Hydrobiologia (2005) 543: 135–145
DOI 10.1007/s10750-004-6951-z

Primary Research Paper

Across-reach consistency in macroinvertebrate distributions among litter patch types in Japanese headwater streams

Sohei Kobayashi[1,2,*] & Takashi Kagaya[1]
[1]*Laboratory of Forest Zoology, Graduate School of Agricultural and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan*
[2]*Present address: Geohazards Division, Disaster Prevention Research Institute, Kyoto University, Gokasho, Uji, Kyoto 611-0011, Japan*
*(*Author for correspondence: Tel.: +81-774-38-4288, E-mail: skob@slope.dpri.kyoto-u.ac.jp)*

Received 16 April 2004; in revised form 14 October 2004; accepted 30 November 2004

Key words: channel characteristics, pool-riffle, patch type composition, hydraulics, accumulating litter, assemblage structure

Abstract

Different types of litter patches with contrasting macroinvertebrate assemblages have been observed within a stream reach. This study examined whether distributions of macroinvertebrates among three litter patch types (riffle, middle, edge) were consistent between reaches with different channel characteristics in headwater streams in central Japan. Mass of leaves per unit area was significantly higher in riffle and edge patches than in middle patches, which was consistent between reaches, while no consistent pattern was evident between reaches for mass of either woody material or small litter fragments. Distribution among the patch types was consistent between reaches for 11 out of 13 dominant macroinvertebrate taxa; density was highest in riffle patches for 5 taxa and in middle patches for 5 taxa. Although we previously related densities of some taxa to mass of woody material or small litter fragments, hydraulic characteristics (water depth, current velocity), which were consistent between reaches, may be more important determinants of macroinvertebrate distributions among the patch types, even within pools (i.e. middle and edge patches) where current is uniformly low. The results of this study indicate that a reach-scale macroinvertebrate community structure associated with litter is likely to vary according to litter patch type composition, which would be affected by channel characteristics of the reaches.

Introduction

Viewing streams as a mosaic of patches promotes our understanding of heterogeneous stream ecosystems (Pringle et al., 1988; Palmer et al., 2000). Different habitats or patch types with contrasting faunal assemblages have been demonstrated in many stream reaches (Huryn & Wallace, 1987; Armitage et al., 1995; Angradi, 1996; Kobayashi & Kagaya, 2004). Relative composition of patch types within stream reaches can vary temporally (Armitage & Cannan, 2000) and spatially among reaches with different channel forms (Inoue & Nunokawa, 2002), and might affect the community structure of stream biota at reach or larger spatial scales.

Plant litter from terrestrial vegetation is a major energy resource in headwater streams draining forests (Fisher & Likens, 1973; Webster & Meyer, 1997). Benthic macroinvertebrates are often dominated by detritivores (belonging to shredder or collector functional groups) and their predators, which obtain energy directly or indirectly from litter, and macroinvertebrate biomass and production have been shown to change according to the amount of litter retained on the streambed

(Dobson & Hildrew, 1991; Richardson, 1991; Wallace et al., 1999).

Physical heterogeneity in headwater reaches often causes litter to accumulate as discrete patches. Different types of litter patches have been recognized based on the size or hydraulic characteristics (current velocity, streambed topography) of retentive devices (Casas, 1997; Kobayashi & Kagaya, 2002; 2004). Kobayashi & Kagaya (2002; 2004) have identified four types of litter patches; one that formed on riffles and three that formed on different locations in pools (middle, alcove, edge), and have demonstrated differences in the structure and production of macroinvertebrate assemblages among these patch types. For instance, densities of stonefly shredder taxa were higher in riffle patches than in pool patches (a mix of middle, alcove, edge patches), while those of caddisfly shredder taxa showed the inverse pattern (Kobayashi & Kagaya, 2002), and within pools, densities of caddisfly shredder taxa were highest in middle patches, while densities of most stonefly shredder taxa were highest in edge patches (Kobayashi & Kagaya, 2004). Kobayashi & Kagaya (2002; 2004) have suggested that headwater reaches vary in community structure of litter-associated macroinvertebrates according to the relative composition of the four litter patch types (riffle, middle, edge, alcove), which is likely to be affected by channel morphology.

