

Fish foraging effects on benthic assemblages along a warm-temperate stream: differences among drift feeders, benthic predators and grazers

Mikio Inoue and Masanobu Miyayoshi

Inoue, M. and Miyayoshi, M. 2006. Fish foraging effects on benthic assemblages along a warm-temperate stream: differences among drift feeders, benthic predators and grazers. – *Oikos* 114: 95–107.

In streams, physical and biotic conditions change from the headwaters to the mouth, shaping longitudinal patterns in community structure. We examined how fish foraging effects on periphyton and benthic invertebrates changed along a longitudinal gradient of a warm-temperate stream in southwestern Japan. We established three study sites according to changes in the composition of fish feeding guilds (upper site characterized by drifting-invertebrate feeders, *Oncorhynchus masou*; middle site by benthic invertebrate feeders, *Rhinogobius* spp.; lower site by the presence of periphyton grazers, *Sicyopterus japonicus*), and performed two manipulative experiments to examine effects of different fish assemblages on periphyton and benthic invertebrate abundances. Results of an enclosure experiment suggested that fishes had no effect on the benthic assemblages at the upper and middle sites whereas fishes reduced the abundances of both periphyton and invertebrates on stone surfaces at the lower site, where both benthic invertebrate feeders and grazers inhabited. A subsequent enclosure experiment showed that the reduction of invertebrate densities at the lower site was caused by the grazers rather than benthic invertebrate feeders. These experimental results suggested that effects of fishes on benthic assemblages are intensified downstream, owing to the occurrence of the grazing fish. Furthermore, observational data based on field sampling suggested that such grazing effects were reflected in longitudinal patterns in periphyton and invertebrate abundances. Overall results emphasize an important role of the grazing fish (*S. japonicus*) in shaping longitudinal patterns in benthic assemblage structure.

M. Inoue and M. Miyayoshi, Dept of Biology, Faculty of Science, Ehime Univ., Bunkyocho 2-5, JP-790-8577 Matsuyama, Japan (inom@sci.ehime-u.ac.jp). Present address for MM: Pacific Consultants Environment Co Ltd., Meinohama-eki, Minami 1, Nishi-ku, JP-819-0006 Fukuoka, Japan.

Fishes are a major vertebrate component of aquatic communities. They occupy various trophic roles, such as carnivore, herbivore, detritivore and omnivore, consuming a large amount of organisms. Therefore, feeding activities of fishes potentially have great influences on other community members. In lotic systems, however, effects of fishes on benthic invertebrate abundance are controversial (Allan 1983, Thorp 1986, Cooper et al. 1990, Wooster and Sih 1995). Although earlier studies tended to show little or no effect of fish predation on

invertebrate abundance (reviewed by Allan 1983, Thorp 1986), a growing number of studies has detected strong effects (Power 1992, Nakano et al. 1999, reviewed by Matthews 1998). Such variation in the strength of fish foraging effects on invertebrates has been explained by factors including differences in prey exchange rates (Cooper et al. 1990), habitat complexity (Power 1992, Rosenfeld 2000), and functional roles of predators (Dahl and Greenberg 1996, Dahl 1998) and prey (Rosenfeld 2000).

Accepted 18 November 2005
Subject Editor: Lennart Persson

Copyright © OIKOS 2006
ISSN 0030-1299

Cooper et al. (1990) suggested that much of the variation in predator impacts observed by field experiments can be explained by prey exchange rates. That is, in habitat patches where prey immigration rates are high (e.g. experimental cages with large mesh sizes), predator impacts (i.e. reduction of prey) can be offset by rapid immigration, whereas predator impacts tend to be evident in patches with low immigration rates (e.g. experimental cages with small mesh sizes). The predator impact is affected also by refuge availability for prey. For example, fish predation caused a strong trophic cascade on simple smooth substrate (e.g. bedrock, tile) whereas no effect was found in complex substrates (e.g. gravel with interstitial spaces) (Power 1992, Rosenfeld 2000). Another important aspect is foraging modes of fishes. In their review, Dahl and Greenberg (1996) suggested that benthic feeders have larger effects on invertebrate density than drift-feeding fishes. This finding has been supported by a subsequent field experiment (Dahl 1998). Fish foraging effects on invertebrates are caused not only through predation; grazing and detritivorous fishes have strong impacts on benthic invertebrates via resource depletion and/or modification of abiotic conditions (e.g. sediment distribution) (Flecker 1992, 1996, Gelwick et al. 1997). These indirect effects can be much greater than direct effects of predation (Flecker 1992).

Overall, the types and strengths of such interactions in communities vary greatly depending on environmental conditions, including experimental settings. Therefore, the variation in interaction strength should be evaluated in the context of natural environmental conditions. A useful approach to this is to conduct manipulative experiments simultaneously at multiple sites along environmental gradients (Menge et al. 1994, March et al. 2002). It is also important to examine whether interactions detected by controlled manipulations are reflected in patterns of community structure under natural conditions (McIntosh and Townsend 1996, Usio and Townsend 2004).

In streams, physical and biotic conditions change from the headwaters to the mouth, shaping longitudinal patterns in community structure (Vannote et al. 1980, Rahel and Hubert 1991). Thus the composition of fish feeding guilds also changes along longitudinal gradients. In temperate regions, headwater reaches shaded by riparian canopy are dominated by drifting-invertebrate feeders (e.g. salmonids), with benthic invertebrate feeders replacing them or co-occurring downstream (Rahel and Hubert 1991). Furthermore, periphyton grazers occur in unshaded downstream reaches where auto-trophic production is high (Lotrich 1973, Rahel and Hubert 1991). Fish foraging effects may vary along longitudinal gradients, according to such changes in fish guild composition. In this study, we examined how fish foraging effects on benthic invertebrates change along a longitudinal gradient in a warm-temperate stream of

southwestern Japan. We first describe longitudinal patterns in periphyton and benthic invertebrate abundances. Next, we present results of two field experiments that were designed to assess (1) if fish effects differ longitudinally and (2) if fishes of different feeding guilds have different effects. On the basis of the observational data and experimental results, we discuss the importance of fish foraging effects in shaping longitudinal patterns of benthic assemblages.

Methods

Study sites

The study was conducted in Kumomo Stream (32°50'N, 132°55'E; catchment area: 10.2 km²), a second-order stream that discharges directly into the Pacific Ocean on the southwestern coast of Shikoku, southwestern Japan. The stream originates at an elevation of 500 m and flows 10 km before entering the sea. Most of the catchment is covered with conifer plantations (*Cryptomeria japonica* and *Chamaecyparis obtusa*) and evergreen broad-leaved forests; only a small portion (0.2 km², i.e. 1.9% of the catchment) in the lower part is used for agriculture (rice paddy) and residence.

The stream is inhabited by at least 11 species of fishes (Table 2). Headwater reaches are dominated by a fluvial population of red-spotted masu salmon (*Oncorhynchus masou*), which are gradually replaced by cyprinids (*Zacco temminckii*, *Tribolodon hakonensis*) as water temperature increases downstream. The most abundant fishes in middle to downstream reaches are benthic fishes of the family Gobiidae (*Rhinogobius*, *Sicyopterus*). Considering the longitudinal changes in fish assemblage composition, we selected three study sites along the course of the stream (upper, middle and lower sites; Tables 1 and 2).

