

Flow rate mediates the competitive influence of a grazing caddisfly on mayflies

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The Glossosomatid caddisflies, which are stream-insect grazers, have been found to negatively affect the densities of mayfly grazers through intensive periphyton exploitation. The grazing efficiency of a Glossomatid caddisfly, however, is known to decrease with increasing current velocity. A manipulative field experiment was conducted to test the hypotheses that the presence of *Glossosoma* sp. decreased the densities of three mayfly grazers, *Baetis thermicus*, *Cinygmula* sp. and *Paraleptopblebia chocorata*, and that the decrease was stronger in slower stream-flow conditions. The experiment followed a two-factorial design with flow conditions and *Glossosoma* densities as the main factors. The periphyton biomass in conditions of reduced *Glossosoma* density was greater than in natural *Glossosoma* densities, but was not affected by flow conditions. In partial contradiction of the experimental hypothesis, the experimental reduction in *Glossosoma* density resulted in a higher density of *Baetis*, irrespective of flow conditions. The grazing activity of *Glossosoma* would not be affected by the flow variations that were employed in the present experiment. The reduction in *Glossosoma* density resulted in higher densities of *Cinygmula* and *Paraleptopblebia* only in fast-flow conditions, a result that did not support the experimental hypotheses. The competitive influence of *Glossosoma* on these mayflies might be altered by flow conditions causing differences in the resource structure.

Key words: flow mediation; *Glossosoma*; interspecific competition; mayflies; stream insect grazers.

INTRODUCTION

Numerous studies have shown competition to be one of the most important structuring forces in natural communities (see reviews by Connell 1983; Schoener 1983; Hairston 1989). Despite the classical competitive-exclusion principle, which predicts that competing species cannot coexist on a single resource (Lotka 1925; Volterra 1926), abiotic environmental stress has been shown to offset the tendency for a few superior species to win out, permitting multiple species to co-occur and thus enhance community diversity (McAuliffe

1984a; Chesson 1986; Warner *et al.* 1993). Thus, the magnitude of the role of competition in organizing community structures can be regarded as variable, depending on environmental spatio-temporal variations (Dunson & Travis 1991; Taniguchi & Nakano 2000).

In streams, which generally appear to be physically harsh environments, abiotic factors might have an especially strong influence on community dynamics compared with other habitats (Hynes 1970). However, the potential importance of biological interactions such as competition in structuring lotic communities has recently been emphasized (Allan 1995). For invertebrate grazers, in particular, considerable evidence exists that species compete with each other for the periphyton, a limiting resource (Feminella & Hawkins 1995). Field experiments have demonstrated that the heterogeneous distributions of various grazers are determined by periphyton abundance (Hill & Knight 1988; Hart & Robinson 1990;

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Winterbourn 1990), where smaller periphyton biomass results in reduced growth and survivorship (Lamberti *et al.* 1987; Feminella & Resh 1990; Hill 1992). Moreover, a high density of a single grazer species is known to result in detrimental consequences for other grazers, by lowering periphyton biomass (McAuliffe 1984b; Lamberti *et al.* 1987; Kohler 1992).

Lotic habitats, however, are typically characterized by heterogeneous physical conditions, even within a local area (Nowell & Jumars 1984). The action of flowing water is a dominant physical feature, which mediates many physiological processes that influence the distribution and abundance of both periphyton and invertebrate grazers (Stevenson 1983; Vaughn 1986). Physiological tolerance to water flow varies among organisms, resulting in flow mediation, for example, in predator–prey (Hansen *et al.* 1991) and grazer–periphyton (Poff & Ward 1995) interactions. The strength of competitive interactions among invertebrate grazers can also vary spatially with local flow conditions. Nevertheless, little attention has been paid to the influence of flow on competitive outcomes between invertebrate grazers.

Glossosomatid caddisflies are commonly dominant grazers on hard substrates in Japanese (Kuranishi & Kuhara 1994; Sameshima & Sato 1994) and North American streams (McAuliffe 1984b; Hart 1987; Kohler 1992). McAuliffe (1984b) and Kohler (1992) demonstrated that the exclusion of Glossosomatid caddisflies from local areas resulted in increased densities of mobile grazers (e.g. mayflies), suggesting a strong competitive influence of the former on the latter through intensive periphyton exploitation. However, the grazing efficiency of a Glossosomatid caddisfly was found to decrease with increasing current velocity (Poff & Ward 1992). Therefore, flow conditions can be expected to mediate the competitive influence of the caddisfly on other invertebrate grazers when there exist different physiological tolerances to flow. In the present study, we performed a manipulative field experiment to test two hypotheses: (i) the presence of Glossosomatid caddisflies reduces the periphyton and hence limits colonization by grazing mayflies in a local habitat patch; and (ii) that such limitation, if it occurs, becomes weaker with increasing flow speed.

