Riffle topography and water flow support high invertebrate biomass in a gravel-bed river
Author(s): Sohei Kobayashi, Kunihiko Amano and Satoru Nakanishi
Source: *Freshwater Science*, Vol. 32, No. 3 (September 2013), pp. 706-718
Published by: The University of Chicago Press on behalf of Society for Freshwater Science
Stable URL: http://www.jstor.org/stable/10.1899/12-080.1
Accessed: 25-04-2018 23:01 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://about.jstor.org/terms

Society for Freshwater Science, The University of Chicago Press are collaborating with JSTOR to digitize, preserve and extend access to *Freshwater Science*

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

Freshwater Science, 2013, 32(3):706–718
© 2013 by The Society for Freshwater Science
DOI: 10.1899/12-080.1
Published online: 4 June 2013

Riffle topography and water flow support high invertebrate biomass in a gravel-bed river

Sohei Kobayashi[1], Kunihiko Amano[2], AND Satoru Nakanishi[3]

Water Environment Research Group, Public Works Research Institute, 1-6 Minamihara, Tsukuba, Ibaraki, 305-8516, Japan

Abstract. We compared biomass and community structure of macroinvertebrates among 3 flow zones (deep, rapid, flat) of riffles at 3 sites in a gravel-bed river. We evaluated bed stability in these zones with a 2-dimensional hydrodynamic simulation over a range of discharge levels. Deep zones had higher flow velocity and coarser bed materials than other zones. Rapid zones were shallower with higher flow velocity than flat zones. The probability of bed movement was greatest in rapid zones and was lowest in deep zones based on bed shear stress and the size of bed materials. Total macroinvertebrate biomass was dominated by filterer insects and was highest in deep zones and lowest in rapid zones across the sites. This trend was most conspicuous for taxa that build retreats on stones, such as net-spinning caddisflies, which have a sessile life form and prefer stable environments. The trend was less apparent for taxa that move freely on the bed, such as baetid and heptageniid mayflies. The macroinvertebrate community differed between the middle and peripheral areas at deep zones. Peripheral areas were dominated more by taxa that stay under stones. The channel bed topography in deep zones of riffles is likely to support high macroinvertebrate biomass by providing greater bed stability and higher water flow, the combination of which is relatively uncommon in gravel-bed rivers.

Key words: gravel-bed rivers, riffles, bed topography, invertebrate biomass, bed stability, hydraulic simulations.

The abundance and community structure of benthic organisms within a river reach are shaped by riverbed topography and the spatial patterns of flow that affect the transport and retention of materials (Huryn and Wallace 1987). The importance of effects of flow attributes, such as velocity and shear stress, on the distribution of benthic organisms has been well demonstrated (e.g., Extence et al. 1999, Gore et al. 2001, Dolédec et al. 2007), and has led to recent predictions of human-caused changes in species/abundance through hydrologic simulations (Mérigoux et al. 2009, Dunbar et al. 2010). The nature of riverbed material, which affects suitability for colonization by benthic organisms (Minshall 1984, Duncan et al. 1999), also varies with bed topography. Various systematic classifications of bed topography are used to describe river reaches (e.g., Bisson et al. 2006), but correspondence between the distribution of benthic organisms and such classifications has not been demonstrated fully, and mechanisms that link benthic organisms with bed topography are not well defined.

Gravel-bed rivers are commonly described by 2 major topographic features, riffles and pools, which alternate between shallow areas with fast flow and deep areas with slow flow in a channel (Leopold et al. 1964, Kani 1981). Riffles often support more biomass and production of benthic invertebrates than pools (Logan and Brooker 1983, Grubaugh et al. 1997, Nishimura et al. 2001). The higher flow velocities of riffles can increase activity and growth of invertebrates by supporting greater amounts of O_2 and food (Hart and Finelli 1999). However, higher flow velocities also are associated with increased shear stress that can impede settlement of individuals through scouring (Brooks et al. 2005, Morales et al. 2006). Differences in benthic community structure

[1] Present address: Disaster Prevention Research Institute, Kyoto University, Gokasho, Uji, Kyoto, 611-0011, Japan. E-mail: kobayashi.sohei.8u@kyoto-u.ac.jp

[2] Present address: Hamamatsu Office of River and National Highway, Ministry of Land, Infrastructure, Transport, and Tourism, 266, Nazuka, Hamamatsu, Shizuoka, 430-0811, Japan. E-mail: amano-k92ta@cbr.mlit.go.jp

[3] E-mail address: nakanisi@pwri.go.jp

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

between pools and riffles are widely recognized, but processes that may affect biomass and production of invertebrates in different habitats within pools or riffles are not as well described as those between pools and riffles.

Flow and bed materials vary at fine spatial scales within pool–riffle sequences, and this variability can affect biomass and structure of the benthic community. In gravel-bed rivers, riffles form at the submerged portion of bar fronts where the bed slope is greater than in areas immediately upstream or downstream (Knighton 1998). The bed of the upstream side of a riffle is relatively flat and gentle, and it gradually unifies to run further upstream. Runs often are identified as discrete habitat units, in which velocity and depth are intermediate between those of riffles and pools (Jowett 1993). The invertebrate community often differs between riffles and runs (Pridmore and Roper 1985, Nishimura et al. 2001, Osmundson et al. 2002), so variations in the invertebrate community also are expected along a short distance within riffles. In contrast, the bed of the downstream side of a riffle is more incised and flow is more constricted before it enters a pool further downstream. Invertebrates in such deep areas have been sampled quantitatively less frequently than invertebrates in other riffle habitats because of hazardous flows. Nevertheless, a comparison of benthic community structure among different flow zones within riffles would provide fundamental information for understanding the links between bed topography and benthic organisms in gravel-bed rivers.

Bed stability can be an important factor differentiating benthic communities in topographically different areas. Spatial distribution and habitat use of benthic invertebrates within a reach typically have been examined with respect to flow attributes under low and normal flows (e.g., base flow) (Extence et al. 1999, Dolédec et al. 2007). However, benthic communities often are disturbed by scours of bed materials during high flows, and the effects of such disturbances can last a few months to years (Niemi et al. 1990). Therefore, invertebrate community structure may vary according to disturbance legacies (Strayer 1999, Matthaei and Townsend 2000), as well as flow attributes under normal flows. Bed stability, which is determined by the combination of flow and bed characteristics (Lorang and Hauer 2003, Schwendel et al. 2010), is likely to vary within a reach and to have significant effects on community structure, especially in gravel-bed rivers where flows and bed materials vary at small spatial scales associated with bed topography.

Our goal was to assess relationships between macroinvertebrate community structure and channel bed topography within riffles of a gravel-bed river. We tested for differences in invertebrate biomass among flow zones and between middle and peripheral flow areas within riffles. We examined the physical conditions that may affect invertebrate biomass in gravel-bed rivers by estimating the probability of bed disturbance with a 2-dimensional (2D) hydrodynamic simulation with a series of discharge levels and substrate sizes observed in the study reaches. We also examined the effect of bed stability on benthic invertebrate community structure based on their use of the stream bed and feeding method (Kobayashi et al. 2010).

Methods

Study site

We worked at 3 riffles in the middle reach of the Chikuma River, which flows north through Nagano Prefecture (Fig. 1A) into the Niigata Prefecture where the stream is called the Shinano River. The Shinano River is the longest in Japan (367 km). The study sites were within a 9-km reach with elevation of 400 to 450 m asl. The drainage area above the lowest site is ~2400 km^2, and the reach has a mean bankfull width of 220 m and mean channel gradient of 0.5% (stream order 6–7). The channel is relatively straight with a meandering thalweg and has alternating bars that occur periodically first along one bank and then along the opposite bank (see Gordon et al. 2004) with a pool–riffle structure. The median grain size (D_{50}) in the reach was 30–50 mm (Chikuma Ecology Research Group, unpublished data). Large cobbles (128–256 mm) and boulders (256–512 mm) were prevalent especially on the beds around riffles. The baseflow discharge at the study sites was 30 to 40 m^3/s (Appendix S1; available online from: http://dx.doi.org/10.1899/12-080.1.s1). Water level typically rises during the snowmelt period from late March to May, and major storms occur during the typhoon season from late June to October. Because of nutrient loading from agricultural activities in the upper river reaches and from nearby urban areas, the concentrations of total N and P (TN: 1.5–2.5 mg/L, TP: 0.1–0.2 mg/L) and primary production (3.2–4.2 g C m^{-2} d^{-1}) were generally high in the reach (Chikuma Ecology Research Group, unpublished data).