The upper, middle and lower sites were established at 7.3, 4.8 and 1.7 km upstream from the stream mouth, respectively. Although both upper and middle sites were located in conifer plantations, streamside vegetation contained evergreen broad-leaved trees and the channel was shaded by riparian canopy. At the lower site, the stream was less shaded, with a conifer plantation on one bank and rice paddy on the other side. Fish fauna in the upper site was characterized by a simple assemblage dominated by red-spotted masu salmon. This species is a typical drift feeder, feeding on both terrestrial and aquatic invertebrates (Nakano 1995). Both middle and lower sites were dominated by *Rhinogobius* species, which forage benthic invertebrates on the bottom (Inoue et al. 2005). The lower site supported a high density of a grazing goby (*Sicyopterus japonicus*), which exclusively feed on periphyton (Dotu and Mito 1955). Therefore, the upper, middle and lower sites were characterized by a drifting-invertebrate feeder, benthic invertebrate feeders

Table 1. General descriptions of the three study sites in Kumomo Stream.

Variable	Upper	Middle	Lower
Elevation (m)	320	110	10
Canopy cover (%)	80.0	70.6	19.0
Summer water temperature (min–max:°C)	18.3–21.3	20.0–22.8	21.3–24.5
Winter water temperature (min–max:°C)	10.5–12.0	11.0–12.5	10.5–12.5
Wetted channel width (mean and SD: m)	4.2 (1.6)	6.0 (2.1)	7.4 (1.7)
Water depth (mean and SD: cm)	25.5 (14.0)	26.5 (13.5)	39.5 (28.7)
Substrate composition (%)			
sand-gravel	6.0	11.8	13.0
pebble	17.0	10.6	6.0
cobble	33.0	31.7	62.0
boulder	34.0	45.9	17.0
bedrock	10.0	0.0	2.0

and a periphyton grazer, respectively, although benthic invertebrate feeders occurred at all sites.

At each site, we quantified fish abundance and stream habitat characteristics to provide general descriptions of the study sites (Tables 1 and 2). Fish density was estimated in riffles during July–August 2001 using the removal method of DeLury (1951). A riffle at each site was blocked with 5-mm mesh seines at the upper and lower ends (riffle length: 17, 13 and 11 m at upper, middle and lower sites, respectively), and three removal passes were made using an electrofishing unit (Model 12 Backpack Electrofisher, Smith-Root Inc.). Stream size (channel width and water depth), substrate composition, canopy cover and water temperature were quantified in a reach including pool-riffle sequences at each site (reach length: 76, 76 and 95 m at upper, middle and lower sites, respectively). Equally spaced transects with five equally spaced measuring points were set along each reach (4 m intervals at the upper site, and 5-m intervals at the middle and lower sites). Wetted channel width was measured at each transect and water depth was measured at each point. The dominant substrate type within a 25 × 25-cm quadrat at each point was classified as

sand-gravel (particle size < 17 mm), pebble (17–64 mm), cobble (65–256 mm), boulder (> 256 mm) or bedrock; substrate composition was expressed by their relative frequencies. Each measuring point was classified as being covered by canopy or not, to estimate percent canopy cover (frequency of covered points). These habitat surveys were conducted during August 2001. Water temperature was recorded in both summer and winter. A maximum–minimum thermometer was placed at each site from 23 July to 28 August 2001. Maximum and minimum temperatures were recorded four times at intervals of 5–10 days and were averaged to represent summer water temperature. Winter water temperature was represented by the maximum and minimum temperatures recorded during the period from 21 to 23 December 2002.

Field sampling for longitudinal patterns

At each site, we sampled periphyton and benthic and drifting invertebrates to describe longitudinal patterns in their abundances. Although drift was sampled only in

Table 2. Fish species found in Kumomo Stream. The density was estimated in a riffle at each site. Species that were not captured from the study riffles but found in pools are denoted by asterisks. Food abbreviation: TI =terrestrial invertebrate, AI =aquatic invertebrate; Guild abbreviation: DIF =drifting-invertebrate feeder, BIF =benthic-invertebrate feeder, PG =periphyton grazer.

Species	Main food	Feeding guild	Density (N m ⁻²)		
			Upper	Middle	Lower
Salmonidae					
<i>Oncorhynchus masou</i>	TI, AI	DIF	0.32	0.02	
Gobiidae					
<i>Rhinogobius</i> sp. LD	AI	BIF	0.03		
<i>Rhinogobius</i> sp. DA	AI	BIF	0.26	0.84	0.14
<i>Rhinogobius</i> sp. CO	AI	BIF		1.15	2.92
<i>Rhinogobius</i> sp. CB	AI	BIF			0.17
<i>Chaenogobius urotaenia</i>	AI	BIF			0.04
<i>Sicyopterus japonicus</i>	algae	PG			1.44
Osmeridae					
<i>Plecoglossus altivelis</i>	algae	PG			*
Cyprinidae					
<i>Zacco temminckii</i>	TI, AI, algae	DIF/BIF/PG		0.10	0.21
<i>Tribolodon hakonensis</i>	TI, AI, algae	DIF/BIF/PG		*	*
Anguillidae					
<i>Anguilla japonica</i>	Fish, AI	Piscivore/BIF	0.04	0.02	0.09

summer (August 2001), periphyton and benthic invertebrates were sampled in both summer and winter (December 2002). In winter, the effects of fishes on benthic invertebrates and periphyton are probably weaker than in summer, because the feeding activities of most fish decline in winter. In particular, grazing effects of *S. japonicus* are negligible, because they hibernate underneath cobbles or boulders (Dotu and Mito 1955).

Periphyton was sampled from the mainstream of riffles. We collected cobbles (longest dimension: 15–20 cm) from riffles at each site on 8–10 August 2001 for summer samples (six cobbles per site) and on 21 and 22 December 2002 for winter samples (ten cobbles per site). Periphyton on the surface of each cobble was removed from a 5 × 5-cm area with a toothbrush, and preserved in 5% formalin in the field. The samples were filtered onto precombusted and preweighted glass-fiber filters (Whatman GF/C) and dried at 60°C for 24 h. The filters were weighed, ashed at 550°C for 3 h, and reweighed to determine ash-free dry mass (AFDM) as a measure of periphyton standing crop.

In summer, to assess autotrophic production, we also measured accumulation rate of periphyton using enclosure cages (see “Experiment 1” for details). We placed 10 enclosure cages in riffles at each site. In each enclosure cage, bare cobbles, which were taken from dried bars and brushed to remove organic layers, were exposed for 15 days (from 24, 25 and 26 July 2001 at lower, middle and upper sites, respectively), after which one cobble per cage was sampled. Standing crop of periphyton on a 5 × 5 cm area of each cobble was measured as described above to obtain accumulation rate per 15 days under fish-free conditions (i.e. in enclosure).