It is unclear whether the differences in macroinvertebrate assemblage structure between the litter patch types are ubiquitous across headwater reaches with different channel characteristics, such as discharge and channel slope, which determine the form and flow of pools and riffles (Wohl et al., 1993; Buffington et al., 2002). Kobayashi & Kagaya (2002; 2004) have demonstrated that litter patch types differed in litter characteristics, for example, mass of leaves (>16 mm) per unit area was higher in riffle patches than in pool patches, and was highest in edge patches within pools, while mass of woody detritus (16–100 mm) and small litter fragments (1–16 mm) was highest in middle patches. It has been supposed that litter characteristics were responsible for the differences in macroinvertebrate densities between these patch types, and also hydraulic characteristics between riffle patches and pool patches. Hydraulic characteristics of each patch type, which are also thought to affect accumulating litter, may vary according to the channel characteristics of reaches. As a consequence, macroinvertebrate distributions among the patch types may also vary in reaches with different channel characteristics.

The differences in reach-scale macroinvertebrate community structure according to patch type composition partly depend on across-reach consistency in macroinvertebrate distributions among patch types. Macroinvertebrate distribution among patch types is said to be consistent if among-type variation in density is larger than among-reach variation in the distribution. The objective of this study was to determine whether macroinvertebrate distributions among litter patch types were consistent over reaches with different channel characteristics.

Sites and methods

Study site

The study was conducted in headwater streams of the Arakawa River drainage basin, in the Tokyo University Forest, Chichibu, Saitama, central Japan (138°56′ E, 35°57′ N). The study area is situated in a wet-temperate climate region, with high summer rainfall and little precipitation but some snowfall in the winter. Annual precipitation ranges from 1300 to 1600 mm in the Tokyo University Forest, and most of the watersheds are largely covered by secondary deciduous forest. The streams were underlained by graywacke and sandstone of the paleozoic era and most flow through steep and narrow valleys with riparian vegetation usually dominated by maples (*Acer* spp.), shioji (*Fraxinus platypoda*), sawagurumi (*Pterocarya rhoifolia*), katsura (*Cercidiphyllum japonicum*), fusazakura (*Euptelea polyandra*), horse chestnut (*Aesculus turbinata*), keyaki (*Zelkova serrata*), and hornbeams (*Carpinus* spp.). Stream water in the area was characterized by neutral or higher pH (7–8), low electrical conductivity (<100 μS/cm) and NO_3–N concentration (<2 mg/l) (The Tokyo University Forest, unpublished data).

Three stream reaches were selected where pool-riffle or step-pool sequences occurred and litter patches were present most of the year round, but where channel size and slope varied as much as possible. The three stream reaches were located in different watersheds (Kudonosawa, Higashitani, Akagisawa), 4–15 km apart from each other, and 100–150 m long. The Kudonosawa reach (KU) is where we have previously examined the differences in macroinvertebrate assemblages between the litter patch types (Kobayashi & Kagaya, 2002; 2004). The Higashitani reach (HI) was largest in size and lowest in slope, while the Akagisawa reach (AK) was smallest in size and highest in slope (Table 1). Each stream reach consisted of 20–30 sequences of slow-flowing scour pools and fast-flowing riffles, with bottom being mainly sand, gravel, and cobbles in pools, and cobbles and boulders in riffles. Mean width and depth of pools and riffles varied among the reaches (Table 1). The altitude of the study reach was higher in AK (1200 m) compared to the others (HI = 600, KU = 800). A few small reservoirs were constructed for erosion control in HI at >500 m upstream of the reach.

Litter patch samplings

Natural litter patches were sampled from each study reach in winter (December 2001), spring (March 2002), and summer (June 2002). All samplings were done at baseflow. Four samples (two or three samples in summer when litter patches were sparse) were collected from each of three patch types (riffle, middle, edge) in each reach; riffle patches are those that formed in riffles, middle patches are those that formed on mid channel near the thalweg in pools, and edge patches are those that formed at shorelines near pool ends (Kobayashi & Kagaya 2002, 2004). Alcove patches, which formed on the side of pools, were omitted from sampling because there were few in the AK reach (0–3 patches). All samples were taken randomly from different riffles or pools using a Surber sampler (0.25 mm mesh). For litter patches covering > 400 cm^2 of the streambed, a portion (400 cm^2) of the patch was collected using a rubber-framed quadrat (20 × 20 cm opening); after placing the frame on a patch, all the organic matter was washed into the sampler net. For litter patches <400 cm^2, the whole litter accumulation was collected after measuring the patch area (200–400 cm^2). Water depth and current velocity at 1–2 cm above the patch using a portable current meter (Tanida et al., 1985) were measured for each sample, however all of middle and edge patches had a current velocity < 0.056 m/s, the lower detection limit of the meter. Samples were fixed in 10% formalin and returned to the laboratory for processing.

