



## Habitat characteristics and trophic structure of benthic macroinvertebrates in a forested headwater stream

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### ABSTRACT

Three channel reaches with different habitat characteristics were selected to test the variability in community structure of benthic macroinvertebrates by comparing the relative abundance of functional feeding groups among the reaches. The important factors influencing the spatial and temporal organization of community structure were explored using nonmetric multidimensional scaling (NMS). The habitat characteristics in the reaches were different in terms of habitat type, hydrological factors, and substrate composition. The first headwater reach was classified as a step-pool reach with similar relative areas of riffle and pool habitats. The second mid-reach and the third down reach had greater areas of pool habitat followed by runs and riffles whose proportions were similar between the latter two reaches. The relative abundances of functional feeding groups were different among the surveyed reaches. Gammarid shredders predominated in the upper reach, and chironomid collector–gatherers and collector–filterers were in greater abundance in the two lower reaches. The proportions of gammarids were minor in the mid and downstream reaches. NMS ordination indicated that the proportion of substrates < 8 mm, discharge, and water depth mainly determined the spatial and temporal distribution of samples based on the macroinvertebrate community in the study reaches. These results suggest that different habitat characteristics result in a distinct community structure in each reach.

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### Introduction

Aquatic organisms including stream insects are affected by various physical environments that can be organized hierarchically according to the spatial scale of the river network within landscapes (Minshall, 1988; Poff, 1997). The physical environments of rivers are controlled by landscape components whose relative importance varies according to spatial scale. Climate controls the hydrological cycle and river water temperature regimes at the greatest scale. Source of flow, watershed topography, and geology affect sediment supply and water chemistry in the meso-scale. Land cover, network position (e.g., stream order), and valley landform influence vegetation type, flood intensity, and morphodynamic processes (e.g., hydraulic geometry, habitat volume, sediment size range, and riparian condition) in the smallest scale (Snelder and Biggs, 2002). These physical factors allow many stream reaches to encompass diverse habitats (Frissell et al., 1986; Montgomery

and Buffington, 1997) and exert influences not only on community structure but also on ecosystem functions (e.g., Minshall, 1984; Hury and Wallace, 1987; Smock et al., 1992).

A number of studies have demonstrated the relationship between heterogeneity among habitat patches in stream reaches and benthic macroinvertebrate communities. Minshall and Robinson (1998) measured 21 environmental variables including physical, chemical, and organic matter resources and examined the relationship between habitat heterogeneity and macroinvertebrate community structure. They found that biotic properties such as the diversity index were dependent on habitat heterogeneity in a reach, and that the proportion of shredders was correlated with stream size, implying longitudinal changes in food availability. Similarly, a study in three segments of a Missouri stream, encompassing a full range of physical and hydraulic conditions, showed that community composition, diversity, and relative densities of some functional feeding groups were highly correlated with hydraulic variables and benthic organic matter (Doisy and Rabeni, 2001). They concluded that variation of local factors in a stream segment has the greatest influence on the invertebrate community.

Several researchers have been interested in examining the effect of habitat type on the function of stream ecosystems by considering the spatial distribution of invertebrates among various habitats.

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Benke et al. (1984) measured invertebrate productivity on snag, sandy bottom, and muddy benthic habitats in a subtropical blackwater river in the Lower Coastal Plain of Georgia. They found that the snag habitat was responsible for much higher taxa diversity and invertebrate biomass and for 15–16% of production, although the effective substrate area of the snag habitat was only about 6%. It was concluded that the community structure categorized by a functional feeding group (FFG) was different between snag and benthic habitats. In a study comparing distribution of FFGs among different habitats in an Appalachian mountain stream, Huryn and Wallace (1987) showed that the functional structure of benthic macroinvertebrates is the result of the relative contributions of each habitat (riffle, pool, or bedrock-outcrop) in the total stream area.

Benthic macroinvertebrates are one of the major biota in streams and are composed mainly of aquatic insects, crustaceans, and mollusks. These organisms are the link between primary food sources (algae, microorganisms, and detritus) and their predators (fish) in a stream food web (Cummins, 1974) and have been widely used as indicators to evaluate the quality of stream ecosystem health (e.g., Resh et al., 1996; Barbour et al., 1999). Under the physically heterogeneous environments of streams, benthic macroinvertebrates have evolved distinct morpho-behavioral feeding strategies that are the basis of categorizing diverse benthic macroinvertebrates into several functional groups (Cummins and Klug, 1979). The feeding mechanisms of different FFGs are adapted to the physical environment of different habitat types within a stream segment. For example, a higher proportion of shredders is observed in headwaters flowing through a deciduous forest with a dense canopy. Scrapers are abundant in mid-reaches with an open canopy (Webster et al., 1995; Grubaugh et al., 1996), whereas collector-gatherers dominate pool habitats (Lemly and Hilderbrand, 2000), and collector-filterers prefer to colonize high-flow water positions providing higher feeding rates (Huryn and Wallace, 1988; Georgian and Thorp, 1992). These observations suggest that variability among habitat types, if considered along with the feeding mechanism of different macroinvertebrate taxa, would result in different but predictable community structures according to the physical characteristics of different habitats.

A stream can be seen as a hierarchical system of several levels between stream segments and single substrate particles according to the channel classification and the associated spatial scale proposed by Frissell et al. (1986) and Montgomery and Buffington (1998). This classification system suggests that a stream segment ( $10^2$ – $10^4$  m scale) includes various types of channel reaches ( $10$ – $10^3$  m scale) composed of different habitat types or channel units (1–10 m scale). It is possible that a channel reach type may have a different combination of relative areas of channel units in a stream segment, resulting in channel reaches with different habitat characteristics even when the reaches are very short and are located at intervals of reach scale.

The objectives of this study were to determine i) if the distribution of macroinvertebrate FFGs changes according to variations in the type of channel reaches closely located within a short stream segment, and ii) which habitat characteristics are important in shaping the macroinvertebrate community structure in the spatial and temporal domain.

## Materials and methods

### Study reaches

This study was conducted in the headwater reaches of Bongseonsa Stream located in the Gwangneung Forest, Korean National Arboretum of the Korea Forest Research Institute (Pocheon-si, Gyeonggi-do, Republic of Korea; Fig. 1). This forest has been preserved for more than 500 years; thus, minimizing anthropogenic disturbances. The stream passes through the natural forest and has kept its undisturbed characteristics as a forest stream whose riparian zones are covered with dense mixed deciduous vegetation in varying degrees along the stream