Benthic invertebrates were sampled from riffles using individual cobbles as sampling units. Ten cobbles (longest dimension: 15–20 cm) were sampled from the mainstream of riffles at each site on 27 and 28 August 2001 and 21 and 22 December 2002. During sampling, a hand net with 0.25 mm mesh was placed immediately downstream of the cobble to catch dislodged invertebrates. Invertebrates were brushed from the cobble into a pan of water and the contents of the pan were sieved with the hand net. Invertebrates were preserved in 10% formalin in the field, sorted in the laboratory, and identified to family or order, with the exception of Tipulidae. Tipulids were identified to either *Antocha* or other tipulids, because the life mode of the former is different from the latter in that *Antocha* larvae build and live in a silk tube attached to a stone surface. Invertebrate density was expressed as the number of individuals per 100-cm² area of cobble surface. The surface area of each cobble was estimated from the weight of aluminum foil needed to completely wrap the cobble, using a regression relating foil weight to surface area.

Drifting invertebrates were sampled in a riffle at each site using drift nets (0.25-mm mesh, 25 × 25-cm opening) for 30 min. The sampling was conducted three times (from 09.00 h on 10 August and 09.00 and 17.00 h on 11 August), with three drift nets being set on each occasion (9 samples in total per site). To estimate the volume of water sieved, current velocity was measured at the center of the net openings using a current meter (Model CR-7, Cosmo Riken Inc., Kashihara). Six samples of benthic invertebrates, as a source of drift, were collected from riffles using a Surber sampler (0.0625-m² quadrat, 0.25 mm mesh) to quantify drift propensity. Both drift and Surber samples were preserved in 10% formalin in the field, sorted and identified to the same taxonomic level as above. Drift propensity was calculated for each taxon at each site as: the mean density in drift samples (the number of individuals per 100 m³ sieved water) divided by the mean density in the Surber samples (m⁻²) (Miyasaka and Nakano 1999).

To examine longitudinal differences in the abundances of periphyton and benthic and drifting invertebrates, we used analysis of variance (ANOVA) on log₁₀-transformed data. For periphyton accumulation rate, which was measured only in summer, among-site differences were examined using one-way ANOVA and subsequent Tukey-HSD multiple comparison test. For periphyton standing crop, two-way ANOVA with site and season as main factors was used. When a site or interaction effect was significant, among-site differences were examined separately by season, using Tukey-HSD test. Similarly, site effects on benthic invertebrate density were analyzed using two-way multivariate analysis of variance (MANOVA), whereas one-way MANOVA was used for drifting invertebrate density. In these MANOVAs, densities of total and four numerically dominant taxa (Baetidae, Heptageniidae, Chironomidae and *Antocha*) were treated as response variables. When a MANOVA was significant, univariate ANOVAs were performed for each variable. All analyses were performed using SPSS (SPSS Inc. 1997).

Experiment 1: among-site differences in fish effects

To examine longitudinal differences in fish foraging effects on benthic invertebrates and periphyton, we conducted an enclosure experiment in riffles at each site during the summer of 2001, using pairs of open and enclosure cages. The cages were made of 6 mm mesh and a wooden frame (40 × 50 × 40 cm). The mesh size was small enough to exclude most adult fish, but large enough to allow access by most invertebrates. Enclosure cages had mesh cloth on all the four sides and floor to exclude fishes, whereas open cages were open on the downstream end to allow fishes to freely enter. The floor of the cages was covered with gravel (5–20 mm in

diameter, 2–3 cm in depth), which was collected from dried bars and washed in flowing water.

In each cage, three plastic trays and four cobbles were placed as substrates for benthic invertebrates and periphyton, respectively. Each tray for invertebrates ($17 \times 11 \times 3$ cm) contained a cobble (longest dimension: 12–20 cm) underlain by gravel (2 cm deep in the tray). The cobbles were taken from riffles, with invertebrates on their surfaces being removed before they were placed on the tray. Care was taken not to disturb periphyton on the cobble surfaces while removing invertebrates. For periphyton, four cobbles taken from riffles in the same manner as for the trays were placed in each cage. In addition to these cobbles from the stream (i.e. with periphyton), four bare cobbles were placed to quantify accumulation rate of periphyton to assess autotrophic production (see above: “Field sampling for longitudinal patterns”).

Ten pairs of open and enclosure cages were arranged along riffles at each site, with the two cages within each pair being positioned contiguous to each other. To establish a “cageless” treatment, three trays for invertebrates and four cobbles (from the stream) for periphyton were placed around each pair of the cages. A fence of coarse mesh (130×40 cm; 6×6 cm mesh) was placed 50–100 cm upstream from each pair of cages for protection against large debris. The cages and fences were fixed using metal stakes and wire, and were cleaned daily throughout the experiment to prevent accumulation of trapped debris. The trays and cobbles for each treatment were placed on 24, 25 and 26 July 2001 at the lower, middle and upper sites, respectively. We measured water depth and current velocity at the center of each cage and at each of the four cobbles outside the cages to assess differences in habitat conditions among the treatments. Current velocity was measured at the surface, mid-depth and bottom at each point with a current meter (Model CR-7, Cosmo Riken Inc., Kashihara). Current velocity in each cage was represented by the mean value of the three velocities. Water depth and current velocity for cageless treatment at each location were represented by the mean values (four depths, 12 velocities). Current velocity did not differ significantly among the three treatments at each site (ANOVA, treatment effect: $F_{2,18} = 0.09$ – 1.08 ; $P = 0.361$ – 0.911 ; Table 3), although water depth differed ($F_{2,18} = 9.78$ – 12.12 ; $P < 0.001$): water depth in the cageless treatment was significantly greater than that in open and enclosure treatments (Table 3).

One cobble per treatment was sampled for periphyton on days 3, 9 and 15. For invertebrates, one tray per treatment was sampled once on day 12. We used only three cobbles and one tray per treatment for periphyton and invertebrate sampling, respectively, although four cobbles and three trays had been set. Invertebrates on the cobble surface and those in the gravel trays were

sampled separately. The cobble on a tray was collected with a hand net (0.25-mm mesh) placed immediately downstream; the tray was subsequently sampled in the same manner. Standing crop of periphyton (AFDM $\text{mg } 25 \text{ cm}^{-2}$) and density of invertebrates on cobble surfaces (number 100 cm^{-2}) and in gravel trays (number per tray = number 187 cm^{-2}) were quantified by the same procedures as those applied for the observational data on longitudinal patterns.

Differences in periphyton standing crop and invertebrate density among treatments were analyzed separately by site. For periphyton, we used a repeated measures ANOVA with day as the repeated measure, treatment as the main factor, and locations of ten pairs of cages as a blocking factor. If a repeated measures ANOVA detected a significant treatment effect or treatment \times day interaction effect, the treatment effect was examined separately by day using ANOVA (factor: treatment, block) and subsequent Tukey-HSD multiple comparison test. Effects on benthic invertebrate densities (total density and four dominant taxa on cobble surfaces and in gravel trays) at each site were analyzed using MANOVA (factor: treatment, block). When a MANOVA was significant, univariate ANOVAs and subsequent Tukey-HSD multiple comparison tests were performed for each variable. All variables were \log_{10} -transformed prior to analysis.