Riffles developed at bar fronts, which typically extended downstream from one bank to the opposite bank. The riffles examined in our study developed near the upstream end of the bar fronts where the banks and bar fronts were close together. The flow at

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

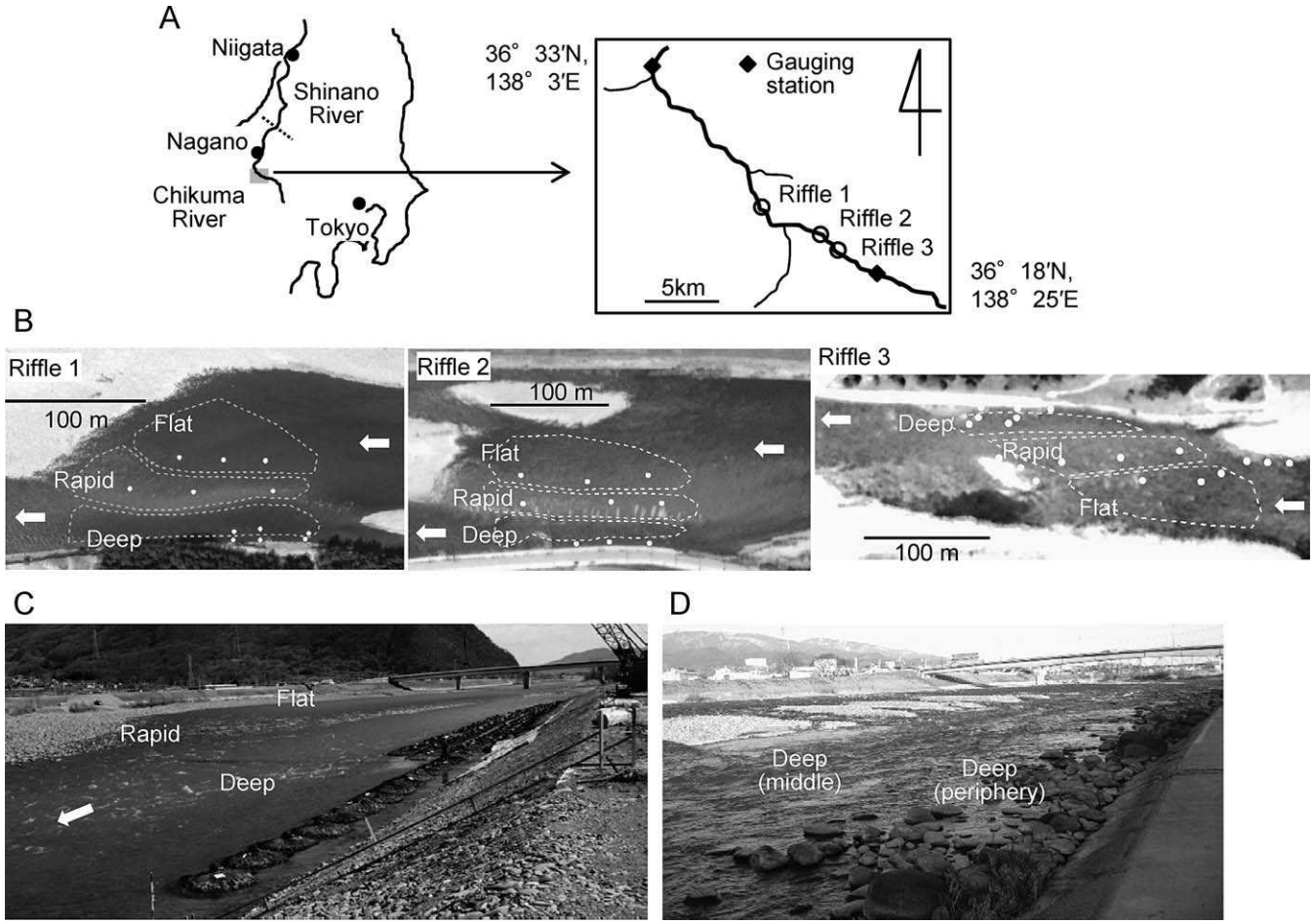

FIG. 1. A.—Maps showing the location of study sites in the Chikuma River. B.—Aerial photographs of the 3 sites showing the area of the flow zones (deep, rapid, flat) and the sampling positions. C.—Photograph of the 3 flow zones in riffle 1. D.—Photograph of the middle and periphery of the deep zone in riffle 2.

each riffle diverged at the upstream side and converged at the downstream side (Fig. 1B). At the center of the riffles, water flow was almost orthogonal to the bar front and the channel. This feature was most conspicuous in riffle 2 and least conspicuous in riffle 3.

Field measurements and samplings

We conducted topographic surveys and collected invertebrate samples in early March 2007 (riffle 1, riffle 2) and early March 2008 (riffle 3). Flow was normal but slightly higher than 1 wk before our sampling (according to hydrologic data available at 2 nearby gauging stations; Fig. 1A, Appendix S1). Several small floods occurred in winter before our sampling. Large floods occurred in summer 6 to 8 mo before our sampling. One of these was the 2nd largest since 1950.

We measured bed topography at each site and used these measurements for the hydrodynamic simulation. We measured cross-sectional topography with a total station (DTM-B10CLG, Nikon Trimble, Tokyo, Japan) at 13 to 14 transects usually spaced at 20-m intervals along 250 to 300-m reaches in riffles 1 and 2. We centered the surveyed area on the focal riffle and included the entire bankfull width. We recorded the water level at each transect and used it to calibrate the hydrodynamic simulation. At riffle 3, we surveyed bed topography with a global positioning system (GPS; Leica GPS1200, Leica Geosystems AG, St Gallen, Switzerland) at almost 800 randomly selected points along a 500-m reach.

We defined 3 zones within riffles (deep, rapid, flat; Fig. 1B–D) when the invertebrates were sampled. Deep zones were areas downstream of bar fronts with a concave bed topography that resulted in deeper flows. Flows were fast and turbulent with rough water surfaces (Fig. 1C, D). Rapid zones were the areas of bar fronts with convex bed topography

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

and steeper bed slopes. Flows were shallow with rough and white surface. Flat zones were upstream of bar fronts and had gentler bed slopes and greater depth than rapid zones, and they gradually unified to runs (relatively smooth water surface and deeper) further upstream. We also distinguished middle and periphery for each zone. The periphery was an area with significantly reduced depth and velocity relative to the middle and usually covered an area <1 m from the bank (edge of water) (Fig. 1D).

Our initial sampling design was to collect invertebrates from locations in the middle of deep, rapid, and flat zones, and in the periphery of deep zones with 3 replications for each zone. However, we were unable to collect samples in the middle of the deep zone of riffle 2. We collected extra samples in the middle of rapid and flat zones in riffle 2, in the middle of the deep zone in riffle 3, and in the periphery of rapid and flat zones in riffle 3. We avoided sampling areas that were too shallow and may have been dewatered within a month.

We used a 50 × 50-cm Surber sampler (mouth opening: 50 × 50 cm, mesh size: 0.5 mm, catch bag length: 1 m) to sample invertebrates. Within each sampling area, we washed all stones to a depth that was difficult to dig by hand (usually <10 cm), and we counted all surface stones exposed to the water column. We classified the surface stones into a size class: 1) large gravels (32–64 mm), 2) small cobbles (64–128 mm), 3) large cobbles (128–256 mm), 4) boulders (256–512 mm). We calculated the mean size class over all stones as a substrate index (range: 1–4). We preserved materials other than stones in 5% formalin. We measured water depth and current velocity at 0.6(depth) at each sampling location with a steel rod and an electromagnetic current meter (VE20; Kenek Co., Tokyo, Japan) before invertebrate sampling.