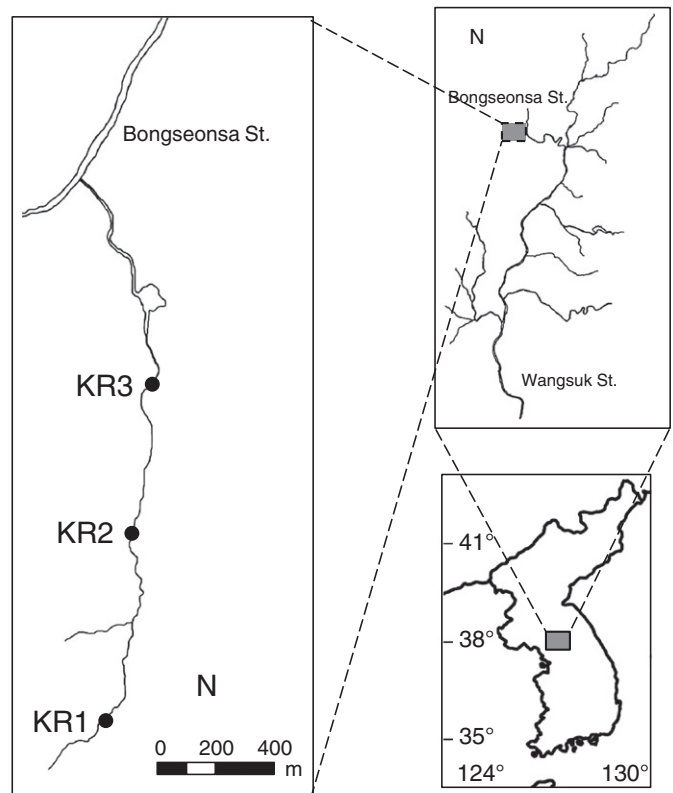


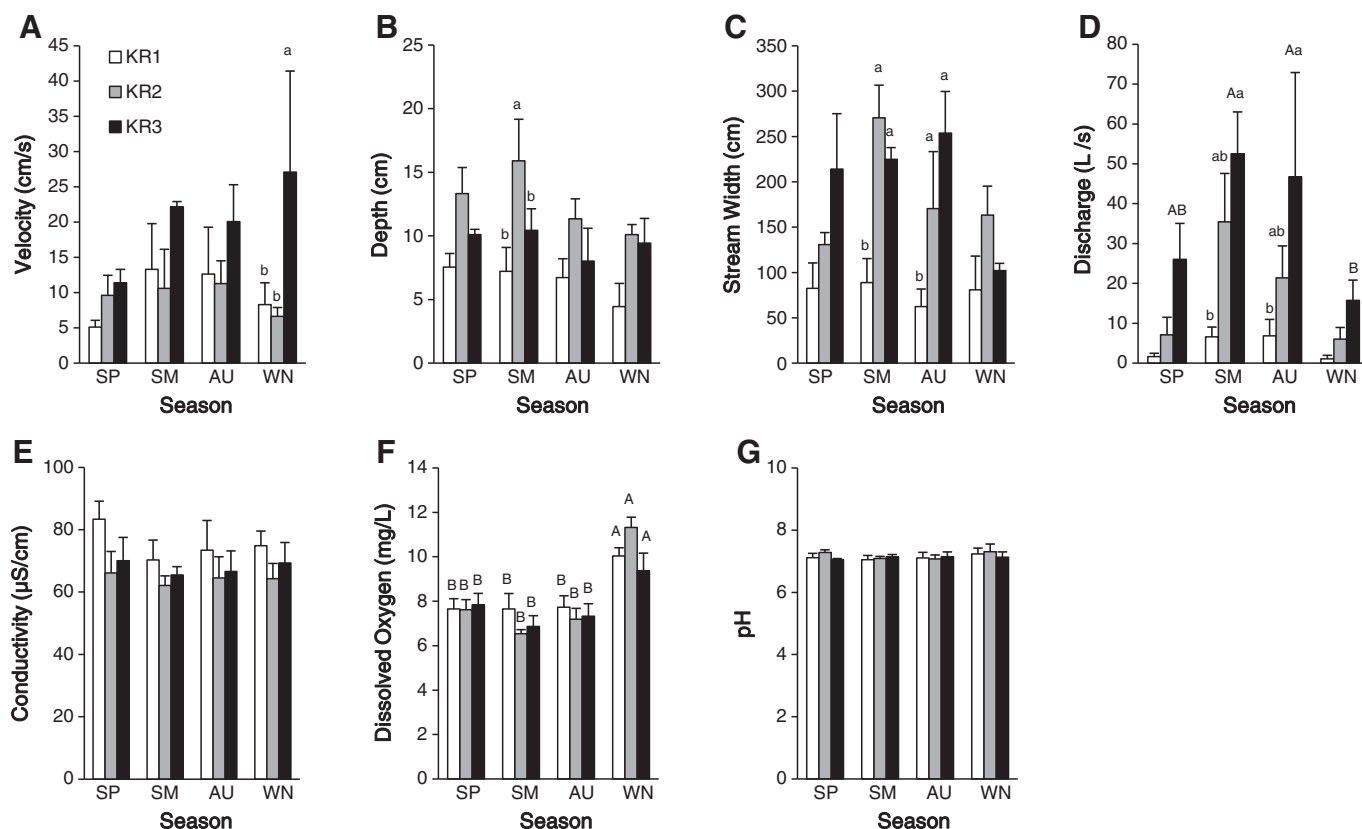
Fig. 1. Location of three study reaches in Bongseonsa Stream, Pocheon, Korea.

corridor from the source to downstream reaches. The main energy source of the stream ecosystem is provided by riparian vegetation in the form of organic detritus and associated microbial assemblages (Hall et al., 2000, 2001). Riparian vegetation mainly consists of red-leaved hornbeam (*Carpinus laxiflora*, Betulaceae), heartleaf hornbeam (*Carpinus cordata*, Betulaceae), and konara oak (*Quercus serrate*, Fagaceae) in the headwater reach, mixed with needle fir (*Abeis holophylla*, Pinaceae), Korean pine (*Pinus koraiensis*, Pinaceae), and Japanese larch (*Larix kaempferi*, Pinaceae) in the downstream reaches.

Three sampling reaches, KR1, KR2, and KR3, from upstream to downstream were surveyed, which were about 500 (between KR2 and KR3) to 600 m (between KR1 and KR2) apart from each other (Fig. 1). KR1 was located in the first-order headwater stream, which is close to the source of the stream, and KR2 and KR3 were in the second-order downstream. KR1 was relatively narrow and mainly composed of a chain of small pools and riffles connected by short runs. The KR2 and KR3 habitats (i.e., channel units) were dominated by pools followed by runs and short riffles. The riparian canopy of KR1 was almost completely closed but was less closed in KR2. The canopy at KR3 was partly closed.

### Macroinvertebrates

Three replicates of benthic macroinvertebrates were collected from each study reach using a Suber sampler (30 cm × 30 cm, 100 µm mesh size; Eaton et al., 2005). Samples were collected once every season from summer 2006 to spring 2009. All sediments from the randomly chosen sampling points in the reaches were washed in the current to separate the benthos and organic detritus into the net. The samples inside the net were rinsed on a sieve (100 µm mesh size) to remove silt and were preserved in 95% ethanol in the field. Macroinvertebrates were sorted under a dissecting microscope and were preserved in 70% ethanol in the laboratory for further analysis. The stored macroinvertebrates were identified to the lowest feasible



**Fig. 2.** Seasonal variation in hydrological and water quality factors in each sampling reach for (A) current velocity, (B) water depth, (C) stream width, (D) discharge, (E) conductivity, (F) dissolved oxygen, and (G) pH. SP, spring; SM, summer; AU, autumn; WN, winter. Values are mean  $\pm$  standard error. Significant differences (Tukey's test,  $P < 0.05$ ) in the factors among the sampling reaches within each season are indicated by small letters, and among the seasons in each reach are indicated by capital letters.

taxonomic level under a microscope; species or genus level for aquatic insects (except chironomids), genus level for gammarids (Yoon, 1995; Merritt and Cummins, 1996; Smith, 2001), and family level for oligochaetes (Brinkhurst and Jamieson, 1971; Brigham et al., 1982). Chironomids were identified to genus for samples collected during summer 2006 to spring 2008 and to family thereafter (Wiederholm, 1983). The number of individuals in each taxon was counted and converted to a number per square meter. Mean densities of macroinvertebrates were calculated for each reach at every sampling date to provide a seasonal mean density in each reach for the sampling years.

Macroinvertebrates were further classified into FFGs according to Merritt and Cummins (1996) and Monakov (2003): shredders (SHR), collector-gatherers (CLG), collector-filterers (CFL), engulfing predators (PRD), and scrapers (SCP). Seasonal mean density was calculated for each FFG. The total density of chironomids over the period of summer 2008–spring 2009 was assigned to each FFG according to the mean relative abundances of chironomid FFG at each sampling reach during summer 2006–spring 2008, which were identified to genus as described above.