Table 1. Physical features of the three study reaches. Channel width and depth represent mean (1SD) of 20–30 pools and riffles

	HI	KU	AK
Altitude (m)	600	800	1200
Drainage area (ha)	720	188	64
Baseflow discharge (m^3/s)	0.10–0.19	0.02–0.03	no data
Channel slope (m/m)	0.07	0.14	0.28
Channel width (m)			
Pools	2.9 (1.2)	2.8 (1.1)	2.2 (1.0)
Riffles	0.8 (0.4)	0.5 (0.2)	0.6 (0.2)
Channel depth (cm)			
Pools	41 (21)	37 (10)	40 (23)
Riffles	16 (7)	12 (10)	8 (7)

In the laboratory each sample was washed through two nested sieves (16 and 1 mm mesh), and the sieve contents were then separated into either litter or macroinvertebrate fractions. We classified litter into one of four categories: particulate organic matter (POM: <16 mm diameter), leaves (>16 mm diameter), small woody detritus (SWD: 16–100 mm length), and large woody detritus (LWD: >100 mm length). However, LWD was excluded from further analyses because of its rare occurrence (<5% of samples). The three remaining categories were dried at 60 °C for 48 h, weighed (g/m^2). Macroinvertebrates were identified to the lowest level possible (usually genus or species) and counted (no./m^2). Each taxon was assigned to a functional feeding group according to Merritt & Cummins (1996) and Kagaya (1990, unpublished data).

Statistical analysis

A mixed-model 3-way analysis of variance (ANOVA) (Zar, 1999) with patch type and season as fixed factors and reach as a random factor was performed to examine whether differences in water depth, mass of litter categories (leaves, SWD, POM), and densities of dominant taxa (mean density in one of the patch types was >500 individuals/m^2 in at least 2 reaches) among the litter patch types were consistent over any stream reaches. The effects of patch type and patch type × season interaction were tested using mean square of patch type × reach interaction and patch type × reach × season interaction as an error term, respectively. If either of these effects is significant, the difference among the patch types is considered to be consistent over any set of reaches. Multiple mean comparisons were done using Tukey's test for significant ANOVAs. When effect of interaction (patch type × reach, patch type × season, patch type × reach × season) was significant, multiple mean comparisons were made after 1-way ANOVA, using Fisher's protected least significance difference (PLSD). Data in seasons of low occurrences were excluded (that is, <50% of samples in all patch types) in the analysis of dominant taxa. Litter and macroinvertebrate data were rank-transformed to improve the normality and homogeneity of variances, which also yield identical results as for nonparametric ANOVA (Zar, 1999). It was not possible to test the difference in current velocity among patch types because the velocity of middle and edge patches was lower than the detection limit of the meter (5.6 cm/s), therefore we only examined difference in current velocity of riffle patches between reaches by a mixed model 2-way ANOVA with season as a fixed factor and reach as a random factor. All the preceding analyses were performed using SYSTAT (version 8, SPSS Inc., Chicago, Illinois).

Detrended correspondence analysis (DCA) ordination was performed each season using PC-ORD (multivariate analysis of ecological data, version 4, MjM Software design, Glenden Beach, Oregon) to examine whether differences in taxonomic composition of macroinvertebrate assemblages among the patch types were consistent between the study reaches. Log-transformed densities of 20 dominant taxa were used for calculating the relative abundance of each taxon before the analysis. A fixed model 2-way ANOVA for DCA score 1 with reach and patch type as factors was performed for each season.

Table 2. Results of mixed model 3-way ANOVA with patch type and season as fixed factors and reach as a random factor for water depth

Source of variation	*df*	*MS*	*F*-value and probability
Patch type	2	11054.38	273.10***
Patch type × reach	4	40.48	0.86
Season	2	304.39	2.19
Reach × season	4	138.91	2.94**
Patch type × season	4	177.54	1.52
Patch type × reach × season	8	116.47	2.47*
Reach	2	70.14	1.49
Error	69	47.18	

The full sources of variation in the analysis are shown. MS used for calculating *F*-value differed according to the source of variation; patch type: patch type × reach, season: reach × season, patch type × season: patch type × reach × season, others: error. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Results

Differences in hydraulic and litter characteristics among litter patch types

Effect of patch type was significant for water depth of litter patches (Table 2). Depth was significantly higher in middle patches than in other patches over reaches ($p < 0.001$), but effects of reach and patch type × season and patch type × reach interactions were not significant (Table 2, Fig. 1). A significant effect of patch type × reach × season interaction was detected in water depth; the depth in middle patches was significantly higher than in the other patches in all cases but during summer in HI. Current velocity of riffle patches did not differ significantly among the reaches ($F_{2,87} = 0.42$, $p = 0.66$) (Fig. 1). Since current velocity of middle and edge patches was nearly 0 (<5.6 cm/s) in all the reaches, it follows that differences in current velocity among the three patch types varied little among the reaches.