We took periphyton samples from 3 undisturbed stones (small or large cobbles) near the invertebrate sampling point. We rinsed each stone gently in water and brushed a 25-cm^2 area over a pan. We pooled the sloughed materials from the 3 stones and kept samples cool and dark after collection.

The flow was too deep and fast in the middle of deep zones for individuals to sample invertebrates without a device to obstruct the flow. We used an excavator to fill 1-m^3 polypropylene sand bags and to place them in the water. We placed several sand bags in a line perpendicular to the flow ~3 to 5 m upstream from the sampling points. We placed the bags close together and sometimes stacked them vertically because single bags were often moved by the current. The bed disturbance associated with the bag placement appeared minimal because little flushing of fine bed materials was observed. We needed 10 to 20 min to place the sand bags at a sampling point, and we sampled soon after the placement. We were unable to sample the middle of the deep zone of riffle 2 because of excavator failure.

Laboratory procedure

We washed invertebrate samples on a 1-mm-mesh sieve and separated invertebrates from other materials in a white tray filled with water. We identified macroinvertebrates to the lowest possible taxonomic level (usually genus or species). We weighed individuals to the nearest 0.1 mg after drying at 60°C for 48 h, divided dry mass (DM) by the area of quadrat (0.25 m^2), and expressed it as biomass (g/m^2). We summed biomass at the genus level, except for Chironomidae, which we summed at the subfamily level. We classified taxa by feeding group (grazers, filterers, deposit feeders, and predators) according to Merritt and Cummins (1996) and Kobayashi et al. (2010) and by 6 bed-residence types based on their mode of living (living in fixed retreat, living in portable case, free living) and settling position in the bed (surface, interstones, interior) according to Kobayashi et al. (2010). The surface fixed-retreat type included taxa that build retreats on the top or side of the stones on the bed surface (most net-spinning caddisflies [e.g., *Hydropsyche*], tube-building caddisflies, and a cranefly [e.g., *Antocha*]). The interstones fixed-retreat type included a net-spinning caddisfly (*Stenopsyche*) that builds retreats between or under stones. The surface portable-case type included taxa that construct portable cases and stay on the top or sides of surface stones (cased caddisflies [e.g., *Glossosoma*]). The surface free-living type included taxa without a retreat/case that stay on the top or sides of surface stones (streamlined mayflies [e.g., *Baetis*], blackflies). The interstones free-living type included taxa without a retreat/case that require loose interstices between or under the stones (thicker mayflies [e.g., *Drunella*, *Epeorus*], large-bodied stoneflies, and dobsonflies). The interior free-living type included taxa that can burrow into relatively tight interstices or sand and pebbles under the surface stones (e.g., flexible-bodied worms and leeches, flat-bodied water pennies and flatworms, and other burrowers).

We filtered periphyton samples through glass-fiber paper (Whatman® GF/C, mean pore size = 1.2 μm). We extracted chlorophyll from ½ of the paper with 99.5% ethanol in cool and dark conditions for 6 h. We measured the extracted pigments with a spectropho-

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

tometer (UV-2200A; Shimadzu Co., Kyoto, Japan). We used the remaining ½ of the paper to measure ash-free dry mass (AFDM) by weighing after drying at 60°C for 48 h and combusting at 700°C for 2 h. We divided chlorophyll *a* (Chl *a*) and AFDM values by the sampling area (75 cm^2) and expressed values as mg/m^2 or g/m^2.

Statistical analysis

We tested differences in environmental variables and invertebrate biomasses among the flow zones across riffles with a mixed model analysis of variance (ANOVA) using flow zone as a fixed factor and site (i.e., riffle) as a random factor. We could not conduct an ANOVA with a fully factorial design using the whole data set (i.e., 4 levels of flow zone, 3 levels of site) because we lacked data for the middle of the deep zone in riffle 2. Instead, we conducted 2 ANOVAs. One excluded the middle of deep zones (i.e., 3 levels of flow zone and 3 levels of site), and one excluded riffle 2 (i.e., 4 levels of flow zone and 2 levels of site). When the effect of flow zone (fixed factor) was significant, we used Tukey's multiple comparisons to identify means that differed (ANOVA 1: among the middle of rapid zones, middle of flat zones, and periphery of deep zones; ANOVA 2: between the middle of deep zones and each of the middle of rapid zones, middle of flat zones, and periphery of deep zones). We log(x)-transformed all dependent variables to normalize their distributions and standardize the variance structure. We used R (version 2.15.0; R Development Core Team, Vienna, Austria) to run these analyses. We set $\alpha = 0.05$ to indicate statistical significance for all tests.

We used nonmetric multidimensional scaling (NMDS) ordination to measure the major trends in community structure among flow zones across the riffles. NMDS is a procedure for plotting communities in 2-dimensional space, such that the distances between communities correspond to their dissimilarities. We ran NMDS in PC-ORD (version 5; MjM Software, Gleneden Beach, Oregon) with Sørensen's distance as the distance measure. We log(x)-transformed the biomass data before the analysis.

Hydrodynamic simulation

We used River2D (Steffler and Blackburn 2002) to simulate spatial configurations of flow in each site to estimate the shear stress acting on the river bed for various discharge levels. We created 300- to 500-m channel reaches in which meshes (a unit of calculation, ~5-m scale) based on the field topographic data were distributed uniformly. We simulated flow around riffles for some discharge levels experienced during the 3 mo before invertebrate sampling (25–350 m^3/s) including low flows and small floods (see Appendix S2 for more details on the running conditions of the simulation; available online from: http://dx.doi.org/10.1899/12-080.1.s1).

Results from the River2D model included water depth, depth-averaged flow velocity, and shear stress (N/m^2), which is the hydraulic force to move bed materials, at each computational mesh. We extracted these hydraulic variables for the area of each flow zone, and compared shear stress (τ) with critical shear stress (τ_c) needed to initiate movement of bed materials,

$$\tau_c = \theta_c g d(\rho_s - \rho)$$

where ρ_s and ρ are the density of a particle (2650 kg/m^3) and of water (1000 kg/m^3), respectively, g is the acceleration of gravity (9.807 m/s^2), and d is the grain size (m). For the constant, θ_c, we used 0.045, which is often adopted for streams with coarse bed materials (Duncan et al. 1999, Lorang and Hauer 2003). We compared the ratio of τ to τ_c among the flow zones by assuming that the probability of bed movement increases with the ratio.

Results

Observed flow and bed attributes

Water depth and flow velocity were significantly higher at the middle of deep zones than the middle of flat zones and the periphery of deep zones across the riffles (Table 1). The middle of rapid zones was shallower than the middle of flat zones and had higher flow velocity than the periphery of deep zones. Part of the rapid zone (eastern or upstream side in each riffle, Fig. 1B) always was shallowest and had relatively low flow velocity. Except at these locations, flow velocity of rapid zones was quite similar to that of deep zones. Bed material size (based on substrate index) was significantly larger at the middle and periphery of deep zones than the middles of rapid and flat zones across the riffles. The mean value of 3.1 in the middle of deep zones indicated the prevalence of large cobbles and boulders, whereas the mean value of 2.4 in the middle of rapid and flat zones indicated the prevalence of small and large cobbles. The periphery of rapid and flat zones (sampled only in riffle 3) was shallower (0.13–0.26 m) and had higher flow velocity (0.23–0.31 m/s) and smaller bed materials (2.4–2.8) than the periphery of deep zones.

