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Kobayashi, Sohei; Oshima, Yurika; Nakanishi, Satoru; Nakata, Kazuyoshi; Amano, Kunihiko

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LONGITUDINAL VARIATION IN PHYSICAL CHARACTERISTICS AND MACROINVERTEBRATE COMMUNITIES OF RIFFLES IN THE TOYO RIVER, JAPAN

Sohei Kobayashi^{1,2}, Yurika Oshima¹, Satoru Nakanishi¹,
Kazuyoshi Nakata¹, and Kunihiko Amano³

¹ Researcher, River Restoration Team, Public Works Research Institute,
Minamihara, Tsukuba, Ibaraki 305-8516, Japan

² E-mail: skoba55@pwri.go.jp

³ Team Leader, River Restoration Team, Public Works Research Institute

ABSTRACT

We surveyed longitudinal changes in physical characteristics and macroinvertebrate communities of riffles and examined physical-biological relationships at the segment scale in the Toyo River, Japan. Bed-material size was larger in upland and mountain reaches, bed stability was greater in lowland reaches, and flow velocity was greater in confined valley and upland reaches. The macroinvertebrate community was characterized by taxa that require a stable environment in lowland reaches and taxa that require large interstices under stones in upland and mountain reaches. Some linear relationships between physical variables and biomass of invertebrate groups suggest the possibility of predicting macroinvertebrate biomass and community structure of riffles from reach- and segment-level characteristics (e.g., discharge, slope) by considering combinations of flow and bed characteristics of riffles.

Keywords: gravel-bed river, longitudinal pattern, riffles, bed materials, bed stability, flow velocity, macroinvertebrate community, biomass, functional feeding groups, life form types

1. INTRODUCTION

The biological communities and ecosystem functions of rivers are largely governed by hydrogeomorphic characteristics that are structured hierarchically in temporal-spatial scales (Frissell et al., 1986; Hildrew and Giller, 1994). Although organisms often respond to small-scale variations in physical environments (i.e., patch and habitat scale), the range, frequency, and combinations of physical variables within an area are determined by hydrogeomorphic features of large spatial scales (reach, segment, and watershed). Understanding physical-biological relationships at large spatial scales is necessary for predicting the distributions of biological communities at broad spatial scales, but general patterns at these levels remain unclear.

A riffle is an area with relatively shallow depth and fast flow, and it is one of the common landscape types in rivers worldwide (Kani, 1944; Frissell et al., 1986). Due to the rapid circulation of oxygen and a ready supply of nutrients and organic matter, the biomass and production of benthic organisms and material uptake from the water column are considered to be high in riffles (Huryn and Wallace, 1987). Although riffles cover a limited portion of the river landscape, they have important roles in food webs and material cycles in river systems.

Many benthic species in riffles require and use flow for their survival and growth (e.g., insects that feed on transported organic materials). Thus, flow velocity is considered to be one of the most important factors determining the abundance and community structure of benthic

invertebrates (Statzner et al., 1988). In addition, benthic invertebrates have species-specific life forms, and the use of bed surface/interstices and bed-stability requirement vary according to these life forms. Therefore, invertebrate communities in riffles are assumed to be strongly link to particular flow levels and types of bed materials. Although physical-biological relationships have been examined in many studies of stream invertebrates (e.g., Mérioux and Dolédec, 2004; Brooks et al., 2005), most of them focused on small spatial scales. Relationships at larger scales (i.e., reach, segment) have been poorly explored (Statzner et al., 1988; Grown and Davis, 1994).

To improve our understanding of physical-biological relationships in rivers, we examined (a) longitudinal changes in physical and macroinvertebrate characteristics of riffles from mountain to lowland segments, and (b) physical-macroinvertebrate relationships at the reach and segment scale. After characterizing the important physical factors determining the biomass of different macroinvertebrate groups, we discuss the possibility of predicting macroinvertebrate biomass and community structure based on reach- and segment-level characteristics.

