

Predatory fish impact on competition between stream insect grazers: a consideration of behaviorally- and density-mediated effects on an apparent coexistence pattern

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Miyasaka, H., Genkai-Kato, M., Kuhara, N and Nakano, S. 2003. Predatory fish impact on competition between stream insect grazers: a consideration of behaviorally- and density-mediated effects on an apparent coexistence pattern. – *Oikos* 101: 511–520.

A manipulative field experiment and theoretical analyses of a simple competition model were used to show how exploitative competition between a caddisfly (*Glossosoma* sp.) and three mayfly grazers (*Ameletus* sp., *Baetis thermicus* and *Cinygmula* sp.) was mediated by a predatory fish, freshwater sculpin (*Cottus nozawae*). The field experiment followed a two-factorial design, with *Glossosoma* densities (natural vs reduced) and sculpin presence (present vs absent) as treatments. Diet analysis revealed that all four prey species were eaten under the natural condition and the sculpin preferred mayfly grazers to *Glossosoma*. Our experiment showed that although mayfly densities in the presence of either sculpin or *Glossosoma* were lower than in the no-sculpin plus reduced-*Glossosoma* treatment, no difference in mayfly densities was found between the following three treatments: sculpin plus natural-*Glossosoma*, no-sculpin plus natural-*Glossosoma*, and sculpin plus reduced-*Glossosoma*. These results indicated that fish predator produced no effects additive to the competitive operation on the mayfly density, and also that competitive operation of *Glossosoma* on the mayfly densities produced no additional effects to fish predators. In addition, although the competitive effect of the mayflies on *Glossosoma* could not be manipulated in isolation, the density of *Glossosoma* in the presence of sculpin was greater than that in the absence of sculpin in the natural-*Glossosoma* treatment. Thus, the densities of these competing grazers either stayed the same or increased in the presence of the fish predator relative to predator-free treatments. A theoretical model, developed to explain the experimental results here, predicted that the densities of the two competing prey under predation pressure could be simultaneously greater than those under predator absent conditions when the behaviorally-mediated effects of the predator were strongly operative. Although we were unable to distinguish experimentally the two different effects of predator on the prey competition, the behaviorally- and density-mediated effects, the reality of the behaviorally-mediated effects in the experiment was discussed.

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Predators have often been found to have important roles in promoting the coexistence of competing prey species, influencing competitive interactions among

their prey (Paine 1966). To examine coexistence mechanisms of similar prey species, classification of predation effects on the outcome of competition has been at-

Accepted 15 November 2002

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ISSN 0030-1299

tempted in a series of theoretical studies (Holt 1985, Miller and Kerfoot 1987, Kotler and Holt 1989). First, predators have been predicted to alter the competitive outcomes by reducing local prey population densities, by facilitating dispersal behavior as well as by direct removal due to predation (density-mediated effect, sensu Kotler and Holt 1989, Norrdahl and Korpimäki 1993, Mol 1996; Fig. 1). Intensive exploitation by predators occasionally results in the local extinction of prey populations and a decline in the number of species in a prey guild (Harper 1969, Spiller and Schoener 1994). However, an intermediate level of predation can decrease the intensity of competition by lowering the densities of prey populations and, accordingly, enhance the likelihood of coexistence (Paine 1966, 1974, Tokeshi 1998). Second, predators which can induce changes in the foraging behavior and/or habitat use of prey (Persson 1991, Skelly 1994, Werner and Anholt 1996) have the potential for altering the intensity and direction of competition among the prey species (behaviorally-mediated effect, sensu Kotler and Holt 1989; Fig. 1), when behavioral responses to the predators differ between the prey species (Schmitt 1981, 1982, Kuhara et al. 1999). The behaviorally-mediated effects are considered to play a role in promoting coexistence of competitors by lowering individual performance (Wootton 1992). In recent years, the major concern of community ecologists has shifted from direct, density-mediated to indirect, behaviorally-mediated effects on competition (Kerfoot and Sih 1987, Beckerman et al. 1997). In reality, both effects, interacting in complex ways, would alter competitive processes and determine the conditions of species coexistence (Kotler and Holt 1989). Nevertheless, only a few studies have examined

such confounded effects in natural systems, where prey species compete for a limited resource and share a common predator (Brown et al. 1988, Wootton 1992).

In lotic systems, the potential importance of biological interactions in structuring communities has been increasingly emphasized (Allan 1995). In particular, the operation of exploitative competition among invertebrate grazers has been evidenced from the fact that a high density of one grazer species resulted in detrimental consequences for other guild members, by lowering periphyton availability (McAuliffe 1984, Lamberti et al. 1987, Kohler 1992). In addition, some field experiments in stony streams have also provided much evidence for negative impacts of predators on both the abundance (reviewed by Wooster 1994) and activities (reviewed by Wooster and Sih 1995) of invertebrates. In this study, using a manipulative field experiment, we examined whether the predatory fish, freshwater sculpin (*Cottus nozawae*), mediated competitive interactions between the caddisfly (*Glossosoma* sp.) and the mayfly grazers (*Ameletus* sp., *Baetis thermicus* and *Cinygmula* sp.; Fig. 1). Subsequently, a simple theoretical model based on the experimental setting was developed to explain the mechanisms behind the experimental results, because we were unable to experimentally distinguish the two effects of predator, density- and behaviorally-mediated ones. We hypothesized in the model that (1) the predator alters the relative abundance of the competitors and thereby reduces the intensity of competition (density-mediated effect) and (2) the predator can also induce changes in the prey behavior such that the prey reduce their grazing time on the surface of substrata to avoid predation (behaviorally-mediated effect).

