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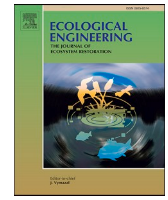

Impacts of flood retention dams on benthic invertebrates by affecting bed material size and disturbance in reservoir and downstream sections

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ABSTRACT

The impacts of Flood Retention Dams (FRDs), designed solely for flood control and featuring bottom outlets at the riverbed level, on benthic invertebrate communities have not been sufficiently elucidated. This study investigated the impact of FRDs on benthic invertebrate communities downstream and reservoirs, focusing on differences in riverbed conditions and bed disturbances caused by reservoir sedimentation. We compared benthic invertebrate communities and riverbed conditions at upstream, reservoir, and downstream sites from seven FRDs in Japan. The average community similarity between the upstream and downstream sites across the seven dams was 0.73, comparable to unregulated streams. They were not related to the duration of dam operation, indicating minimal long-term impacts on downstream communities. However, the community similarity between the upstream and reservoir sites was notably lower, at 0.66. Reservoir sites had smaller grain sizes and softer substrates with narrower interstitial spaces than upstream sites. Consequently, taxes that inhabit or move across stone surfaces were more common in reservoirs. Conversely, taxa that prefer stable beds and larger body sizes were less frequent. Additionally, we found that reservoir sedimentation fluctuations, which indicates riverbed disturbance pattern, influence the similarity of invertebrate communities between upstream and downstream sites. To conclude, FRDs have negligible impacts on benthic invertebrate communities at DS sites; smaller grain sizes modulate these communities at RS sites. Predicting reservoir sedimentation fluctuations supports the design of FRDs with minimal impacts on benthic invertebrates.

1. Introduction

Flood mitigation by dams is one of the most effective measures against increasingly severe flood disasters (e.g., Ehsani et al., 2017; Thomas et al., 2021); however, dams negatively impact stream ecosystems, particularly by interrupting sediment continuity (e.g., Katano et al., 2009; Kondolf, 1997; Petts and Gurnell, 2005). A Flood Retention Dam (FRD) is dedicated solely to flood control whose bottom outlets are installed at the riverbed level (Poulard et al., 2010; Sumi, 2008). FRD reservoirs typically remain empty under non-flood conditions. When a flood occurs, the bottom outlets restrict the flow rate, allowing the reservoir to temporarily store the flood and reduce flood damage in downstream areas. These FRD designs are considered optimal structures for sediment sluicing or flushing (Aoyama et al., 2009; Lai and Shen, 1996; Onda and Sumi, 2017), indicating minimal impact on the natural sediment regime. Thus, FRDs have the potential to provide flood control functions without significantly impacting the riverine ecosystems.

FRDs have been constructed in various countries and regions worldwide. In the United States, by 1922, the Miami Conservancy District (MCD) had constructed five FRDs, called ‘Dry Dams’ (Miami Conservancy District, 2024). These dams were implemented as cost-effective flood mitigation measures, offering early flood control functionality within a limited budget (Purcell, 2002; Sumi, 2008). In contrast to large-scale FRDs in the United States (Sumi, 2008), in European regions, multiple small-scale FRDs, also known as hydraulic flood retention basins (Scholz, 2007), are strategically distributed across the headwater areas of basins for flood mitigation in downstream urban areas (Patek, 2014; Sumi, 2009). The concept of decentralized FRDs across the basin offers the advantage of mitigating flood risks while conserving riverine ecosystems and the local landscape (Fedorov et al., 2016; McMinn et al., 2010; Terêncio et al., 2020; Wang et al., 2021). More than 20 FRDs have been constructed in Japan since the 1960s (Sumi, 2008). Initially, small-scale FRDs, comparable to European ones, were primarily built to protect farmland from floods. Since 2005,

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medium-scale FRDs have been constructed to protect downstream urban areas from flood damage. More recently, in response to the increasing severity of flood damage, plans for larger-scale FRDs comparable to the Dry Dams in the United States are underway (K. Kobayashi et al., 2024).

Although FRDs are advantageous structures for maintaining sediment continuity, sediment still accumulates in their reservoirs, though to a lesser extent than in storage dams (Morris and Fan, 1998; Nakamura et al., 2024; Sumi, 2008), potentially altering riverbed conditions within the reservoir and downstream. The reservoir sedimentation process during large-scale floods can be described in two stages (Sakka et al., 2009; Sumi et al., 2012): During a large-scale flood, various grain-sized sediments accumulate in the reservoir because the reservoir becomes a still-water zone. Subsequently, towards the end of the floods, as the water level recedes, sediment transport capacity is restored. However, the reduced flow rate at this stage hinders the complete flushing of deposited materials, mainly the coarser sediments. The bed materials are selectively transported based on their grain size and accumulate at locations corresponding to their size for an extended period (Sumi et al., 2012, 2014). Sediment released downstream of the FRD at the end of the flood is also expected to be deposited in the downstream channel because of lower sediment transport capacity, which is often problematic with sediment flushing operations (Kondolf and Wilcock, 1996). The coarse-grained deposits in the reservoir and fine deposits downstream can alter riverbed material sizes within the reservoir and downstream (Shirai et al., 2011). Sediment accumulated in the reservoir after large-scale floods may be gradually supplied downstream by subsequent small to medium-scale floods. Fine deposits downstream may also be flushed out, resulting in minimal changes to bed material size. Even in such cases, however, the pattern of bed disturbance caused by sediment supply differs from that of unregulated streams. Hence, sedimentation in FRD reservoirs can alter riverbed conditions in both the reservoirs and downstream areas, particularly in bed material size and disturbance.

The bed material size and disturbance pattern change caused by the reservoir sedimentation indicate an alteration in the benthic invertebrate community. Firstly, each grain size class serves distinct ecological functions (Apitz, 2012; Gore et al., 2001). For instance, medium-sized grains contribute to the diversity of benthic invertebrates by providing habitats suitable for a broader range of species (S. Kobayashi et al., 2011). Meanwhile, sand and gravel are essential case-building materials for case-bearing caddisflies (Katano et al., 2009), but excessive fine deposits can harm benthic invertebrates by reducing habitat quality (Buendia et al., 2013; Espa et al., 2013; S. Kobayashi et al., 2023; Wood and Armitage, 1997). Secondly, the bed disturbance affects the abundance and composition of the invertebrate community. After bed disturbance, unstable riverbeds are colonized by species such as *Baetis* (Mackay, 2011). Over time, as the riverbed stabilizes, species that prefer stable substrates, such as *Hydropsyche*, begin to dominate (Cardinale et al., 2004; Statzner et al., 1999). Hence, sediment deposition in FRD reservoirs can alter bed material size and disturbance patterns, potentially changing the benthic invertebrate community. However, the impacts of FRDs on benthic invertebrates by affecting bed conditions have not been sufficiently documented.