Chl *a* and AFDM of periphyton were highest at the middle of deep zones, followed by the periphery of

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

TABLE 1. Mean (±1 SD) values of physical and periphyton variables for each flow zone according to field surveys, and the results of mixed model analyses of variance (ANOVAs) and subsequent Tukey's tests. Means with the same superscript are not significantly different. $n = 3$ riffles. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variables	Middle of deep	Middle of rapid	Middle of flat	Periphery of deep	ANOVA without middle of deep		ANOVA without riffle 2	
					F	*p*	*F*	*p*
Depth (m)	0.65 ± 0.02[a]	0.21 ± 0.06[c]	0.40 ± 0.08[b]	0.26 ± 0.02[bc]	10.86	***	16.85	***
Velocity (m/s)	1.40 ± 0.05[a]	1.10 ± 0.20[ab]	0.72 ± 0.10[b]	0.10 ± 0.02[c]	31.64	***	28.08	***
Substrate index	3.1 ± 0.0[a]	2.4 ± 0.1[b]	2.4 ± 0.2[b]	2.9 ± 0.4[a]	6.96	**	7.29	**
Periphyton Chl *a* (mg/m^2)	73.0 ± 62.3[ab]	9.3 ± 6.1[b]	8.4 ± 3.7[b]	25.9 ± 3.6[a]	4.87	*	16.13	***
Periphyton AFDM (g/m^2)	24.1 ± 18.6[a]	5.0 ± 2.2[b]	4.3 ± 1.0[b]	17.4 ± 3.2[a]	27.17	***	31.84	***

deep zones (Table 1). The variation of Chl *a* and AFDM was relatively high in the middle of deep zones, and only AFDM differed between the middle of deep zones and other zones. The high variation could be attributed to patchy development of the filamentous algae *Cladophora glomerata* (L.) Kützing in the middle of deep zones (e.g., values as high as 417 mg/m^2 Chl *a* and 124 g/m^2 AFDM). Such growth of *C. glomerata* was not observed in rapid and flat zones. Dense growth of another filamentous algae, *Hydrurus foetidus* (Villars), was observed in rapid zones 1 mo before our sampling, but it had disappeared by the sampling date.

Macroinvertebrate biomass and community structure

Total macroinvertebrate biomass was significantly higher at the middle and periphery of deep zones than at the middle of rapid and flat zones (Fig. 2A). The difference between the middle of deep zones and rapid zones was 4.6- to 19-fold across riffles. The biomass of filterers, the most dominant functional feeding group in many samples, was significantly higher at the middle and periphery of deep zones than at the middle of rapid and flat zones (Fig. 2A). This pattern reflected the distribution of *Hydropsyche* and *Stenopsyche* (Appendix S3; available online from: http://dx.doi.org/10.1899/12-080.1.s1). The biomass of grazers was significantly higher in the middle and periphery of deep zones than in the middle of rapid zones. The biomass of predators, which was dominated by *Onychogomphus* and *Dina*, was significantly higher in the periphery of deep zones than in the other zones, with a 5- to 10-fold difference between the periphery and middle of deep zones. A similar trend was observed for deposit-feeders. The total biomass in the periphery of rapid and flat zones was low (1.0–2.0 g/m^2) and dominated by grazers (54–66%).

Invertebrate distribution among the flow zones also differed according to bed-residence type. The biomass of the surface fixed-retreat type was significantly higher at the middle of deep zones than at the middle of rapid and flat zones (Fig. 2B) and reflected the distribution of *Psychomyia*, *Cheumatopsyche*, *Hydropsyche*, *Potamyia*, and *Antocha*. Its biomass was also significantly higher at the periphery of deep zones than at the middle of rapid zones. A similar distribution was observed for the surface portable-case type, which was dominated by *Glossosoma*. The biomass of the interstones fixed-retreat type (*Stenopsyche*) was significantly higher at the periphery of deep zones than at the middle of rapid and flat zones. The biomass of the interior free-living type differed markedly between the periphery of deep zones and other zones and reflected the distribution of *Dugesia*, Oligochaeta, *Dina*, and *Onychogomphus*. The difference in biomass of the surface free-living and interstones free-living types among flow zones was unclear and varied among taxa. For example, the biomass of *Baetis* (surface free-living type), *Drunella*, *Epeorus*, and *Rhithrogena* (interstones free-living type) tended to be higher at the middle of rapid and flat zones than at the middle and periphery of deep zones, whereas the biomass of *Simulium* (surface free-living type), *Uracanthella*, and *Torleya* (interstones free-living type) was significantly higher at the middle or periphery of deep zones. The biomasses of all bed-residence types except the interstones free-living type were lower at the periphery of rapid and flat zones than at the periphery of deep zones.

Differences in macroinvertebrate community structure among flow zones also were evident in the NMDS ordination (Fig. 3). Communities at the middle of rapid and deep zones and the periphery of deep zones were almost completely separated from each other along axis 1. Communities at the middle of flat zones were between communities at the middle of rapid and deep zones. The communities at the periphery of rapid and flat zones were almost completely separated from the others along axis 2.

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

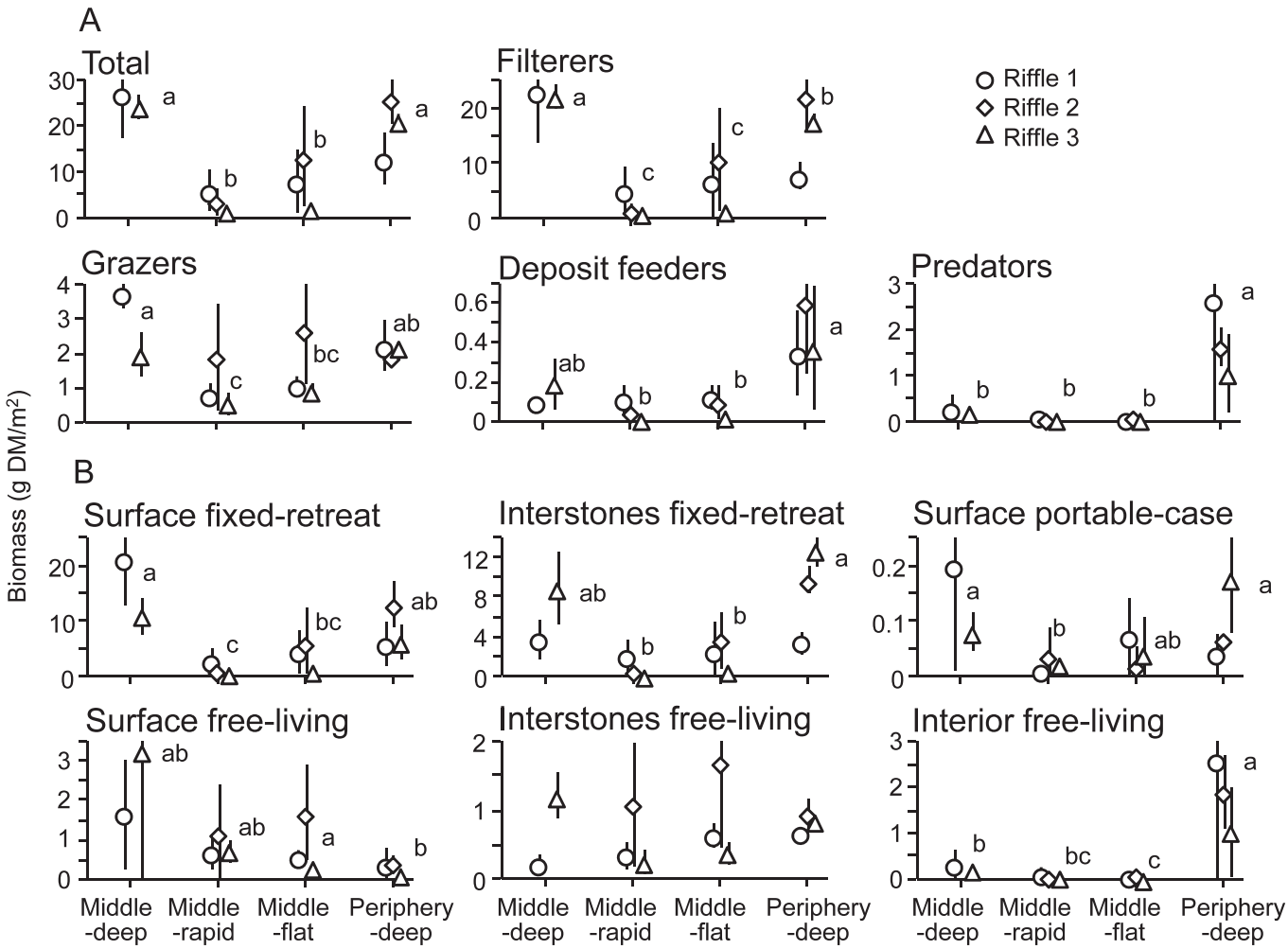

FIG. 2. Mean (±1 SD) biomass of total macroinvertebrates and feeding groups (A), and bed-residence types (B) in different flow zones. Groups with the same letters are not significantly different among flow zones based on mixed model analysis of variance and subsequent Tukey's test. DM = dry mass. $n = 3$ riffles.