2. METHODS

Physical and macroinvertebrate surveys were conducted in the main stem and some tributaries of the Toyo River (watershed area: 724 km²), one of the major rivers in the Ise-Bay area of Japan. According to national surveys of the water environment, the Toyo River is one of the cleanest major rivers in Japan. The Toyo is a gravel-bed river with bed-material size varying longitudinally along the 77-km length of the main stem, which allowed us to examine longitudinal patterns and physical-biological relationships. We surveyed 14 sites along the main stem and 4 sites in different tributaries (watershed range: 18–660 km², reach slope range: 0.0005–0.02 m/m) (Figure 1). The 14 sites along the main stem were classified into different reach groups (lowland, confined valley, upland, mountain) for convenience when making the longitudinal comparisons. Baseflow discharge ranged from 0.7 to 10.6 m³/s. At all study sites, pH was almost neutral (range: 7.4–8.6), concentrations of nitrate, phosphate, and particulate organic matter (POM) were usually low (NO₃-N: <1 mg/L, PO₄-P: <0.05 mg/L, POM: <2 mg/L). These concentrations increased toward the downstream directions and two tributaries (Tsuge, Ebi) also had higher concentrations. Water temperature ranged from nearly 0 °C in winter and to 24 °C in summer at the uppermost site (Sakai) and from 5 to 30 °C at the lowest site (Gejo).

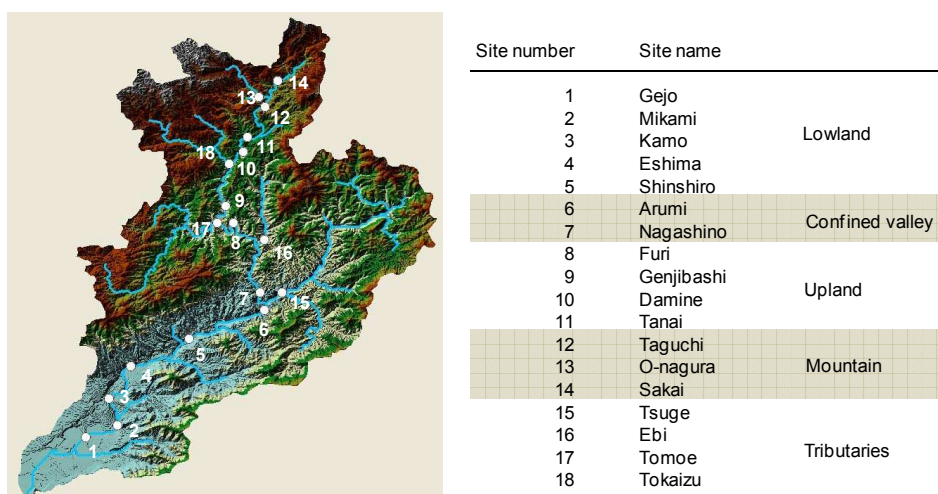


Figure 1 A map of the Toyo River watershed and location of the 18 study sites

A riffle was defined here as a zone where the water surface was relatively steep and rough within a reach. At each site, flow width, longitudinal length, and water surface slope of riffles were measured. Horizontal and vertical distance between two consecutive riffles was also measured to calculate reach slope and the proportion of riffle in the total reach length. Bed-material size, flow depth and velocity, and streambed stability were evaluated as physical variables of the riffles. Mean bed-material size was determined by direct measurements of bed-surface materials at 5 to 10 positions in each riffle. Diameter of all main particles was recorded in at each position. Flow depth and velocity of riffles were indirectly evaluated using the width and slope of each riffle and baseflow discharge. Bed stability was evaluated as the ratio of observed bed-material size to the critical particle size that is mobile during a 1-yr flood. Erosive tractive force on the bed during flood [$u_* = \sqrt{(ghi)}$, where g is gravitational acceleration, h is mean water depth, and i is energy slope] was determined using channel slope and water level at a 1-yr flood, and the equation [$U_{*c}^2 = 80.9d$, where d is particle diameter] was used to estimate critical particle size.

Macroinvertebrates were collected in riffles four times, each in a different season (March, August, and November 2007, and February 2008). At each survey, 0.09-m² quadrat samplings were done at three positions in each riffle using a Surber net (mesh size: 0.25 mm). Samples were immediately preserved in 10% formalin. In the laboratory, samples were washed on a 1-mm mesh sieve and invertebrates on the sieve (i.e., macroinvertebrates) were identified, mostly to the genus level, and weighed after drying at 60 °C for 48 h to calculate biomass (g/m²). Macroinvertebrates were classified by functional feeding groups and life form types, which provide useful information on food resources and physical habitats, respectively of invertebrates. We followed Merritt and Cummins (1996) for these classifications, but we modified some classifications of life form types with more focus on living space and movement style of invertebrates. Features of each invertebrate group are listed in Table 1.