Therefore, in this study, the impact of FRDs on benthic invertebrate communities in downstream channels and reservoirs was quantitatively evaluated, focusing on differences in riverbed conditions and bed disturbances caused by reservoir sedimentation. Seven FRDs in Japan were selected as study sites, and benthic invertebrate samples were collected from the reference site (upstream site) and impact sites (reservoir and downstream reaches). If an FRD sufficiently maintains the natural sediment regime, the invertebrate communities at the impact sites will resemble those at the reference site. In particular, we addressed the following three research questions: (1) How similar are the benthic invertebrate communities at the reference site to those at the impact sites? (2) What is the relationship between the taxa characterizing the communities at the impact sites and the riverbed conditions? (3) How does the difference in riverbed disturbance due to reservoir sedimentation affect community similarity between the impact and the reference site?

2. Materials and methods

2.1. Description of study sites

Seven FRDs were selected from Japan as study sites: the Sotomasuzawa Dam (1), Rentaki Dam (2), Ohtao Dam (3), Sagadani Dam (4), Masudagawa Dam (5), Takamatsu Dam (6), and Nishinotani Dam (7) (Fig. 1, Table S1). Sasakura Dam, a storage-type dam, was also selected as a control for comparison with the FRDs. These dams are of intermediate size, positioned between the smaller FRDs in Europe and the larger ones in the United States (Fig. S1). Sotomasuzawa and Rentaki were constructed in the Kitakami River Basin, Iwate Prefecture. Sagadani, Ohtao, Masudagawa, and Sasakura were built in the Masuda River Basin in Shimane Prefecture. Takamatsu was constructed in the Takamatsu River Basin in the Kagoshima Prefecture. Nishinotani was built in the Shin River basin in Kagoshima Prefecture. The Masudagawa and Nishinotani dams, built in 2005 and 2012, respectively, are relatively new compared with the other dams in this study, which were built between 1957 and 1969.

The FRDs examined in this study have one or two bottom outlets (Table S1). The detailed photographs of the bottom outlet area are shown in Table S2. Slide gates were installed in the bottom outlets of the Sotomasuzawa, Rentaki, and Takamatsu dams, whereas the other dams had gateless structures. The dams can regulate the flood more efficiently and flexibly through gate operation; however, these three FRDs rarely close gates, except for periodic inspections by the dam office staff. Therefore, the effects of the presence or absence of a gate on the sediment transport were negligible.

The dam administrators provided the data from the reservoir sedimentation surveys conducted over the past 10 years. The reservoir sedimentation rate (SR) was calculated by dividing the latest volume by the gross reservoir capacity. The sedimentation rate ranges from −0.8 % to 10.2 % (Table 1, Fig. S2). It can be categorized into groups with near-zero sedimentation rates (Rentaki, Ohtao, Sagadani, and Masudagawa) and those with relatively high sedimentation rates (Sotomasuzawa, Takamatsu, and Nishinotani). The low-SR group consisted of dams with steep reservoir topography, whereas the high-SR group included dams with flat reservoir topography. The sedimentation volume's coefficient of variation (CV) was calculated using available data from the past 10 years, ranging from 0.01 to 3.32 (Table 1).

The SR varied annually in response to the flood intensity, as indicated by annual maximum discharge or annual maximum 24-h precipitation (Fig. S2). Sotomasuzawa, where no significant floods have occurred in the past decade (average annual maximum discharge of 14.09 m^3/s), shows a low CV in sedimentation volume. Although no discharge data are available for Takamatsu, the stable SR suggests that no significant floods have occurred in the past decade. In Sagadani, the SR decreased in years with low discharge and increased in years with high discharge, resulting in the highest CV among the seven dams. Rentaki exhibited a trend similar to Sagadani's; however, its CV was not as large. Nishinotani experienced a sharp increase in SR owing to a major flood in 2019. In Ohtao, the SR decreases annually due to slope failures within the reservoir, with significant reductions observed during years of high discharge. In Masudagawa, no clear relationship was observed between the flood intensity and SR.

2.2. Field investigation

2.2.1. Sampling locations and season

We collected benthic invertebrate samples and data for riverbed conditions from a reference site and two impact sites. The reference site was established in the upstream channel of the reservoir (upstream site:

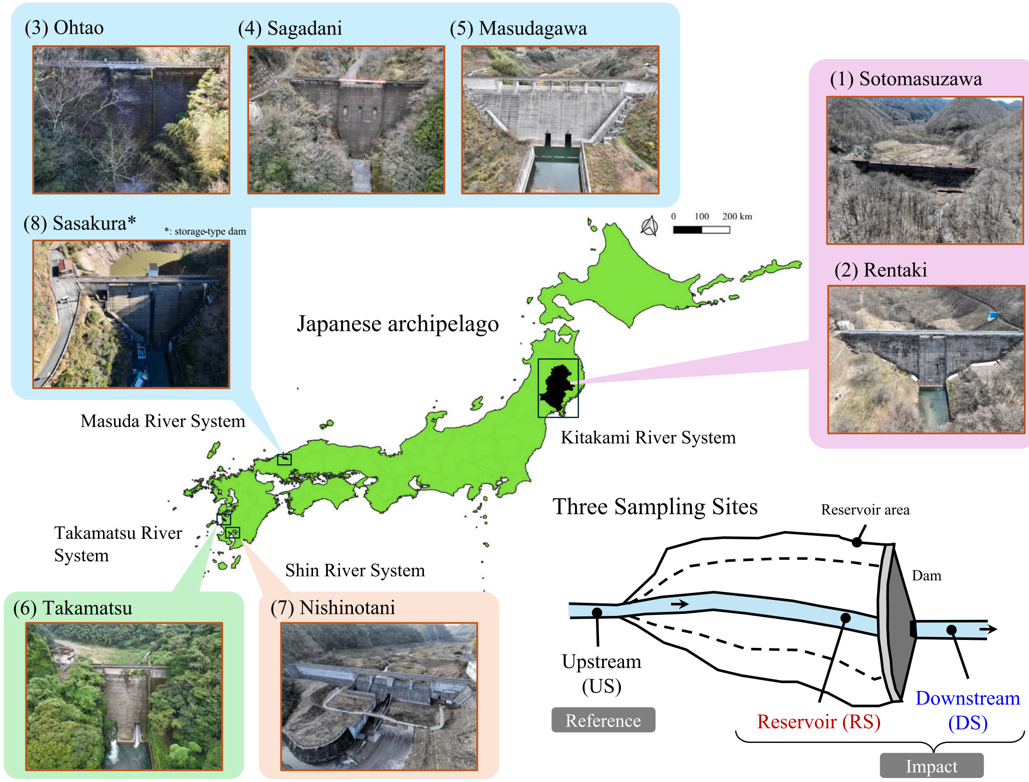

Fig. 1. Locations of eight study sites (seven flood retention dams and one storage-type dam) and a sketch of three sampling locations: the upstream site (US), the reservoir site (RS), and the downstream side (DS).

Table 1
Summary of reservoir sedimentation rate and coefficient of variable of the sedimentation volume calculated using available data from the past 10 years. The number in parentheses in the sedimentation rate line indicates the year the bathymetric survey was conducted.