Hydrodynamic simulation

Simulations of normal flow at each site showed spatial patterns in flow velocity and depth (Fig. 4A–C, see Appendix S4 for 2-dimensional patterns; available online from: http://dx.doi.org/10.1899/12-080.1.s1) that were in agreement with the field measurements. For instance, deep zones were characterized by deeper and partly faster flow (at the middle), whereas rapid zones were characterized by shallower and partly faster flow (shallower areas [upstream- or eastern-side] had low velocities). Current velocity measured at each sampling point was correlated with the simulated current velocity at the nearest mesh (Pearson's moment, riffle 1: $r^2 = 0.83$, riffle 2: $r^2 = 0.66$, riffle 3: $r^2 = 0.90$). Because of their greater water depth and velocity, deep zones had greater unit-width discharge (median discharge = 0.84–0.98 m^3/s) than rapid zones (0.11–0.20 m^3/s) and flat zones (0.23–0.72 m^3/s).

For normal flows, τ was greater at rapid than at deep and flat zones especially in riffle 1 and riffle 2 (Fig. 4A, B) and the plots for rapid zones were closer to isoclines of higher τ than plots for flat and deep zones. The median value among all plots for each flow zone shows the changes in τ with discharge (see Fig. 5A for riffle 2 results, Appendix S5 for riffle 1 and 3 results; available online from: http://dx.doi.org/10.1899/12-080.1.s1). As discharge increased, the differences in median τ among the flow zones tended to be small or the median τ at deep and flat zones exceeded that at the rapid zones. τ_c was 87.4 N/m^2 for rapid and flat zones (based on bed grain size = 12 cm, corresponding to substrate index = 2.4), and 142 N/m^2 for deep zones (bed grain size = 19.5 cm, substrate index = 3.1). The

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

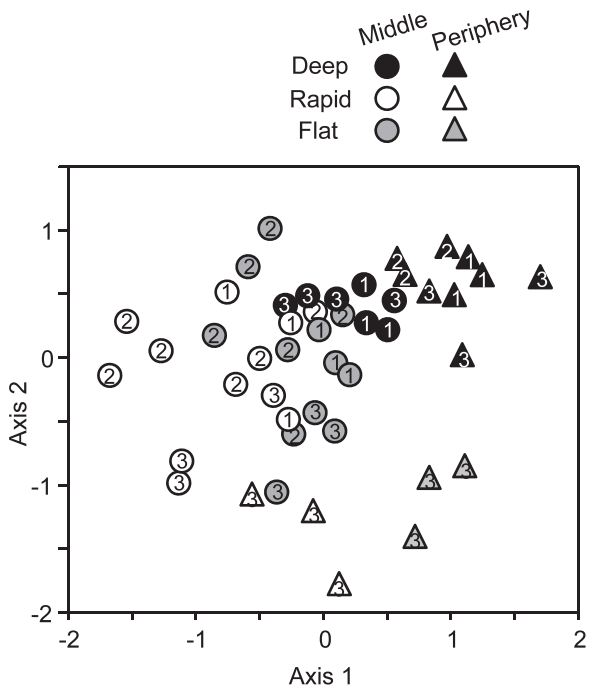

FIG. 3. Nonmetric multidimensional scaling ordination of macroinvertebrate communities plotted for all sampling points across riffles. The numbers in symbols denote the identity of the riffle from which the sample was collected.

percentage of τ-values > τ_c was low for all discharge levels. For example, for lower discharges (<100 m^3/s), the maximum percentage was 7 to 20% at rapid zones, and for the highest discharge, the maximum percentage was 30% in flat zones.

The ratio of median τ to τ_c (an index of the probability of bed movement) was higher in rapid zones than in deep zones for all discharge levels across riffles (Fig. 5B, Appendix S5). The ratio increased with discharge, especially in flat zones, and the ratio in flat zones exceeded that in rapid zones for the largest floods in riffle 1 and riffle 2.

Discussion

Features of invertebrate communities in our study

We observed differences in macroinvertebrate biomass and community structure among the 3 flow zones and between the middle and periphery of the flow zones across riffles. The differences in biomass and community structure were greatest between rapid and deep zones. Biomass and community structure in flat zones were somewhat intermediate between the rapid and deep zones. The hydrodynamic simulation based on topographical data and the field measurements of flow and substrate revealed

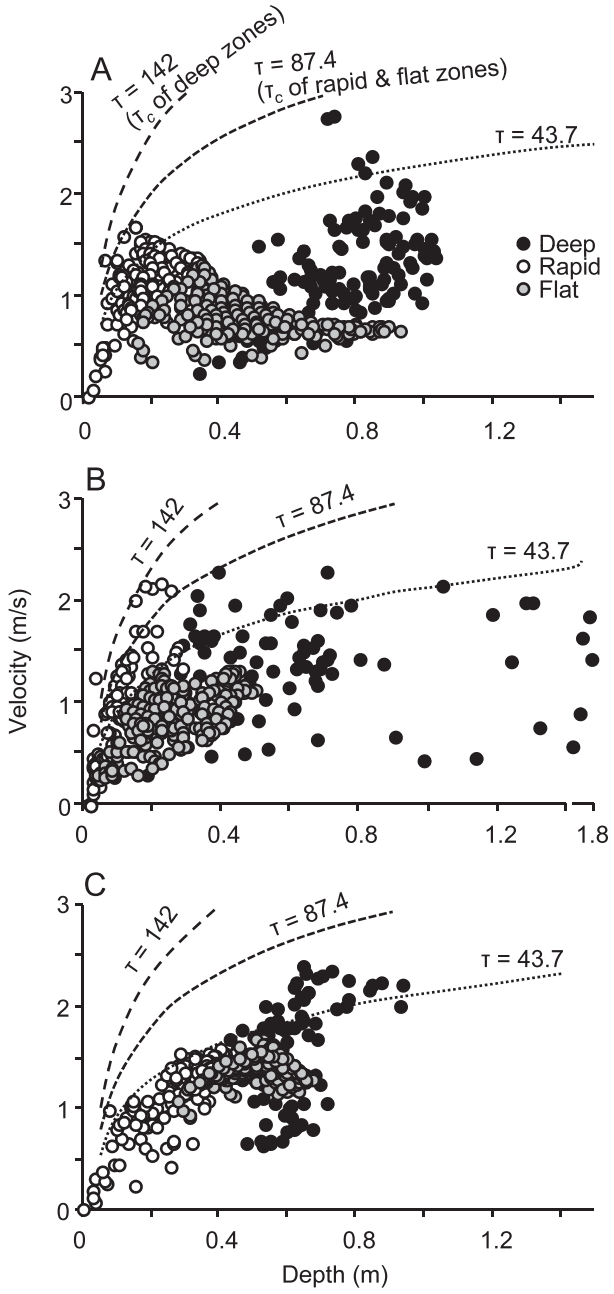

FIG. 4. Depth-averaged flow velocity as a function of depth in the 3 flow zones of riffles 1 (A), 2 (B), and 3 (C) simulated by 2-dimensional hydrodynamic modeling for the discharge of the sampling time. Isoclines of shear stress (τ) are shown.

differences in current velocity, bed-material size, and bed stability among the 3 zones. These physical features probably were reflected in community structure in terms of feeding group and bed-residence type.