Table 1 Features used to classify functional feeding groups and life form types

Functional feeding group	Main food resource	Representative taxa
Grazer	algae and heterotrophic biofilm attached on stones	Baetidae, Ephemerellidae, Heptageniidae, Psychomyiidae, Psephenidae, <i>Antocha</i>
Shredder	coarse particulate organic matter (e.g., leaves)	Nemouridae, Taeniopterigidae
Filterer	transported fine particulate organic matter	Hydropsychidae, <i>Stenopsyche</i> , Simuliidae
Collector	deposited fine particulate organic matter	Oligochaeta, Ephemeridae
Predator	invertebrates	Perlidae, Perlodidae, <i>Rhyacophila</i> , Odonata, Megaloptera
Life form type	Living space/movement style	Representative taxa
Shelter-holder	sessile life form building nest mainly above stones	Hydropsychidae, Psychomyiidae, <i>Antocha</i>
Net-spinner	sessile life form spinning net beneath stones	<i>Stenopsyche</i>
Burrower	burrow inside fine sediment	Oligochaeta, Ephemeridae, Odonata, <i>Hexatoma</i>
Crawler	walk above and beneath stones, final body size < 20 mm	Ephemerellidae, Nemouridae, <i>Rhyacophila</i> , Psephenidae
Bulky-crawler	walk above and beneath stones, final body size > 20 mm	Perlidae, Perlodidae, Megaloptera
Glider	glide above and beneath stones	Heptageniidae
Swimmer	swim above stones and water column	Baetidae, <i>Isonychia</i>
Case-bearer	walk above stones with case made of sand, leaves, etc.	Glossosomatidae, Goeridae

3. RESULTS

3.1 Longitudinal patterns of riffle characteristics

Riffle slope ranged from 0.005 to 0.5 m/m, increasing toward the upstream direction (Figure 2). Variation in riffle slope was smaller than that of reach slope (i.e., 0.0005–0.025 m/m). The longitudinal trend of riffle length was unclear, whereas the distance between two consecutive riffles clearly increased toward the downstream direction. As a consequence, the proportion of riffle in the total reach length decreased toward the downstream direction (Figure 2).

Riffle depth was greater at downstream sites (lowland, confined valley) compared to upstream sites (upland, mountain). In contrast, flow velocity tended to be higher at sites in confined valley and upland reaches compared to sites in lowland and mountain reaches (Figure 2). Bed-material size increased toward the upstream direction in lowland and confined valley reaches and was uniformly high in upland and mountain reaches. The maximum value was recorded at an upland site (Tanai, particle size: 267 mm). Bed stability (i.e., the ratio of observed particle size to critical particle size that is mobile during a 1-yr flood) was relatively high at sites in lowland reaches. All sites in lowland reaches had a ratio larger than 1, whereas many sites in the confined valley, upland, and mountain reaches had a ratio far less than 1.