#### Environmental characteristics

The percentages of three types of habitats (riffle, pool, and run) were estimated in terms of surface area of the sampling reaches. Ninety (KR2) to one hundred (KR1 and KR3) meter long reaches were subdivided into 5 m long segments along the stream channel axis. The habitat types in each segment were identified, and their relative proportions were estimated by visual examination (Bisson and Montgomery, 1996). Stream widths at both ends of the segments were measured to calculate the area of each segment. After multiplying the proportion of habitat types by the segment area, the sums

of the segment areas for different habitat types were divided by the reach area. The relative amount of coarse particulate organic matter (CPOM) was estimated by visually examining the proportion of surface area covered by debris dams on the benthic sediment of each 5-meter long segment in the three study reaches.

Environmental variables were measured in the study reaches. Hydrological factors, including water depth, stream width, and current velocity (2100-C140, Swoffer Instruments, Tukwila, WA, USA) were measured at each macroinvertebrate sampling point as well as along the transect of each reach to calculate discharge at the reach (Gore, 1996). Water quality factors (conductivity, dissolved oxygen [DO] and pH) were measured using a multi-probe meter (CX401, Seachang Instruments) in each reach. Substrate composition was measured by visually examining the relative volume of benthic sediments at the macroinvertebrate sampling points after classifying the sediments into seven size categories according to the diameter of the particles: smaller than 8 mm ( $< 8$  mm), 8–16 mm ( $> 8$  mm), 16–32 mm ( $> 16$  mm), 32–64 mm ( $> 32$  mm), 64–128 mm ( $> 64$  mm), 128–256 mm ( $> 128$  mm), and greater than 256 mm ( $> 256$  mm) (modified from Cummins, 1962).

#### Data analysis

Differences in FFGs (relative abundance), hydrological factors (water depth, stream width, current velocity, and discharge) and water quality factors (DO, pH, and conductivity) were examined with a two-way analysis of variance (ANOVA). When the ANOVA test was significant ( $P < 0.05$ ), Tukey's multiple-comparisons tests were conducted. The ANOVA and Tukey's tests were performed with SPSS 18 (PASW, 2009).

Taxon richness, the Shannon diversity index, and evenness index were calculated for macroinvertebrates in each reach. The Shannon index ( $H'$ ) and the evenness index ( $J$ ) were determined using the

equations below (Ludwig and Reynolds, 1988; McCune and Grace, 2002):

$$H' = - \sum_i^S (p_i) \log_{10}(p_i)$$

and

$$J = \frac{H'}{\log_{10} S}$$

where  $S$  is the number of species, and  $p_i$  is the proportion of individuals belonging to the  $i$ th species. Taxon richness among the three reaches was compared based on the individual-based rarefaction curve (Hurlbert, 1971). The rarefaction curve was generated using the *rarefaction* function with default options (<http://www.jennajacobs.org/R/rarefaction.txt>) in R version 2.15 (<http://cran.r-project.org/>).

Nonmetric multidimensional scaling (NMS) was carried out using species abundance of each sample to examine the spatial and temporal variation of the benthic macroinvertebrate communities in the three reaches. NMS was performed with PC-ORD version 5 based on the Bray–Curtis distance measure with 500 iterations per run. A Monte Carlo test was performed with 50 runs of randomized data and 50 runs of real data to estimate the significance of each dimensionality (McCune and Grace, 2002). To assist in interpreting benthic macroinvertebrate community variation, Pearson correlation coefficients were calculated between the NMS axes and the environmental factors as well as the FFG abundances, using Statistica 8 (StatSoft Inc, 2007). Factors with significant correlations ( $P < 0.05$ ,  $r^2$  cut off value = 0.1) with the axes were visualized on the NMS ordination plot. The environmental variables included hydrological and water quality factors as well as substrate composition in the sampling reaches. The mean density of each FFG in the reaches (#FFG) at each sampling season was also included.

Macroinvertebrate densities were log transformed with  $\ln(x + 1)$  to reduce variance and to fulfill the assumption of normality for statistical analyses. Data for the proportions of FFGs and substrate composition were square root transformed, and the data for hydrological and water quality factors were min–max transformed.

## Results

### Habitat characteristics

The distribution of habitat types in terms of channel units indicated differences in relative habitat areas not only among the types in a reach but also among reaches. The proportion of surface area for the three habitat types (riffle, pool, and run) in KR1 was different from the proportions in KR2 and KR3 (Table 1). The percentage of riffle and pool habitats in KR1 was similar, and the value of the run was smaller than that of the other types. The proportion of pool habitat was the greatest in KR2 and KR3, followed

**Table 1**  
Habitat characteristics in the sampling reaches. The relative proportions of channel unit types are presented as percent surface area in the reach.

Category	Reach		
	KR1	KR2	KR3
Altitude (m)	249	172	156
Surface Area (m <sup>2</sup> )	121.2	162.9	259.6
Channel unit (%)			
Riffle	36.5	12.5	16.0
Pool	36.6	58.0	55.3
Run	26.9	29.5	28.7

**Table 2**

Mean values of each hydrological and water quality variable at the three reaches KR1, KR2, and KR3 ( $n = 12$  for each reach), and the results of a two-way analysis of variance. Significant differences among reaches for each variable (Tukey's test,  $P < 0.05$ ) are indicated by superscript letters.

Variable	Mean			F value		
	KR1	KR2	KR3	Reach	Season	Interaction
Velocity (cm/s)	0.147 <sup>b</sup>	0.141 <sup>b</sup>	0.342 <sup>a</sup>	4.589 <sup>*</sup>	0.856	0.526
Depth (cm)	0.222 <sup>b</sup>	0.525 <sup>ab</sup>	0.370 <sup>a</sup>	11.069 <sup>***</sup>	1.843	0.444
Width (cm)	0.156 <sup>b</sup>	0.493 <sup>a</sup>	0.542 <sup>a</sup>	13.157 <sup>***</sup>	2.501	1.866
Discharge (L/s)	0.041 <sup>b</sup>	0.178 <sup>b</sup>	0.359 <sup>a</sup>	9.996 <sup>***</sup>	3.860 <sup>*</sup>	0.632
Conductivity (μS/cm)	0.516 <sup>a</sup>	0.232 <sup>b</sup>	0.323 <sup>b</sup>	3.479 <sup>*</sup>	0.720	0.144
DO (mg/L)	0.351	0.334	0.279	0.727	23.720 <sup>***</sup>	1.520
pH	0.353	0.413	0.339	0.275	0.487	0.299

\*  $P < 0.05$ .

\*\*\*  $P < 0.001$ .

by runs and riffles. The proportions of runs and riffles were similar to each other in KR2 and KR3. KR1 had smaller differences in proportion among habitat types than the differences in KR2 and KR3.

Variations in hydrological factors were apparent among the reaches, and the differences were not consistent for each factor (Table 2). Current velocity and water depth in KR3 was greater than in KR1 and KR2 in winter and summer, respectively ( $P < 0.05$ , Figs. 2A and B). Stream widths in KR2 and KR3 were greater than those in KR1 during summer to autumn ( $P < 0.05$ , Fig. 2C). Discharge was the only hydrological factor that exhibited a significant difference among the seasons. Discharge during summer and autumn in KR3 was greater than that in KR1 ( $P < 0.01$ , Fig. 2D). None of the water quality factors showed differences among the reaches (Figs. 2E, F and G). In all reaches, DO in winter was significantly greater than that in the other seasons ( $P < 0.05$ , Fig. 2F).

