

## Seasonal Difference in Macroinvertebrate Contribution to the Leaf Litter Breakdown in a Headwater Stream at Mt. Jumbong

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### 점봉산 소하천의 낙엽분쇄에 대한 대형무척추동물 기여도의 계절간 차이

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#### ABSTRACT

Macroinvertebrate contribution to the leaf litter breakdown of *Carpinus cordata* was estimated at headwater streams at Mt. Jumbong (38° 03'N, 128° 25' E) during spring and winter-spring by using two types of litter bag. Coarse-mesh bags with 10 g of leaf litter were placed in a 1st-order stream in April (the spring experiment) and December 1995 (the winter-spring experiment). Fine-mesh bags with 5 g of leaf litter were placed in a nearby 3rd-order stream. The breakdown of *Carpinus* in coarse-mesh bags was rapid, and, in terms of season, leaf litter processed rapidly during spring. Daily mass loss rates of leaf litter ( $-k \pm 1$  SE) were highest for coarse-mesh bags in the spring experiment ( $-0.0429 \pm 0.0048$ ), followed by coarse-mesh bags in the winter-spring ( $-0.0146 \pm 0.0014$ ), fine-mesh bags in the spring ( $-0.0078 \pm 0.0004$ ), fine-mesh bags in the winter-spring experiment ( $-0.0054 \pm 0.0005$ ). Macroinvertebrate contribution to the litter breakdown was estimated by the difference of % leaf litter remaining between coarse-mesh bags and fine-mesh bags. Although shredders were more abundant during the winter-spring, their contribution was greater during the spring (50%) than the winter-spring (22~33%). This result appeared to be due to the change in the chemical composition of leaf litter during processing, and to the seasonal growth patterns of major shredder taxa.

**Key words:** *Carpinus cordata*, *Gammarus* sp., Headwater stream, Litter bags, Litter processing, Macroinvertebrates, Mt. Jumbong

#### INTRODUCTION

Headwater streams draining deciduous forests in a temperate region receive a large amount of litter inputs from riparian vegetation (Fisher and Likens 1973), and these

allochthonous energy are the most important to stream biota (Webster and Benfield 1986). After leaves enter the stream, they are broken down by physical processes such as leaching and abrasion, and biological processes such as microbial degradation and invertebrate feeding (Cummins 1974, Kaushik and Hynes 1968, 1971, Petersen and Cummins 1974). Stream-dwelling macroinvertebrates consuming leaf litter are known as shredder functional feeding group (Cummins 1973), and their importance to leaf litter processing in stream ecosystems have been demonstrated (e.g., Cuffney *et al.* 1990).

During April~June 1995, the author examined macroinvertebrate communities in two headwater streams by using mesh bags which contained leaf litter of *Carpinus cordata* (Chung 1997). Compared with other studies (e.g., Petersen and Cummins 1974, Webster and Benfield 1986), breakdown rate of *Carpinus* seemed to be very rapid. However, since the timing of the experiment did not follow the timing of the autumnal litter input, what observed during that study might not properly describe the general pattern of the leaf litter processing in headwater streams at Mt. Jumbong (Boulton and Boon 1991). To correct this problem, the author carried out a similar experiment during the following winter-spring seasons by using different types of litter bags. The objectives of this study were to compare the processing of *Carpinus* during winter through spring with that observed during spring, and to investigate whether there was any seasonal variation in shredder contribution to the leaf litter breakdown.

## STUDY SITES

This study was conducted in a 1st- and 3rd-order streams. Both streams belong to the 4th-order stream system draining the south-east slope of Mt. Jumbong (38° 03' N, 128° 25' E). The 1st-order site is at about 15~40 m upstream from the confluence of both streams. The 3rd-order site is located about 15~30 m upstream from the confluence. Both sites are covered by a similar riparian vegetation. Dominant tree species are *Quercus mongolica*, *Carpinus cordata*, *Acer* spp., and *Kalopanax pictus*. There was no apparent litter accumulation in the 3rd-order site, but a large amount of leaf litter was often found in pools and debris dams in the 1st-order site. Water temperature was similar in both streams. Daily mean water temperature ranged 0~2°C during December-March, while it increased from 2 to 11°C during the period of April~June.