STUDY SITE AND METHODS

The study was conducted in the Horonai Stream, which runs through the Tomakomai Experimental Forest of Hokkaido University, south-western Hokkaido, Japan (42°43'N, 141°36'E), during March–April 1997. The discharge of this small, cold, spring-fed stream (14 km long, 2–5 m wide, gradient < 1%) was relatively stable (0.21–0.29 m³ s⁻¹) throughout the study period, with no major disturbances occurring. The natural substrate consisted predominantly of pebbles, gravel and sand. A 200-m stretch in a second-order section of the stream, where mean water depth and current velocity were 15 cm and 56 cm s⁻¹, respectively, was selected as a study site. Although canopies of deciduous riparian trees covered the study site almost entirely, the streambed was largely open to sunlight prior to spring leaf development in May. The water temperature was relatively stable (8–10°C) during the study period.

The case-building Glossosomatid caddisfly, *Glossosoma* sp. (undescribed species), was one of the dominant grazers in the stream, where it was univoltine, with adult emergence peaking in June–July. The species was mainly represented by final-instar larvae (body length approximately 6 mm) during the study period.

We conducted a field experiment to examine the competitive influence of *Glossosoma* sp. on the colonization of invertebrate grazers under two different flow conditions. The experiment followed a two-factorial design with flow conditions (fast or slow) and *Glossosoma* densities (natural or reduced) as the main factors. Forty unglazed ceramic tiles (20 cm × 20 cm in area, 6 cm in height) were used as experimental substrates for the grazers. Two months before the start of the experiment, 20 tiles were arranged on the streambed in the study site, along the riffle center, which is characterized by a high current velocity and high water depth (fast-flow treatment). The remaining 20 tiles were placed on the riffle margins, which are characterized by a slow current velocity and shallow depth (slow-flow treatment). Periphyton mats had become sufficiently established on the tiles in both habitats by the beginning of the experiment. On 23 March, we removed all of the invertebrates from the tiles and randomly assigned half of the tiles each to the natural and the reduced *Glossosoma*

treatments, for each of the two flow treatments (i.e. 10 tiles for each of the four treatments). For the reduced *Glossosoma* treatment, a rubber band (1.5 cm wide, 25 cm in circumference) was placed around the edge of each tile and coated with a 2-mm-thick layer of Vaseline (Hoei Pharmaceuticals, Osaka, Japan). *Glossosoma* are unable to colonize the tiles with such barriers (McAuliffe 1984b) because their major mode of movement is crawling rather than entering into drift (Kohler & McPeck 1989). In contrast, *Glossosoma* were allowed to freely colonize tiles for the natural *Glossosoma* treatment. Except for the case-building caddisflies, mobile invertebrate grazers in the stream, such as mayflies, were expected to colonize the tiles, irrespective of Vaseline barriers, because they are commonly found in stream drift (Miyasaka & Nakano 1999). Immediately after the removal of the invertebrates and the Vaseline treatment (where applicable), all of the tiles were returned to their original locations, where the water depth and current velocities just above the tiles were measured using a portable current meter (Tanida *et al.* 1985). Both the depth (mean \pm SE, 22.3 ± 1.5 cm) and current velocity (mean \pm SE, 63.6 ± 1.5 cm s⁻¹) in the fast-flow treatment were significantly greater than those in the slow-flow treatment (depth, 10.5 ± 1.0 cm, $F_{1,38} = 52.52$, $P < 0.001$; current velocity, 50.9 ± 1.2 cm s⁻¹, $F_{1,38} = 44.29$, $P < 0.001$; ANOVA on log₁₀ transformed data was used for both).