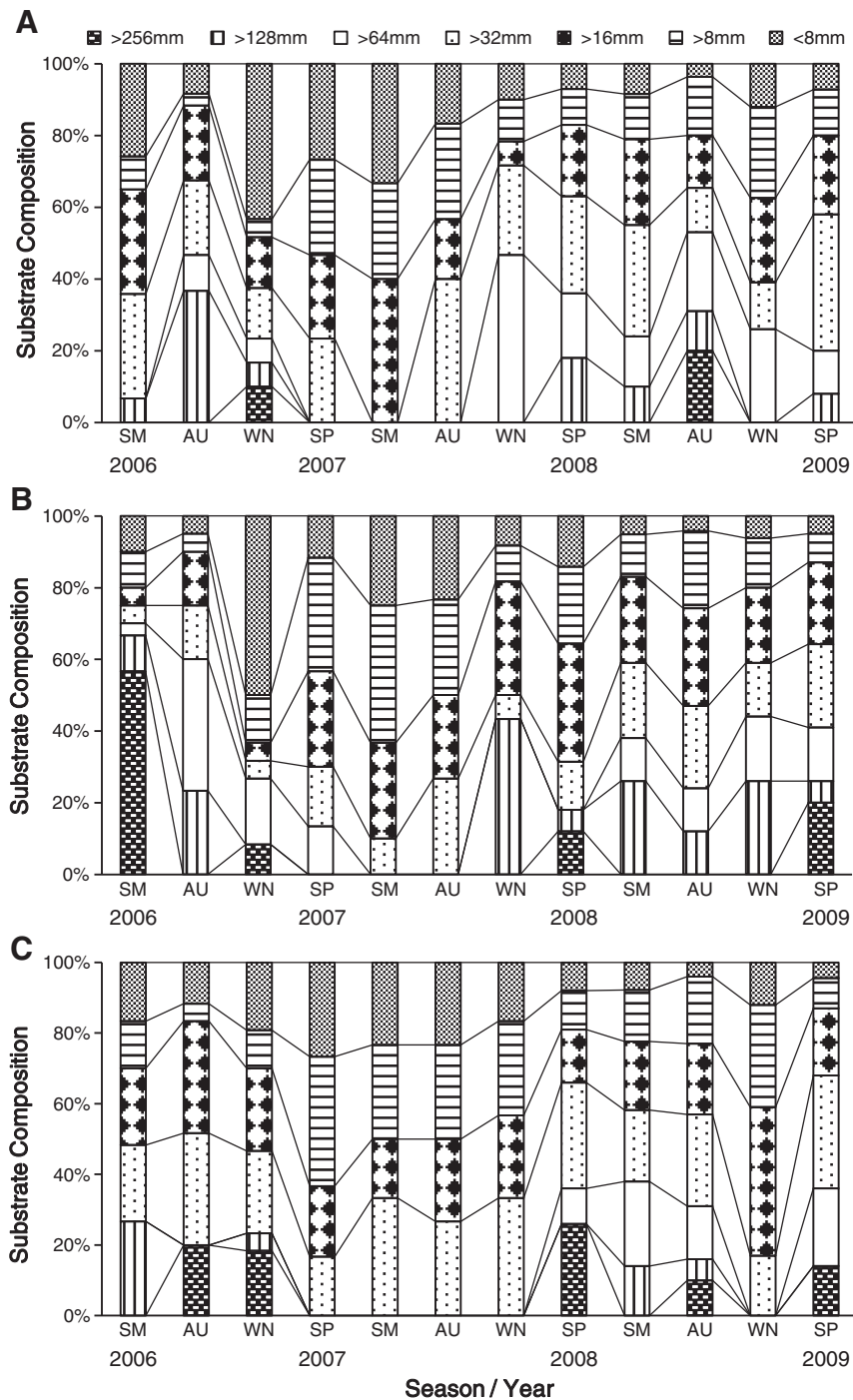
The variation in substrate compositions exhibited a similar overall pattern among the reaches. The proportion of smaller particles ( $< 16$  mm) gradually decreased from winter 2006 to spring 2009 in all reaches (Fig. 3). In contrast, the combined proportions of particles  $\geq 16$  mm showed an increasing pattern during the same years with minor fluctuations. The decrease in the proportion of fine sediments was prominent in the  $< 8$  mm size category during summer 2008 and spring 2009. The relative proportion of coarser particles  $\geq 64$  mm was highly variable.

### Macroinvertebrate community

Seventy-seven macroinvertebrate taxa in 36 families and 10 orders were collected through sampling. The vast majority of macroinvertebrates were included in Insecta. A taxon in Tubificidae (Oligochaeta) and *Gammarus* sp. in Gammaridae (Malacostraca) were also observed. *Gammarus* sp. (Gammaridae, SHR) was the most dominant taxa in KR1, followed by chironomids (Chironomidae, CLG and CFL) and *Ephemera* sp. (Ephemerae, CLG). The dominant taxa in KR2 included chironomids (CLG and CFL), *Gammarus* sp., and *Ephemera* sp. In KR3, chironomids (CLG, CFL, and SHR) were the most abundant taxa, followed by *Choroterpes* sp. (Leptophlebiidae, CLG) and *Gammarus* sp.

The total density of macroinvertebrates increased gradually throughout the study in each reach (Figs. 4A, C and E). The values reached maximums in summer 2008, winter 2008, and summer 2008 for KR1, KR2, and KR3 respectively and then decreased. Although not prominent, taxon richness generally followed the pattern of total density in KR1 and KR2, and maximum richness was observed at the same time as maximum density in both reaches. The greatest taxon richness in KR3 was observed in spring 2007. Species diversity in