Effect of patch type was significant for leaf mass, but not for POM and SWD mass, and effect of patch type × season interaction was not significant for all litter categories (Table 3, Fig. 1). Mass of leaves was significantly higher in riffle and edge patches than in middle patches. Patch type × reach and patch type × reach × season interactions were significant for mass of SWD; the mass was significantly higher in middle patches than in the other patches in KU and AK, but the mass was significantly higher in the different patch types during the different seasons in HI. Mass of SWD and POM showed significant reach effect and were higher in KU than in HI.

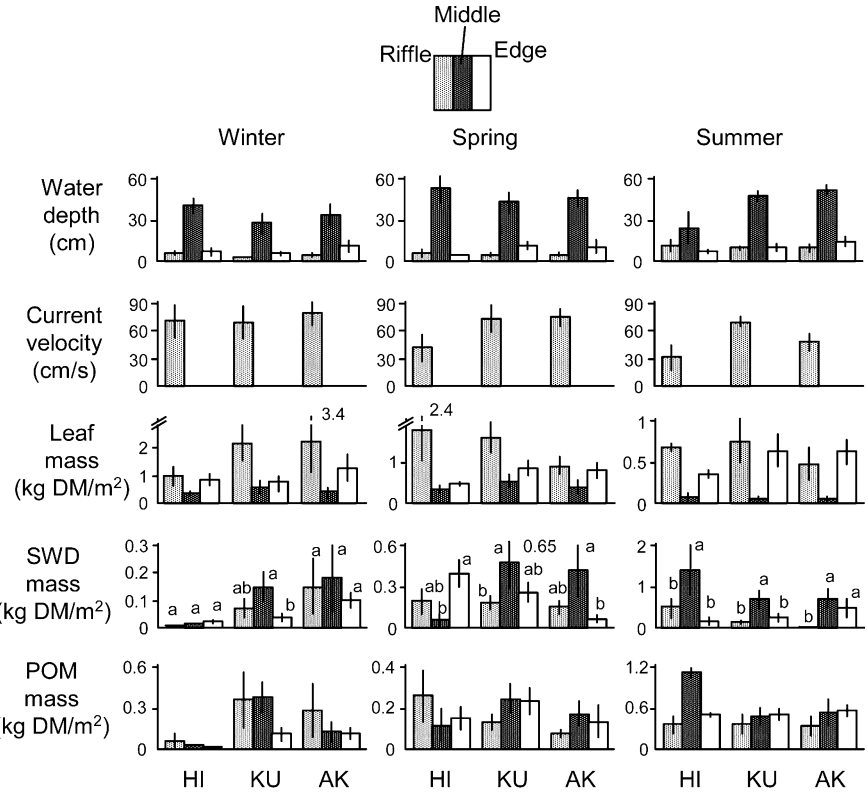

Figure 1. Difference in water depth, current velocity, mass of leaves, small woody detritus (SWD), and particulate organic matter (POM) among litter patch types in Higashitani reach (HI), Kudonosawa reach (KU), and Akagisawa reach (AK) each season. Error bars denote ±1SE. For variables with a significant effect of patch type × reach × season, a significant difference (Fisher's PLSD, $p < 0.05$) among patch types is shown by different superscripts for each reach and season. Current velocity of middle and edge patches was lower than detection limit (5.6 cm/s) of the meter.

Differences in macroinvertebrate assemblage structure among patch types

Of the 13 taxa examined, 7 (Taeniopterygidae, *Nemoura*, *Protonemura*, *Capnia asakawana* Kohno, *Eucapnopsis*, *Lepidostoma complicatum* (Kobayashi), *Lepidostoma satoi* (Kobayashi)) were shredders, 4 (*Ameletus*, *Paraleptophlebia*, *Simulium*, *Brillia*) were collectors, and 2 (Chloroperidae, *Rhyacophila lezeyi* Navás) were predators (Table 4, Fig. 2). Densities of 10 taxa had a significant effect of patch type. For example, densities of Taeniopterygidae, *Nemoura*, *Protonemura*, *R. lezeyi*, and *Simulium* were significantly higher in riffle patches than in the other patches, and those of *Nemoura* and *Protonemura* were also significantly higher in edge patches than in middle patches. In contrast, densities of *Ameletus*, *Paraleptophlebia*, *L. complicatum*, *L. satoi* were significantly higher in middle patches than in the other patches, and density of *Ameletus* was also significantly higher in edge patches than in riffle patches (Table 4). Density of *C. asakawana* was significantly higher in middle patches than in riffle patches. Density of *Eucapnopsis* tended to be highest in riffle patches (patch type effect: $p = 0.052$). Effect of patch type × season interaction was significant for density of Chloroperlidae. Its density was significantly higher in middle patches than in riffle patches during the winter, but not during the spring and summer. A significant effect of reaches was detected for three taxa (Taeniopterygidae, *Nemoura*, *L. satoi*). Effect of patch type × reach interaction was significant for density of *Brillia*, which certainly included many species here. It was significantly higher in riffle patches than in the other patches in HI but not in the other reaches; different species of this genus