## MATERIALS AND METHODS

### Litter bag

Leaf species was selected by examining several debris dams in the studied streams during October 1994. Debris were largely composed of *Quercus mongolica*, *Carpinus cordata*, and *Acer* spp., among which *Carpinus* was selected. Leaves of *Carpinus* were collected during late October to early November from the forest floor near the study site. Leaves were

stored at room temperature until they were used for the experiments. Two types of litter bags were used. Coarse-mesh bags (size: 20×30 cm) containing 10 g of air dried leaf litter were made of 1mm-mesh size nylon cloth with 40 additional openings (size: 2~4×20 mm). Fine-mesh bags (size: 17×25 cm) were made of 0.15 mm-mesh size nylon monofilament netting (Nytex®) to prevent the access of macroinvertebrates to leaf litter. Fine-mesh bags were received 5 g of *Carpinus* to reduce the chance of anaerobic condition within the bag. Fifty coarse-mesh bags and 40 fine-mesh bags were placed in the 1st- and 3rd-order streams, respectively, on April 16, 1995 (the spring experiment: for coarse-mesh bags see Chung 1977) and December 10, 1995 (the winter-spring experiment). Five of coarse-mesh bags and four of fine-mesh bags were retrieved at 2~7 weeks interval until coarse-mesh bags lost more than 90% of their initial mass. Upon retrieval from streams, each bag was transferred to a plastic bag and preserved with 5~8% formalin. In laboratory, leaf litter remained in fine-mesh bags was gently washed with tap water to remove any sediment. There were always some filter-feeding chironomids in fine-mesh bags. But, they were ignored since they would not significantly affect the litter breakdown rates. Leaf litter in coarse-mesh bags was washed off sediments and macroinvertebrates. Macroinvertebrates clinging to bags were hand picked. For later identification sediment and macroinvertebrates retained on 0.125 mm-sieve were preserved in 5~8% formalin containing small amount of phloxine-B dye. Leaf litter remained in bags were oven dried at 60°C for 5 days and weighed (oven-dry weight) and ashed at 500°C for 12hr and re-weighed (ash weight) to the nearest 0.01 g. Ash-free dry mass was determined by subtracting ash weight from oven-dry weight. Leaf processing has been assumed to follow an exponential decay model (Olson 1963, Petersen and Cummins 1974). Daily leaf processing rates ( $-k$ ) were estimated by equation  $m_t = m_0 e^{-kt}$ , where  $m_t$  is the remaining mass (in AFDM) after the time of  $t$ , and  $m_0$  is the initial mass of leaf litter.

### Macroinvertebrates

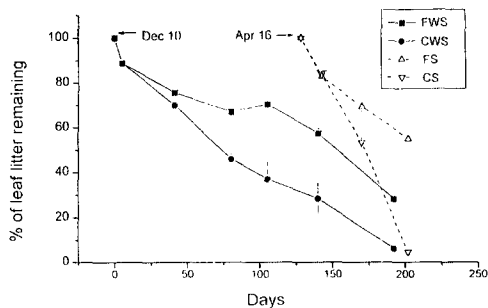
Macroinvertebrates and sediments preserved in formalin solution were passed through nested 1 mm- and 0.125 mm-sieves. All macroinvertebrates retained on 1 mm-sieve and a portion (1/4~1/32) of those passed 1 mm-sieve but retained on a 0.125 mm-sieve were sorted and identified under a dissecting microscope. For identification of insect taxa, Yoon (1988) and Kawai (1985) were used. Macroinvertebrates other than insect taxa were identified to *Gammarus*, Turbellaria, Copepoda or Oligochaeta. Tanypodinae (Chironomidae) was treated as predator, while other chironomids were allocated to collector-gatherer functional feeding group. For Functional feeding group allocation of insect taxa, Merritt and Cummins (1984) was used.

## RESULTS

Leaf litter in coarse-mesh bags broke down significantly faster than those in fine-mesh

bags, and mass loss rates of leaf litter during the winter-spring experiment were lower than those of the spring experiment (Fig. 1). Daily mass loss rates of leaf litter ( $-k \pm 1$  SE) were highest for coarse-mesh bags of the spring experiment ( $-0.0429 \pm 0.0048$ ), followed by coarse-mesh bags of the winter-spring ( $-0.0146 \pm 0.0014$ ), fine-mesh bags of the spring ( $-0.0078 \pm 0.0004$ ), and fine-mesh bags of the winter-spring experiment ( $-0.0054 \pm 0.0005$ ). During the winter-spring experiment, the difference in the mass loss between the coarse- and fine-mesh bags was greatest in late March (33% more mass loss in coarse-mesh bags). During the spring experiment, between bag type mass loss were greatest at the end of the study period, when coarse-mesh bags lost 95% of their initial weight, while fine-mesh bags lost only 45%.