Dam No	1	2	3	4	5	6	7
Dam	Sotomasuzawa	Rentaki	Ohtao	Sagadani	Masudagawa	Takamatsu	Nishinotani
Sedimentation rate [%][1)]	10.2 (2020)	0.6 (2021)	−0.8 (2023)	0.2 (2023)	0.2 (2023)	4.8 (2022)	6.8 (2022)
Coefficient of variation	0.01	0.10	0.61	3.32	0.22	0.05	0.69

1) Reservoir sedimentation rate: the ratio of sedimentation volume to gross reservoir capacity.

US), while the impact sites were located near the bottom outlet within the reservoir (reservoir site: RS) and downstream of the dam (downstream site: DS) (Fig. 1). The RS site experiences a sorting process of grain size by the effects of the bottom outlet, where the grain size becomes smaller closer to the dam (Sumi et al., 2012). At the DS site, reservoir sedimentation can alter the sediment supply volume, grain size, and patterns downstream of the dam, which may lead to changes in substrate conditions compared to the US site. The impact sites were generally located at the riffle closest to the dam body. In cases where artificial disturbances to the riverbed were present, the sites were set at locations far enough to minimize these effects. Table S3 shows the characteristics of the sampling sites, including the distance from the dam, channel slope, and channel width of each study site. To eliminate the impact of riverbed disturbances caused by flood events on the invertebrate community, sampling was conducted during the non-flood season, from October to the following April, from 2021 to 2024.

2.2.2. Benthic invertebrates collection and analysis

Macroinvertebrate samples were collected qualitatively at each site using a Surber net (quadrate size: 0.25 × 0.25 m, mesh size: 0.5 mm). At each site, three or four samples were collected from several locations along the riffle. The sampling locations were selected to ensure that the hydraulic conditions were as similar as possible among the three survey sites. Before collecting the benthic invertebrates, the flow velocity at 60 % depth (using a propeller-type current meter, KENNEK Co.) and the water depth were measured at the center of each quadrat. The samples collected from these locations were combined, fixed with 70 % ethanol, and brought back to the laboratory. The collected samples were washed with a 0.5 mm sieve in the laboratory, and only the samples retained on the sieve were used for analysis. The samples were identified to the lowest possible taxonomic level using a stereomicroscope based on the literature (Kawai and Tanida, 2018; Merritt et al., 1996). The number of individuals in each taxon was divided by the sampling area to calculate the density (individual/m^2).

Each taxon was classified based on its functional feeding group, bed residence type, and flow habitat type. Functional feeding group classification considers the food resources and feeding styles. Based on Merritt et al. (1996) and Takemon (2005), they were classified into five types: Scrapers, Shredders, Gatherers, Filterers, and Predators. The bed-residence type classification considers the invertebrate settling position and mode of living on the riverbed. In this study, we classified these into seven types based on S. Kobayashi et al. (2010): surface retreat, inter-stone retreat, interior retreat, surface case, surface-free, inter-stone free, and interior-free. The flow habitat type classification was based on the preferred flow environment of benthic invertebrates (i.e., lotic or lentic). According to S. Kobayashi (2019), benthic invertebrates are classified into four categories: lotic, sub-lotic, sub-lentic, and lentic.

2.2.3. Riverbed conditions

The grain size distribution (GSD) was analyzed using an image-based method (Auel et al., 2017). A one-meter square area on the riverbed photograph was gridded at 20-cm intervals, and gravels beneath the 36 grid intersections were selected. The maximum length and the perpendicular width were measured for each selected gravel on the computer, and their average value was used as the gravel size. Photographs were taken along the sand bar around each sampling site at least five times, and more than 180 grain-size data points were collected. If there was not enough area to take photographs, the line intersection method was applied, and at least 100-grain size data were collected. The GSD curve was plotted for each site, and the 60th percentile grain size (d_{60}) was used as representative grain size. Bed material size classifications were determined as follows (Blott and Pye, 2012): fine gravel (2–16 mm), coarse gravel (16–64 mm), small cobbles (64–128 mm), large cobbles (128–256 mm), and boulders (256 mm and above).

The relationship between the representative grain size and channel slope was examined for the three sampling sites across seven FRDs. Generally, the bed material size increases with a steeper channel slope in unregulated channels (Mikuniya and Chibana, 2011). In regulated streams, where sediment is in short supply, the representative grain size relative to the slope is typically larger than in unregulated streams (Hatano et al., 2005). Suppose the relationship between the representative grain size and channel slope for FRDs is closer to that of unregulated streams than that of regulated streams. In that case, we can evaluate that FRDs have a lower impact on sediment continuity.

The riverbed softness was gauged by the depth at which a pointed steel rod penetrated the substrate when it was manually driven in (Hyodo et al., 2014). This depth correlates with the availability of interstitial spaces within the riverbed, which is important for benthic invertebrate habitats. Although this measurement method is simple, its results correlate with those obtained using more authoritative methods such as the Hasegawa Soil Penetration Tester (Izumi et al., 2015). In this study, to account for variability in measurements, riverbed softness was measured at least five times near the sampling points at each survey site by the same person conducting the measurements.

2.3. Statistical analysis

A two-way analysis of variance (ANOVA) without replication was conducted to examine the differences in flow velocity, water depth, bed material size, bed density, and taxonomic richness of invertebrates among the three survey sites, with survey sites (three levels) and dams (seven levels) as the main factors. For parameters for which the effect of the survey site was significant, multiple comparisons were conducted using the Tukey method. All data were logarithmically transformed to improve the normality and homogeneity of variances.

The community similarity between the US and other sites was analyzed using the Bray-Curtis similarity index $BC_{US,k}$ (Bray and Curtis, 1957):

$$BC_{US,k} = 1 - \frac{\sum_j^p |n_{US,j} - n_{k,j}|}{\sum_j^p (n_{US,j} + n_{k,j})} \tag{1}$$

Where k is the name of the impact sites (i.e., RS or DS site), p is the total number of taxa collected at the two sites, $n_{i,j}$ is the number of individuals of taxon j at the site i.If the community structure is completely the same, $BC_{US,k} = 1$, and if completely different, $BC_{US,k} = 0$. A Pearson correlation analysis was performed to assess the relationship between the Bray-Curtis similarity between the US and DS sites and factors such as the similarity between the US and RS sites, FRD operation year, or the CV of sedimentation volume. A similarity percentage (SIMPER) analysis was applied to determine the characteristic taxa that had a high contribution to Bray-Curtis similarity (Clarke, 1993). Here, taxa with more than 1 % influence on $BC_{US,k}$ were extracted as indicator taxa:

$$BC_{US,k}^j = \frac{|n_{US,j} - n_{k,j}|}{\sum_j^p |n_{US,j} - n_{k,j}|} \geq 0.01 \tag{2}$$

All statistical analyses were performed using R software (version 4.4.1; R Development Core Team, Vienna, Austria).