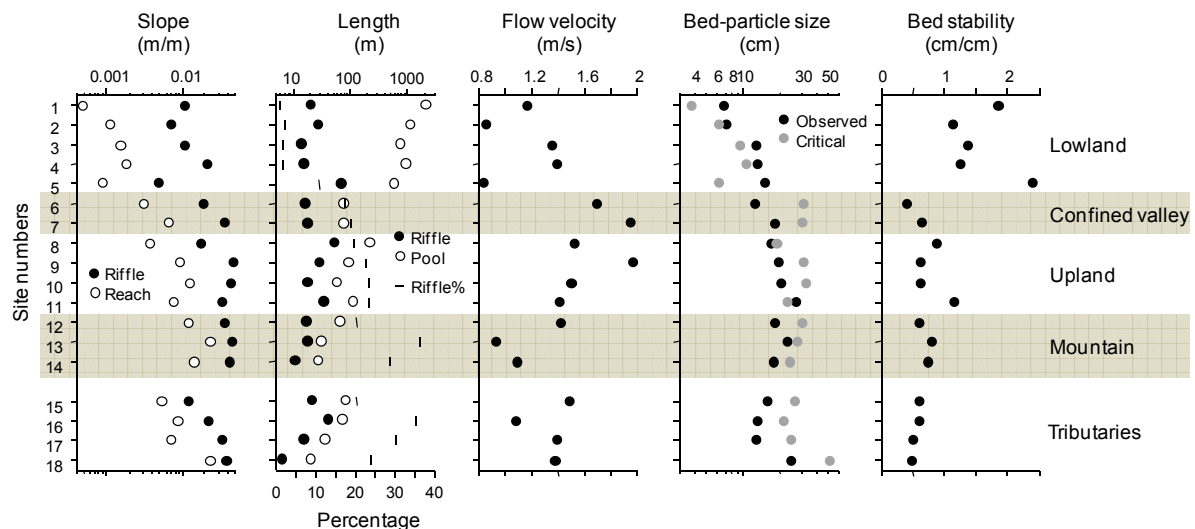


Figure 2 Longitudinal changes in physical characteristics of riffles

3.2 Longitudinal patterns of macroinvertebrate communities

In total, 242 invertebrate taxa were identified during the four seasonal surveys. Most were larvae of mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera) and midges (Diptera, Chironomidae). Total macroinvertebrate biomass was the highest in February or March and the lowest in August (Figure 3). This seasonal change in biomass agreed with what is generally known for stream insects: biomass increases and peaks in winter and spring, and decreases substantially in summer (Hynes, 1970). Mean biomass of macroinvertebrates throughout all seasons was the highest at sites in lowland reaches (the highest: Kamo, 24 g/m²), followed by sites in upland reaches, and it was uniformly low at sites in confined valley and mountain reaches (the lowest: Arumi, 4 g/m²).

Longitudinal differences in taxonomic composition were apparent during all seasons (Figure 4). Ordination by detrended correspondence analysis (DCA) was performed using PC-ORD (version 5, MjM Software, Gleneden Beach, Oregon, USA) to understand the overall patterns of taxonomic composition among study sites based on biomass of all observed taxa.

During all seasons, communities can be separated into four reach types (lowland, confined valley, upland, mountain), with lowland and mountain reaches always situated on the opposite end of the first axis (Figure 4).

The functional feeding groups that dominated total macroinvertebrate biomass were filterer, grazer, and/or predator (Figure 3). Biomass of both filterer and grazer did not show a clear longitudinal trend, but filterer biomass tended to be high at sites in lowland and upland reaches. In contrast, predator biomass was clearly higher at sites in upland and mountain reaches than at sites in lowland and confined valley reaches. Sites with high filterer biomass tended to have high total macroinvertebrate biomass.

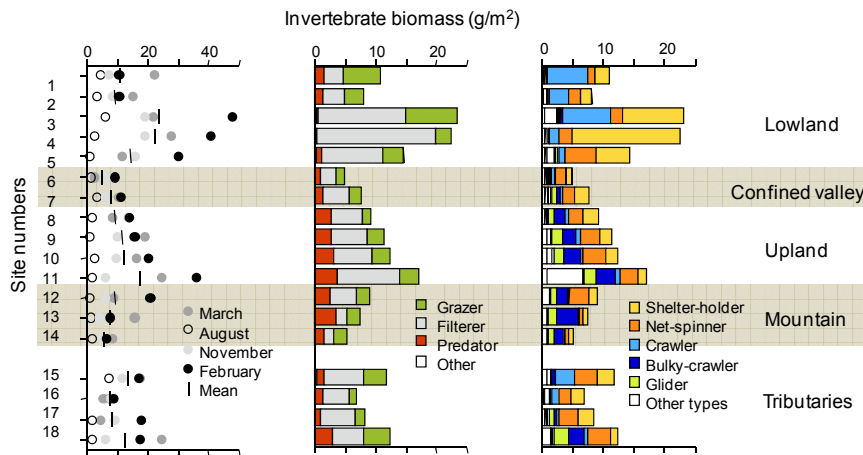


Figure 3 Longitudinal changes in macroinvertebrate biomass and community structure

The life form types that dominated total macroinvertebrate biomass were shelter-holder, net-spinner, crawler, bulky-crawler, and glider (Figure 3). Shelter-holder (mainly caddisflies *Hydropsyche* and *Macrostemum*) and crawler (mainly beetle *Mataeopsephus* and flatworm *Girardia*) dominated at sites in lowland reaches, whereas net-spinner, bulky-crawler (mainly stoneflies *Kamimuria* and *Paragnetina* and dobsonfly *Protohermes*), and glider (mainly mayfly *Epeorus*) dominated at sites in upstream reaches. Sites in lowland reaches tended to be dominated by a small number of taxa.