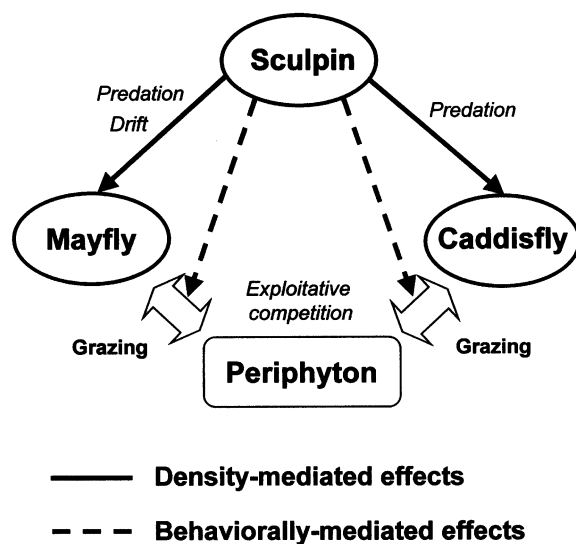


Fig. 1. Two conceptually distinctive effects, density- and behaviorally-mediated, of a predator (sculpin) on the interspecific competition between two grazers (mayfly and caddisfly).

Study system

Glossosomatid caddisfly and some mayfly (e.g. Ameletidae, Baetidae and Heptageniidae) species are generally dominant components of invertebrate grazer assemblages on hard substrates in headwater streams of cool-temperate zone (Fig. 1; see Kuranishi and Kuhara 1994, Kuhara et al. 1999 for Japanese streams, and McAuliffe 1984, Hart 1987, Kohler 1992 for North American streams). McAuliffe (1984), Kohler (1992) and Kuhara et al. (2000) demonstrated that the experimental exclusion of glossosomatid caddisflies from local substrate patches in natural streams resulted in increases in densities of mayfly grazers. In addition, the growth rates of both a glossosomatid caddisfly and a baetid mayfly have been found to be lowered by small periphyton biomass associated with experimentally increased competitor densities in laboratory channels (Kuhara et al. 1999; Fig. 1). Such experimental evidence revealed the operation of exploitative competition between the two types of invertebrate grazers. On

the other hand, predatory sculpin was found to suppress grazing activities of both grazer types in both natural streams (Kohler and McPeck 1989, Kuhara et al. 1999), as well as consuming both (Kuhara et al. 1999). The presence of non-feeding sculpin which was prevented from attacking prey, largely reduced a time budget for periphyton grazing by a baetid mayfly, with only a minor behavioral shift being induced by the sculpin in a glossosomatid caddisfly (Kuhara et al. 2001). Such a difference in behavioral response to the sculpin between the two grazers resulted in asymmetric mediation of their competitive interaction (Kuhara et al. 1999, 2001).

The density- and behaviorally-mediated effects of a predator were expected to influence, in different ways, the competitive system of prey species with different levels of predator susceptibility (Kotler and Holt 1989). Accordingly, a test for the overall impact (i.e. including both behaviorally- and density-mediated effects) of predatory sculpin on the outcome of competition between the mayfly grazers and the glossosomatid caddisfly was required to provide an insight into the apparent coexistence of these grazers (Fig. 1).

Methods

Study site and animals

The field experiment was conducted in the Horonai Stream running through the Tomakomai Experimental Forests (TOEF) of Hokkaido University (42°37'N, 141°20'E), southwestern Hokkaido (northernmost island of the Japanese archipelago), from February to April 1998. Water temperature in this small, cold spring-fed, second-order stream (14 km long and < 1% gradient) ranged from 7 to 9°C during the study. The stream discharge was relatively stable (0.21–0.29 m³ s⁻¹) throughout the study period, with no major disturbances occurring. A 500 m stretch of the stream, 4.0–4.5 km downstream from the headwater spring, was selected as an experimental reach. Mean habitat variables in the experimental reach were stream width (3.6 m), water depth (22 cm) and water current velocity (42 cm s⁻¹). Although riparian forest canopies covered almost the entire stream channel in the experimental reach, the streambed was largely open to sunlight during the study period because of seasonal defoliation.

The density of benthic invertebrates and periphyton biomass in the reach were estimated on 24 February from ten samples collected from ceramic plates (19 × 19 cm area, 1 cm thickness), which had been placed on the streambed for two months, (see sampling protocol below). Dominant periphyton-grazing invertebrates were larvae of a caddisfly (*Glossosoma* sp.) and nymphs of three mayfly species (*Ameletus* sp., *Baetis thermicus* and *Cinygmula* sp.), their mean densities being 250 ± 122

(SE) m⁻², 54 ± 38, 105 ± 85 and 25 ± 20, respectively. Mean periphyton biomass was 120 ± 20 (SE) AFDM µg cm⁻² (see measuring protocol below). The four species accounted for 50.5% of the total number of benthic invertebrates that remained on a 1 mm mesh sieve. In the stream, the larval periods of the four species largely overlapped, their emergence peaking from June to July (N. Kuhara, unpubl.). Other periphyton grazers included in the samples (at much lower densities than the above) were nymphs of five mayfly species (*Epeorus latifolium*, *B. yoshinensis*, *Cincticostella nigra* and *C. okumai*), and larvae of a caddisfly (*Neophylax ussuriensis*) and several chironomid species. The freshwater sculpin, the dominant benthic fish in the stream with local densities ranging from 0.2 to 2.1 m⁻² (H. Miyasaka, unpubl.), is a typical insectivore foraging primarily upon exposed benthic prey on the streambed and is therefore regarded as the major predator of both the *Glossosoma* larvae and mayfly nymphs (Kuhara et al. 1999; H. Miyasaka, unpubl.).