3. Results

3.1. Hydraulic conditions

In this study, benthic invertebrates were collected from riffles, and the hydraulic parameters, i.e., current velocity and water depth, varied slightly among the three sampling sites (Fig. S4). The mean water depth at the reservoir site was significantly smaller than that at the other two sites (F-statics: 5.01, $P = 0.0262$); however, the difference was not substantial (Table 2). There were no significant differences in current velocity among the three survey sites (F-statics: 0.44, $P > 0.05$) (Table 2). Thus, the differences in hydraulic conditions among the three sampling sites can be considered negligible regarding their impact on benthic invertebrate communities.

3.2. Riverbed conditions

Fig. S5 shows the GSD for seven FRDs and a storage-type dam at the upstream (US), reservoir (RS), and downstream (DS) sites of the riffles. There were no significant differences in the representative grain sizes among the three survey sites (F-statics: 3.29, $P > 0.05$) (Table 2). However, in six FRDs, excluding Ohtao, the representative grain size at the RS sites was finer than those at the US and DS sites. The GSD at the US and DS sites for the FRDs were similar, with only a slight variation. However, specific grain-size classes differed between Masudagawa and Takamatsu. In Masudagawa, the GSD of larger cobbles (> 64 mm) was comparable at both the US and DS sites; however, the proportion of gravel (2–64 mm) was higher at the DS site than at the US site. In Takamatsu, the GSD of gravel (2–64 mm) was comparable between the US and DS sites. However, the proportion of small cobbles (64–128 mm) at the DS site was much smaller than that at the US site, whereas the proportions of large cobbles (128–256 mm) and boulders (>256 mm) at the DS site were larger than those at the US site.

Fig. 2 (a) shows the relationship between the representative grain size (with d_{60} used in this study) and channel slope. This figure also includes data for unregulated gravel-bed rivers from Mikuniya and Chibana (2011) and data for downstream channels of storage-type dams from Hatano et al. (2005). For the seven FRDs examined in this study, the data were plotted at positions similar to those of unregulated gravel-bed rivers, differentiating them from the plots corresponding to the downstream channels of storage-type reservoirs. At Sotomasuzawa, Sagadani, Masudagawa, and Takamatsu, the grain size was larger at sites with steeper riverbed gradients. In Rentaki, although there was no significant difference in grain size among the three sites, the channel slopes varied. In Ohtao, although there was no significant difference in the channel slope among the three sites, the grain size varied.

There were no significant differences in riverbed softness among the three survey sites or the seven dams (F-statics: 2.54, $P > 0.05$) (Table 2). However, the mean riverbed softness at the reservoir sites was slightly lower than that at the other sites. In particular, at Sotomasuzawa and Nishinotani, the riverbed softness at the RS site was much greater than that at the other two sites. Fig. 2 (b) shows the relationship between riverbed softness and grain size. The riverbed softness at the reservoir sites for a grain size was greater than that at the upstream sites.

For more detailed data on the riverbed condition, please refer to Table S4.

Table 2
Average values of hydraulic conditions, riverbed conditions, and benthic invertebrate metrics across different survey sites (upstream, reservoir, downstream) and the seven target dams. Results of the two-way analysis of variance (ANOVA) with survey sites (three levels) and target dams (seven levels) as main factors. Results of multiple comparisons using the Tukey method, with significantly different mean values indicated by different letters (a, b, c).

	Mean value													Effect			
	Sampling site						Dam							Sampling site		Dam	
	US		RS		DS		1	2	3	4	5	6	7	*F*	*P*	*F*	*P*
▾ Hydraulic condition																	
Velocity	100.3		101.4		92.1		124.4	88.3	109.2	125.3	83.7	115.5	55.7	0.44		5.24	**
Depth	22	b	17	a	22	b	15	26	15	22	30	17	16	5.01	*	10.10	***
▾ Riverbed condition																	
Grain size	95.7		70.9		111.4		72.3	91.7	87.6	80	134.2	126.6	56.2	3.29		2.30	
Bed-softness	4		9		5		5	6	4	5	6	6	12	2.54		0.66	
▾ Benthic invertebrate																	
Density	3883		4237		3006		1743	1653	2435	2073	8148	5519	4389	0.20		2.37	
Taxa	35		30		34		33	40	28	42	38	33	19	1.96		8.86	***

*:$P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

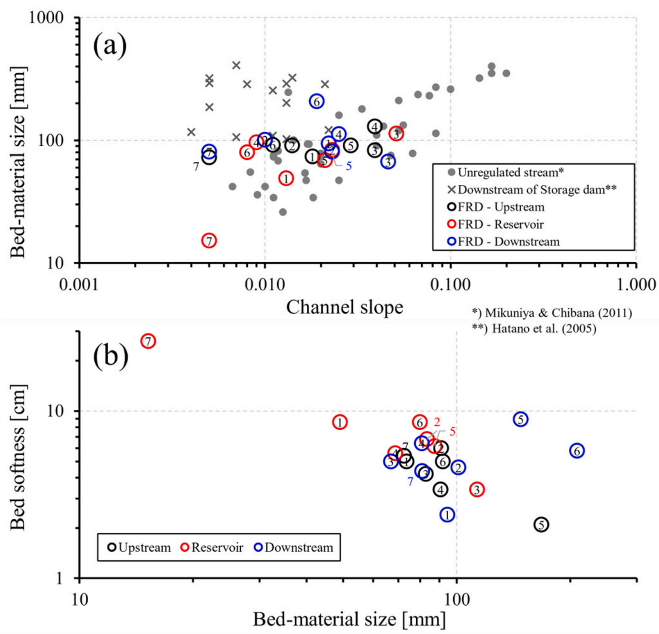

Fig. 2. Characteristics of riverbed conditions: (a) relationship between bed-material size and channel slope, (b) relationship between bed softness and bed-material size.

3.3. Benthic invertebrate community

3.3.1. Total density and taxonomic richness

There were no significant differences in invertebrate density (F-statics: 0.20, $P > 0.05$) or number of taxa (F-statics: 1.96, $P > 0.05$) among the three survey sites (Table 2). However, the number of taxa at the RS sites was smaller than at the other sites, particularly in Sotomasuzawa, Sagadani, Takamatsu, and Nishinotani (Fig. S6 (a)). In Sagadani, Takamatsu, and Nishinotani, the number of taxa at the DS sites was also smaller than that at the US sites. The differences in population density among the three survey sites across the seven FRDs were small (Fig. S6 (b)). In Sasakura, a storage-type dam, the number of taxa downstream was considerably lower than upstream, although the population density showed little difference.