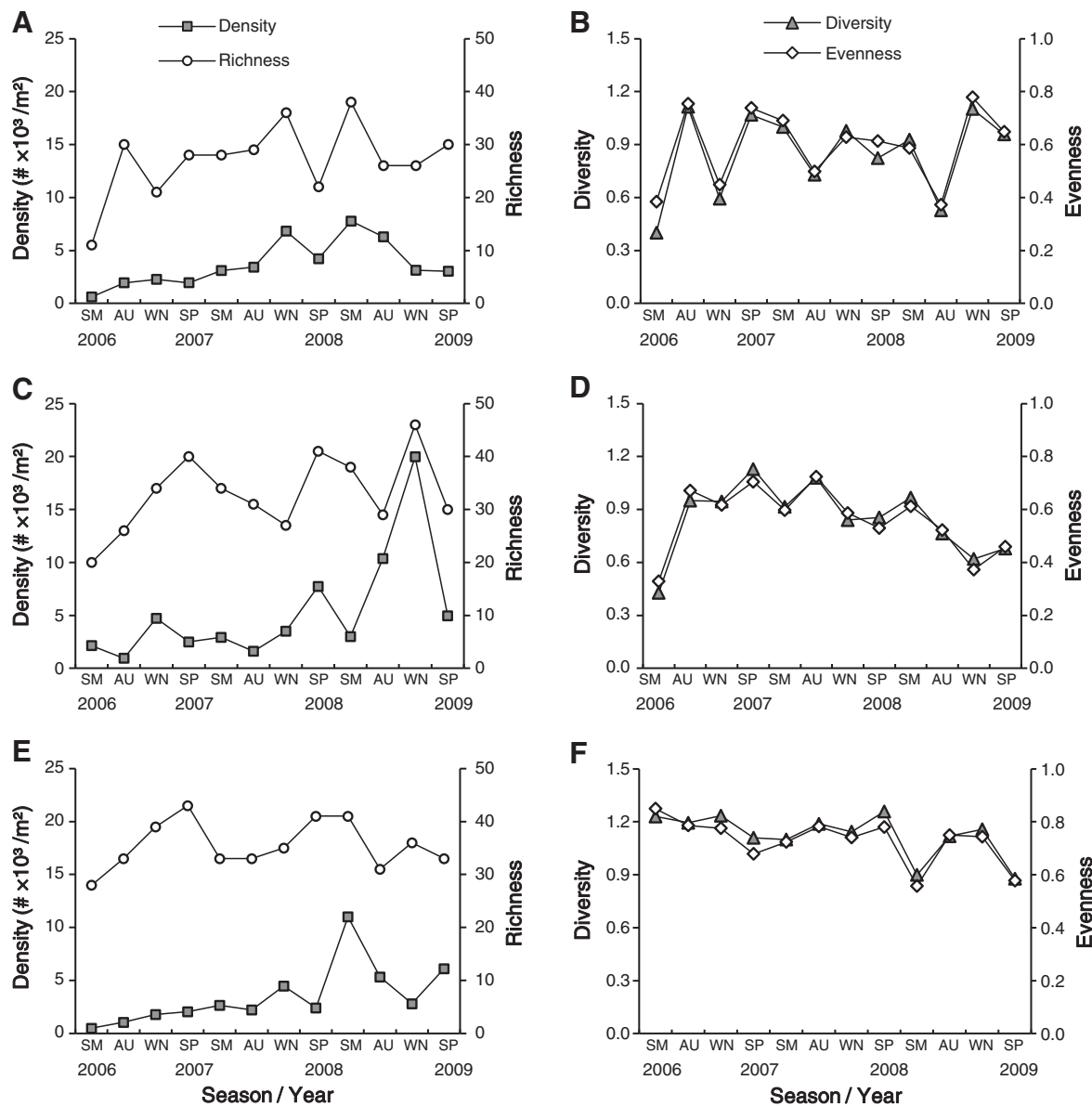




**Fig. 3.** Variation in substrate composition in (A) KR1, (B) KR2, and (C) KR3 during each season and sampling period. Values are the percentage of each size category. Abbreviations for the seasons are the same as in Fig. 2.

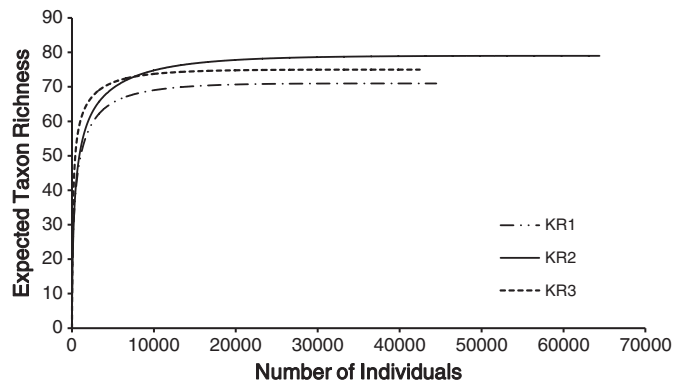
summer 2006 was the lowest in both KR1 and KR2 but was the greatest in KR3 (Figs. 4B, D and F). The variation in species diversity overlapped with that of evenness. Mean differences between diversity and evenness indexes were 0.256 (KR1), 0.287 (KR2), and 0.397 (KR3). When the total densities were the greatest in KR2 and KR3, the values of diversity and evenness reached the second lowest and the lowest in the reaches, respectively (Figs. 4C–F). These contrasts were mainly caused by higher densities of chironomids (CFL, CLG, and PRD) in KR2 during winter 2008 and of *Ephemera* sp., chironomids (CFL), *Oyamia* sp. (Perlidae, PRD), and a few SHR taxa including *Gammarus* sp., *Georodes* sp. (Lepidostomatidae), and

chironomids (SHR) in KR3 during summer 2008. The reverse relationship between high density and low diversity/evenness was consistent throughout the study years in KR2 and KR3. This pattern was not observed in KR1. The variation in diversity and evenness followed that of taxon richness in KR1 (Figs. 4A and B). When the taxon richness estimates were compared with the lowest number of individuals observed in KR3 during summer 2006, the estimates were similar between KR1 (41) and KR2 (42), whereas the value was 52 in KR3. When the greatest number of individuals was observed in KR2 during winter 2008, the estimated taxon richness was 71, 78, and 75 for KR1, KR2, and KR3, respectively, reaching the asymptotes (Fig. 5).



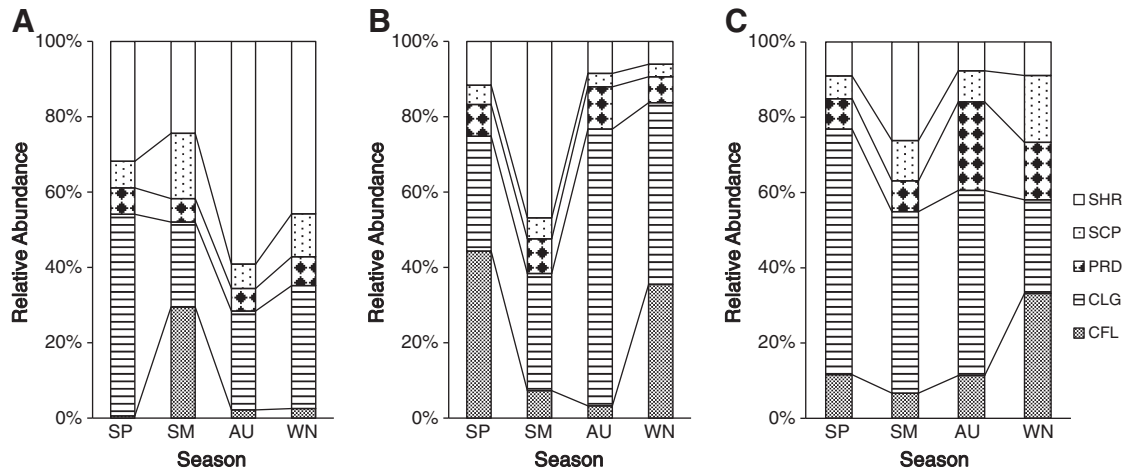
**Fig. 4.** Variation in total density, taxon richness, diversity, and evenness in (A and B) KR1, (C and D) KR2, and (E and F) KR3 during each season and sampling period. Abbreviations for the seasons are the same as in Fig. 2.

The relative abundances of the FFG suggested variation in macroinvertebrate community structure among the reaches. The compositions of FFG were similar between KR2 and KR3 but were



**Fig. 5.** Individual-based rarefaction curve for three sampling reaches, KR1, KR2, and KR3.

somewhat different between KR1 and the other two reaches. However, the overall variation in the percentage of any FFG among the seasons was not different in every reach. The relative abundances of five FFGs were significantly different in all seasons for every reach ( $P < 0.001$ ), except summer in KR1. The overall relative abundances were the highest for SHR followed by CLG in KR1 ( $P = 0.002$ , Fig. 6A). Shredders showed the greatest percentage in autumn, and the value decreased gradually through winter to summer in KR1. The relative abundance of CLG was the lowest in summer and the greatest in spring. Collector-gatherers exhibited their greatest relative abundance in KR2 and KR3, and the value was the lowest for SCP overall ( $P < 0.050$ , Figs. 6B and C). Collector-gatherers had the greatest relative abundance in KR2 during autumn and winter. Shredders showed their greatest percentage in summer, but were minor during spring, autumn, and winter. Collector-filterers were highly abundant in spring and winter in KR2 (Fig. 6B). Collector-gatherers were in their highest relative abundance in KR3 during spring to autumn, and their percentage was lower than the CFL value during winter. The relative abundance of SHR was the second largest among FFG in summer and remained minor during the other seasons in KR3.