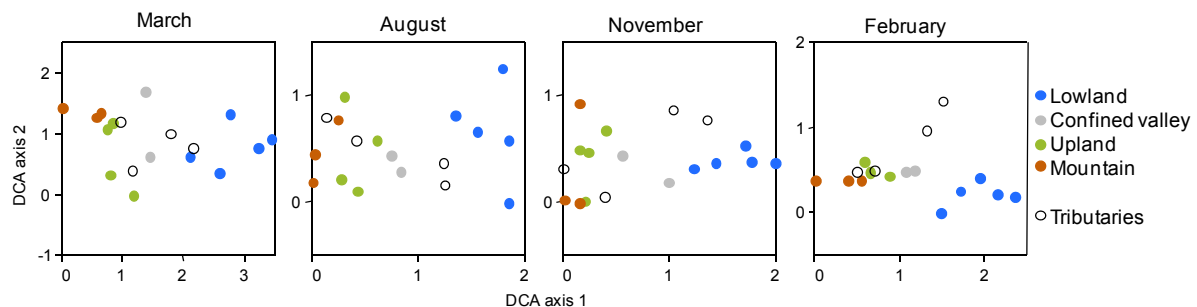


Figure 4 DCA ordination plots of 18 macroinvertebrate communities

3.3 Relationships between physical variables and invertebrate biomass

Simple linear regressions were performed to examine relationships between physical variables and macroinvertebrate biomass using flow depth, flow velocity, bed-material size, and bed stability as independent variables. No single variable was significantly correlated with total macroinvertebrate biomass (Table 2, Figure 5). Among the dominant functional feeding groups, grazer biomass was positively correlated with bed stability, and predator

biomass was positively correlated with particle size most strongly. No correlation with physical variables was found for filterer biomass. Among the dominant life form types, shelter-holder biomass was positively correlated with depth and bed stability, whereas bulky-crawler and glider were positively correlated with bed-material size most strongly. Crawler biomass was negatively correlated with bed-material size. Net-spinner biomass tended to be higher at sites with high flow velocities, and a positive correlation with flow velocity was seen when a site with exceptionally high biomass was removed from the analysis ($r = 0.56$, $p = 0.019$, Figure 5).

Stepwise multiple regressions were performed to test whether multiple physical variables explain macroinvertebrate biomass better than a single variable, but biomass was not explained better by two or more variables.

Table 2 Standard regression coefficient (r) and significance of correlation ($*p < 0.05$, $**p < 0.01$, $***p < 0.001$) in simple linear regression of invertebrate biomass by riffle characteristics

	Independent variable			
	Depth	Flow velocity	Bed-material size	Bed stability
Total macroinvertebrates	0.28	-0.03	0.09	0.44
Grazer	0.34	-0.18	-0.11	0.48 *
Filterer	0.36	0.19	-0.01	0.35
Predator	-0.56 *	-0.05	0.66 **	-0.29
Shelter-holder	0.51 *	0.01	-0.42	0.49 *
Net-spinner	0.30	0.33	0.18	0.04
Crawler	0.65 **	-0.25	-0.65 **	0.50 *
Bulky-crawler	-0.57 *	0.32	0.87 ***	-0.40
Glider	-0.67 **	0.26	0.89 ***	-0.50 *

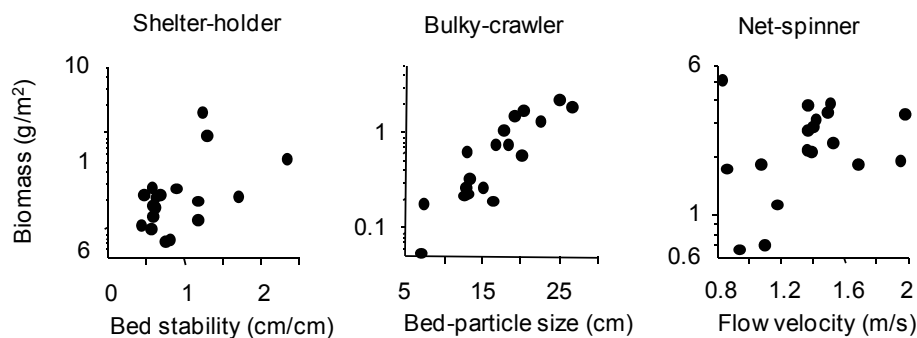


Figure 5 Some relationships between invertebrate biomass and riffle characteristics