3.3.2. Community similarities between reference and impact sites

The Bray-Curtis similarity index was calculated to compare the benthic invertebrate community structures between US and DS or US and RS (Fig. 3 (a)). For the seven FRDs, the community similarity values between the US and DS ranged from 0.62 to 0.79. In contrast, the Bray-Curtis similarity between the US and DS sites in Sasakura, a storage-type dam, was lower at 0.55. A significant Pearson correlation was observed between the Bray-Curtis similarity of the US and DS sites and that of the US and RS sites ($R^2 = 0.7935$; $P = 0.0071$) (Fig. 3 (b)). In Rentaki, Masudagawa, and Takamatsu, the community similarity between the US and DS sites was comparable to that between the US and RS sites. In contrast, for Sotomasuzawa, Ohtao, Sagadani, and Nishinotani, the community similarity between the US and RS sites was lower than that between the US and DS sites (0.56, 0.68, 0.47, and 0.62, respectively). No significant relationship was found between the Bray-Curtis similarity and log-transformed operation time ($R^2 = 0.0249$; $P = 0.7356$) (Fig. 3 (c)). No significant relationship was found between the Bray-Curtis similarity of the US and DS sites and the log-transformed coefficient of variation of sedimentation volume ($R^2 = 0.5319$; $P = 0.0629$) (Fig. 3 (d)). Because bathymetric surveys at Sotomasuzawa and Rentaki have been conducted only three times in the past decade, these two dams were excluded from the analysis. This time, a significant relationship was found between similarity and the coefficient of variation ($R^2 = 0.8881$; $P = 0.0165$).

3.3.3. Characteristic taxa at the downstream and reservoir site

Table 3 summarizes the characteristic taxa identified at the DS and RS sites compared to those at the US sites, as analyzed using SIMPER. At the DS sites, scrapers (at three dams) and shredders (at four dams) were more frequently observed in terms of feeding groups, whereas collectors (at five dams) were more common at the US sites. Regarding bed residence types, interior free taxa (at three dams) occurred more frequently at the DS sites. Regarding flow habitat types, sub-lentic taxa (at four dams) were more common at DS sites, whereas sub-lotic taxa (at four dams) were more prevalent at US sites. *Heptageniidae* and *Baetis* were representative scraper taxa frequently found at the DS sites, whereas *Nemouridae*, *Obipteryx*, and *Tipula* were common shredder taxa. *Rhyacophila*, *Ephemera*, and *Tipula* were the representative interior free-type taxa frequently observed at the DS sites (Table S5). In summary, the DS sites of the FRDs were characterized by taxa that relied on algae or litter as food resources (scrapers and shredders), inhabited sand/gravel substrates (interior free), and preferred slow-flow conditions (sub-lentic). However, taxa that rely on detritus as a food resource (collectors) were less frequently observed at downstream sites.

At the RS sites, shredders (at three dams) were more frequently observed in terms of feeding groups, whereas filterers (at five dams) and predators (at three dams) were more common at the US sites. Regarding bed-residence types, surface free (at five dams) and surface cases (at three dams) occurred more frequently at the RS sites, whereas surface retreat (at four dams), inter-stone-free (at three dams), and interior-free (at four dams) were more frequent at the US sites. *Lepidostoma*, *Obipteryx*, and *Nemouridae* were representative shredder taxa frequently found at the RS sites. *Baetidae* and *Simuliidae* were typical surface-free

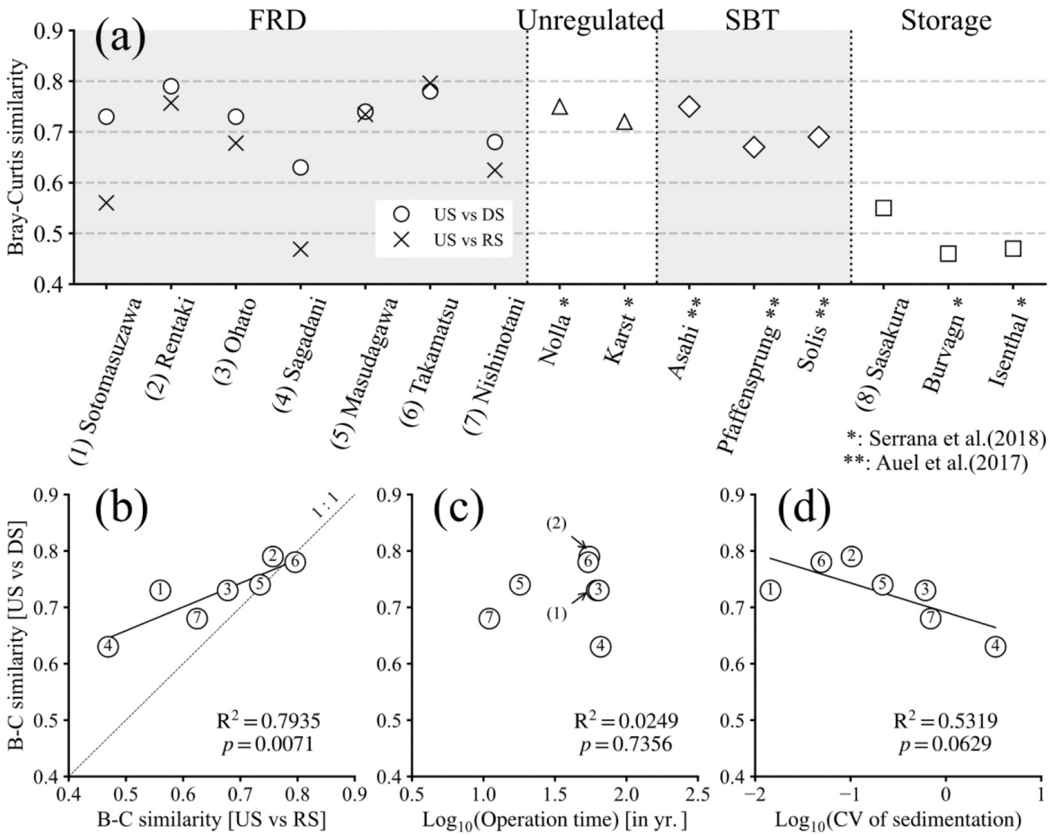

Fig. 3. Community similarity between reference and impact sites: (a) comparison between upstream (US) and impact sites (downstream: DS or reservoir: RS) at flood retention dams (FRDs), unregulated streams, storage dams with sediment bypass tunnels (SBTs), and storage dams without sediment management; (b) comparison of DS-DS and US-DS similarities; (c) comparison with log-transformed operation time; (d) comparison with sedimentation volume variability. The numbers in the plots of (b) ~ (d) correspond to the dam numbers in Fig. 1.

taxa, whereas *Lepidostoma* and *Glossosoma* were common surface-case taxa. In contrast, *Hydropsyche* surface retreat-type filterers were infrequent at the RS sites of all five dams, except at Ohtao and Masudagawa. *Perlidae* (e.g., *Kamimuria* and *Paragnetina*) and *Protohermes grandis*, inter-stone free-type predators, were typically less frequent at the RS sites than at the US sites. *Psephenidae* and *Rhyacophila*, interior free-type taxa, were also less frequent at the RS sites (Table S6). In summary, the RS sites of the FRDs were characterized by taxa that relied on litter as a food resource (shredders) and inhabited the surface of substrates (surface case/free). However, taxa that relied on detritus (filterers) or animals (predators) as food resources, inhabited stable substrates (surface retreat), and porous or sand/gravel beds (inter-stone/interior free) were less frequently observed at the RS sites.