Table 3. Results of mixed model 3-way ANOVA with patch type and season as fixed factors and reach as a random factor for mass of leaves, small woody detritus (SWD), and particulate organic matter (POM); effects of season and reach × season interaction are omitted. Results of multiple comparisons by Tukey's test are also shown for a significant effect of patch type and reach

Litter category	*n*	*F* value and probability					Multiple comparison	
		Patch type	Patch type × reach	Patch type × season	Patch type × reach × season	Reach	Patch type	Reach
Leaves	96	42.45**	1.04	0.49	1.04	2.96	R,E > M	
SWD	96	2.32	3.13*	0.69	5.37***	4.47*		KU > HI
POM	96	1.94	0.49	1.73	0.83	5.14**		KU > HI

HI – Higashitani reach; KU – Kudonosawa reach; R – riffle patches; M – middle patches; E – edge patches. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 4. Results of mixed model 3-way ANOVA with patch type and season as fixed factors and reach as a random factor (or 2-way ANOVA with type as a fixed factor and reach as a random factor) for densities of dominant taxa and DCA score 1; effects of season and reach × season interaction are omitted. Results of multiple comparisons by Tukey's test are also shown for a significant effect of patch type and reach

	n	*F* value and probability					Multiple comparison	
		Patch type	Patch type × reach	Patch type × season	Patch type × reach × season	Reach	Patch type	Reach
Dominant taxa								
Ameletus	72	174.02***	0.70	0.00	1.46	2.01	M > E > R	
Paraleptophlebia	72	36.91**	1.40	0.06	3.18*	0.93	M > R,E	
Taeniopterygidae	72	150.18***	0.75	0.60	2.08	5.10**	R > M,E	AK > HI
Nemoura	96	55.65***	1.78	3.40	3.52**	5.32**	R > E > M	AK > HI
Protonemura	96	84.47***	0.86	1.86	1.04	0.39	R > E > M	
Capnia asakawana Kohno	36	10.32*	1.64			1.48	M > R	
Eucapnopsis	36	6.79	1.89			0.64		
Chloroperlidae	96	1.24	0.98	6.04*	0.41	1.34		
Rhyacophila lezeyi Navás	96	34.53**	1.49	1.12	1.72	0.95	R > M,E	
Lepidostoma complicatum (Kobayashi)	60	34.04**	1.22	2.40	0.61	1.30	M > R,E	
Lepidostoma satoi (Kobayashi)	72	32.91**	1.57	5.61	1.15	4.56*	M > R,E	HI > AK
Simulium	96	265.49***	0.44	1.30	2.36*	2.01	R > M,E	
Brillia	36	0.08	3.79*			2.01		
DCA score 1								
Winter	36	175.31***	0.85			1.49	R > E > M	
Spring	36	82.81***	2.82			0.44	R > E > M	
Summer	24	88.13***	1.20			0.38	R > E > M	

HI – Higashitani reach; AK – Akagisawa reach; R – riffle patches; M – middle patches; E – edge patches. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