Experiment 2: effects of predation vs grazing

To separate effects of fish grazing and predation, we conducted an enclosure experiment in riffles at the lower site during the summer of 2002. Ten sets of three cages, which were identical to the enclosure cages used in the experiment 1, were arranged along riffles, with the following three treatments randomly assigned: (1) no fish, (2) predator (*Rhinogobius* sp. CO, 2 fish per cage: 10 fish m^{-2}), and (3) grazer (*S. japonicus*, 1 fish per cage: 5 fish m^{-2}). *Rhinogobius* sp. CO and *S. japonicus* added were 6.9 ± 0.8 cm (6.1 – 9.3 , $N = 20$) and 9.1 ± 0.8 cm (7.6 – 10.3 , $N = 10$) in total length, respectively (mean \pm SD, range). Predatory fish were represented by *Rhinogobius* sp. CO (benthic invertebrate feeder), which was numerically dominant at the lower site, and were stocked at a higher density than that of grazing fish to simulate their relative abundance under natural conditions at the lower site (Table 2). Although densities of both species in the cages were 3–4 times higher than natural densities estimated from overall area of a riffle (Table 2), the densities in the cages were within the natural range of local densities because their distribution was patchy within riffles.

On 27 July 2002, cages were placed in the stream and stocked with fishes; each cage included two plastic trays and three cobbles (from riffles) as substrates for benthic

Table 3. Water depth and current velocity in each treatment of experiment 1 and 2 (mean and SD). Water depth differed among the treatments in experiment 1: data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test within each site.

Experiment	Site	Treatment	Water depth (cm)	Current velocity (cm s^{-1})
Experiment 1	Upper	Cageless	24.7 (4.6) _a	16.1 (7.0)
		Open	22.4 (5.6) _b	17.2 (9.4)
		Exclosure	22.0 (5.5) _b	16.1 (6.4)
	Middle	Cageless	24.5 (3.3) _a	26.2 (11.0)
		Open	20.0 (2.7) _b	24.5 (8.2)
		Exclosure	19.4 (2.0) _b	25.0 (7.9)
	Lower	Cageless	23.8 (4.0) _a	22.7 (8.2)
		Open	19.0 (5.1) _b	22.5 (6.8)
		Exclosure	18.6 (5.0) _b	21.5 (7.7)
Experiment 2	Lower	No fish	21.7 (4.4)	24.8 (10.0)
		Predator	20.2 (4.4)	25.5 (10.6)
		Grazer	21.1 (5.4)	25.7 (8.9)

invertebrates and periphyton, respectively. The plastic trays for invertebrate sampling were identical to those used in the experiment 1. Water depth and current velocity were measured at the center of each cage. Both depth and velocity did not differ significantly among the treatments (depth: $F_{2,12} = 0.81$, $P = 0.469$; velocity: $F_{2,12} = 0.45$, $P = 0.647$; Table 3). One cobble per cage was sampled for periphyton on days 10 and 14; one tray per cage was sampled once for benthic invertebrates on day 14. At the end of the experiment, we found escapement of *S. japonicus* from three cages. Therefore, data from the three locations were excluded from the analysis. Periphyton standing crop and invertebrate densities were quantified and treatment effects on these were analyzed using repeated measures ANOVA or MANOVA. Detailed procedures for sampling, quantifications and statistical analyses were the same as those applied in the experiment 1.

Results

Longitudinal patterns

Accumulation rate of periphyton significantly differed among the three sites ($F_{2,27} = 26.36$, $P < 0.001$), with considerably higher rates occurring at the lower site (Fig. 1). A site effect was significant also on periphyton standing crop (site: $F_{2,42} = 50.26$, $P < 0.001$; season: $F_{1,42} = 6.19$, $P = 0.017$; site \times season: $F_{2,42} = 1.45$, $P = 0.247$), with that at the middle and lower sites being greater than at the upper site in both summer and winter (Fig. 1). Longitudinal pattern of the standing crop was different from that of the accumulation rate. In summer, although statistically insignificant, the mean standing crop of periphyton at the lower site was lower than that at the middle site, contrasting periphyton accumulation rate, which exhibited an exceedingly high value at the lower site.

Effects of site, season and their interaction were significant on overall benthic invertebrate densities

(MANOVA, site: $F_{10,102} = 18.48$, $P < 0.001$; season: $F_{5,50} = 22.66$, $P < 0.001$; site \times season: $F_{10,102} = 11.55$, $P < 0.001$). Univariate ANOVAs showed that their longitudinal patterns differed seasonally (Fig. 2). Significant site \times season interactions were found for all taxa except baetid mayflies (Baetidae: $F_{2,54} = 0.63$, $P = 0.539$; others: $F_{2,54} = 9.28$ – 44.72 , $P < 0.001$). In summer, the lower site had the lowest total density. In contrast, total density in winter increased downstream, mainly due to increases in chironomids and *Antocha*. Densities of chironomids and *Antocha* at the lower site were low in summer,

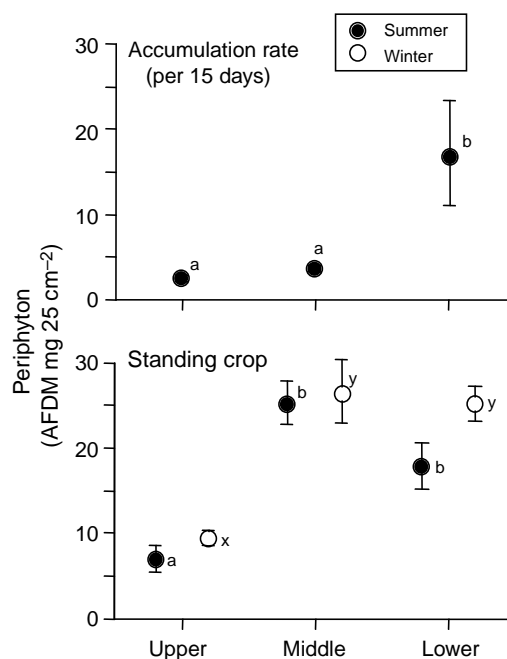


Fig. 1. Accumulation rate and standing crop of periphyton at each site along the stream. Accumulation rate was quantified only in summer. Data are shown as mean \pm 1 SE. Data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test after analysis of variance.

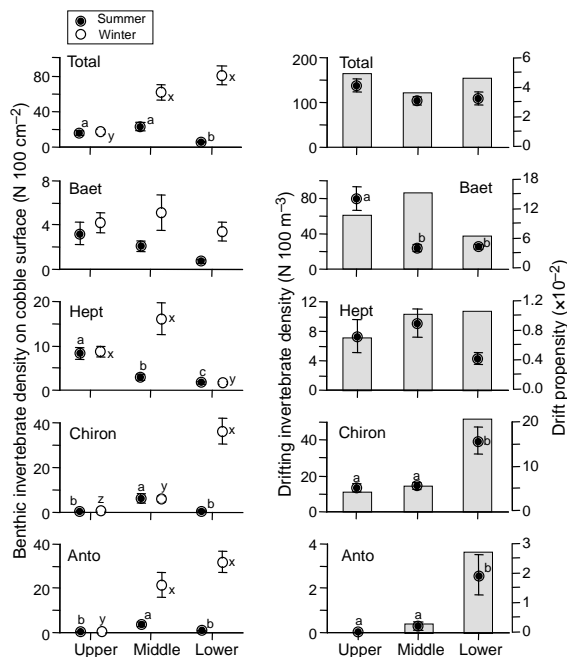


Fig. 2. Densities of benthic and drifting invertebrates at each site along the stream. Data are shown as mean \pm 1 SE; shaded columns in the right panels indicate drift propensity. Drift samples were taken only in summer. Data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test after analysis of variance. Total = total invertebrates; Baet = Baetidae; Hept = Heptageniidae; Chiron = Chironomidae; Anto = *Antocha*.

but became very high in winter, shaping patterns of downstream increases.