On 12 April (day 21 of the experiment), we washed all of the invertebrates from the upper surface of the tiles into a 100- μ m-mesh Surber net sampler (25 cm \times 25 cm area, 100 cm long; Miura-Rika Inc., Sapporo, Japan), by gently rubbing the tile surface by hand. A number of grazers that was sufficient for analysis colonized the tiles within the experimental period (Nakano *et al.* 1999). The samples were preserved in a 5% formalin solution for later analysis. Immediately following the invertebrate collection, periphyton was removed from the whole upper surface of the tiles by brushing and preserved in 1% formalin solution for later analysis. Invertebrate samples were sieved once by using a 1-mm mesh and identified under a binocular microscope. Subsamples of a well-mixed epilithon suspension were collected with glass-fiber filters (GF/C; Whatman International, Maidstone, England), which had been pre-

combusted at 450°C for 2 h. The filters were dried at 60°C for 24 h, weighed to the nearest 0.01 mg, combusted at 550°C for 3 h and reweighed to obtain an ash-free dry mass (AFDM). We used the AFDM as an index of periphyton biomass.

By the end of the experiment, three species of mayflies, *Baetis thermicus* Ueno (Baetidae), *Cinygmula* sp. (Heptageniidae) and *Paraleptophlebia chocorata* Imanishi (Leptophlebiidae), in addition to *Glossosoma*, were found to be dominant components of the invertebrate grazer guild. On pooling the samples, these species were found to represent 68.5% of the total number of invertebrate grazers collected. In addition to the above, the grazer guild included six species of mayflies, *Epeorus latiforium* Ueno (Heptageniidae), *Baetis yoshinensis* Gose (Baetidae), *Cincticostella nigra* (Ueno), *Cincticostella okumai* Gose, *Epebemerella aurivillii* (Bengtsson) (Ephemerellidae); and *Ameletus* sp. (Ameletidae); a caddisfly, *Neophylax ussuriensis* (Martynov) (Uenoidae) and several species of chironomid flies, although the densities of all these species were much lower than those of the three main species. Only the three dominant mayfly species, plus *Glossosoma* were included in the analyses.

We performed two-way ANOVA on periphyton biomass and the density of each grazer species, with flow conditions and *Glossosoma* manipulations as main factors and tiles as replicates. When the interaction terms in the ANOVA were significant, multiple comparisons among the four treatments were conducted after one-way ANOVA, using Student–Newman–Keuls' tests. Log₁₀ x or log₁₀ ($x + 1$) transformations were used in order to minimize any deviations from normality and the homogeneity of variances. For all the tests, the α value of 0.05 was used for statistical significance.

RESULTS

Glossosoma and periphyton

The Vaseline barriers effectively prevented *Glossosoma* larvae from colonizing the upper surface of the tiles (Fig. 1). Two-way ANOVA revealed significant treatment effects (Table 1), where an average of only 0.4 individuals colonized the tiles in the reduced *Glossosoma* treatment (11

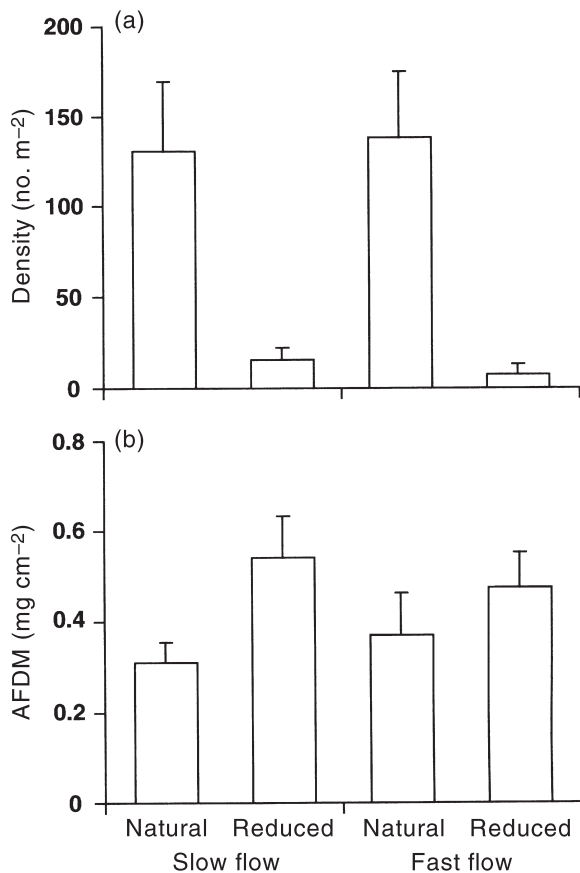


Fig. 1. (a) Density of colonizing *Glossosoma* and (b) ash-free dry mass (AFDM) of periphyton in four experimental treatments: natural *Glossosoma* levels in slow-flow conditions, reduced *Glossosoma* levels in slow-flow conditions, natural *Glossosoma* levels in fast-flow conditions, and reduced *Glossosoma* levels in fast-flow conditions. Data are mean \pm SE; $n = 10$.