In Sasakura, a storage dam, collectors and filterers at the DS site were more frequently observed in feeding groups, whereas scrapers were more common at the US site. Regarding bed-residence types, surface retreat, inter-stone retreat, and interior free occurred more frequently at the RS sites, whereas surface case and surface free were more frequent at the US sites. Regarding flow habitat types, sub-lentic taxa were more common at DS sites (Table S5). In summary, the DS site of Sasakura was characterized by taxa relying on detritus as food resources (collectors and filterers), stable beds (surface retreat, inter-stone retreat), sand and gravel beds (interior free), or slow flow (sub-lentic). In contrast, the US site was characterized by taxa relying on algae (scrapers), sand and gravel as case material (surface case), and cobble surfaces (surface free).

4. Discussion

4.1. Riverbed material size at the reservoir and downstream sites of FRD

Generally, the bed material size increases with channel slope in unregulated rivers (Mikuniya and Chibana, 2011). Based on the slope-to-grain size relationship, the grain size in rivers regulated by FRDs can be compared with that in unregulated rivers. The relationships in the US, RS, and DS sites were similar to those in unregulated rivers and distinctly different from those downstream storage dams (Hatano et al., 2005). This suggests that FRDs have a minimal impact on downstream bed material size.

Although GSDs were similar between US and DS overall among the surveyed dams, a difference was evident for a particular grain size class in Masudagawa and Takamatsu (Fig. S5, Table S4). In Masudagawa, gravel was more abundant in the DS than at the US site. This is probably because sediment is mainly released downstream at the end of flood events when the reservoir shifts from a dammed-up condition to a free-flowing condition with reduced stream power from the flood peak (Sakka et al., 2009). The absence of fine sediment deposition at DS sites of other dams could be attributed to gradual flushing during small to medium-scale floods after a large flood (Kondolf and Wilcock, 1996). Similar conditions may potentially occur at Masudagawa in the future.

In Takamatsu, small cobbles were less prevalent, and boulders were more abundant (Fig. S5, Table S4). The shapes of many boulders at the DS site appeared sharper than those at the US site, suggesting that they were not fluvially transported upstream but were supplied laterally from mountain slopes. The reduced presence of small cobbles in the DS site appears to be influenced not only by the unique sediment transport dynamics within the reservoir but also by the structural characteristics

Table 3
Frequent occurrence of benthic invertebrate categories (feeding group, bed-residence type, and flow habitat type) in comparisons of (1) downstream vs. upstream and (2) reservoir vs. upstream based on SIMPER analysis.

		(1) DS site vs. US site[1]							(2) RS site vs. US site[2]						
		Sotomasuzawa	Rentaki	Ohtao	Sagadani	Masudagawa	Takamatsu	Nishinotani	Sotomasuzawa	Rentaki	Ohtao	Sagadani	Masudagawa	Takamatsu	Nishinotani
Feeding Group	scrapers	U	U	D			D	D		U	R		U	R	
	shredders	D	D	U	D	U	D	U	R		U	R	U	R	U
	collectors	U	U	U	U	D	U			R	U		R		U
	filterers	D	U	D	U			U	U	U		U	R	U	U
	predators				D	D	U	U				U		U	U
Bed Residence Type	surface retreat	U	U		D	D		U		U	R	U	R	U	U
	inter-stone retreat	D									R	U			
	surface case	U			U	U	D	U	R	R				R	U
	surface free			D	U		D		U	R		R	R	R	R
	inter-stone free		U		D	D				U	U		R		U
	interior free	D	D	U		U	U	D	R	R		U	U	U	U
Flow Habitat Type	lotic		U			D			U			U	R		
	sub-lotic	U	U		U			U		U					U
	sub-lentic	D	D		D		D	U	R	U		R	U		U

1) "D" represents groups more common downstream, while "U" represents groups more common upstream.
2) "R" represents groups more common in the reservoir site, while "U" represents groups more common upstream.

of the dam. First, unlike the other FRDs, the bottom outlets of Takamatsu are located several meters above the riverbed (Fig. 1, Table S2), which results in a reduced bed slope near the bottom outlets, promoting sediment deposition. Additionally, the stilling basin downstream of the dam has a small opening (i.e., a single 1-m-wide slit), which also could promote sediment accumulation within the stilling basin (Fig. S3). The replenishment of small cobbles from the reservoir and stilling basin, which has been practiced downstream of storage dams worldwide (Kondolf et al., 2014; Mörtl et al., 2023), can potentially improve this condition.

Due to sediment sorting processes, FRD reservoirs are characterized by unstable riverbed conditions with smaller bed-material sizes (Sumi et al., 2012). For all FRDs, excluding Ohtao, the bed-material size at the RS sites was smaller than that at the US and DS sites (Fig. 2, Fig. S5). The bed material size becomes smaller as it approaches the dam body in the RS site because bed materials are selectively transported based on their grain size as the reservoir water level recedes in the later stages of floods (Sumi et al., 2012, 2014). This was particularly evident in Masudagawa, Sotomasuzawa, and Nishinotani (Fig. S5).

Many FRDs exhibit smaller channel slopes at RS sites than the US sites, with Masudagawa, in particular, showing an exceptionally small slope at the RS site (Table S3). This is likely a key factor contributing to the significantly smaller bed material size at the RS site than at the US site. The small slope at the RS site is suspected to result from backwater effects caused by the bottom outlet (Morris and Fan, 1998), although a quantitative evaluation of this effect remains a future task. A more comprehensive data collection effort will be necessary to discuss this further.

In reservoirs where the stream channel width is narrower relative to the reservoir bottom width, such as Sotomasuzawa and Nishinotani (Table S2), the bed material size at RS sites tends to be smaller than that at US sites (Fig. S5). This phenomenon is likely influenced not only by the reservoir topography but also by the size of the bottom outlet. The stream channel width is proportional to the square root of the flushing discharge (Atkinson, 1996; Morris and Fan, 1998), which suggests that a larger bottom outlet leads to higher stream power within the reservoir. FRDs with smaller bottom outlets in flat valley reservoirs are expected to exhibit lower stream power, resulting in much finer grains. Understanding the relationship between reservoir topography, bottom outlets, and bed material size at RS sites requires further data collection from more FRDs.

4.2. *Limited impacts of FRD on the invertebrate community in the downstream*

Sediment deficiency downstream storage reservoirs modulate downstream benthic invertebrate communities, often leading to differences from upstream reference sites. The Bray-Curtis similarity between upstream and downstream sites was lower for storage dams, averaging 0.49 across three dams—two in Switzerland (Serrana et al., 2018) and the Sasakura Dam in Japan from this study—than for unregulated streams, which averaged 0.74 across two rivers in Switzerland (Serrana et al., 2018) (Fig. 3 (a)). The characteristics of the community observed at the Sasakura Dam DS site correspond to the general pattern of benthic invertebrate communities influenced by dams (Hatano et al., 2005; Katano et al., 2009; S. Kobayashi et al., 2023).