Overall drift densities differed significantly among the three sites (MANOVA, $F_{10,42} = 6.06$, $P < 0.001$, Fig. 2). Subsequent univariate ANOVAs indicated that site effects were significant on baetids ($F_{2,24} = 19.59$, $P < 0.001$), chironomids ($F_{2,24} = 7.89$, $P = 0.002$) and *Antocha* ($F_{2,24} = 9.14$, $P = 0.001$). For chironomids and *Antocha*, longitudinal patterns in drift density were different from those in benthic density (in summer). Their drift densities at the lower site were considerably higher than at the other two sites in spite of their lower benthic densities at the lower site. Consequently, drift propensities of chironomids and *Antocha* were highest at the lower site.

Among-site differences in fish effects

In experiment 1, a significant treatment effect on standing crop of periphyton was detected at the lower site (treatment: $F_{2,18} = 35.49$, $P < 0.001$; treatment \times day: $F_{4,36} = 3.39$, $P = 0.019$, Fig. 3), while no significant effects were found at the upper (treatment: $F_{2,18} = 0.36$, $P = 0.700$; treatment \times day: $F_{4,36} = 0.408$, $P = 0.802$) and middle sites (treatment: $F_{2,18} = 1.22$, $P = 0.319$;

treatment \times day: $F_{4,36} = 0.668$, $P = 0.618$). At the lower site, periphyton standing crop in enclosure cages was higher than in open and cageless treatments (Fig. 3).

Similarly, MANOVAs on invertebrate densities showed that treatment effects were significant only at the lower site (upper: $F_{16,24} = 0.79$, $P = 0.679$; middle: $F_{20,20} = 1.08$, $P = 0.434$; lower: $F_{20,20} = 3.74$, $P = 0.002$, Fig. 4). At the lower site, fish effects were more apparent on cobble surfaces than in gravel trays. In cobble samples, significant effects of treatment were detected for all taxa except heptageniids, with their densities being higher in enclosure than in open and cageless treatments (Table 4, Fig. 4). In gravel-tray samples, treatment effects were significant on heptageniids and chironomids (Table 4, Fig. 4). Heptageniid density was significantly higher in cageless than in enclosure treatments. Conversely, chironomid density was higher in enclosure than in cageless treatments. In both cases, however, their densities did not differ significantly between open and enclosure treatments.

Effects of predation vs grazing

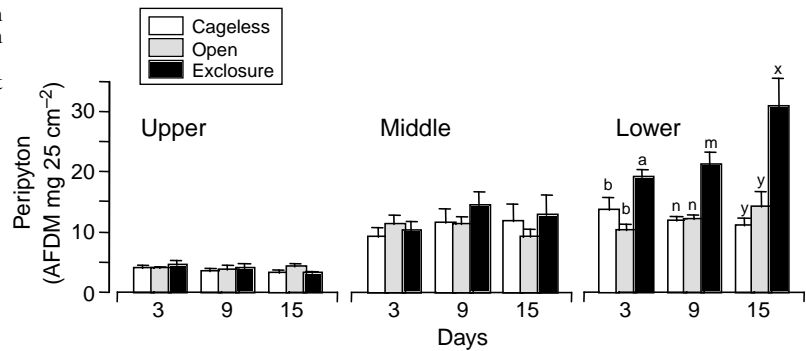
In experiment 2, significant effects of both treatment and treatment \times day interaction were detected for periphyton standing crop (treatment: $F_{2,12} = 15.86$, $P < 0.001$; treatment \times day: $F_{2,12} = 5.72$, $P = 0.018$, Fig. 5). Subsequent separate ANOVAs and multiple comparison tests indicated that periphyton standing crop in the grazer treatment was significantly lower than that in the predator and no fish treatments on both days 10 and 14 (Fig. 5).

For invertebrates, MANOVA detected a significant overall difference among the three treatments ($F_{20,8} = 10.41$, $P = 0.001$). Results of subsequent univariate ANOVAs were similar to those from experiment 1 (Table 5, Fig. 6). In cobble samples, treatment effects were detected for all taxa except heptageniids. Densities of total invertebrates, baetids and chironomids on cobble surfaces in the grazer treatment were significantly lower than those in the other two treatments. Although mean density of *Antocha* in the grazer treatment was the lowest, it was not significantly different from that in the no fish treatment. In gravel-tray samples, a treatment effect was significant only for chironomids, with their densities being lowest in the grazer treatment.

Discussion

Our enclosure experiment showed that fish effects on benthic invertebrates differed longitudinally: their effects were significant only at the lower site where both grazing and predatory fishes occurred. The second experiment at the lower site revealed that benthic invertebrate density

Fig. 3. Standing crop of periphyton in each treatment in experiment 1 at each site. Data are shown as mean \pm 1 SE. Data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test after analysis of variance.



was reduced by grazing rather than predation. Furthermore, our field observations suggest that grazing effects were reflected in longitudinal patterns in periphyton and invertebrate abundances. These findings emphasize an important role of fish grazing in shaping longitudinal patterns in benthic assemblage structure.

Fish predation effects on benthic invertebrate density at the middle site were expected to be larger than those at the upper site, because total fish density was higher at the middle site than at the upper site (Table 2) and benthic predatory fishes tend to have greater effects on prey density than drift-feeding fishes (Dahl and Greenberg 1996, Dahl 1998). However, no significant effects were found at the middle site as well as at the upper site. The lack of any significant effect of predation at the upper and middle sites may be related with the movement (immigration/emigration) of prey. Rapid prey

immigration can compensate for a loss of prey density caused by fish predation (Cooper et al. 1990). At the middle site of Kumomo Stream, we previously examined prey immigration rates and fish predation effects in relation to current velocity, using experimental cages similar to those used in the present study (Inoue et al. 2005). The previous results indicated that prey immigration rates tended to increase and fish predation effects tended to decrease with current velocity; as a result, reductions in density of a prey taxon (chironomids) by fishes were found in pools, whereas fishes had weak or no effects on them in riffles. Because the present experiments were conducted in riffles, effects of fish predation may have been obscured by a high immigration rate of prey.