individuals per m^2), compared with an average of 5.4 individuals in the natural treatment (133 individuals per m^2). Neither flow speed nor interaction effects was significant (Table 1), indicating that the flow speed did not influence the colonization by *Glossosoma* or alter the effect of the Vaseline barriers on such colonization.

The reduction of *Glossosoma* density from the Vaseline barriers resulted in greater periphyton biomass (Fig. 1). Two-way ANOVA revealed that the *Glossosoma* treatment significantly influenced periphyton AFDM (Table 1), with that for the reduced *Glossosoma* treatment being 1.5-fold that for the natural treatment. There were no significant flow-speed or interaction effects (Table 1).

Mayfly grazers

The experimental reduction of *Glossosoma* density resulted in a greater density of *Baetis* irrespective of flow speed (Fig. 2). Two-way ANOVA revealed a significant *Glossosoma* density effect (Table 1), where the density of *Baetis* was greater in the reduced than in the natural *Glossosoma* treatments. *Baetis* density did not differ significantly between flow speeds (Table 1). It was clear that the effect of *Glossosoma* on *Baetis* density was independent of flow speed because there was no significant interaction effect (Table 1).

In contrast, the flow speed altered the influence of *Glossosoma* on the other two mayfly densities (Fig. 2). Two-way ANOVA on the density of *Cinygmula* revealed that *Glossosoma*, flow condition and

Table 1 Two-way ANOVA for the effects of *Glossosoma* density and stream flow rate on the density of *Glossosoma* sp., periphyton ash-free dry mass and the densities of three mayflies, *Baetis thermicus*, *Cinygmula* sp. and *Paraleptophlebia chocorata*

	<i>Glossosoma</i> treatment		Source of variation		<i>Glossosoma</i> \times flow	
	<i>F</i>	<i>P</i>	Flow treatment <i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Glossosoma</i>	32.57	<0.001	0.07	0.799	0.30	0.589
Periphyton	5.47	0.025	<0.01	0.950	0.22	0.639
<i>Baetis</i>	5.91	0.020	0.69	0.413	<0.01	0.991
<i>Cinygmula</i>	6.24	0.017	9.43	0.004	7.46	0.010
<i>Paraleptophlebia</i>	0.46	0.504	6.46	0.016	5.14	0.030

For all sources of all response variables, d.f. were 1 and 36.