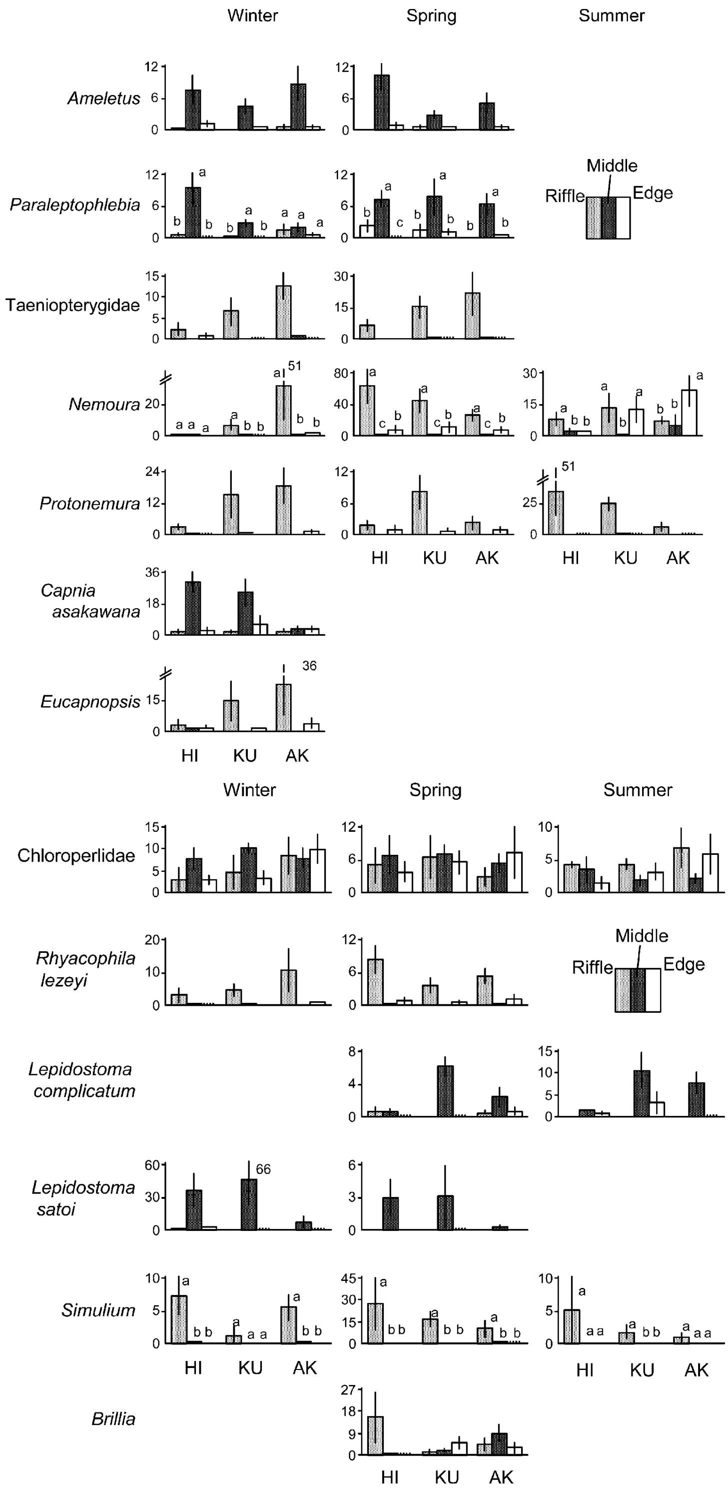

Figure 2. Difference in densities ($\times$100 individuals/m^2) of dominant macroinvertebrate taxa among litter patch types in Higashitani reach (HI), Kudonosawa reach (KU), and Akagisawa reach (AK) each season. Error bars denote $\pm$1SE. For taxa with a significant effect of patch type $\times$ each $\times$ season, a significant difference (Fisher's PLSD, $p < 0.05$) among patch types is shown by different superscripts for each reach and season.

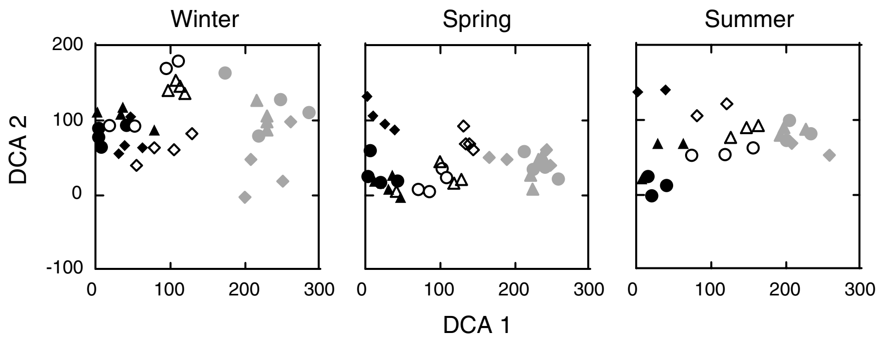

Figure 3. DCA (detrended correspondence analysis) ordination of litter patch macroinvertebrate assemblages of all the study reaches each season. The color of the plots denotes litter patch type (riffle – gray; middle – dark; edge – white) and the shape of the plots denotes reach (Higashitani – diamond; Kudonosawa – circle; Akagisawa – triangle). The ordination is based on proportion of log-transformed densities of 20 dominant taxa.

might occur in the different reaches. Effect of patch type × reach × season interaction was significant for densities of *Paraleptophlebia*, *Nemoura*, and *Simulium*. Density of *Nemoura* was significantly higher in riffle patches than in the other patches during the winter and spring except during the winter in HI, and was significantly higher in edge patches than in middle patches during the spring and summer except during the summer in HI. Density of *Paraleptophebia* was significantly higher in middle patches than in the other patches in all cases but during the winter in HI. Density of *Simulium* was significantly higher in riffle patches than in the other patches except during the winter in KU and during the summer in HI and AK.