**Fig. 6.** Seasonal variation in the relative abundance of functional feeding groups (FFGs) in (A) KR1, (B) KR2, and (C) KR3. Values are presented as the percentage of each FFG.

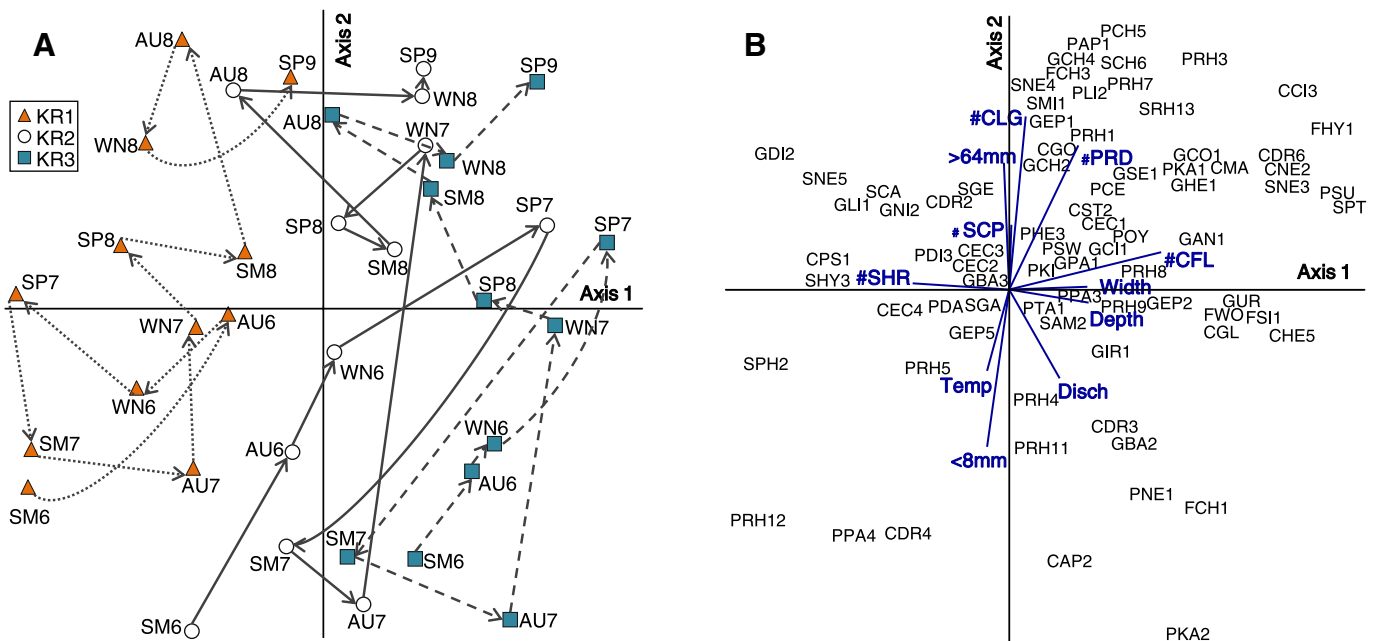
Predators showed a similar pattern with SHR but in different seasons (Fig. 6C). The proportions of SCP and PRD were relatively constant among seasons in the reaches.

#### Ordination of the macroinvertebrate community

The NMS ordination plot indicated that the samples at each sampling time and reach could be distinguished based on similarities in community composition (Fig. 7). The final stress of the NMS ordination was 13.77 (three axes), which was in the range of stress values for most ecological community data (10–20), indicating an acceptable solution (McCune and Grace, 2002). A two-dimensional ordination explained 55.4% of the variance ( $r^2=0.399$  for axis 1,

$r^2=0.185$  for axis 2), and the Monte Carlo test implied that the axes explained significantly more variance than expected by chance ( $P=0.02$ ).

The ordination clearly showed both temporal changes and spatial distribution of the sampling units in the three reaches (Fig. 7A). Spatial variation in the samples was distinguished on axis 1, whereas temporal changes were revealed on axis 2. All KR1 samples were located on the left part of axis 1, whereas the KR3 samples were located on the right part of axis 1. The KR2 samples were mostly located between those of KR1 and KR3. The KR1 samples completed the annual cycle in the lower left part of the ordination during the first 2 years and moved to the upper left part for the third year. Those of KR2 were found below axis 1 during summer 2006–autumn 2007



**Fig. 7.** Nonparametric multidimensional scaling (NMS) ordination of samples with species density of benthic macroinvertebrates in space and time (A). Environmental factors and functional feeding group (FFG) density were visualized on the biplot with a taxa score map (B). Sampling reaches are marked with three-digit labels (season-code/year), and macroinvertebrate species are marked with three- or four-digit labels (FFG-code/taxon-acronym/species #). Season codes are the same as in Fig. 1. Years are 6, 2006; 7, 2007; 8, 2008; 9, 2009. FFG codes are C, scrapers; F, collector–filterers; G, collector–gatherers; P, predators; S, shredders. Taxon acronym represents the first two letters of the genus or family name (see Appendix A for details). Species # is given as the serial number of the species when multiple species are included in the genus or multiple taxa in a family.

and then moved to the upper right part of the ordination. The KR3 samples were observed on the right part of the ordination during all years and followed a similar route to those of KR2.

Factors with significant correlations with the NMS axes ( $P < 0.05$ ) were displayed on the ordination (Fig. 7B). Axis 1 was positively correlated with the abundance of collector-filterers (#CFL,  $r = 0.56$ ), water depth ( $r = 0.41$ ), stream width ( $r = 0.40$ ), and the abundance of predators (#PRD,  $r = 0.38$ ), and was negatively correlated with shredder abundance (#SHR,  $r = -0.45$ ). Axis 2 was correlated positively with the abundances of collector-gatherers (#CLG,  $r = 0.60$ ), predators (#PRD,  $r = 0.55$ ), and scrapers (#SCP,  $r = 0.37$ ) as well as substrate category  $> 64$  mm ( $r = 0.51$ ), and was negatively correlated with the particles  $< 8$  mm ( $r = -0.57$ ), discharge ( $r = -0.43$ ), and water temperature ( $r = -0.41$ ).

## Discussion

### Habitat morphology, organic matter availability, and FFG structure

The results suggest that differences in the predominant FFGs among the reaches were related to differences in habitat characteristics in the study reaches in terms of geological channel morphology and organic matter input. KR1 habitat characteristics classified the reach as a step-pool reach. That reach had a discontinuous assembly of large stones, coupled with relatively higher elevations and a steep slope, which created a series of small pools and riffles (Table 1) in the form of steps (Montgomery and Buffington, 1997). Larger sediments act as barriers for the accumulation of CPOM called debris dams. Debris dams are mainly composed of detritus from riparian vegetation (Fisher and Likens, 1973; Benfield, 1997) and play a key role in the function of forested stream ecosystems (Bilby and Likens, 1980; Abelho and Graça, 1998; Allan and Castillo, 2007). The narrow stream channel in KR1 was shaded heavily with a dense forest canopy providing allochthonous organic matter input to the stream. The stream channel was also confined by steep banks where fallen leaves had accumulated and slid down into the channel, creating year-round energy input.