Manipulative field experiment

To examine the impacts of predatory sculpin on the outcome of competitive interactions between *Glossosoma* and the three dominant mayflies, a manipulative field experiment was conducted for forty days, from 25 February to 5 April. The experiment followed a two-factorial design with *Glossosoma* (competitor) densities (natural vs reduced) and sculpin (predator) presence (present vs absent) as factors. Thus, four treatments were established; (1) no-sculpin plus reduced-*Glossosoma*, (2) no-sculpin plus natural-*Glossosoma*, (3) sculpin plus reduced-*Glossosoma*, and (4) sculpin plus natural-*Glossosoma*. On 18 February (one week before the beginning of the experiment), forty columnar enclosures (1 m high, 1 m in diameter, with 10 mm wire mesh coated with rubber) were arranged in the experimental reach. Each enclosure was separated from those immediately adjacent by greater than 5 m of unmanipulated streambed. The four treatments (ten replicates) were randomly assigned to the forty enclosures.

Ceramic plates (19 × 19 cm area, 1 cm thickness) were used as experimental substrates so as to minimize unplanned variance in grazer densities. The plates had been placed on the streambed near the experimental reach for the previous two months, so that a sufficient natural periphyton mat had been established at the beginning of the experiment (Nakano et al. 1999). On 25 February (the beginning of the experiment), all invertebrates on the plates were removed by gently rubbing the surface by hand. For the reduced-*Glossosoma* treatment, a rubber band (1.5 cm wide × 25 cm circumference) was placed around the edge of each plate and coated with a 2 mm thick layer of vaseline to prevent *Glossosoma* from grazing periphyton on the

upper surface (Kuhara et al. 2000), of which a major movement mode was crawling, from colonizing the plates (McAuliffe 1984, Kuhara et al. 2000). In contrast, *Glossosoma* was allowed to freely colonize the plates in the natural-*Glossosoma* treatments. Apart from case-building caddisflies, *Neophylax* as well as *Glossosoma*, mobile invertebrate grazers in the stream such as mayflies, were expected to colonize the plates irrespective of the vaseline barriers, because they were commonly found in stream drift (Miyasaka and Nakano 1999). After all of the fishes had been removed from the enclosures by a backpack electrofishing unit (Model 12, Smith-Root Inc., Vancouver, WA, USA), we placed three ceramic plates, with and without the vaseline barrier, on the streambed inside each enclosure for the reduced- and natural-*Glossosoma* treatments, respectively. Sculpin (males, 85–118 mm in total length) were collected in the Horonai Stream (outside the experimental reach) using the electrofishing unit (see above), just prior to the introduction of two individuals into each of the enclosures (1.6 m⁻² density) used for the sculpin present treatments. The 10 mm mesh of the enclosures prevented fish from entering or leaving each enclosure, while allowing all stream invertebrates to pass through freely (Miyasaka and Nakano 1999). Enclosures were cleaned by brushing four times per day (every six hours) over the experimental period, owing to the reduction of current velocity by leaf litter blocking the enclosure mesh.

On 6 April (day 41 of the experiment), benthic invertebrates were collected simultaneously from the upper surface of the three plates in each enclosure with three connected Surber net samplers (225 µm mesh, 25 × 25 cm quadrat, 100 cm long, Miurarika Inc., Sapporo, Japan). Invertebrate samples were preserved in 5% formalin solution for later analysis. Periphyton was removed from the entire upper surface of the plates by brushing, and preserved in 1% formalin solution. The invertebrate samples were sieved 1 mm mesh and identified under a binocular microscope. Samples of well-mixed periphyton suspension were collected with Whatman GF/C-filters (Whatman International Ltd., Maidstone, UK) that 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 ash-free dry mass (AFDM) for periphyton biomass. Mean benthic invertebrate density (m⁻²) and mean periphyton biomass (µg cm⁻²) were then determined for the three plates (sub-samples).

After the experiment, we collected 101 sculpin individuals from the stream within the experimental reach during 1600 h–0400 h (dark hours) using the electrofishing unit (see above), in order to analyze their diets. The captured sculpin were 94 ± 3 (SE) mm in total length. Stomach contents were collected by stomach pumping with a 2 cm³ pipette, so as to flush prey

items from the entire stomach region (Giles 1980), and preserved in 5% formalin solution. After that we collected benthic invertebrate samples (n = 24) on the stream bed in the experimental reach with the Surber net sampler (see above). Invertebrates found in the sculpin diet and the benthic sample were identified and counted under a binocular microscope. We compared the fractional composition of each item (*i*) found in the guts of the sculpins (*r_i*) to its fractional composition in the available prey invertebrates (*p_i*) using Ivlev's electivity index (1961):

$$E_i = (r_i - p_i) / (r_i + p_i)$$

Values of *E_i* range from -1 to +1, indicating avoidance (negative values) and preference (positive). Values close to zero indicate that the predator does not display preference nor avoidance for prey item *i*.