Predatory fishes can cause both increases and decreases in prey drift rates (emigration rates) (Wooster

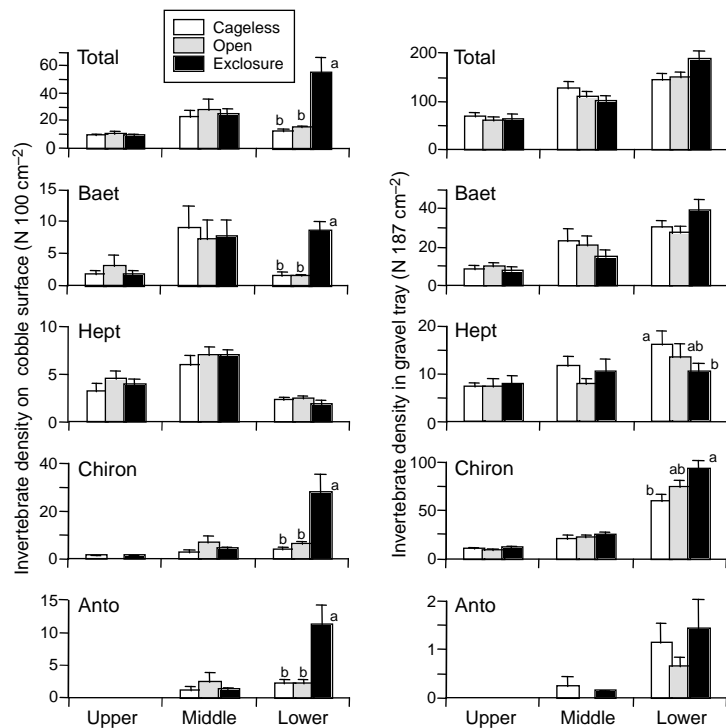


Fig. 4. Benthic invertebrate densities in each treatment in experiment 1 at each site. Data are shown as mean \pm 1 SE. Data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test after analysis of variance. See Fig. 2 for abbreviations.

Table 4. Summary of univariate ANOVAs testing for effects of treatment (cageless, open, and enclosure) on invertebrate densities on cobble surface and in gravel tray in experiment 1 at the lower site. df = 2, 18 for treatment effect; df = 9, 18 for block effect. Bold characters indicate statistical significance.

	Cobble surface		Gravel tray	
	F	P	F	P
Total density				
treatment	18.40	<0.001	3.25	0.062
block	1.15	0.378	1.53	0.210
Baetidae				
treatment	21.17	<0.001	2.53	0.108
block	1.24	0.333	4.23	0.004
Heptageniidae				
treatment	0.91	0.419	7.85	0.004
block	2.36	0.058	23.07	<0.001
Chironomidae				
treatment	13.56	<0.001	4.96	0.019
block	0.62	0.766	0.88	0.561
<i>Antocha</i>				
treatment	14.48	<0.001	0.54	0.595
block	2.23	0.071	1.63	0.182

and Sih 1995). In the latter case, predator-induced reductions in prey emigration can also obscure negative effects of predation on prey density (Wooster and Sih 1995, McIntosh et al. 1999). However, if behavioral responses of invertebrate prey to fish predators are elicited from chemical cues (fish odor) (McIntosh et al. 1999, Miyasaka and Nakano 2001), the lack of any predation effects on prey density at the upper and middle sites in the present experiment cannot be explained by predator-induced reductions in prey emigration. In the experiment 1, conditions of different treatments (cageless, open, enclosure) were likely to be similar in terms of fish odor, because our experimental units were small and positioned contiguous to each other.

Our experimental results corroborate previous work by Flecker (1992), who reported that, in a neotropical stream, indirect effects of grazing fishes on invertebrate densities were much greater than direct effects (consumption of invertebrates) of predatory fishes. At the

lower site of our stream, the predatory goby did not reduce the density of any invertebrates, whereas the grazing goby reduced not only periphyton standing crop, but also the density of baetids, chironomids and *Antocha*, resulting in a significant reduction in total invertebrate density on cobble surfaces. Probable mechanisms behind the reductions of invertebrates by fish grazers include resource depletion, bioturbation and intimidation by fish (Flecker 1992, Pringle et al. 1993, Gelwick et al. 1997).

Flecker (1992) attributed reductions of the abundance of most insect taxa by grazing fishes to factors associated with sediment removal (e.g. resource depletion, bioturbation). However, in the case of a baetid mayfly, he suspected that the reduction of its density was due to intimidation by grazing fishes rather than resource removal, because his experiment showed that this baetid was not negatively affected by manual sediment removal, which mimicked grazing effects (in the absence of grazing fishes). In our case, however, intimidation by fishes cannot account for the reduction of baetid mayflies. If intimidation influenced baetid mayflies in our stream, their density should have been reduced also by the predatory goby. Nevertheless, the predatory goby had no effect on baetid mayflies. Therefore, the reduction of baetids in our stream is most likely caused by resource depletion. The grazing goby reduced periphyton standing crop on stone surfaces. Reduced periphyton can increase emigration rates of invertebrates (Hildebrand 1974, Kohler 1985), and also may decrease immigration rates owing to the avoidance by colonizers, resulting in low invertebrate densities. Such effects of periphyton abundance on colonization/emigration dynamics have often been reported for baetid mayflies (Kohler 1985, Kuhara et al. 2000, Miyake et al. 2003),

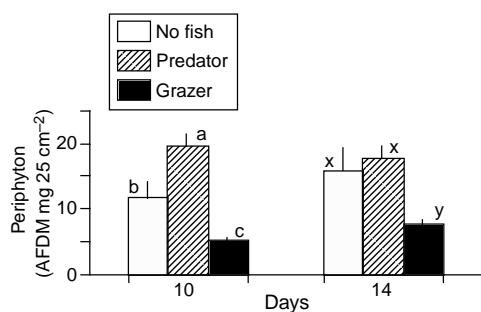


Fig. 5. Standing crop of periphyton in each treatment in experiment 2 at the lower site. Data are shown as mean \pm 1 SE. Data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test after analysis of variance.

Table 5. Summary of univariate ANOVAs testing for effects of treatment (no fish, predator, and grazer) on invertebrate densities on cobble surface and in gravel tray in experiment 2. df = 2, 12 for treatment effect; df = 6, 12 for block effect. Bold characters indicate statistical significance.

	Cobble surface		Gravel tray	
	F	P	F	P
Total density				
treatment	19.83	<0.001	1.70	0.225
block	0.56	0.752	2.80	0.061
Baetidae				
treatment	8.73	0.005	0.02	0.984
block	2.21	0.114	4.97	0.009
Heptageniidae				
treatment	0.87	0.445	2.08	0.168
block	2.22	0.113	4.69	0.011
Chironomidae				
treatment	17.03	<0.001	4.08	0.044
block	1.26	0.342	1.11	0.412
<i>Antocha</i>				
treatment	14.51	<0.001	0.39	0.687
block	1.11	0.410	0.98	0.479

which are mobile swimmers (Forrester 1994, Inoue et al. 2005). On the other hand, for tube-building clingers attaching to stone surfaces, such as *Antocha* and some

chironomids, bioturbation, as well as resource depletion, may be responsible for their reductions by the grazing fish. These attaching insects may be dislodged from stone surfaces while fish are grazing, and periphyton removal from stone surfaces should result in modification of physical structure of their habitat. A similar interpretation has been made by Pringle et al. (1993), who reported reductions of sediment and chironomids from substrate surfaces by feeding activities of omnivorous shrimps.