The organic debris dams in KR1 were colonized by gammarids in great abundance, which are classified as SHR and ingest CPOM in general (Bärlocher and Kendrick, 1975; Kostalos and Seymour, 1976; Tiegs et al., 2008). The presence of debris dams in detritus-based headwater stream ecosystems is crucial to retain organic matter, allowing the energy to be processed into finer sizes within the upstream reaches rather than being exported to downstream reaches in a CPOM form (Bilby and Likens, 1980), while supporting the higher relative abundance of shredders (Smock et al., 1989). Hawkins and Sedell (1981) indicated that the density of shredders was significantly correlated with the amount of CPOM in four streams with various physical characteristics. Compared to downstream reaches of KR2 and KR3, a higher amount of CPOM was observed throughout the study in KR1. The channel morphology plus CPOM availability supported the high abundance of shredders, particularly *Gammarus* sp. in KR1, which exhibits patchy distribution in leaf packs (Covich and Thorp, 2001; Cushing and Allan, 2001). The seasonal variation in the relative abundance of SHR in KR1 also suggested that the occurrence of SHR in the upstream reach might be tightly related to CPOM availability. The proportion was the greatest in autumn when food sources were abundant and decreased gradually through winter and summer (Fig. 6A) with a decline of CPOM due to decomposition. The same annual cycle was repeated during the study years.

The KR2 and KR3 channel characteristics may approximate the downstream reaches of a pool-riffle reach type, although both reaches did not exactly match the description of reach type (Montgomery and Buffington, 1997). The reaches oscillated laterally to some degree and displayed a sequence of bigger pools and riffles in a smaller proportion (Table 1). Pool spacing was greater than that in KR1. With a lack of

confining valley walls, channel width was greater than that in KR1 (Table 2), resulting in larger width-to-depth ratios. Such characteristics made the canopy cover in KR2 and KR3 more open than that in KR1. Both less dense riparian cover (lower input) for a food source and microhabitat as well as scarce in-stream structure accumulating organic debris (lower retention) contributed to the smaller values of CPOM stock in the reaches and *Gammarus* sp. densities (except in summer 2006 and 2007, refer to Fig. 6B). The lateral input of CPOM from the stream banks was also limited, as the banks were not as steep as those in KR1. Loose accumulations of decaying leaves laying in the sediment were mainly observed in the shallow edges of large pools in KR2 and KR3, which were mixed with fine particulate organic matter utilized by collector-gatherers and probably SHR-chironomids as well (Cummins and Klug, 1979). Considering the feeding mechanism of collector-gatherers, they are expected to prefer slow-flowing depositional habitats (Berg, 1995). The higher proportion of pool habitats in KR2 and KR3 may have favored the higher relative abundances of CLG in the reaches (Figs. 6B and C). The NMS ordination plots showed that CLG taxa, except a few, were located near the KR2 and KR3 sampling units (Fig. 7).

Snelder and Biggs (2002) assumed that the variation in dominant environmental factors results in the physical and biotic component patterns of rivers at a given spatial scale. Our results are consistent with the observations of previous studies. A study by Wohl et al. (1995) concluded that local geomorphology and related physical parameters affect the differences in the FFG structure of benthic macroinvertebrates and the distribution of organic matter in the three types of habitats. Huryn and Wallace (1987) showed that the physical characteristics of specific habitats determine resource availability and mode of delivery to consumers. They reported that the distribution of secondary production of different FFGs was higher in habitats whose characteristics are suitable for certain groups of FFG. For example, collector-filterers exhibited high production in habitats with high velocity and low retention of organic matter, and CLG and SHR production were highest in pool habitats with slower currents and accumulating organic matter. In two grassland streams in New Zealand, the variation in organic matter availability was important in the proportions and biomass of CGL and CFL (Thompson and Townsend, 1999).

### Trophic structure and environmental variables

The temporal changes of samples in the ordination suggest that the decreases in the proportion of fine particles ( $< 8$  mm) coupled with increases in the densities of CLG and PRD as well as the proportion of coarse substrates ( $> 64$  mm), might explain the shift in the positions of the samples to the upper part of axis 2 for the third year in all reaches. The changes in FFG composition in KR1 during the third year were mainly related to the increase in the densities of CLG (spring 2008 and 2009) and CFL (summer 2008, Fig. 6A). Such changes contributed to the greater increase in total densities in the samples (Fig. 4A). The increases in total density during autumn–winter 2008 in KR2 (Fig. 4C) were due to higher densities of CLG (autumn–winter 2008) and CFL (winter 2008, Fig. 6B). Higher densities of CLG and SHR in KR3 resulted in the maximum total density in summer 2008 (Fig. 4E). The abundance of CLG was higher during summer 2008–spring 2009 with recurring high density of CFL during each winter, resulting in a seasonal variation in FFG composition in KR3 (Fig. 6C). The proportions of substrate  $< 8$  mm were lower during spring 2008–spring 2009 in all reaches (Fig. 3A).

However, the spatial changes in samples were more transparent to discriminate shifts in community structure of benthic macroinvertebrates than temporal changes. The horizontal discrimination of samples from each reach was related to the geographic distribution of sampling reaches, which displayed differences in hydrological factors such as water depth and stream width (Fig. 7). Although the



variables were not always significantly different among the reaches, the mean values of stream width and water depth were generally the lowest in KR1 and the highest in KR3 (Table 2, Fig. 2). Doisy and Rabeni (2001) reported similar results with an ordination analysis of macroinvertebrate data from a study conducted in three stream segments (upper, middle, and lower) of a stream. They showed that macroinvertebrate communities are segregated based on their geographic position in the stream with a longitudinal gradient from the upper to lower segment.

Differences in SHR and CFL densities were also identified on the horizontal discrimination. The relative proportion of SHR was higher in KR1 than that in the other reaches except summer in KR2 (Fig. 6). The dominant SHR taxon was *Gammarus* sp., which was highly abundant in KR1 through the study and was relatively abundant in KR2 as well. The dominant SHR group in KR3 was chironomids followed by *Gammarus* sp. The reduced values of hydrological factors in KR1, coupled with large stones, may have enhanced retention of CPOM which is a favorable food and microhabitat of gammarid shredders (Tiegs et al., 2008). It has been demonstrated that the transport distance of leaves in streams increases with increasing depth, velocity, stream width, and discharge (Wallace et al., 1995; Brookshire and Dwire, 2003). The abundance of CFL was higher in KR2 and KR3 than that in KR1 due to the predominance of chironomids, followed by *Simulium* sp., *Cheumatopsyche* sp., *Hydropsyche orientalis*, and *Wormaldia* sp. (Figs. 6 and 7). In contrast to shredders, the filter-feeding species in KR2 and KR3 may have benefited from the increased current (Huryn and Wallace, 1988; Georgian and Thorp, 1992). Collector–filterers generally construct silken catchnets or use ‘feeding brushes’ (e.g., cephalic fans of *Simulium* sp.) to catch food

particles transported via the current (Wallace and Merritt, 1980; Berg, 1995; Wiggins, 1996).

## Conclusion

The community structure of benthic macroinvertebrates classified into FFGs was variable even among three reaches closely located in a short stream segment (about 1 km length). This suggests that the variation in the trophic structure was affected by habitat characteristics in each channel reach, including channel morphology, proportion of habitat type, and benthic organic matter availability. The benthic community structure in terms of relative abundances of FFGs was distinguished between the upper headwater reach and the lower downstream reaches. The NMS ordination indicated that stream width, water depth, and the densities of shredders and collector–filterers were the main factors determining the differences in community structure. The ordination also revealed temporal variation in community structure within a reach, influenced by the densities of collector–gatherers and predators and the proportions of substrate particles <8 mm and 64–128 mm.