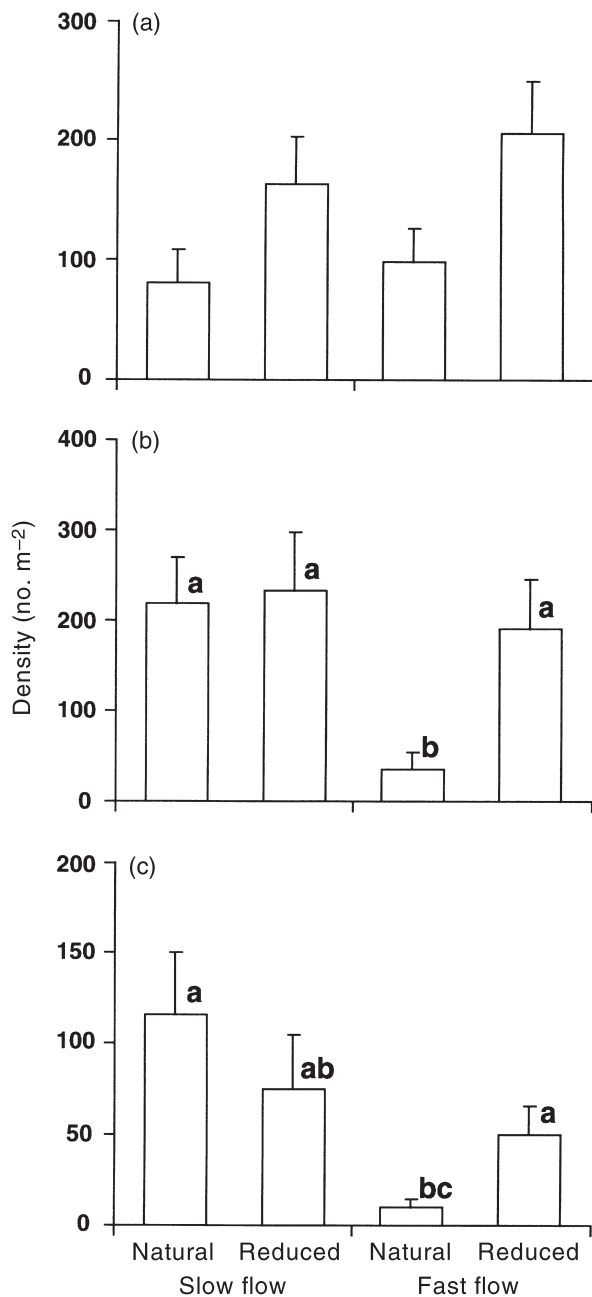


Fig. 2. Densities of three species of mayfly grazers in four experimental treatments: natural *Glossosoma* levels in slow-flow conditions, reduced *Glossosoma* levels in slow-flow conditions, natural *Glossosoma* levels in fast-flow conditions, and reduced *Glossosoma* levels in fast-flow conditions. (a) *Baetis thermicus*; (b) *Cinygmula* sp.; (c) *Paraleptophlebia chocorata*. For *Cinygmula* sp. and *P. chocorata*, there is no significant difference ($P \geq 0.05$) between bars with the same letter above (as assessed by Student–Newman–Keuls’ tests). Data are mean \pm SE; $n = 10$.

interaction effects were all significant (Table 1). Subsequent one-way ANOVA showed a significant difference in *Cinygmula* density among the four treatments ($F_{3,36} = 7.71$, $P < 0.001$). The density was lowest under fast flow with natural *Glossosoma* levels, but similar among the remaining three treatments (according to a Student–Newman–Keuls’ test; Fig. 2), indicating that a negative effect of *Glossosoma* on *Cinygmula* density was evident only in the fast-flow treatment. Two-way ANOVA on the density of *Paraleptophlebia* revealed significant flow-speed and interaction effects (Table 1), but no significant *Glossosoma* effects (Table 1). Subsequent one-way ANOVA showed significant differences among the four treatments ($F_{3,36} = 4.02$, $P = 0.015$). The *Paraleptophlebia* density in fast-flow conditions with natural *Glossosoma* levels was lower than those in both fast flow with reduced *Glossosoma* levels and slow flow with natural *Glossosoma* levels, whereas other comparisons were not significant (according to a Student–Newman–Keuls’ test; Fig. 2), indicating that *Glossosoma* influenced *Paraleptophlebia* density only in the fast-flow treatment.

DISCUSSION

The periphyton biomass in the reduced *Glossosoma* treatments was greater than in the natural treatments irrespective of flow condition, with the Vaseline barriers successfully excluding *Glossosoma* from the upper surfaces of the ceramic tiles. However, the densities of the three mayfly grazers on the tiles with such barriers were not lower than those on the unprotected tiles, implying that the barriers do not significantly prevent mayfly colonization. Therefore, reduced periphyton biomass in the natural *Glossosoma* treatment was likely to be a consequence of consumption by *Glossosoma*. Scraping caddisfly larvae, such as Glossosomatidae, with stout, heavily sclerotized mandibles, can remove even tightly adhering diatoms (Hill & Knight 1988) and reduce periphyton biomass in a density-dependent fashion (Feminella & Resh 1990; Kuhara *et al.* 1999). In addition, several field studies have also found increased periphyton biomass to be associated with the experimental reduction of grazing caddisflies, including species of Glossosomatidae (McAuliffe

1984b; Kohler 1992) and Helicopsychidae (Lamberti & Resh 1983).