By supplying sediment to degraded downstream channels through mechanical or hydraulic methods, downstream benthic invertebrate communities can become similar to those upstream (Katano et al., 2021; Kondolf et al., 2014; Nakano et al., 2024). Sediment bypass tunnels (SBTs), which transfer incoming sediment downstream through a tunnel, are among the most successful countermeasures for downstream restorations (Auel et al., 2017; S. Kobayashi et al., 2023; Serrana et al., 2018; Sueyoshi et al., 2024). The Bray-Curtis similarity of benthic invertebrate communities between US and DS sites of SBTs is comparable to that of unregulated streams (Auel et al., 2017; Serrana et al.,

2018) (Fig. 3 (a)). Moreover, the longer the operation period of SBTs, the more the downstream sites approach the conditions of unregulated streams (S. Kobayashi et al., 2023; Serrana et al., 2018).

Seven FRDs in Japan exhibited a Bray-Curtis similarity in benthic invertebrate communities between the US and DS sites, ranging from 0.63 to 0.79. This similarity was comparable to that observed in unregulated streams and significantly higher than those observed in the three storage dams (*t*-test, $P < 0.001$) (Fig. 3 (a)). The operation period did not influence this similarity (Fig. 3 (c)). The minimal impact of FRDs on downstream bed material size suggests that sufficient sediment can be supplied to maintain the diversity of downstream benthic invertebrate communities, similar to the effects of SBTs. This indicates that FRDs have negligible long-term impacts on benthic invertebrate communities by affecting bed material size.

While the overall influence of FRDs on downstream benthic invertebrate communities was minimal, several specific characteristics of the DS site were identified from the SIMPER analysis. Regarding flow habitat type, the sub-lentic type was frequently observed in the DS of the four FRDs (Sotomasuzawa, Rentaki, Sagadani, and Takamatsu) (Table 3). In riverbeds with larger bed material sizes, bed roughness was greater, and the extent of slow-flowing areas increased at the bottom. Except for Sagadani, the DS sites exhibited larger representative grain sizes for the four dams than the US sites, which can contribute to increasing sub-lentic taxa. In Sagadani, the flow velocity in the DS was slightly lower than that in the US, which may have contributed to the increase in sub-lentic taxa.

Like sub-lentic taxa, shredders, which rely on litter or wood tissue as food resources, were observed more frequently in the DS than in the US (Table 3). In riverbeds with larger bed-material sizes, litter may be trapped more often because of the greater bed roughness. Additionally, litter was readily supplied from the reservoir and riparian sites adjacent to the DS sites. Alternatively, because the differences in grain size between the US and DS were small, the differences in the invertebrate community might have been due to subtle differences in the riverbed slope and channel width rather than the influence of FRD (Fig. 2 (a)).

The accumulation of fine-grained sediments in downstream channels, often a concern in sediment flushing operations, was less evident with FRDs. Regarding grain sizes larger than 2 mm, there was no clear difference in fine sediment availability (i.e., 2–16 mm) between the US and DS, at least for the three FRDs (Sotomasuzawa, Rentaki, and Nishinotani) (Fig. S5). However, at the DS of these dams, taxa that require sand or small gravel, i.e., the interior-free type (e.g., *Ephemera*, *Rhyacophila*, and *Tipula*), were more frequently observed than in the US. The representative grain size for these dams was larger than that in the US. Riverbeds with larger grain sizes tend to exhibit higher bed roughness, which may facilitate the accumulation of finer materials (smaller than 2 mm) within the interstitial spaces. Although there was a notably higher presence of gravel (2–64 mm) DS in Masudagawa than in the US (Fig. S5), interior-free taxa were less frequently observed at the DS (Table 3).

In summary, benthic communities in the DS sites exhibited characteristics associated with larger grain sizes than those in the US sites. However, these differences in grain size were likely attributable more to inherent river geomorphology, such as bed slope and channel width, rather than to the FRDs. In addition, many dams did not exhibit a significant deposition of fine sediments in the DS, nor were benthic invertebrates associated with fine sediments.

4.3. Smaller grain size and bed softness modulate invertebrate community in the reservoir of FRDs

Smaller bed-material sizes, softer bed materials, and sediment deposition in the RS sites lead to unstable riverbed conditions and lower community similarity between the US and RS sites. Taxonomic richness and total density at the RS sites were lower at five FRDs: Sotomasuzawa, Rentaki, Sagadani, Takamatsu, and Nishinotani (Fig. S6). Excessive bed disturbance negatively impacts the abundance and diversity of benthic invertebrates (Schwendel et al., 2011). The highly disturbed bed conditions at RS sites suggest the potential to modulate benthic invertebrate communities quantitatively and qualitatively, leading to lower similarity between the US and RS sites (Fig. 3 (b), (c)). The SIMPER analysis identified several specific invertebrate characteristics of the RS sites attributed to smaller grain sizes and larger bed disturbance.

Smaller grain sizes at RS sites (Table 2, Fig. S5) are suitable for taxa that stay or move on the surface of stones but not for large-bodied species that require large interstitial spaces. Firstly, the surface-free type, which includes *Simulidae* and *Baetidae* that stay/move on the surfaces of stones directly exposed to flow, was observed more frequently in the RS of five FRDs (Rentaki, Sagadani, Masudagawa, and Takamatsu) (Table 3, Table S6). Surface case types, which stay/move the surface of stones with a carrying case, were also more common at the RS of three (Sotomasuzawa, Rentaki, and Takamatsu) (Table 3). A riverbed of smaller grain sizes forms a smoother surface, increasing the area exposed to flow (Yen, 1992). This type of riverbed is considered suitable for taxa that stay or move on the surface of stones. Additionally, because *Simulidae* and *Baetidae* are taxa that colonize early after disturbance (Mackay, 2011), their frequent presence suggests that RS sites are frequently disturbed environments. Secondly, the RS had less frequent predators and inter-stone-free types, such as *Kamimuria*, *Paragnetina*, and *Protohermes grandis* (Table S6). These large-bodied species require relatively large interstitial spaces (S. Kobayashi et al., 2023). The riffles at the RS, composed of relatively smaller grain, appeared to lack the suitable larger interstitial spaces necessary for these large species, rendering the habitat less favorable for them.

RS sites with unstable riverbeds with smaller and softer substrates were considered unsuitable for retreat-type filterers, which prefer stable substrates. Filterers and retreat types were less frequent in the RS than in the US for the five FRDs (Sotomasuzawa, Rentaki, Sagadani, Takamatsu, and Nishinotani) (Table 3). Although surface-free-type filterers, such as *Simuliidae,* were occasionally more frequent, retreat-type filterers (e.g., *Stenopsyche* sp., *Hydropsyche* sp., and *Cheumatopsyche* sp.) were not commonly observed in the RS (Table S6). However, in Masudagawa, despite the smaller grain sizes and greater riverbed softness observed in the RS than in the US (Table S4), retreat-type taxa frequently occurred in the RS. Masudagawa US had the largest representative grain size among all FRDs (Fig. 2 (a), Fig. S5). Although the US of Masudagawa has larger and more stable substrates, the smaller substrates at the RS may provide more suitable conditions for retreat-type taxa because some of the taxa (e.g., *Hydropsyche*) prefer depressions on gravel surfaces at the boundaries between bed material (Cardinale et al., 2004; Statzner et al., 1999) and rather than interstitial spaces between large stones (Takao et al., 2006).