Our observation of the lowest invertebrate biomass in rapid zones differs from the generally recognized

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

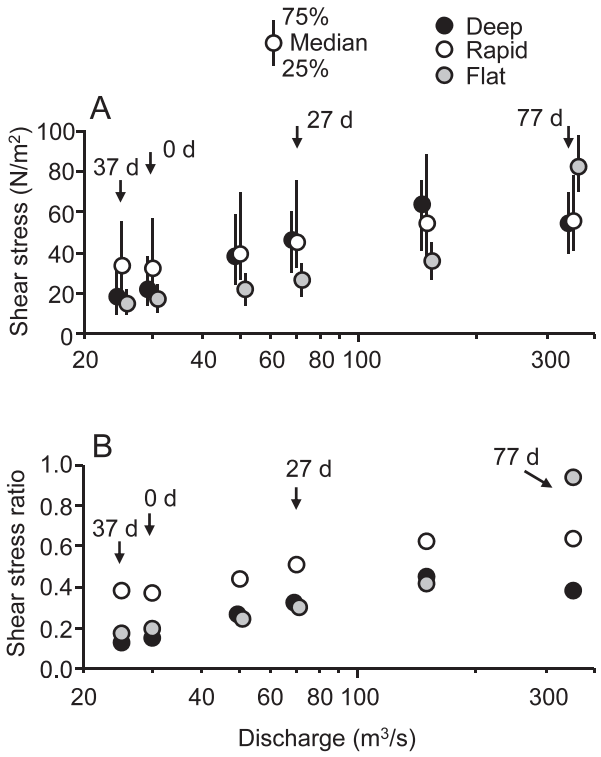

FIG. 5. Median shear stress (with 25 and 75% values) (A) and shear stress ratio (median shear stress to critical shear stress) (B) in the 3 flow zones in riffle 2 for the discharge levels experienced within 3 mo before sampling simulated by 2-dimensional hydrodynamic modeling (see Appendix S5 for the results of riffles 1 and 3). Arrows indicate number of days before sampling.

pattern of high invertebrate biomass in riffles. Riffles generally support higher biomass than runs and pools (Pridmore and Roper 1985, Nishimura et al. 2001, Osmundson et al. 2002). Rapid zones have physical features that are most recognizable as riffles (i.e., shallowness and swiftness of flow; Jowett 1993) among the 3 zones, but invertebrate biomass was lower in rapid than in flat zones, which have physical features much like those of runs. The biomass of filterers, which prefer fast current conditions and are often the dominant group in riffles (Grubaugh et al. 1997, Nishimura et al. 2001), was particularly low in rapid zones. Thus, current velocity alone cannot explain the lower biomass in rapid zones.

We found exceptionally high levels of invertebrate biomass in deep zones (25–30 g DM/m^2). Invertebrate biomass typically ranges from <1 to 10 g DM/m^2 even in riffles with high biomass (Quinn and Hickey 1990, Nishimura et al. 2001, Osmundson et al. 2002). The biomass in deep zones was comparable to the annual invertebrate biomass in a reach of an Appalachian river (20–25 g AFDM/m^2) that had particularly high invertebrate production (nearly 200 g AFDM m^{-2} y^{-1}) (Grubaugh and Wallace 1995). Much higher biomass (>50 g DM/m^2) has been reported at the outlets of lakes and dams (Parker and Voshell 1983, Wotton 1988), but these high levels of biomass are uncommon in unregulated rivers. Quantitative sampling in deep, fast flowing areas has rarely been reported especially for high-order streams and rivers. Rempel et al. (2000) sampled in a large gravel-bed river in Canada to a depth of 3 m using a weighted grab sampler, but they found fewer invertebrates in deeper areas (>1.5 m) than in shallower areas (<0.5 m). Our study may be the first to use large sand bags to permit quantitative sampling in fast current conditions. We think the effects of reduced flow velocity on invertebrate communities at the time of sampling were minimal because sampling began soon after the current was reduced.

Factors differentiating invertebrate biomass and community structure among flow zones

The hydrodynamic simulations and the differences in bed material size suggest that the probability of bed movement was highest and, thus, bed stability was lowest in rapid zones during normal flows and small floods. Values of τ that exceeded τ_c were restricted to a small region of the rapid zones (up to 20%), so the extent of bed movement in rapid zones may be small. We estimated mean τ at each discharge level, but entrainment of bed materials may be more related to instantaneous τ, which is much greater than the mean, generated by flow fluctuations and turbulence (Lorang and Hauer 2003). Moreover, smaller bed materials could have been entrained and could have abraded larger materials (Schwendel et al. 2010) or could have induced entrainment of larger materials during collisions (Lorang and Hauer 2003). The bed appeared stable in flat zones during normal flows, but the probability of bed movement in flat zones increased and exceeded that in rapid zones during larger floods. The bed in deep zones is likely to be stable during all discharges experienced in the 3 mo preceding our sampling. Despite greater flow velocities in deep zones, smaller water-surface slopes (associated with a concave bed profile) and larger bed materials contribute to this stability.

The difference in bed stability between rapid and deep zones probably was reflected in the development of periphyton. Lower periphyton biomass and Chl *a* in rapid zones suggests that the beds in rapid zones were relatively unstable. *Hydrurus foetidus*, which covered the beds in rapid zones 1 mo before

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

we sampled, usually is found on scoured and bare stones (Elber and Schanz 1990, Wellnitz and Rader 2003). Thus, the temporal dominance of this species before and its disappearance at our sampling time would both indicate the unstable nature of rapid zones. Periphyton biomass and Chl *a* were higher in deep than in rapid zones, and we frequently observed *C. glomerata* on the bed in deep zones. Growth and development of *C. glomerata* is largely restricted to stable stones in fast current conditions (Bergey et al. 1995, Okada and Watanabe 2007). Thus, the dense growth of *C. glomerata* suggests that the bed in deep zones was stable.

Differences in macroinvertebrate community structure among flow zones probably are associated with variation in the requirements for substrate stability among bed-residence types. Higher biomass in deep than in rapid zones was most apparent for the surface fixed-retreat type. This type included net-spinning caddisfly taxa that are often abundant in stable environments, such as lake outlets, regulated rivers, and on large wood debris in sandy rivers (Parker and Voshell 1983, Benke et al. 1984, Malmqvist et al. 1991). The caddisfly, *Hydropsyche*, was the most dominant taxon. This genus is considered to be a climax genus because it dominates the latter stages of community succession in riffle beds in Japanese rivers (Tsuda and Gose 1964). Taxa in the surface fixed-retreat type are regarded as preferring stable substrates because of their sedentary lifestyle. The biomass of the surface portable-case type (i.e., cased caddisflies) also was greater in deep than in rapid zones. Cased caddisflies are not sedentary, but they are competitively dominant grazers in relatively stable environments, such as in spring streams and regulated rivers (Cobb et al. 1992, Kohler 1992, Wootton et al. 1996). In contrast, the difference in biomass of surface and interstones free-living taxa among the flow zones was unclear, or the biomass tended to be greater in rapid zones than in deep zones. One such taxon was *Baetis*, which is a rapid colonizer of disturbed patches (Mackay 1992) and competitively inferior (Malmqvist et al. 1991, Kohler 1992). The interstones free-living type included *Rhithrogena* and *Epeorus*, which prefer porous beds (i.e., more interstices between stones in the beds) (Minshall 1967, Lubini and Sartori 1994). The beds of rapid zones appeared porous because the stones moved readily in response to our walking during the surveys, whereas stones did not move freely in deep zones. Thus, the higher biomass of these interstones free-living taxa in rapid zones may be associated with the porous nature of the beds and with bed instability.