Abundance of all macroinvertebrates was higher in the winter-spring experiment than those in the spring experiment, largely due to *Nemoura* and chironomids (Table 1). During the winter-spring experiment, the mean number of *Nemoura* was 14-times greater than that of the spring experiment. Most of them were young nymphs. While 8 mm was the largest body length class of *Nemoura* nymphs collected, individuals of <2 mm represented near 96% of the total individuals. Abundances of non-insect taxa were quite similar between experiments (Table 1). *Gammarus* was the only non-insect taxon whose abundance



**Fig. 1.** Percent of initial leaf litter remaining ( $\pm 1$  SE in ash free dry mass) of *Carpinus cordata* in streams. Litter bags were placed in the 1st-order stream on April 16, 1995 (the spring experiment) or on December 10, 1995 (the winter-spring experiment).  $N=5$  for coarse-mesh bags, and  $n=4$  for fine mesh bags. FWS=fine-mesh bags of the winter-spring experiment, CWS=coarse-mesh bags of the winter-spring experiment, FS=fine-mesh bags of the spring experiment, CS=coarse-mesh bags of the spring experiment. Data for CS were from Chung (1997).

was significantly higher in the winter-spring than in the spring experiment.

Macroinvertebrate communities associated with coarse-mesh bags were dominated by collector-gatherers, followed by shredders and predators. Other functional feeding groups such as scrapers or filterers were very rare and contributed less than 5% of the total macroinvertebrate abundance in both experiments. Abundances of most taxa belong to three dominant functional groups did not appear to closely related to time of year or the amount of leaf litter remaining in bags (Table 2). Collector-gatherers and shredders tended to increase when 40-60% of initial mass of *Carpinus* remained, but they often bounced back later and maintained relatively high abundances at the end of the experiments. Predators did not exhibit any distinct temporal pattern either.

**Table 1.** Mean numbers of macroinvertebrates per bag over the entire sampling period. Litter bags were placed in a 1st-order stream on April 16, 1995 (the spring experiment) or December 10, 1995 (the winter-spring experiment). N=15 for the spring experiment, and n=29 for the winter-spring experiment. Functional group allocation was based on Merritt and Cummins (1984). Data for the spring experiment were from Chung (1977). CG=Collector-gatherer, CF=Collector-filterer, Pr=Predator, Sc=Scraper, S=Shredder.

Taxa	Spring Experiment	Winter-spring Experiment	Functional group
<b>Ephemeroptera</b>			
<i>Baetis</i>	5.5±1.7	21.7±5.5	CG
Ephemerellidae	0.5±0.5	0.2±0.1	CG
<i>Cinictostella tshernovae</i>	1.7±0.7	16.0±3.9	CG
<i>Drunnella cryptomeria</i>	0.7±0.4	0	CG
<i>Ephemerella</i> sp.	1.2±0.6	0	CG
<i>Ephemera strigata</i>	1.0±0.6	0.2±0.1	CG
<i>Cinygmula</i>	0.9±0.7	0	CG
<i>Ecdyonurus dracon</i>	0	0.8±0.3	Sc
<i>Ecdyonurus kibunensis</i>	0.2±0.2	0.2±0.1	CG
<i>Ecdyonurus</i> sp.	0.3±0.3	0	Sc
<i>Heptagenia</i>	0.1±0.1	0	Sc
<i>Paraleptophlebia chocoata</i>	30.7±7.2	34.6±6.4	CG
<i>Ameletus montanus</i>	1.5±0.8	1.7±0.8	CG
Total	43.9±8.0	75.3±12.6	
<b>Plecoptera</b>			
<i>Capnia</i>	0.1±0.1	0	S
<i>Sweltsa</i>	6.5±1.9	14.5±2.6	Pr
<i>Rhopalopsale</i>	3.9±2.3	1.8±0.6	S
<i>Amphinemura coreana</i>	1.1±1.1	4.0±2.8	S
<i>Nemoura</i>	34.5±4.5	521.1±66.8	S
<i>Yoraperla</i>	0.1±0.1	1.8±1.2	S
Perlidae	0.5±0.5	0	Pr
<i>Isoperla</i>	1.5±0.6	1.2±0.4	S
<i>Pteronarcyctis</i>	0	1.2±0.5	S
<i>Scopura</i>	1.3±0.6	1.0±0.7	S
Total	49.6±6.0	546.7±67.9	
<b>Trichoptera</b>			
<i>Micrasema</i>	0.1±0.1	0	?
<i>Goerodes</i>	7.3±2.5	10.8±4.2	S
<i>Hydatophylax nigrovittatus</i>	0.3±0.2	1.5±1.0	S
<i>Psilotreta</i>	5.2±1.5	2.0±0.8	Sc
<i>Plectrocnemia</i>	0.3±0.2	0	Pr
<i>Rhyacophila articulata</i>	0.9±0.4	1.8±0.3	Pr
<i>Rhyacophila brevicephala</i>	1.5±0.7	1.0±0.3	Pr
<i>Rhyacophila shikotsuensis</i>	0.1±0.1	0.6±0.1	Pr
Total	15.6±3.9	17.6±4.6	