Shredders, which rely on leaves or wood tissue as a food resource, occurred more frequently in the RS than in the US in the three FRDs (Sotomasuzawa, Sagadani, and Takamatsu) (Table 3). During flood events, reservoirs store flood water and accumulate litter. Riffles of medium-sized gravel also exhibit bed roughness that facilitates leaf litter trapping (S. Kobayashi et al., 2010). Thus, FRD reservoirs may not only promote the accumulation of litter but also create conditions that enhance their retention and utilization by benthic invertebrates.

4.4. Effect of reservoir sedimentation on invertebrate communities and possible measures

The differences in benthic invertebrate communities between US and DS sites are attributed to variations in bed disturbance caused by reservoir sedimentation. For the seven FRDs, the community similarity between the US and DS ranged from 0.63 to 0.79, which correlated with the CV in the reservoir sedimentation volume (Fig. 3 (d)). The higher CV suggests that the sediment supply pattern, or riverbed disturbance pattern, differs significantly between the downstream and upstream channels of the FRD. During the phase of increased sedimentation volume in the reservoir, the DS site exhibited a more stable riverbed with a limited sediment supply than the US site, and vice versa. Therefore, in the decision-making process for designing new FRDs, it is essential to consider changes in bed material size and disturbance patterns due to reservoir sedimentation to predict their impacts on benthic invertebrate communities.

The patterns of variation in sedimentation volume can be classified into three types: oscillating (Sagadani) and rapid increase (Nishinotani). In Ohtao, the reservoir sedimentation volume continuously decreases, which is attributed to changes caused by slope failure within the reservoir rather than erosion of deposits. In Sagadani, the long-term average sedimentation volume was close to zero, but the fluctuation (increase or decrease) in sedimentation volume was the highest. Reservoir sedimentation in Sagadani tends to increase with more significant annual maximum inflows and decrease during years with smaller inflows (Fig. S2). This pattern suggests that sediment deposited in the reservoir after larger-scale floods is subsequently supplied downstream during smaller to medium-scale floods. In reservoirs like Sagadani, the bed material size at the DS site may remain similar to that at the US site; however, bed disturbance could differ significantly.

The wider and flatter reservoir topography, such as Nishinotani, may facilitate sediment accumulation and resist erosion. Therefore, due to large-scale floods, the reservoir sedimentation volume increases rapidly. In Nishinotani, the rapid increase in sedimentation volume in 2019 was caused by a large flood (Fig. S2). The erosion of accumulated sediments is limited to the channel area, while deposits in the floodplain are not eroded (Morris and Fan, 1998; Nakamura et al., 2024), making it relatively high among the dams studied. Sotomasuzawa, like Nishinotani, has a similar reservoir topography, and its reservoir sedimentation volume is also high. However, no large-scale floods have occurred in the past decade, resulting in minimal changes to the reservoir sedimentation volume. This suggests that in wider and flatter reservoirs, the variation in reservoir sedimentation volume is influenced mainly by large-scale floods. A significant amount of sediment has accumulated in the reservoirs of Nishinotani and Sotomasuzawa, which might be expected to influence the bed material size at the DS sites. However, this was not the case (Fig. 2 (a), Fig. S5). A longer timeframe may be required for such dams to impact the bed material size at the DS sites.

Predicting the impacts of new FRDs on benthic invertebrate communities requires estimating the magnitude of reservoir sedimentation volume fluctuations. However, because these fluctuations depend on individual flood events, accurately estimating them remains challenging. During the decision-making stage for designing new FRDs, it is essential to evaluate how dam design, particularly the bottom outlet geometry, influences reservoir sedimentation volume fluctuations. Therefore, developing methodologies to predict these fluctuations is crucial to minimizing the impacts of FRDs on benthic invertebrate communities.

To minimize their impact on benthic invertebrate communities, sediment management techniques for FRDs should also be considered. Sediment augmentation may be effective for dams such as Sagadani, where sediment volumes fluctuate (Mörtl et al., 2023). This involves excavating the sediment once it reaches a certain level and redistributing it downstream. For broad and flat reservoirs such as Nishinotani, uniform sediment deposition can lead to rapid increases in the sediment volume. In such reservoirs, along with excavation, installing flow-guiding structures is a potential mitigation measure (Tietz et al., 2024). Using these structures, the reservoir's flow and sediment deposition patterns could be controlled, reducing the sediment trapping rate during large flooding events.

5. Conclusions

In this study, the impact of FRDs on benthic invertebrate communities in downstream channels and reservoirs was quantitatively evaluated, focusing on differences in riverbed conditions and bed disturbances caused by reservoir sedimentation. Data on benthic invertebrates and riverbed conditions at the upstream, reservoir, and downstream sites of seven FRDs in Japan were analyzed. The community and bed-material size similarity between the upstream and downstream sites resembled those in unregulated gravel-bed rivers. It was not linked to the number of years of operation. This suggests minimal long-term effects of FRDs on downstream benthic invertebrate communities and riverbed conditions. However, the community similarity between the upstream and reservoir sites was relatively low. The riverbed conditions at the reservoir sites included smaller grain sizes, flatter profiles, and a softer substrate with narrower interstitial spaces compared to those at the upstream sites. This resulted in a higher frequency of taxa observed on stone surfaces at the reservoir sites, while taxa inhabiting stable beds, those with larger body sizes were less frequent. The study also found that invertebrate community similarity between upstream and downstream sites correlated with the coefficient of the reservoir sedimentation volume variable, suggesting that changes in bed disturbance patterns caused by reservoir sedimentation may affect benthic invertebrate communities. To conclude, FRDs have negligible impacts on benthic invertebrate communities at DS sites. However, at RS sites, smaller grain sizes modulate these communities. The extent to which FRDs affect benthic invertebrate communities may depend on changes in bed disturbance caused by reservoir sedimentation. From a practical viewpoint, predicting the magnitude of reservoir sedimentation fluctuations can inform dam designs that minimize impacts on benthic invertebrate communities.

CRediT authorship contribution statement

Ryota Nakamura: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sohei Kobayashi:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sameh Ahmed Kantoush:** Writing – review & editing. **Tetsuya Sumi:** Validation, Supervision, Project administration, Funding acquisition.

Declaration of generative AI and AI-assisted technologies in the writing process

While preparing this work, the authors used DeepL, DeepL Write, and Grammarly to improve sentences and correct grammatical mistakes. After using these tools, the authors reviewed and edited the content as needed and took full responsibility for the publication's content.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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