DCA ordination showed a difference in taxonomic composition of macroinvertebrate assemblages among the three patch types (Fig. 3). Although there were some overlaps between middle and edge patches during the winter and spring, assemblages were largely grouped according to patch type over the three reaches along the first axis. Riffle and middle patches were mostly separated throughout all seasons. In contrast, assemblages were not clearly separated by reaches in all seasons. DCA score 1 differed significantly between the three patch types across all reaches, but not between the reaches in all seasons (Table 4).

Discussion

The three study reaches differed in channel characteristics (channel size and slope), but there were no clear differences in hydraulic characteristics (water depth, current velocity) of each litter patch type between the reaches. In contrast, a consistent pattern between reaches was less obvious for litter characteristics. Although leaves were more abundant in riffle and edge patches than in middle patches over reaches, POM showed no clear difference among the patch types in all the reaches, and SWD was abundant in middle patches in KU and AK while no clear difference in HI. Previous studies conducted in KU demonstrated that POM mass was higher in pool patches than in riffle patches (Kobayashi & Kagaya, 2002), and was higher in middle patches than in edge patches within pools (Kobayashi & Kagaya, 2004). Comparisons of data between this study and the previous studies reveal that in this study POM mass in middle patches is less than half, while that in edge and riffle patches is >2-fold. The formation mechanism of middle patches is thought to differ from that of the other patches; in middle patches litter settles and accumulates according to its weight, while in riffle and edge patches litter becomes entangled with streambed or bank materials by the force of flow. Consequently, litter in middle patches is more likely to be swept away when the flow increases. According to the differential impacts of high flow events among the patch types, relative mass of POM among the patch types might differ according to the annual hydrograph. Assuming the differential impacts of high flows among the patch types, relative mass among the patch types might also vary between reaches with different flow regime. The higher SWD mass in the different patch types during the different seasons in HI might be due to a high flow fluctuation because of its larger channel size.

Distributions of many taxa and the analysis of taxonomic composition are suggesting that differences in macroinvertebrate assemblage structure between the patch types are consistent over reaches. It has been suggested that both hydraulic and litter characteristics cause differences in macroinvertebrate assemblages between litter patch types (Kobayashi & Kagaya, 2002; 2004). Small differences in hydraulic characteristics of each litter patch type between the reaches probably contributed to the across-reach consistency of the macroinvertebrate distributions. Litter characteristics such as leaf mass can also contribute to the consistency of macroinvertebrate distributions, but not all litter characteristics that were thought to be important seem to have an effect. In the previous study within pools (Kobayashi & Kagaya, 2004), the highest densities of *L. complicatum* and other shredder taxa in middle patches were thought to be related to POM or SWD mass, but density of *L. complicatum* in this study was higher in middle patches despite no clear difference in either POM or SWD mass among the patch types. Little focus has been paid to the hydraulic characteristics within pools owing to a uniformly low current velocity, but it might play an important role in macroinvertebrate distributions. For example, the distance from the thalweg to a litter patch might affect drifting macroinvertebrates that colonize the patch, resulting in a higher abundance of some taxa in middle patches compared to edge patches.

The consistency of macroinvertebrate distributions among the litter patch types across reaches of different channel size and slope indicates that the similar distributions occur in different reaches within this area where channel size and slope are at least in the range of this study. Current is an important factor affecting macroinvertebrate distributions (Minshall & Minshall, 1977; Hart & Finelli, 1999), and differences in macroinvertebrate assemblages of litter accumulations between lotic and lentic conditions have been shown in streams of other regions (Richardson, 1992; Wallace et al., 1995; Casas, 1997). Thus, some differences in macroinvertebrate assemblages between litter patches of riffles and pools are likely for many stream reaches. On the other hand, the generality of a difference between middle and edge patches is less certain, because variation of water depth and distance from the thalweg within pools, which might have caused the variation in litter retention and in macroinvertebrates among the patch types in our reaches, may be small in other reaches. Verification of the effects of hydraulic and litter characteristics on macroinvertebrate distributions, as well as surveys on more other reaches are therefore required.