Food availability and bed stability may have contributed to the high invertebrate biomass in deep zones. Organic matter associated with periphyton was more abundant in deep zones. Periphyton includes many inedible materials, such as filamentous algae (*C. glomerata*), but some grazing taxa are likely to benefit from bed stability and continuous accumulation of algae and other microbes in deep zones. Moreover, the greater supply of transported particulate organic matter (POM) associated with discharge is likely to support high invertebrate biomass in deep zones, which are largely dominated by filterers (85–90%). High biomass and production of filterers have been observed consistently in the outlets of lakes and impoundments with high amounts or quality of transported POM (Mackay and Waters 1986, Wotton 1988, Huryn and Wallace 2000). We did not measure transported POM, but its availability would be especially high in deep zones with highest unit-width discharge. However, we are unable to explain why filterer biomass also was high in the periphery of deep zones with low velocities and discharges. In contrast, invertebrate biomass, especially of filterers, was very low at the periphery of rapid and flat zones. Velocity is locally low in the periphery of deep zones, but the supply of transported POM may be maintained by flow turbulence and lateral mixing of water between middle and periphery in deep zones.

The difference in community structure between the middle and periphery of deep zones may be associated with differences in interstitial spaces in bed materials and current velocity. One feature of the periphery was the higher biomass of deposit feeders there than elsewhere. Deposited detritus may be more available in the periphery because of low current velocity. Moreover, most deposit-feeding taxa belong to the interior free-living type that burrows into interstitial spaces under stones. The biomass of predators, many of which were of the interior free-living type, also was greater in the periphery than middle. In addition, filterers in the periphery were dominated by *Stenopsyche*, which builds retreats under or between stones (Tsuda 1959), and *Cheumatopsyche*, which tends to prefer the lower side of stones (Wallace 1975, Rutherford and Mackay 1985). The size of bed materials was similar between the middle and periphery of deep zones, but embeddedness of these materials by fine sediment appeared different. The surface cobbles and boulders were rarely embedded in the periphery, whereas they were heavily embedded in the middle of deep zones (Appendix S6; available online from: http://dx.doi.org/10.1899/12-080.1.s1). It seems atypical that less-fine sediment occurred in the periphery, where current velocity was low, than in the deep zone. However, fine sediment, such as sand, which is easily moved by flow, may be

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

prone to transport to deeper areas (i.e., from the periphery to the middle; Table 1) where it is deposited between the main materials. In this context, the spaces beneath surface stones might be more available for invertebrates in the periphery than in the middle of deep zones. The largest invertebrates observed in our study, a dobsonfly *Protohermes grandis* (Thunberg), which probably requires a large space for hiding, was found only in the periphery of deep zones.

Topography and bed characteristics supporting high invertebrate biomass

Conditions that ensure both sufficient habitat and sufficient food supply are required to yield high invertebrate biomass. High biomass and production of invertebrate communities dominated by either filterers or grazers occur in river reaches with a stable flow environment in temperate regions (Huryn and Wallace 2000, Hall et al. 2006). Thus, a certain extent of environmental stability, especially for substrate that allows continuous colonization and growth by invertebrates, is essential for high biomass. Food supply (periphyton production or transported POM) is also essential for high biomass and production (Mackay and Waters 1986, Wotton 1988, Hall et al. 2006), and flow velocity is an important determinant of the supply of transported POM for filterers. Moreover, flow velocity and bed stability are often interrelated. Higher flow velocity is typically associated with higher τ, and areas that provide both stability and food supply for benthic invertebrates are relatively uncommon especially in unregulated gravel-bed rivers. The necessary conditions would be satisfied at fast-flow areas with deposition of exceptionally large bed materials or bed topography like that of the deep zones in our study.

Other bed characteristics that could potentially promote the settlement of invertebrates are the surface texture of bed materials and the interstitial spaces between the bed materials (Flecker and Allan 1984, Way et al. 1995). More interstitial spaces could increase invertebrate biomass in the middle of deep zones by promoting the colonization by interstones invertebrates, including large predators (perlid stoneflies and dobsonflies) and *Stenopsyche*, which are keystone species of high total biomass in Japanese rivers (Nishimura et al. 2001).

Topography–invertebrate relations in longer time scales

We observed patterns of invertebrate distribution that were consistent across the 3 riffles, and we would expect similar distribution patterns in other riffles in the study area. However, we captured the patterns in a limited period (early spring of 2 consecutive years), so caution should be used when extrapolating our findings to other seasons. Invertebrate activity and the time required for community recovery after a disturbance vary depending on temperature and season (Wallace 1990, Mackay 1992). Invertebrate colonization and community recovery are expected to be more rapid in warmer seasons. Differences in community structure among flow zones may be less apparent in warmer seasons because of faster colonization of invertebrates of disturbed areas (i.e., rapid zones). However, disturbance will be more frequent in warmer seasons because of snowmelt and rain (Appendix S1), which may keep invertebrate biomass in rapid zones low.

On a longer time scale, bed characteristics of each flow zone could change. The bed topography of the riffles we studied seems to have been formed by severe floods that occurred 6 to 8 mo before our survey. Thus, beds consisted of newly deposited cobbles and gravels. The beds in the rapid zones were unstable at the time of sampling, but they should stabilize as the mobile (i.e., finer) materials are removed and stable (coarser) materials remain and as the bed slope of rapids becomes gentler. On the other hand, cobbles in deep zones may gradually become embedded by fine sediment until the next large flood. Thus, bed characteristics of each flow zone, which are important determinants of invertebrate community structure, will change over time and will vary with the magnitude of and the time since floods. Understanding temporal changes in bed characteristics is the next step for understanding relationships between bed topography and community structure.

Acknowledgements

We thank the Chikuma River Office in the Ministry of Land, Infrastructure, Transport, and Tourism, and Josho and Koshoku fisheries for supporting our research and providing channel and hydrological data or other useful information. Y. Oshima worked together in the field and played important roles in building a good relationship with offices and fisheries. K. Nakata and M. Fujiwara assisted our fieldwork. We also thank M. D. Bryant for reviewing and improving our manuscript.

Literature Cited

BENKE, A. C., T. C. V. ARSDALL, AND D. M. GILLESPIE. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecological Monographs 54:25–63.

BERGEY, E. A., C. A. BOETTIGER, AND V. H. RESH. 1995. Effects of water velocity on the architecture and epiphytes of

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

Cladophora glomerata (Chlorophyta). Journal of Phycology 31:264–271.

BISSON, P. A., D. R. MONTGOMERY, AND J. M. BUFFINGTON. 2006. Valley segments, stream reaches, and channel units. Pages 23–50 *in* F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. 2nd edition. Elsevier, Amsterdam, The Netherlands.

BROOKS, A. J., T. HAEUSLER, I. REINFELDS, AND S. WILLIAMS. 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. Freshwater Biology 50:331–344.

COBB, D. G., T. D. GALLOWAY, AND J. F. FLANNAGAN. 1992. Effects of discharge and substrate stability on density and species composition of stream insects. Canadian Journal of Fisheries and Aquatic Sciences 49:1788–1795.

DOLÉDEC, S., N. LAMOUROUX, U. FUCHS, AND S. MÉRIGOUX. 2007. Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. Freshwater Biology 52:145–164.

DUNBAR, M. J., M. L. PEDERSEN, D. CADMAN, C. EXTENCE, J. WADDINGHAM, R. CHADD, AND S. E. LARSEN. 2010. River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores. Freshwater Biology 55: 226–242.

DUNCAN, M. J., A. M. SUREN, AND S. L. R. BROWN. 1999. Assessment of streambed stability in steep, bouldery streams: development of a new analytical technique. Journal of the North American Benthological Society 18:445–456.

ELBER, F., AND F. SCHANZ. 1990. Algae, other than diatoms, affecting the density, species richness and diversity of diatom communities in rivers. Archiv für Hydrobiologie 119:1–14.

EXTENCE, C. A., D. M. BALBI, AND R. P. CHADD. 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. Regulated Rivers: Research and Management 15: 543–574.

FLECKER, A. S., AND J. D. ALLAN. 1984. The importance of predation, substrate and spatial refugia in determining lotic insect distribution. Oecologia (Berlin) 64:306–313.