**Table 1.** Continued

Taxa	Spring Experiment	Winter-spring Experiment	Functional group
Coleoptera			
Elmidae	1.0±0.6	0.3±0.3	S
Helodidae	0	0.8±0.2	?
Total	1.0±0.6	1.1±0.4	
Diptera			
Atheridae	0	0.2±0.2	Pr
Ceratopogonidae	0.6±0.3	0.1±0.1	Pr
CG-Chironomidae	168.6±48.2	254.3±52.6	CG
Tanypodinae	22.1±5.3	11.7±3.3	Pr
<i>Dixa</i>	0.2±0.1	0	CG
Empididae	0.7±0.5	0.1±0.1	Pr
<i>Pericoma</i>	0.2±0.1	2.5±0.9	CG
<i>Prosimulium</i>	0	0.2±0.1	CF
<i>Antocha</i>	0	<0.1	Pr
<i>Dicranota</i>	3.9±1.0	2.7±1.4	Pr
<i>Hexatoma</i>	0.2±0.1	0.3±0.2	Pr
<i>Ormosia</i>	0.0±0.0	0.1±0.1	CG
<i>Pedicia</i>	0	<0.1	Pr
<i>Pilaria</i>	0	<0.1	Pr
<i>Tipula</i>	0	0.2±0.2	S
Total	196.5±47.7	272.4±55.6	
Non-Insects			
Copepoda	1051.9±210.1	1023.8±226.9	CG
<i>Gammarus</i>	76.4±11.0	139.9±23.9	S
Oligochaeta	20.5±7.0	16.5±8.5	CG
Turbellaria	39.5±17.0	26.3±12.9	Pr
Total	1368.6±257.2	1206.5±221.4	
Insect Total	305.6±49.7	913.2±105.4	
Non-Insect Total	1188.3±219.9	1206.5±221.4	
Macroinvertebrate Total	1494.9±214.4	2119.7±293.3	

## DISCUSSION

High water temperature during spring appeared to be responsible to the rapid processing of *Carpinus* in fine-mesh bags. Since macroinvertebrate action and physical abrasion are virtually eliminated by the fine-mesh netting, leaf litter in fine-mesh bags should be processed by microbes. Microbial decomposition is closely related to the water temperature (Webster and Benfield 1986). High water temperature increase litter decomposition by increasing microbial activity (Short and Smith 1989, Subberkropp *et al.* 1975). If it is assumed that 1,000 degree-days accumulation is required to process 90% of

**Table 2.** Mean numbers of individuals per bag ( $\pm 1$  SE) of major taxa of each functional group on each sampling date. Litter bags were placed in a 1st-order stream on April 16, 1995 (the spring experiment) or December 10, 1995 (the winter-spring experiment). Data for the spring experiment were from Chung (1997). N=5, except on 96/04/28 where n=4.