The results of this study indicate that a reach-scale macroinvertebrate community structure associated with litter patches is likely to vary according to litter patch type composition of the reaches as well as the absolute macroinvertebrate density in litter patch and the absolute amount of litter patch in the reaches. This study tells little about the factors determining litter patch type composition of reaches, however, since the formation of each litter patch type varies among pools or riffles within a particular reach (personal observation), channel characteristics such as channel size and slope, which control the form and flow of pools and riffles (Wohl et al., 1993; Buffington et al., 2002), are expected to play some roles. Future clarification of the relationship between channel characteristics and litter patch type composition will help determine the relationships between channel characteristics and biotic community structure and the ecosystem function of forested streams. In turn this will help predicting the effects of channel modifications on stream ecosystems.

Acknowledgements

We thank the employees of The Tokyo University Forest in Chichibu for their support and for providing stream chemical data, T. Shimizu for identifying Capniidae, and K. Kudo, K. Yoshinaga, K. Sasakawa, M. Wakabayashi for providing assistance and helpful advice on this study.

References

Angradi, T. R., 1996. Inter-habitat variation in benthic community structure, function, and organic matter storage in three Appalachian headwater streams. Journal of the North American Benthological Society 15: 42–63.

Armitage, P. D. & C. E. Cannan, 2000. Annual changes in summer patterns of mesohabitat distribution and associated macroinvertebrate assemblages. Hydrological Process 14: 3161–3179.

Armitage, P. D., I. Pardo & A. Brown, 1995. Temporal constancy of faunal assemblages in mesohabitats: application to management. Archiv für Hydrobiologie 133: 367–387.

Buffington, J. M., T. E. Lisle, R. D. Woodsmith & S. Hilton, 2002. Controls on the size and occurrence of pools in coarse-grained forest rivers. River Research and Applications 18: 507–531.

Casas, J. J., 1997. Invertebrate assemblages associated with plant debris in a backwater of a mountain stream: natural leaf packs vs. debris dam. Journal of Freshwater Ecology 12: 39–49.

Dobson, M. & A. G. Hildrew, 1992. A test of resource limitation among shredding detritivores in low order streams in southern England. Journal of Animal Ecology 61: 69–78.

Fisher, S. G. & G. E. Likens, 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43: 421–439.

Hart, D. D. & C. M. Finelli, 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Annual Review of Ecology and Systematic 30: 363–395.

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

Inoue, M. & M. Nunokawa, 2002. Effects of longitudinal variations in stream habitat structure on fish abundance: an analysis based on subunit-scale habitat classification. Freshwater Biology 47: 1594–1607.

Kagaya, T., 1990. Processing and macroinvertebrate colonization of leaf detritus in a mountain forest stream in Japan (in Japanese). Bulletin of The Tokyo University Forest 82: 157–176.

Kobayashi, S. & T. Kagaya, 2002. Difference in litter characteristics and macroinvertebrate assemblages of between litter patches in pools and riffles. Limnology 3: 37–42.

Kobayashi, S. & T. Kagaya, 2004. Litter patch types determine macroinvertebrate assemblages in pools of a Japanese headwater stream. Journal of the North American Benthological Society 23: 78–89.

Merritt, R. W. & K. W. Cummins (eds), 1996. An Introduction to the Aquatic Insects of North America. 3rd edn. Kendall/Hunt, Debuque, Iowa.

Minshall, G. W. & J. N. Minshall, 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (USA) stream. Hydrobiologia 55: 231–249.

Palmer, M. A., C. M. Swan, K. Nelson, P. Silver & R. Alvestad, 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. Landscape Ecology 15: 563–576.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme & M. J. Winterbourn, 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7: 503–524.

Richardson, J. S., 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72: 873–887.

Richardson, J. S., 1992. Food, microhabitat, or both? Macroinvertebate use of leaf accumulations in a montane stream. Freshwater Biology 27: 169–176.

Tanida, K., K. Yamashita & A. Rossiter, 1985. A portable current meter for field use. Japanese Journal of Limnology 46: 219–221.

Wohl, E. E., K. R. Vincent & D. J. Merritts, 1993. Pool and riffle characteristics in relation to channel gradient. Geomorphology 6: 99–110.

Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69: 409–442.

Wallace, J. B., J. R. Webster & J. L. Meyer, 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 52: 2120–2137.

Webster, J. R. & J. L. Meyer (eds), 1997. Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.

Zar, J. H, 1999. Biostatistical analysis. 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.