Statistical analyses

For the experimental data, the enclosures (or enclosures) were considered as replicates. To test for the effects of both sculpin (predator) presence (present vs absent) and *Glossosoma* (competitor) manipulations (natural vs reduced) on the densities of the three mayfly grazers and the periphyton biomass, a two-way multiple analysis of variance (MANOVA) was employed, with a separate two-way ANOVA being subsequently conducted for each mayfly species and periphyton. When the interaction terms in these two-way ANOVAs were significant, pair-wise comparisons among the four treatments were conducted using Fisher's PLSD tests after a significant treatment effect was confirmed by one-way ANOVAs. Also, in order to examine the effects of the sculpin and the vaseline barrier on *Glossosoma* density in the presence of its competitors (mayfly grazers), a two-way ANOVA was performed on the density of the *Glossosoma*, with sculpin (present vs absent) and vaseline barrier (with vaseline vs without vaseline) as factors. Log₁₀(x + 1) transformations for exact values were made in order to minimize deviations from normality and homogeneity of variances. For all tests, an alpha value of 0.05 was used for statistical significance.

Theory

Consider a simple competitive system in which two prey grazers compete with each other for a limited resource (periphyton):

$$\frac{dX_M}{dt} = a_{M0} - (a_{MM} + b_G a_{MG} X_G + d_M Y) X_M \quad (1a)$$

$$\frac{dX_G}{dt} = a_{G0} - (a_{GG} + b_M a_{GM} X_M + d_G Y) X_G \quad (1b)$$

where X_M denotes the density of mayflies; X_G , the density of *Glossosoma*; and Y , the density of predator. We assume here that the predator density is constant, following the present experimental design. Parameter a_{i0} is the immigration rate of prey i ($i = M, G$) into the system considered; a_{ii} , the intraspecific competition coefficient; a_{ij} , the interspecific competition coefficient (impact of j on i ($i \neq j$)); and d_i , the per-capita per predator rate of prey i removal from the system by a combination of predation and emigration due to predator avoidance (density-mediated effects). Parameter b_i ($0 \leq b_i \leq 1$) describes the behaviorally-mediated effects of the predator on prey i . We assume that the predator can reduce the grazing time of prey on the surface of stones, which results in reduction in the interspecific competition for the shared resource (smaller $b_i a_{ji} X_i$). The smaller the value of b_i (therefore smaller $b_i a_{ji} X_i$), the greater the behaviorally-mediated effect of the predator on prey i . There is no behaviorally-mediated effect when $b_i = 1$.

Results

Sculpin diets

Both nymphs of the three mayflies (*Ameletus*, *Baetis* and *Cinygmula*) and larvae of *Glossosoma* were found in the diets of 101 sculpin individuals collected from an experimental reach (Fig. 2). In addition to the four grazers, *Drunela* and *Gammaridae* were especially eaten by the sculpin. In the Ivlev's electivity index, the sculpin preferred *Ameletus* and *Baetis* to *Glossosoma* (Fig. 2).

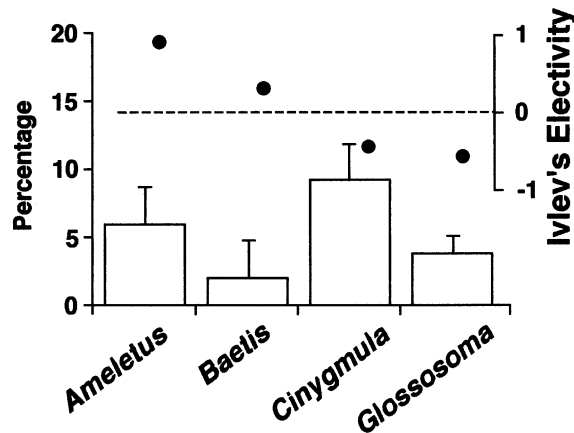


Fig. 2. Diet composition within sculpin guts (left scale) and predation preference (right scale) by sculpin on the three mayfly grazers, *Ameletus* sp., *Baetis thermicus* and *Cinygmula* sp., and the one caddisfly, *Glossosoma* sp. Data with regard to the diet composition given as means \pm SE ($n = 101$).

Field experiment

The presence of either predator (sculpin) or competitor (*Glossosoma*) produced a negative influence on the densities of the three mayfly grazers (Fig. 3) and the periphyton biomass (Fig. 4). Two-way MANOVA on the mayfly grazer densities and the periphyton biomass revealed significant *Glossosoma* and sculpin effects, with the interaction effect also being significant (Table 1). For each species of mayfly grazer, separate two-way ANOVAs revealed that *Glossosoma*, sculpin and interaction effects were all significant (Table 2). The predatory sculpin influenced the competitive operation of *Glossosoma* on the densities of the three mayflies, and the *Glossosoma* also influenced the effect of predator on the mayfly densities. Subsequent one-way ANOVAs showed significant differences in density among the four treatments of *Ameletus* ($F_{3,36} = 8.87$), *Baetis* ($F_{3,36} = 8.05$) and *Cinygmula* ($F_{3,36} = 12.89$, $P < 0.001$ for all). Pair-wise comparisons over all four treatments revealed that their densities were highest in the no sculpin plus reduced-*Glossosoma* treatment, but similar among the remaining three (Table 3, Fig. 3), indicating that predatory sculpin introduced no effects additional to the competitive impacts of *Glossosoma* on the mayfly densities and competitive operation of *Glossosoma* produced no additional effects to the fish predator. For the periphyton biomass, separated two-way ANOVA revealed that the *Glossosoma* manipulation significantly reduced the periphyton biomass: the biomass was 1.7 times greater in the reduced-*Glossosoma* treatment than in the natural-*Glossosoma* treatment (Table 2, Fig. 4). There were no significant sculpin or interaction effects, indicating that the effect of *Glossosoma* on the periphyton biomass was independent of the sculpin presence. The reduced *Glossosoma* density due to the vaseline