GORDON, N. D., T. A. MCMAHON, B. L. FINLAYSON, C. J. GIPPEL, AND R. J. NATHAN (EDITORS). 2004. Stream hydrology: an introduction for ecologists. John Wiley and Sons, West Sussex, UK.

GORE, J. A., J. B. LAYZER, AND J. MEAD. 2001. Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. Regulated Rivers: Research and Management 17:527–542.

GRUBAUGH, J. W., AND J. B. WALLACE. 1995. Functional structure and production of the benthic community in a Piedmont river: 1956–1957 and 1991–1992. Limnology and Oceanography 40:490–501.

GRUBAUGH, J. W., J. B. WALLACE, AND E. S. HOUSTON. 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. Freshwater Biology 37:581–596.

HALL, R. O., M. F. DYBDAHL, AND M. C. VANDERLOOP. 2006. Extremely high secondary production of introduced snails in rivers. Ecological Applications 16:1121–1131.

HART, D. D., AND C. M. FINELLI. 1999. Physical-biological coupling in steams: the pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematics 30:363–395.

HURYN, A. D., AND J. B. WALLACE. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology 68:1932–1942.

HURYN, A. D., AND J. B. WALLACE. 2000. Life history and production of stream insects. Annual Review of Entomology 45:83–110.

JOWETT, I. G. 1993. A method for objectively identifying pool, run, and riffle habitats from physical measurements. New Zealand Journal of Marine and Freshwater Research 27:241–248.

KANI, T. 1981. Stream classification in ''Ecology of torrent-inhabiting insects'' (1944): an abridged translation. Physiology and Ecology Japan 18:113–118.

KNIGHTON, D. 1998. Fluvial forms and processes: a new perspective. Arnold, London, UK.

KOBAYASHI, S., S. NAKANISHI, Y. OSHIMA, AND K. AMANO. 2010. Physical characteristics and macroinvertebrate biomass of riffles in the Toyo River, Aichi Prefecture. Japanese Journal of Limnology 71:147–164 (in Japanese with English abstract).

KOHLER, S. L. 1992. Competition and the structure of a benthic stream community. Ecological Monographs 62: 165–188.

LEOPOLD, L. B., M. G. WOLMAN, AND J. P. MILLER. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, California.

LOGAN, P., AND M. P. BROOKER. 1983. The macroinvertebrate faunas of riffles and pools. Water Research 17:263–270.

LORANG, M. S., AND F. R. HAUER. 2003. Flow competence and streambed stability: an evaluation of technique and application. Journal of the North American Benthological Society 22:475–491.

LUBINI, V., AND M. SARTORI. 1994. Current status, distribution, life cycle and ecology of *Rhithrogena germanica* Eaton, 1985 in Switzerland: preliminary results (Ephemeroptera, Heptageniidae). Aquatic Sciences 56:388–397.

MACKAY, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49:617–628.

MACKAY, R. J., AND T. F. WATERS. 1986. Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67:1680–1686.

MALMQVIST, B., S. RUNDLE, C. BRÖNMARK, AND A. ERLANDSSON. 1991. Invertebrate colonization of a new, man-made stream in southern Sweden. Freshwater Biology 26:307–324.

MATTHAEI, C. D., AND C. R. TOWNSEND. 2000. Long-term effects of local disturbance history on mobile stream invertebrates. Oecologia (Berlin) 125:119–126.

MÉRIGOUX, S., N. LAMOUROUX, J. OLIVIER, AND S. DOLÉDEC. 2009. Invertebrate hydraulic preferences and predicted impacts of changes in discharge in a large river. Freshwater Biology 54:1343–1356.

MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms

MINSHALL, G. W. 1984. Aquatic insect–substratum relationships. Pages 358–400 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger, New York.

MINSHALL, J. N. 1967. Life history and ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae). American Midland Naturalist 78:369–388.

MORALES, Y., L. J. WEBER, A. E. MYNETT, AND T. J. NEWTON. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. Journal of the North American Benthological Society 25: 664–676.

NIEMI, G. J., P. DEVORE, N. DETENBECK, D. TAYLOR, A. LIMA, J. PASTOR, J. D. YOUNT, AND R. J. NAIMAN. 1990. Overview of case studies on recovery of aquatic systems from disturbance. Environmental Management 14:571–587.

NISHIMURA, N., T. NOBUMOTO, AND H. MITSUHASHI. 2001. Biomass of benthic macroinvertebrates in sixteen rivers, western Japan with special reference of environmental factors. Bulletin of the Hoshizaki Green Foundation 5: 161–206 (in Japanese with English abstract).

OKADA, H., AND Y. WATANABE. 2007. Distribution of *Cladophora glomerata* in the riffle with reference to the stability of streambed substrata. Landscape and Ecological Engineering 3:15–20.

OSMUNDSON, D. B., R. J. RYEL, V. L. LAMARRA, AND J. PITLICK. 2002. Flow–sediment–biota relations: implications for river regulation effects on native fish abundance. Ecological Applications 12:1719–1739.

PARKER, C. R., AND J. R. VOSHELL. 1983. Production of filter-feeding Trichoptera in an impounded and a free-flowing river. Canadian Journal of Zoology 61:70–87.

PRIDMORE, R. D., AND D. S. ROPER. 1985. Comparison of the macroinvertebrate faunas of runs and riffles in three New Zealand streams. New Zealand Journal of Marine and Freshwater Research 19:283–291.

QUINN, J. M., AND C. W. HICKEY. 1990. Characterization and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. New Zealand Journal of Marine and Freshwater Research 24:387–409.

REMPEL, L. L., J. S. RICHARDSON, AND M. C. HEALEY. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. Freshwater Biology 45:57–73.

RUTHERFORD, J. E., AND R. J. MACKAY. 1985. The vertical distribution of hydropsychid larvae and pupae (Trichoptera: Hydropsychidae) in stream substrates. Canadian Journal of Zoology 63:1306–1315.

SCHWENDEL, A. C., R. G. DEATH, AND I. C. FULLER. 2010. The assessment of shear stress and bed stability in stream ecology. Freshwater Biology 55:261–281.

STEFFLER, P., AND J. BLACKBURN. 2002. Two-dimensional depth averaged model of river hydrodynamics and fish habitat: River2D user's manual. University of Alberta, Alberta, Canada.

STRAYER, D. L. 1999. Use of flow refuges by unionid mussels in rivers. Journal of the North American Benthological Society 18:468–476.

TSUDA, M. 1959. Some problems on the standing crop of benthic communities of running waters, especially the importance of net-spinning caddis-worms. Japanese Journal of Limnology 20:86–91 (in Japanese).

TSUDA, M., AND K. GOSE. 1964. On the succession of aquatic insect communities in rapids of the river. Physiology and Ecology Japan 12:243–251 (in Japanese with English summary).

WALLACE, J. B. 1975. Food partitioning in net-spinning Trichoptera Larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona*, and *Macronema zebratum* (Hydropsychidae). Annals of the Entomological Society of America 68: 463–472.

WALLACE, J. B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. Environmental Management 14:605–620.

WAY, C. M., A. J. BURKY, C. R. BINGHAM, AND A. C. MILLER. 1995. Substrate roughness, velocity refuges, and macroinvertebrate abundance on artificial substrates in the lower Mississippi River. Journal of the North American Benthological Society 14:510–518.

WELLNITZ, T., AND R. B. RADER. 2003. Mechanisms influencing community composition and succession in mountain stream periphyton: interactions between scouring history, grazing, and irradiance. Journal of the North American Benthological Society 22:528–541.

WOOTTON, J. T., M. S. PARKER, AND M. E. POWER. 1996. Effects of disturbance on river food webs. Science 273: 1558–1561.

WOTTON, R. S. 1988. Very high secondary production at a lake outlet. Freshwater Biology 20:341–346.

Received: 23 May 2012
Accepted: 5 April 2013

This content downloaded from 128.193.164.203 on Wed, 25 Apr 2018 23:01:03 UTC
All use subject to http://about.jstor.org/terms