Taxa	Spring experiment				Winter-spring experiment			
	95/04/30	95/05/28	95/06/28	96/01/20	96/02/28	96/03/24	96/04/28	96/06/19
<b>Collector-Gatherers</b>								
Chironomidae	136.4 $\pm$ 39.6	133.8 $\pm$ 21.2	235.6 $\pm$ 143.8	135.0 $\pm$ 33.8	227.8 $\pm$ 108.8	416.6 $\pm$ 110.3	435.2 $\pm$ 213.3	92.8 $\pm$ 15.4
Copepoda	743.4 $\pm$ 64.8	1702.8 $\pm$ 446.6	709.4 $\pm$ 317.5	361.6 $\pm$ 173.9	1175.0 $\pm$ 466.3	1446.4 $\pm$ 500.4	794.0 $\pm$ 428.8	1296.0 $\pm$ 761.2
Others	78.8	368.8	89.0	51.4	60.0	106.4	141.3	118.4
Total	958.6	2205.4	1034.0	548.0	1462.8	1969.4	1370.5	1507.2
<b>Predators</b>								
Tanypodinae	23.8 $\pm$ 7.6	31.6 $\pm$ 12.8	11.0 $\pm$ 4.6	2.0 $\pm$ 2.0	15.2 $\pm$ 5.6	12.8 $\pm$ 5.5	26.4 $\pm$ 15.4	5.2 $\pm$ 3.5
<i>Turbellaria</i>	57.8 $\pm$ 49.9	40.4 $\pm$ 15.8	20.2 $\pm$ 10.1	11.0 $\pm$ 7.4	6.8 $\pm$ 2.0	3.0 $\pm$ 1.0	4.3 $\pm$ 3.6	102.2 $\pm$ 51.9
<i>Suctisa</i>	11.6 $\pm$ 3.7	7.0 $\pm$ 3.2	1.0 $\pm$ 0.6	17.2 $\pm$ 4.5	21.8 $\pm$ 3.9	16.4 $\pm$ 6.7	16.3 $\pm$ 8.4	1.2 $\pm$ 0.4
Others	11.4	15.4	3.8	5.2	7.0	5.6	19.5	5.4
Total	104.6	94.4	36.0	35.4	50.8	37.8	66.4	114.0
<b>Shredders</b>								
<i>Gammarus</i>	69.2 $\pm$ 11.4	97.8 $\pm$ 18.8	62.2 $\pm$ 24.8	89.8 $\pm$ 34.4	181.6 $\pm$ 57.3	190.0 $\pm$ 86.5	99.0 $\pm$ 19.0	131.0 $\pm$ 40.1
<i>Nemoura</i>	29.8 $\pm$ 9.2	27.6 $\pm$ 3.8	46.0 $\pm$ 8.0	545.0 $\pm$ 116.5	767.8 $\pm$ 221.9	380.8 $\pm$ 100.1	455.3 $\pm$ 123.9	443.4 $\pm$ 135.5
<i>Goeroides</i>	14.4 $\pm$ 6.5	5.8 $\pm$ 1.7	1.8 $\pm$ 0.9	0.6 $\pm$ 0.4	4.0 $\pm$ 1.6	16.4 $\pm$ 6.8	29.8 $\pm$ 22.4	6.8 $\pm$ 3.3
Others	1.16	17.8	1.2	4.8	7.6	3.0	4.6	36.8
Total	115.0	149.0	111.2	640.2	961.0	590.4	588.7	618.0

leaf litter (Hanson and Cummins: cited from Meyer and Johnson 1983), 590 degree-days accumulated from late March to the end of the experiment in mid June correspond to 50~55% of mass loss of initial leaf litter. This estimate was fairly close to the observed value (42%: decreased from 70% to 28%) that occurred during the same time period.

Macroinvertebrate, especially shredders, contribution to leaf litter breakdown in this study appeared to vary with the season of leaf litter input to a stream, as denoted by Anderson and Sedell (1979). Macroinvertebrates in coarse-mesh bags of the winter-spring experiment seemed to feed on *Carpinus* until late March when 37% of initial leaf litter remained. By that time, their contribution to leaf breakdown (average % of leaf litter remaining of fine-mesh bags minus that of coarse-mesh bags) was 33% and was in a close agreement with those found by Petersen and Cummins (1974). Petersen and Cummins postulated that the remained leaf litter would be processed further by the microbial and invertebrate action. However, in spite of high abundances of shredders, shredder action appeared to be minimal on these skeletonized leaf litter during the period of March through June. On the other hand, in the spring experiment, 95% of new *Carpinus* in coarse-mesh bags disappeared during the similar time period of year. Here, macroinvertebrate contribution was estimated to represent near 50% mass loss of the leaf litter. Such variation in the macroinvertebrate contribution to the leaf litter breakdown appeared to be due to the change in the chemical composition of leaf litter during processing as well as the different growth periods of dominant shredders in the study stream (e.g., Grafius and Anderson 1979, 1980). The skeletonized leaf litter has been known to have relatively high content of refractory materials such as lignin (Gessner 1991). Gessner and Chauvet (1994) reported that lignin reduced fungal activities on leaf litter, which, in turn, should reduce the leaf litter palatability to shredders.