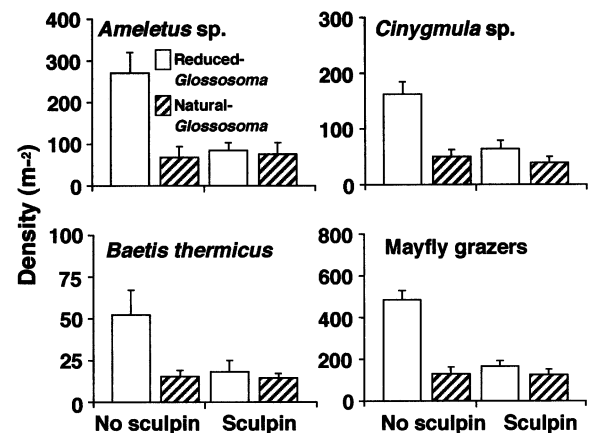


Fig. 3. Effect of treatments on the densities of three mayfly grazers, *Ameletus* sp., *Baetis thermicus* and *Cinygmula* sp. and total mayfly grazers, including the above three species. Data given as means \pm SE ($n = 10$).

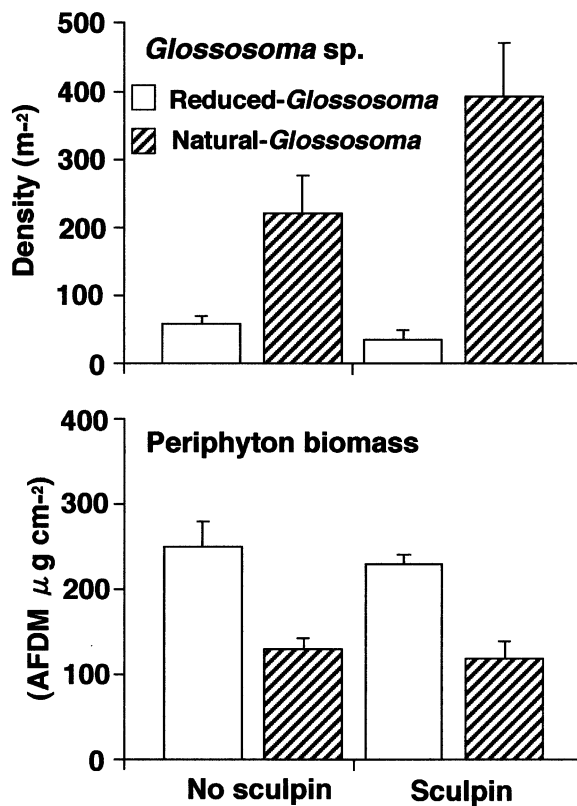


Fig. 4. Effect of treatments on the density of *Glossosoma* sp. and the periphyton biomass. Data given as means \pm SE (n = 10).

Table 1. Two-way MANOVA for the densities of three mayfly grazers and the periphyton biomass.

Factor	df	Hotelling-Lawley trace	P
<i>Glossosoma</i>	4	17.11	<0.001
Sculpin	4	4.45	0.006
<i>Glossosoma</i> \times Sculpin	4	3.41	0.019
Error	33		

barrier resulted in increased periphyton biomass (Fig. 4).

For the *Glossosoma* density in the presence of mayfly competitors, two-way ANOVA revealed significant effects of the vaseline barrier ($F_{1,36} = 39.87$, $P = < 0.001$) and interaction between vaseline barrier and *Glossosoma* ($F_{1,36} = 5.54$, $P = 0.024$); the predator effect was not significant ($F_{1,36} = 0.16$, $P = 0.689$; Fig. 4). The effect of the vaseline barrier on the *Glossosoma* density was influenced by the presence of predatory sculpin. Subsequent one-way ANOVA showed a significant difference in the density of *Glossosoma* among the four treatments ($F_{3,36} = 15.19$, $P < 0.001$; Fig. 4). Pair-wise comparisons over all treatments revealed that the *Glos-*

sosoma density in the presence of both sculpin and mayfly grazers was significantly greater than that in the presence of mayflies only ($P = 0.039$). Moreover, the *Glossosoma* densities without the vaseline barrier were significantly greater than that with the barrier ($P < 0.008$ for all combinations); under the vaseline barrier conditions, there was no significant difference in the *Glossosoma* density between sculpin and no-sculpin treatments ($P > 0.689$ for all combinations). These indicate that the vaseline barrier was primarily effective in preventing *Glossosoma* larvae from colonizing the upper surface of the plates so treated. Only 1.7 individuals colonized the plates (47 m^{-2}) in the reduced-*Glossosoma* treatments, compared with 11.1 individuals (307 m^{-2}) in the natural-*Glossosoma* treatments (Fig. 4).