In contrast to baetids, chironomids and *Antocha*, the density of heptageniids was not reduced by fishes in both experiment 1 and 2. Because heptageniids generally feed on periphyton, the grazing goby was expected to have negative effects on their density through periphyton removal. Although it is unclear why heptageniids were not negatively affected through periphyton removal, similar cases can be found in some previous studies assessing effects of riparian canopy on invertebrate abundance. It was reported that heptageniid abundance in unshaded reaches (e.g. clear-cut areas), where periphyton tends to be more abundant, was not higher than in reaches with overhanging canopy, while other taxa (e.g. baetids, chironomids) were more abundant in unshaded reaches (Behmer and Hawkins 1986, Dudgeon 1988, Stone and Wallace 1998, but see *Cinygmula* in Behmer and Hawkins 1986). Heptageniids prefer smooth substrate surfaces to rough surfaces (Clifford et al. 1992). The lack of positive effects of periphyton abundance on heptageniid density might be related with their preference for smooth surfaces, because development of periphyton layer affect substrate-surface conditions.

Longitudinal patterns in benthic assemblages and their seasonal shifts shown by the field data are consistent with our experimental results. In summer, accumulation rate of periphyton (under fish-free

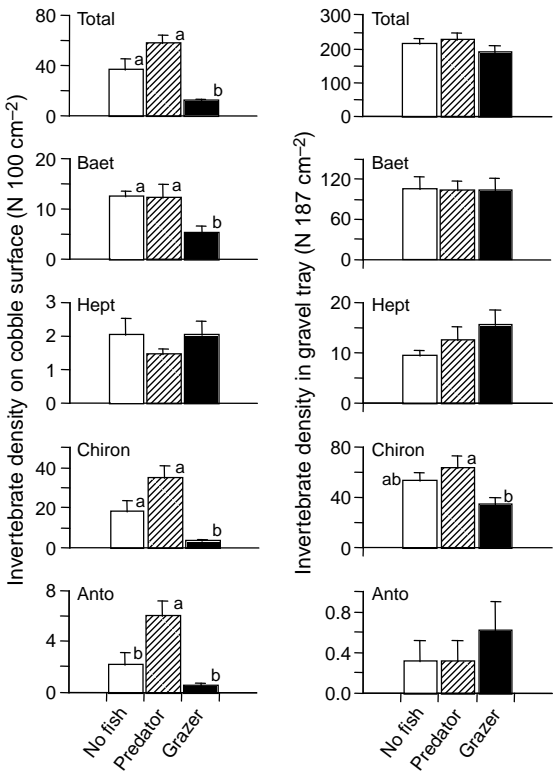


Fig. 6. Benthic invertebrate densities in each treatment in experiment 2 at the lower site. Data are shown as mean \pm 1 SE. Data denoted by the same letter are not significantly different ($P > 0.05$) by Tukey-HSD test after analysis of variance. See Fig. 2 for abbreviations.

conditions) varied longitudinally, with considerably higher rates at the lower site. Nevertheless, the mean standing crop at the lower site was lower than that at the middle site, although the difference was not statistically significant. These results indicate effective removal of periphyton by the grazing goby under natural conditions. Probably, longitudinal patterns in invertebrate densities in summer also reflected grazing effects shown by the experiments. In general, benthic invertebrates are more abundant in unshaded downstream reaches than in upper reaches shaded by riparian canopy, owing to higher autotrophic production in the former (Grubaugh et al. 1996). Chironomids typically exhibit positive responses to increases in light intensity and autotrophic production (Newbold et al. 1980, Behmer and Hawkins 1986, Stone and Wallace 1998). Similarly, *Antocha* tends to be more abundant in unshaded downstream reaches than in upper reaches (Grubaugh et al. 1996, Nunokawa and Inoue 1999). In our stream, however, summer densities of chironomids, *Antocha* and total invertebrates at the lower site, where autotrophic production was high, were significantly lower than those at the middle site. This suggests that the grazing goby has negative effects on invertebrates associated with stone surfaces, affecting longitudinal patterns in their abundances. This is furthermore corroborated by the data from winter. In winter, when the grazing goby hibernates, the densities of total invertebrates, chironomids and *Antocha* at the lower site became very high, exhibiting downstream increases along the stream.

The effects of the grazing goby on chironomids and *Antocha* may have involved increases of their drift propensity. Generally, the density of invertebrate drift increases with their benthic density (Hildebrand 1974, Walton 1980). Therefore, the drift densities of chironomids and *Antocha* at the lower site are expected to be lower than those at the middle site, in accordance with their benthic densities (Fig. 2). Nevertheless, their drift densities at the lower site were considerably higher, resulting in high values of the drift propensity. It has frequently been reported that fishes can increase the drift propensity of prey invertebrates through feeding activities or the presence of fishes per se (e.g. chemical cue) (Forrester 1994, Miyasaka and Nakano 1999, 2001, but see McIntosh et al. 1999, reviewed by Wooster and Sih 1995). Furthermore, reduction of resources can induce emigration, resulting in higher drift rates (Hildebrand 1974, Kohler 1985, Siler et al. 2001). Therefore, it is plausible that the grazing fish at the lower site increased the drift rates of invertebrates through resource depletion or grazing activities, which disturb stone surfaces (Gelwick et al. 1997). However, most studies examining the effects of fishes or resource levels on invertebrate drift have dealt with predatory fishes (e.g. trout, sculpin) and mobile mayflies (e.g. baetids) (Hildebrand 1974, Kohler 1985, Forrester 1994, McIntosh et al. 1999,

Miyasaka and Nakano 1999, 2001); information on drift mechanisms of epilithic insects, such as chironomids and *Antocha*, is scarce. Therefore, although our field data provide circumstantial evidence for increased drift rates by the grazing fish, experimental studies are needed to test such effects.

Overall, the results of the present study illustrate interactions among autotrophic resources, invertebrates and fishes along a longitudinal gradient of a stream. Because autotrophic production increases downstream, unshaded downstream reaches can support populations of grazing fishes, which in turn depress periphyton abundance, resulting in negative effects on benthic invertebrates. Traditionally, longitudinal patterns in the abundance and assemblage structure of benthic invertebrates have been examined in relation to longitudinal changes in energy base (autochthonous vs allochthonous, benthic vs drifting) and/or physical characteristics (e.g. flow, substrates) (Vannote et al. 1980, Grubaugh 1996, Rice et al. 2001). However, resource-mediated interactions with fishes have rarely been reported as a factor behind observed longitudinal patterns, probably because most studies were conducted in cool-temperate streams where grazing fishes were absent or negligible. Grazing fishes are known as strong interactors in tropical (Power 1990, Flecker 1992, Flecker and Taylor 2004) and some temperate streams (*Camptostoma*: Power et al. 1985, Gelwick et al. 1997). Similarly, the present results from a warm-temperate stream suggest that effects of the grazing goby, *Sicyopterus japonicus*, are strong enough to affect longitudinal patterns of benthic assemblages.

Several fish species of specialized grazers, such as some sicydiine gobies (e.g. *Sicyopterus*, *Lentipes*; Fitzsimons et al. 2002), southern grayling (*Prototroctes*; Berra 1982) and ayu (*Plecoglossus altivelis*; Iguchi and Hino 1996), are distributed among coastal and island streams of the Pacific Ocean, from temperate regions of the Western Pacific (e.g. eastern coast of Australia, New Zealand, Japan) through tropical islands of Micronesia to Hawaiian islands (Fitzsimons et al. 2002, McDowall 2004). The fact that these grazers are amphidromous species, which obligatorily migrate between freshwater and the ocean, has important management implications. Human activities that block upstream migration of the grazing fishes, such as dams, impoundments and water pollution, can exert their influences not only downstream but also upstream direction: disappearance of the grazing fishes from reaches above barriers is likely to cause dramatic changes in structure and function of stream communities.