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## Appendix A. List of taxa recorded in the study reaches during sampling

Acronym	Class	Order	Family	Species	FFG
SAM2	Insecta	Plecoptera	Nemouridae	<i>Amphinemura coreana</i>	SHR
SCA	Insecta	Plecoptera	Capniidae	<i>Capnia</i> sp.	SHR
SCH6	Insecta	Diptera	Chironomidae	n/a	SHR
SGA	Malacostraca	Amphipoda	Gammaridae	<i>Gammarus</i> sp.	SHR
SGE	Insecta	Tricoptera	Lepidostomatidae	<i>Georodes</i> Kub	SHR
SHY3	Insecta	Tricoptera	Limnephilidae	<i>Hydatophylax nigrovittatus</i>	SHR
SMI1	Insecta	Tricoptera	Brachycentridae	<i>Micrasema</i> Kua	SHR
SNE3	Insecta	Plecoptera	Nemouridae	<i>Nemoura</i> Kua	SHR
SNE4	Insecta	Plecoptera	Nemouridae	<i>Nemoura</i> Kub	SHR
SNE5	Insecta	Plecoptera	Nemouridae	<i>Nemoura</i> tau	SHR
SPH2	Insecta	Tricoptera	Phryganopsychidae	<i>Phryganopsyche latipennis</i>	SHR
SPT	Insecta	Plecoptera	Pteronarcidae	<i>Pteronarcis macra</i>	SHR
SRH13	Insecta	Plecoptera	Leuctridae	<i>Rhopalopsale mahunkai</i>	SHR
CAP2	Insecta	Tricoptera	Limnephilidae	<i>Apatania</i> Kua	SCP
CCI3	Insecta	Ephemeroptera	Heptageniidae	<i>Cinygmula</i> Kua	SCP
CDR2	Insecta	Ephemeroptera	Ephemerellidae	<i>Drunella cryptomeria</i>	SCP
CDR3	Insecta	Ephemeroptera	Ephemerellidae	<i>Drunella</i> sp. 1	SCP
CDR4	Insecta	Ephemeroptera	Ephemerellidae	<i>Drunella</i> sp. 2	SCP
CDR6	Insecta	Ephemeroptera	Ephemerellidae	<i>Drunella aculea</i>	SCP
CEC1	Insecta	Ephemeroptera	Heptageniidae	<i>Ecdyonurus bajkovae</i>	SCP
CEC2	Insecta	Ephemeroptera	Heptageniidae	<i>Ecdyonurus dracon</i>	SCP
CEC3	Insecta	Ephemeroptera	Heptageniidae	<i>Ecdyonurus kibunensis</i>	SCP
CEC4	Insecta	Ephemeroptera	Heptageniidae	<i>Ecdyonurus levis</i>	SCP
CGL	Insecta	Tricoptera	Glossosomatidae	<i>Glossosoma</i> Kua	SCP
CGO	Insecta	Tricoptera	Limnephilidae	<i>Goera japonica</i>	SCP
CHE5	Insecta	Coleoptera	Helodidae	n/a	SCP
CMA	Insecta	Coleoptera	Psephenidae	<i>Mataeopsephus</i> Kua	SCP
CNE2	Insecta	Tricoptera	Uenoidae	<i>Neophylax ussuriensis</i>	SCP
CPS1	Insecta	Tricoptera	Odontoceridae	<i>Psilotreta kisoensis</i>	SCP
CST2	Insecta	Coleoptera	Elmidae	<i>Stenelmis</i> sp.	SCP
PAP1	Insecta	Tricoptera	Rhyacophilidae	<i>Apsilochorema</i> Kua	PRD
PCE	Insecta	Diptera	Ceratopogonidae	n/a	PRD
PCH5	Insecta	Diptera	Chironomidae	n/a	PRD

(continued on next page)

## Appendix A (continued)

Acronym	Class	Order	Family	Species	FFG
PDA	Insecta	Odonata	Gomphidae	<i>Davidius lunatus Bartenev</i>	PRD
PD13	Insecta	Diptera	Tipulidae	<i>Dicranota Kua</i>	PRD
PHE3	Insecta	Diptera	Tipulidae	<i>Hexatoma Kua</i>	PRD
PKA1	Insecta	Plecoptera	Perlidae	<i>Kamimuria coreana</i>	PRD
PKA2	Insecta	Plecoptera	Perlidae	<i>Kamimuria</i> sp.	PRD
PKI	Insecta	Plecoptera	Perlidae	<i>Kiotinal decorata</i>	PRD
PLI2	Insecta	Diptera	Tipulidae	<i>Limnophila</i> sp.	PRD
PNE1	Insecta	Plecoptera	Perlidae	<i>Neoperla coreensis</i>	PRD
POY	Insecta	Plecoptera	Perlidae	<i>Oyamia nigribasis</i>	PRD
PPA3	Insecta	Megaloptera	Corydalidae	<i>Parachauliodes continentalis</i>	PRD
PPA4	Insecta	Plecoptera	Perlidae	<i>Paragnetina flavotincta</i>	PRD
PRH1	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila articulata</i>	PRD
PRH11	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila</i> sp. 1	PRD
PRH12	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila</i> sp. 2	PRD
PRH3	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila clemens</i>	PRD
PRH4	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila Kua</i>	PRD
PRH5	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila Kub</i>	PRD
PRH7	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila narvae</i>	PRD
PRH8	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila nigrocephala</i>	PRD
PRH9	Insecta	Tricoptera	Rhyacophilidae	<i>Rhyacophila shikotsuensis</i>	PRD
PSU	Insecta	Diptera	Athericidae	<i>Suragina Kua</i>	PRD
PSW	Insecta	Plecoptera	Chloroperlidae	<i>Sweltsa nikkoensis</i>	PRD
PTA1	Insecta	Diptera	Tabanidae	<i>Tabanus</i> sp.	PRD
GAN1	Insecta	Diptera	Tipulidae	<i>Antocha Kua</i>	CLG
GBA2	Insecta	Ephemeroptera	Baetidae	<i>Baetiella tuberculata</i>	CLG
GBA3	Insecta	Ephemeroptera	Baetidae	<i>Baetis fuscatus</i>	CLG
GCH2	Insecta	Ephemeroptera	Leptophlebiidae	<i>Choroterpes altiocularis</i>	CLG
GCH4	Insecta	Diptera	Chironomidae	n/a	CLG
GCI1	Insecta	Ephemeroptera	Ephemerellidae	<i>Cincticostella levanidovae</i>	CLG
GCO1	Insecta	Collembola	Entomobryidae	<i>Collembola</i> sp.	CLG
GDI2	Insecta	Diptera	Dixidae	<i>Dixa</i> sp.	CLG
GEP1	Insecta	Ephemeroptera	Heptageniidae	<i>Epeorus curvatus matsumura</i>	CLG
GEP2	Insecta	Ephemeroptera	Heptageniidae	<i>Epeorus pellulus</i>	CLG
GEP5	Insecta	Ephemeroptera	Ephemeridae	<i>Ephemera strigata</i>	CLG
GHE1	Insecta	Collembola	Entomobryidae	<i>Heteromurus</i> sp.	CLG
GIR1	Insecta	Ephemeroptera	Heptageniidae	<i>Iron aesculus</i>	CLG
GLI1	Oligochaeta	Tubificida	Tubificidae	<i>Limnodrilus</i> sp.	CLG
GNI2	Insecta	Ephemeroptera	Baetidae	<i>Nigrobaetis bacillus</i>	CLG
GPA1	Insecta	Ephemeroptera	Leptophlebiidae	<i>Paraleptophlebia chororata</i>	CLG
FCH1	Insecta	Tricoptera	Hydropsychidae	<i>Cheumatopsyche Kua</i>	CFL
FCH3	Insecta	Diptera	Chironomidae	n/a	CFL
FHY1	Insecta	Tricoptera	Hydropsychidae	<i>Hydropsyche orientalis</i>	CFL
FSI1	Insecta	Diptera	Simuliidae	<i>Simulium</i> sp.	CFL
FWO	Insecta	Tricoptera	Philopotamidae	<i>Wormaldia Kua</i>	CFL

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