Graphical analyses of the theory

Here, we present the results of the model system represented by eq. 1a and b using a graphical approach. The isocline of prey species i is given by the following equation:

$$X_i = \frac{a_{i0}}{a_{ii} + b_j a_{ij} X_j + d_i Y} \quad (2)$$

where $j \neq i$.

First, we consider the case where there is no predator (i.e. $Y = 0$ and $b = 1$), second, only density-mediated effects of predator ($Y > 0$ and $b = 1$) and finally, both density- and behaviorally-mediated effects of predator are present ($Y > 0$ and $b < 1$).

When the predator is absent, the isoclines of prey, M (mayfly grazers) and G (*Glossosoma*), are described by two curves (convex downward), intersecting the X_M -axis at $X_M^{00} = a_{M0}/a_{MM}$ and the X_G -axis at $X_G^{00} = a_{G0}/a_{GG}$, respectively (black curves in Fig. 5). The equilibrium densities of the two competing prey (X_M^{0C} , X_G^{0C}) are given by the crossing point of the prey isoclines. It is clear from Fig. 5 that the equilibrium density of prey i ($i = M, G$) in the absence of its competitor are greater than in the presence of the competitor ($X_i^{00} > X_i^{0C}$).

Let us consider the case where predators are present and produce density-mediated effects only ($Y > 0$ and $b = 1$). As the density-mediated effects (d) become larger, the prey isoclines approach the origin, intersecting the X_M -axis at $X_M^{P0} = a_{M0}/(a_{MM} + d_M Y)$ and the X_G -axis at $X_G^{P0} = a_{G0}/(a_{GG} + d_G Y)$ (red curves in Fig. 5). The crossing point (X_M^{PC} , X_G^{PC}) of the two prey isoclines can locate within the inner region (dotted region in Fig. 5) produced by the two black isoclines (as no predator effects were considered), depending on the d_M and d_G values. Compared with the no predator condition (the crossing point of black curves: X_M^{0C} , X_G^{0C}), the density-mediated effects of the predator can be predicted to lead to either of the following two cases, with regard to

Table 2. Separated two-way ANOVAs for the densities of three mayfly grazers and the periphyton biomass.

Species	Factor	df	<i>F</i>	<i>P</i>
<i>Ameletus</i> sp.	<i>Glossosoma</i>	1	7.44	0.010
	Sculpin	1	10.63	0.002
	<i>Glossosoma</i> × Sculpin	1	8.55	0.006
	Error	36		
<i>Baetis thermicus</i>	<i>Glossosoma</i>	1	7.60	0.010
	Sculpin	1	9.63	0.004
	<i>Glossosoma</i> × Sculpin	1	6.95	0.012
	Error	36		
<i>Cinygmula</i> sp.	<i>Glossosoma</i>	1	11.89	0.002
	Sculpin	1	19.21	<0.001
	<i>Glossosoma</i> × Sculpin	1	7.54	0.009
	Error	36		
Periphyton	<i>Glossosoma</i>	1	30.12	<0.001
	Sculpin	1	0.34	0.562
	<i>Glossosoma</i> × Sculpin	1	0.11	0.736
	Error	36		

Table 3. *P*-values of pair-wise comparisons using Fisher's PLSD for each mayfly grazer density.

Combination of treatments	Species		
	<i>Ameletus</i> sp.	<i>Baetis thermicus</i>	<i>Cinygmula</i> sp.
No-sculpin, reduced- <i>Glossosoma</i> vs no-sculpin, natural- <i>Glossosoma</i>	0.001	0.003	<0.001
No-sculpin, reduced- <i>Glossosoma</i> vs sculpin, reduced- <i>Glossosoma</i>	0.004	0.006	0.001
No-sculpin, reduced- <i>Glossosoma</i> vs sculpin, natural- <i>Glossosoma</i>	0.002	0.003	<0.001

the prey densities (the crossing point of red curves: X_M^{PC} , X_G^{PC}): (1) the densities of both prey species decrease, or (2) the density increases in one prey species, but decreases in the other. In other words, the prey densities in the presence of both a predator and a competitor can not together achieve a level greater than those in the presence of a competitor only.

Then, let us consider the case where both density- and behaviorally-mediated effects of predators are operative ($Y > 0$ and $b < 1$). As the behaviorally-mediated effects become stronger (decreases in b_M and b_G), the isoclines of prey *M* and *G* move away from the origin with the X_M - and X_G -intercepts unchanging (blue curves in Fig. 5). In the extreme situation where the behaviorally-mediated effects of the predator are too strong to exert any interspecific competition between grazers (i.e. $b_M = 0$ and $b_G = 0$), it can be seen (from eq. 2) that the isoclines of prey *M* and *G* become linear and respectively perpendicular to the X_M - and X_G -axis, resulting in $X_M = X_M^{P0}$ and $X_G = X_G^{P0}$ (green lines in Fig. 5). Thus, the crossing point (\hat{X}_M^{PC} , \hat{X}_G^{PC}) of the two isoclines can locate within the inner region (yellow region in Fig. 5) surrounded by the prey isoclines in the case where only density-mediated effects are present (red isoclines) and the isoclines in the extreme situation (green lines). Accordingly, the densities of both prey in the presence of both the predator and competitor can be simultaneously greater than those in the presence of only a competitor if

$$X_M^{P0} > X_M^{0C} \text{ and } X_G^{P0} > X_G^{0C} \quad (3)$$

This means that the effects of predation on the densities of the two prey species should be smaller than the effects of competition.