4. DISCUSSION

We demonstrated the longitudinal distribution (i.e., variations at reach and segment scales) of riffle macroinvertebrate communities, and some correlations between dominant invertebrate groups and certain physical characteristics of riffles. A classification of macroinvertebrates according to life form types provides some plausible mechanisms to explain the relationships between physical variables and invertebrate communities. Lowland reaches had high total biomass and the community was characterized by a dominance of shelter-holders and crawlers. Shelter-holders would prefer stable substrates to build their nests. Crawlers were dominated by a beetle, *Mataeopsephus*, and *Mataeopsephus* is likely to prefer

stable environments due to their poor dispersing abilities. Despite small bed materials, bed stabilities were shown to be high in lowland reaches, which agrees with the dominance of shelter-holders and crawlers at these sites. In addition, a positive relationship between bed stability and biomass was evident for shelter-holders. Thus, bed stability in lowland reaches seems to sustain high macroinvertebrate biomass by enabling accumulations of invertebrate groups that possess sessile or nearly a sessile life form.

Macroinvertebrate communities of confined valley, upland, and mountain reaches were characterized more by net-spinners, bulky-crawlers, and/or gliders, and upland reaches showed the highest total biomass among the three reach types. A strong positive relationship between bed-material size and biomass of bulky-crawlers probably indicates that large-bodied invertebrates require large interstices underneath stones, which are created by the existence of large stones, for them to hide and stay. A strong relationship with particle size was also evident for gliders. Due to their gliding movement style, gliders prefer smooth substrates, and large bed materials seem to be preferable for gliders because of the availability of large surface area for movement each substrate rather than the availability of large interstices. Net-spinner (*Stenopsyche*) showed a marginally significant positive relationship with flow velocity. Because *Stenopsyche* is a filterer, it prefers fast flows that supply large amounts of transported organic materials. However, because the *Stenopsyche* builds nets and stays underneath stones, the biomass is also more or less affected by bed-materials size and bed stability. Based on these relationships with physical variables, the high total macroinvertebrate biomass in upland reaches is likely maintained by a combination of large bed-materials and fast flow.

Not all functional feeding groups showed clear relationships with physical variables. Biomass of predators was high in upland and mountain reaches and was positively correlated with bed-material size. Because most predators are bulky-crawlers, the existence of interstices underneath large stones is likely to contribute to the high biomass of predators in upland and mountain reaches. In contrast, biomass of grazers tended to be high in lowland reaches and was positively correlated with bed stability. A beetle, *Mataeopsephus*, made the greatest contribution to the high grazer biomass in lowland reaches. When this taxon was removed, grazer biomass was strongly correlated with bed-material size ($r = 0.79, p < 0.001$), reflecting the biomass of gliders and swimmers. The biomass of filterers, which comprise a large portion of total macroinvertebrate biomass, did not show a clear relationship with any physical variables, and the longitudinal pattern was also unclear. Different life form types contributed to the biomass of filterers among reaches (e.g., shelter-holders in lowland reaches and net-spinners in upstream reaches). It appears that relationships between physical variables and biomass of each functional feeding group depend largely on the life form types included in each group.

Our study suggested that flow velocity, bed-material size and bed stability are important factors determining biomass and community structure of riffles. We hypothesize that combinations of these variables determine the potential carrying capacity of each invertebrate group (i.e., life form type) and, hence, the potential total invertebrate biomass of riffles. Because these riffle characteristics are largely determined by reach- and watershed-level characteristics (e.g., discharge, channel slope, width, sediment supply), invertebrate biomass and community structure could be ultimately predicted from such large-scale characteristics. In order to make these predictions, knowledge of the relationships between large-scale characteristics and riffle characteristics are needed. However, spatial variations in riffle characteristics and their relationship with biological features have not been explored well in either geomorphologic or ecological studies. The longitudinal variation of riffle characteristics shown in this study (e.g., flow velocity, bed stability, proportion of riffle in reach length) would provide fundamental information for understanding the spatial variation

of riffle characteristics. Finally, although we examined the Toyo River, which has relatively clean water and a short longitudinal distance, longitudinal variations in water temperature and chemistry might also have affected the distribution of the invertebrate community. Further studies are needed to separate the effects of these factors from the effects of flow and bed characteristics and to gain a better understanding of the relative importance of flow and bed characteristics on invertebrate distributions.

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