*Gammarus* appeared to be responsible to much of the different pattern of *Carpinus* breakdown in coarse-mesh bags. *Gammarus* was the second abundant shredder taxon in both experiments. But, considering their large body size and the year-round existence in the study stream, they should be the most important shredder in the study stream. Therefore, detritus dynamics in the study stream can not be understood without considering their feeding ecology and the seasonal growth pattern. For insect shredders, Grubbs and Cummins (1996) demonstrated that some species grow in either autumn and/or winter, while others showed either spring and/or summer growth. According to Cummins *et al.* (1989), *Gammarus* belongs to the spring-summer shredder populations and should feed mostly on rather slowly decomposing leaf species such as oak, since most of the rapidly disappearing leaf species will be unavailable by spring when their feeding rates increase. However, it is questionable if their argument is valid to headwater streams in Korea. For two consecutive years, the author observed that most of the leaf litter stored within wetted areas of the study stream disappeared after monsoon in July. Also, oak leaves seemed to be a less attractive diet to *Gammarus*. Coarse-mesh bags containing oak leaves contained much fewer *Gammarus* (unpublished data). Therefore, during summer, *Gam-*



*marus* probably feed on diets such as small organic particles, algae or moss (Bärlocher 1983). Also, lateral leaf litter inputs from stream banks or inputs of green leaves from the riparian vegetation would provide valuable resources to *Gammarus* and other shredders (McArthur *et al.* 1986, Stout and Taft 1985).

Considering their abundances, *Nemoura* might also be important to leaf litter breakdown. However, since most of them are small individuals, they would not be so important as what represented by their abundances. In general, aquatic insects are omnivores, and their diet preference changes as they grow. Many shredding insects tend to feed on fine organic particles when they are young, but later they switch to large organic particles such as leaf litter or even to animal tissues (Anderson and Cummins 1979).

Overall, this study shows that macroinvertebrates are important to the process of large particulate organic matters in headwater streams at Mt. Jumbong. Among shredders *Gammarus* appeared to be most important to detritus dynamics in the 1st-order stream. *Neomura*, the most abundant shredder taxon, may be similarly important, too. However, under the situation where feeding ecology or seasonal growth patterns of most shredder species are largely unknown, such conclusions can be biased to species of high biomass or of high abundance.

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## 적 요

점봉산 소하천에서 봄과 겨울 동안 대형무척추동물의 까치박달 (*Carpinus cordata*) 낙엽분해에 대한 기여도가 측정되었다. 대형무척추동물의 출입이 허용되는 큰 망목 주머니에는 10g, 이들이 차단된 작은 망목 주머니에는 5g의 낙엽이 넣어져 1995년 4월 (봄)과 12월 (겨울) 두 차례에 걸쳐 하천에 넣어졌다. 낙엽주머니는 큰 망목 주머니속 낙엽 대부분이 분쇄될 때까지 일정 간격으로 수거되어 낙엽의 중량감소 양상과 낙엽주머니의 대형무척추동물상 조사에 이용되었다. 낙엽의 중량감소율은 투입시기에 관계없이 큰 망목 주머니에서 높았으며, 계절적으로는 봄이 겨울보다 빨랐다. 낙엽의 하루 당 중량감소율은 봄의 큰망목 주머니에서 0.0429%로 가장 높았으며, 그 다음은 겨울의 큰망목 주머니 (0.0146%), 봄의 작은 망목 주머니 (0.0078%), 겨울의 작은 망목 주머니 (0.0054%)의 순이었다. 낙엽분해에 대한 대형무척추동물의 기여도는 큰 망목 주머니에 남아있는 낙엽의 비율 (%)과 작은 망목 주머니에 남아있는 낙엽의 비율의 차이로 구하였다. 봄에 하천에 설치된 주머니에서는 대형무척추동물의 기여도가 50%로 나타났으나, 겨울의 낙엽 주머니에서는 22~33%로 적었다. 그러나 낙엽을 섭식하는 것으로 알려진 shredder 기능군의 주머니 당 밀도는 12월의 낙엽주머니에서 더 높았다. shredder가 많았음에도 그들의 기여도가 낮았던 것은 낙엽이 분쇄되면서 낙엽의 화학적 조성이 변화하여 shredder의 선호성이 감소하였을 뿐만 아니라 *Gammarus*와 같은 주요 낙엽섭식성 대형무척추동물이 가을-겨울이 아닌 주로

봄과 여름에 성장하기 때문인 것으로 생각된다.

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