Discussion

The present experimental results clearly showed that the presence of either the predator (sculpin) or the competitor (*Glossosoma*) produced a negative influence on the populations of mayfly grazers. *Glossosoma* only suppressed mayfly densities in the absence of predators (Fig. 3, and simultaneously corresponding to $X_M^{0C} < X_M^{00}$ in Fig. 5), by reducing periphyton biomass (Fig. 4). Predators only affected mayfly grazers in the absence of competition from caddisfly grazers (Fig. 3, and corresponding to $X_M^{P0} < X_M^{00}$ in Fig. 5). Indeed, we found not only mayfly grazers but also *Glossosoma* in the stomach contents of sculpin captured in natural reaches of the Horonai Stream. However, an electivity index analysis revealed that the sculpin preferred the *Ameletus* and *Baetis* to the *Glossosoma* (Fig. 2). However, there was no difference in mayfly grazer densities between the sculpin plus natural-*Glossosoma* and no-sculpin plus natural-*Glossosoma* treatments (Fig. 3), indicating that the predator produced no effects additional to the competitive operation on mayfly densities (also, the competitor produced no additional effects to the preda-

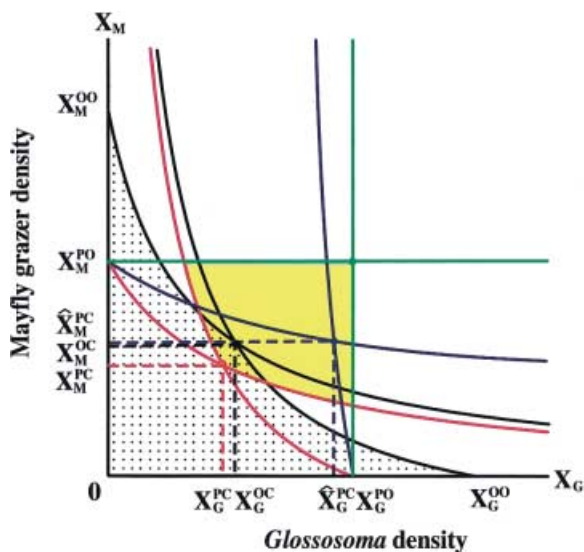


Fig. 5. Graphical analyses of competition between the *Glossosoma* and the three mayfly grazers in the presence and absence of a predator; non-linear isoclines for *Glossosoma* and the mayfly grazers in a simple competitive system (see eqs. 1 in Theory). Black isoclines denote predator absent; red isoclines, only density-mediated effects of the predator present; blue isoclines, both density- and behaviorally-mediated effects of predator present; green isoclines, behaviorally-mediated effects of predator sufficiently strong to overcome competitive effects. For the four colored isoclines, the crossing point of the isoclines represents the coexisting situation between the prey species in a stable equilibrium. Dotted region denotes only density-mediated effects present; yellow region, both density- and behaviorally-mediated effects of the predator present. X_M and X_G denote densities of mayfly grazers and *Glossosoma*, respectively. For X_M and X_G , 00, 0C, P0 and PC denote conditions in the field experiment; 00 = no-predator plus no-competitor, 0C = no-predator plus competitor, P0 = predator plus no-competitor, and PC = predator plus competitor. \hat{X}_M^{PC} and \hat{X}_G^{PC} denote density of prey in the presence of the competitor and both density- and behaviorally-mediated effects of the predator. X_M^{PC} and X_G^{PC} denote density of prey in the presence of the competitor and only density-mediated effects of the predator.

tor effect). These results showed that the confounded effects of predator and competitor could not be represented by a simple arithmetic expression, such as "predation plus competition".

In the field experiment, the densities of both sympatric, competing grazers were not simultaneously reduced by the addition of predator impact (i.e. $\hat{X}_M^{PC} \geq X_M^{0C}$ and $\hat{X}_G^{PC} \geq X_G^{0C}$ were satisfied). The graphical analyses of the theory predicted that the two prey densities in the presence of the predator (X_M^{PC} , X_G^{PC}) were unable to be greater than those in the absence of the predator (X_M^{0C} , X_G^{0C}) at the same time (dotted region in Fig. 5) unless the behaviorally-mediated effects were operative. Thus, only density-mediated effects of the predator could not account for the experimental results. The behaviorally-mediated effects of the sculpin, which weakened the intensity of competition

between the grazers, should be considered to play one of the principal roles in producing the apparent coexistence pattern of *Glossosoma* and mayfly grazers in natural systems. When the behaviorally-mediated effects as well as density-mediated ones, as suggested by Kotler and Holt (1989), were present, there is the potential for the densities of two competing prey species under certain predation pressures (\hat{X}_M^{PC} , \hat{X}_G^{PC}) to be simultaneously greater than respective densities under predator absence conditions (yellow region in Fig. 5). The densities of the mayflies and the *Glossosoma* in the experimental condition with the sculpin plus natural-*Glossosoma* treatment were, in reality, nearly equal to those observed in natural reaches of the Horonai Stream.