For *Baetis*, the experimental result corroborated hypothesis (i), that the presence of *Glossosoma* decreased the colonizing density by reducing periphyton biomass. However, the degree of density reduction in *Baetis* was not affected by flow speed, contrary to the expectation of hypothesis (ii). *Baetis*, which has relatively robust mouthparts compared with other mayfly grazers, is similar to *Glossosoma* in being able to feed on diatoms that adhere tightly to their substrate (Brown 1961). McAuliffe (1984b) and Kohler (1992), for example, demonstrated experimentally that the presence of *Glossosoma* reduced the density of mayfly grazers including Baetidae by lowering the periphyton mass. Wiley and Kohler (1981), however, by direct observation, found no interference interactions that resulted in displacement between Glossosomatidae and Baetidae. Similarly, in our previous experiment in laboratory channels, no behavioral interactions were observed between *Glossosoma* and *Baetis* (N. Kuhara, S. Nakano & H. Miyasaka, pers. obs., 1996). Therefore, any negative effect of *Glossosoma* on *Baetis* could be regarded as occurring through exploitative competition associated with resource depression. Focusing on a local patch, Kohler (1985) found the drift emigration of a baetid mayfly to be high at a low resource level, whereas the immigration rate could be expected to be independent of the *in situ* resource level. In the present experiment, a high periphyton biomass associated with the experimental reduction of *Glossosoma* density would lower the rate of drift emigration and support high *Baetis* density.

One possible explanation for the discrepancy between hypothesis (ii) and the experimental result is that the grazing activity of *Glossosoma* was not affected by the flow variations employed in the present experiment. Poff and Ward (1992) demonstrated that the grazing activity of a Glossosomatid caddisfly, *Agapetus boulderensis* Milne, decreased with current velocity, even when the current velocity was less than 50 cm s^{-1} , which was slower than that used in the present experiment. However, Poff and Ward (1992) also showed that *Agapetus* occupied a greater range of current velocities as larval size increased. Since the *Glossosoma* (body length approximately 6 mm) studied here was much

larger than *Agapetus* (< 3 mm), the former may tolerate a wider range of current velocities than the latter.

Glossosoma lowered the densities of *Cinygmula* and *Paraleptopplebia* in fast-flow conditions, but not in slow. The Vaseline barriers might prevent colonization of these mayflies, because such mayflies frequently use crawling in addition to drifting and swimming as a mode of colonization (Mackay 1992). Even so, this result indicates that the competitive influence of *Glossosoma* was lowered by slow flow rates, as long as the barrier effect on these mayflies did not differ between the flow conditions. The observed trend for these mayflies in the present experiment was completely contrary to the expectation of hypothesis (ii) that the competitive influence of *Glossosoma* should be lowered under fast-flow conditions due to low grazing efficiency. These mayfly grazers, which have collector-gatherer mouthparts but not typical scraper ones, unlike *Glossosoma*, are known to most effectively graze on loosely attached diatoms, rather than those more tightly attached to the substrate (Brown 1961; Hill & Knight 1988). The composition of the periphyton growth forms, which could vary according to flow conditions, would be an important element in the alteration of competitive influence by *Glossosoma*, although the total periphyton biomass did not differ between the two flow conditions in the present experiment. The effect of flow on the accumulation rates of periphyton has been found to differ for different growth forms (Kuhn *et al.* 1981; Robinson & Rushforth 1987). Tightly adherent diatoms, which are usually early colonists, are rather difficult for flow to dislodge, whereas loosely attached forms of later colonists are easily dislodged (Korte & Blinn 1983). In the present study, grazing pressure on the periphyton assemblage by *Glossosoma* would be stronger in the natural *Glossosoma* treatments than in the reduced *Glossosoma* treatments under both flow conditions. However, the contribution of loosely attached diatoms under slow-flow conditions might be greater owing to their greater accumulation rate than fast conditions. Moreover, loosely attached diatoms would wash away easily in fast flow when *Glossosoma* moved or grazed. Grazing by a Glossosomatid caddisfly has been found to alter the periphyton assemblage structure from

late-successional (i.e. loosely attached) to early-successional forms (tightly attached; Poff & Ward 1995). Therefore, under fast-flow conditions, the contribution of such diatoms in natural *Glossosoma* levels might be less than in reduced levels. The competitive influence of *Glossosoma* on *Cinygmula* and *Paraleptophlebia* was probably altered by flow conditions producing differences in the growth-form composition of the periphyton.

In the present experiment, we showed that stream-flow conditions can mediate competitive influence. These results suggested a potential for such mediation to be due to a modification of the resource structure. Further studies concerning the effects of flow and grazer feeding on the composition of periphyton growth forms are needed to clarify the mechanisms of the mediation.

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