hyporheic zone, and macroinvertebrates did not explain the seasonality in the downstream effects in this study.

We need to bear in mind that cotton-strips and their tensile strength loss were used in this study. The observed changes in shape of many cotton strips in 0.5 mm mesh bags in the benthic zone after just 20 days of incubation were considered as the signs of shredder activities. However, the cotton-strips are basically cellulose, and the quality is different from leaf litter. Tensile strength loss is sensitive for fiber cutting by macroinvertebrate activities and fiber maceration by microbial activity, and their relative effects are not known. Thus, the results of this study may underestimate the actual contribution of macroinvertebrate to leaf litter decomposition. To examine the effects of macroinvertebrates on leaf litter decomposition at each site, other approach, preferably use of leaf litter, should also be used.

Comparison of organic matter decomposition rates between the hyporheic zone and the benthic zone

Previous studies that examined the decomposition rates both on the benthic zone and in the hyporheic zone showed contradicting results. For example, Boulton & Quinn (2000) and Peralta-Maraver et al. (2019) that used both cotton-strips and tea bags, and Piscart et al. (2011) and Danger et al. (2012) that used leaf litter, found lower decomposition rates in the hyporheic zone due to lower effects of abrasion from bedload transport and invertebrate and microbial activities. Solagaistua et al. (2015) and Risse-Buhl et al. (2017) that used leaf litter found similar decomposition rates between the benthic zone and the hyporheic zone due to comparable contribution by the microbial community. In intermittent streams, Burrows et al. (2017) used cotton-strips and leaf litter and found higher decomposition rates in the hyporheic zone compared to benthic zone because of consistently saturated conditions. The present study also showed mixing results. The INO River sites showed lower decomposition rates in the hyporheic zone than in the benthic zone from spring to fall, whereas the INU River sites showed similar decomposition rates in the hyporheic zone and the benthic zone in many

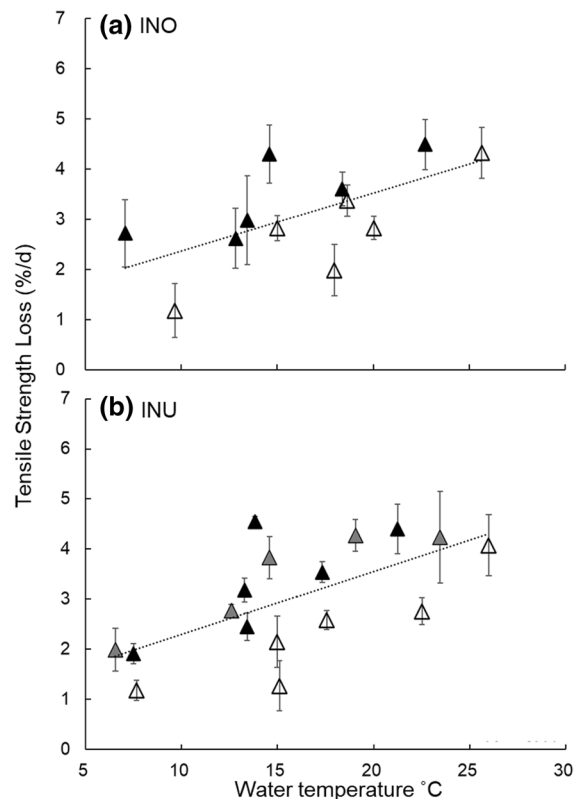


Fig. 8 Relationship between average water temperature during incubation period and tensile strength loss in **a** INO River and **b** INU River. Open symbols indicate downstream sites, black symbols indicate upstream sites and grey indicate tributary site. The lines indicate linear regression relationship ($P < 0.05$)

seasons. The studied rivers were perennial, so the effects of dryness were not expected. Microbial community was not examined in this study, but microbial decomposition rates between benthic zone and hyporheic zone may be similar despite the differences in the physical environment (Risse-Buhl et al., 2017). Macroinvertebrate decomposition rates, in contrast, differ between the hyporheic zone and the benthic zone, where the effects of macroinvertebrate are greater in the benthic zone (Cornut et al., 2010). The contribution of macroinvertebrate examined in this study showed that the effects were small in the hyporheic zone, whereas it was significant in the benthic zone at the same sites (Li et al., 2020). The contribution of macroinvertebrates to decomposition in the benthic zone was larger in the INO River sites, ranging from 23 to 29%, than the INU River sites, ranging from 11 to 20% (Li et al., 2020). Therefore, the difference in

the contribution of macroinvertebrates to decomposition between the benthic zone and the hyporheic zone might have resulted in the lower decomposition rates in the hyporheic zone in the INO River, and comparable decomposition rates in the INU River.

In winter at INU_D, the decomposition rate was significantly higher in the hyporheic zone than in the benthic zone, and a similar trend was also found in other sites, although the differences were not significant. Menéndez et al. (2003) found that the density of macroinvertebrates was more than twofold higher and so was the decomposition rate in the benthic zone in spring–summer, compared to fall–winter. The effects of macroinvertebrate in the benthic zone may become small in winter. The contribution of macroinvertebrate to decomposition in the benthic zone was lowest in winter in the INU River (Li et al., 2020). Due to these seasonal variation in the effects of macroinvertebrate, hyporheic decomposition rates may become comparable to the rates in the benthic zone in winter.

This study demonstrated that the presence of a dam influences decomposition rates not only in the benthic zone but also in the hyporheic zone downstream, that the effects of dams on hyporheic decomposition may depend on season, and that the hyporheic decomposition rates and benthic decomposition rates may be comparable in some seasons in some rivers. These results suggest that the hyporheic zone can be an important zone of decomposition, and it is crucial to examine both benthic and hyporheic zones when addressing the effects of dams and reservoirs on stream ecosystem processes.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by TK and YL. Analysis of hyporheic invertebrates were carried out by AT. The first draft of the manuscript was written by TK and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets obtained during the present study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval This manuscript has not been submitted to any other journals. This manuscript does not contain any studies with human participants or animals under the Japanese Act.

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