A decrease in grazing activity in order to reduce predation risk has been observed in both *Glossosoma* (Kuhara et al. 2001) and a number of mayfly species (e.g. Culp and Scrimgeour 1993, McIntosh and Peckarsky 1996, Peckarsky 1996), including one examined here (*Baetis*; Kuhara et al. 1999). In a laboratory experiment, the use of a profitable but risky habitat (i.e. upper surface of substrate) by *Baetis* was found to largely decrease in the presence of non-feeding sculpin, which involved sub-lethal effects only (Kuhara et al. 1999). The grazing activities of *Glossosoma* have also been observed experimentally to decrease in the presence of non-feeding sculpin during a certain period (morning) of the day in laboratory channels (Kuhara et al. 2001). Such decreases in grazing activities in competing grazers, possibly related to predator avoidance, could result in an increasing accumulation of periphyton biomass and lesser influence of exploitative competition between them.

In the theoretical model, we derived the necessary condition for the situation where neither of the two prey densities in the presence of a predator were smaller than their respective densities in the absence of the predator. For such a situation to be realized, the sole effect of the predator on prey densities should be less than that of the competitor (inequality 3, $X_M^{P0} > X_M^{0C}$ and $X_G^{P0} > X_G^{0C}$). Nevertheless, the experimental result for the mayfly grazers ($X_M^{P0} = X_M^{0C}$) differed somewhat from this necessary condition. One possible reason for such a discrepancy between the theoretical prediction and experimental result is the fact that the exclusion of *Glossosoma* from the upper surface of the plates was incomplete in the experiment. Both mayfly grazers and *Glossosoma* were eaten by sculpin under the natural condition, but the sculpin displayed a preference for mayfly over *Glossosoma* (Fig. 2). *Glossosoma* is known to be invulnerable to sculpin fish in Japanese (Yamamoto et al. 1988) and western streams (Flecker 1984, Greenberg 1991). In addition, in contrast to mayfly nymphs which frequently entered stream drift to avoid predators (Forrester 1994, Miyasaka and Nakano 1999, 2001), such active drift dispersal has not been found for

Glossosoma larvae in the stream (H. Miyasaka, unpubl.). The density-mediated effects, which are assumed to include both predation and dispersal here, of the sculpin on the *Glossosoma* density would be smaller than those on the mayflies (i.e. $d_G < d_M$ in eqs. 1). On the other hand, competitive interactions between these two grazer types have been shown to be rather symmetrical in the absence of sculpin in experimental studies using laboratory channels (Kohler 1992, Kuhara et al. 1999). These imply that the effect of predator on the reduction in the *Glossosoma* density is expected to be smaller than that of competition ($X_G^{P0} > X_G^{0C}$).

The density of *Glossosoma* in the presence of both sculpin and mayfly grazers was greater than that in the presence of mayflies only ($\hat{X}_G^{PC} > X_G^{0C}$), whereas the densities of the mayfly grazers were similar in both conditions ($\hat{X}_M^{PC} = X_M^{0C}$). This difference in the trend between the two grazers could be explained by species-specific differences (b_M and b_G in eqs. 1) in the predator susceptibility in terms of behavioral suppression due to different predation pressures. We found differences in the magnitude of direct predation among the four grazers under natural conditions (*Ameletus* and *Baetis* were frequently preferred over *Glossosoma* by the sculpin). The greater behavioral response by mayflies than caddisflies (i.e. $b_M < b_G$) can be represented by the different positions of the blue lines in Fig. 5 (with the caddisfly isocline being much closer to the vertical, green line). Consequently, the model predicts a greater increase in caddisflies than mayflies. In reality, Kuhara et al. (1999) found that the magnitude of behavioral predator avoidance and therefore growth suppression of *Baetis* were both greater than in *Glossosoma*, in the presence of non-feeding sculpin.

Our results demonstrated predator-mediated inter-specific competition between the prey species, resulting in an increase in the density of the less vulnerable prey species, as has been found in previous studies (Paine 1966, Leibold 1991, Wootton 1992). In these previous studies, however, the increases in density of one prey species were always accompanied by decreases in the densities of other competing prey species. Therefore, it would be possible to simply explain the mechanisms responsible for the latter situation by differences in magnitude of the density-mediated effects among the prey species (e.g. selective predation). In contrast, behaviorally-mediated effects of the predator are necessary parts of the explanation of the present study results, in which the density of neither competing prey species (i.e. only competitive effect was operative) did decrease by the introduction of the predator. Such contradictions among these studies may be primarily attributed to variations in the strength of density- and behaviorally-mediated effects of predators on competing prey species among the targeted systems. Moreover, the theory predicted that the predator could provide non-negative impacts on the densities of more than one

competing prey species when the behaviorally-mediated effect was extremely strong relative to the density-mediated effect. We emphasize that evaluation of the relative importance of both density- and behaviorally-mediated effects provides an insight into the understanding of apparent coexistence patterns of competing species in a system including predators.

Acknowledgements – We are sincerely grateful to M. J. Toda, N. Yamamura and M. Higashi for critical comments on an early draft of the manuscript. We express our sincere thanks to members of the TOEF Stream Ecology Group for invaluable advice during the field studies. We are also grateful to staff of the Tomakomai Research Station, Hokkaido Univ. Forests, for their logistical support. This research was funded by the Japan Ministry of Education, Science, Sport and Culture (grant 09NP1501 to S. Nakano).

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