Acknowledgements – We are grateful to Hisashi Miyatake, Yumiko Akamine, Shin Sone, Yuki Uchida, Masahiro Kunimoto and Chiharu Inoue for their help in the field and/or lab. We also thank Masanori Nunokawa for advice on the

identification of invertebrates. Naotoshi Kuhara, Kenji Yoshino, Yo Miyake and Todd Miller provided helpful advice.

References

- Allan, J. D. 1983. Predator-prey relationships in streams. – In: Barnes, J. R. and Minshall, G. W. (eds), *Stream ecology: application and testing of general ecological theory*. Plenum Press, pp. 191–229.
- Behmer, D. J. and Hawkins, C. P. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. – *Freshw. Biol.* 16: 287–300.
- Berra, T. M. 1982. Life history of the Australian grayling, *Prototroctes maraena* (Salmoniformes: Prototroctidae) in the Tambo River, Victoria. – *Copeia* 1982: 795–805.
- Clifford, H. F., Casey, R. J. and Saffran, K. A. 1992. Short-term colonization of rough and smooth tiles by benthic macroinvertebrates and algae (chlorophyll *a*) in two streams. – *J. N. Am. Benthol. Soc.* 11: 304–315.
- Cooper, S. D., Walde, S. J. and Peckarsky, B. L. 1990. Prey exchange rates and the impact of predators on prey populations in streams. – *Ecology* 71: 1503–1514.
- Dahl, J. 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. – *Oecologia* 116: 426–432.
- Dahl, J. and Greenberg, L. 1996. Impact on stream benthic prey by benthic vs drift feeding predators: a meta-analysis. – *Oikos* 77: 177–181.
- DeLury, D. B. 1951. On the planning of experiments for the estimation of fish populations. – *J. Fish. Res. Board. Can.* 8: 281–307.
- Dotu, Y. and Mito, S. 1955. Life history of a gobioid fish, *Sicydium japonicum* Tanaka. – *Sci. Bull. Fac. Agr. Kyushu Univ.* 15: 213–221 (in Japanese with English summary).
- Dudgeon, D. 1988. The influence of riparian vegetation on macroinvertebrate community structure in four Hong Kong streams. – *J. Zool. Lond.* 216: 609–627.
- Fitzsimons, J. M., Parham, J. E. and Nishimoto, R. T. 2002. Similarities in behavioral ecology among amphidromous and catadromous fishes on the oceanic islands of Hawaii and Guam. – *Environ. Biol. Fish.* 65: 123–129.
- Flecker, A. S. 1992. Fish trophic guilds and the structure of a tropical stream: weak direct vs strong indirect effects. – *Ecology* 73: 927–940.
- Flecker, A. S. 1996. Ecosystems engineering by a dominant detritivore in a diverse tropical stream. – *Ecology* 77: 1845–1854.
- Flecker, A. S. and Taylor, B. W. 2004. Tropical fishes as biological bulldozers: density effects on resource heterogeneity and species diversity. – *Ecology* 85: 2267–2278.
- Forrester, G. E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. – *Ecology* 75: 1208–1218.
- Gelwick, F. P., Stock, M. S. and Matthews, W. J. 1997. Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river ecosystem. – *Oikos* 80: 382–398.
- Grubaugh, J. W., Wallace, J. B. and Houston, E. S. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. – *Can. J. Fish. Aquat. Sci.* 53: 896–909.
- Hildebrand, S. G. 1974. The relation of drift to benthos density and food level in an artificial stream. – *Limnol. Oceanogr.* 19: 951–957.
- Iguchi, K. and Hino, T. 1996. Effect of competitor abundance on feeding territoriality in a grazing fish, the ayu *Plecoglossus altivelis*. – *Ecol. Res.* 11: 165–173.
- Inoue, M., Miyayoshi, M. and Sone, S. 2005. Foraging modes of stream benthic fishes in relation to their predation effects on local prey density. – *Ecol. Res.* 20: 151–161.
- Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. – *Ecology* 66: 1749–1761.
- Kuhara, N., Nakano, S. and Miyasaka, H. 2000. Flow rate mediates the competitive influence of a grazing caddisfly on mayflies. – *Ecol. Res.* 15: 145–152.
- Lotrich, V. A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. – *Ecol. Monogr.* 43: 377–397.
- March, J. G., Pringle, C. M., Townsend, M. J. et al. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. – *Freshw. Biol.* 47: 377–390.
- Matthews, W. J. 1998. Effects of fish in ecosystems. – In: Matthews, W. J. (ed.), *Patterns in freshwater fish ecology*. Chapman & Hall, pp. 565–616.
- McDowall, R. M. 2004. Ancestry and amphidromy in island freshwater fish faunas. – *Fish Fish.* 5: 75–85.
- McIntosh, A. R. and Townsend, C. R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? – *Oecologia* 108: 174–181.
- McIntosh, A. R., Peckarsky, B. L. and Taylor, B. W. 1999. Rapid size-specific changes in the drift of *Baetis bicaudatus* (Ephemeroptera) caused by alterations in fish odour concentration. – *Oecologia* 118: 256–264.
- Menge, B. A., Berlow, E. L., Blanchette, C. A. et al. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. – *Ecol. Monogr.* 64: 249–286.
- Miyake, Y., Hiura, T., Kuhara, N. et al. 2003. Succession in a stream invertebrate community: a transition in species dominance through colonization. – *Ecol. Res.* 18: 493–501.
- Miyasaka, H. and Nakano, S. 1999. Effects of drift- and benthic-foraging fish on the drift dispersal of three species of mayfly nymphs in a Japanese stream. – *Oecologia* 118: 99–106.
- Miyasaka, H. and Nakano, S. 2001. Drift dispersal of mayfly nymphs in the presence of chemical and visual cues from diurnal drift- and nocturnal benthic-foraging fishes. – *Freshw. Biol.* 46: 1229–1237.
- Nakano, S. 1995. Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. – *J. Anim. Ecol.* 64: 75–84.
- Nakano, S., Miyasaka, H. and Kuhara, N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. – *Ecology* 80: 2435–2441.
- Newbold, J. D., Erman, D. C. and Roby, K. B. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. – *Can. J. Fish. Aquat. Sci.* 37: 1076–1085.
- Nunokawa, M. and Inoue, M. 1999. Patterns of benthic insect assemblages in relation to riparian vegetation in a small stream, northern Hokkaido, Japan. – *Jpn. J. Limnol.* 60: 385–397 (in Japanese with English summary).
- Power, M. E. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. – *Ecology* 71: 897–904.
- Power, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. – *Ecology* 73: 1675–1688.
- Power, M. E., Matthews, W. J. and Stewart, A. J. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. – *Ecology* 66: 1448–1456.
- Pringle, C. M., Blake, G. A., Covich, A. P. et al. 1993. Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. – *Oecologia* 93: 1–11.
- Rahel, F. J. and Hubert, W. A. 1991. Fish assemblages and habitat gradient in a Rocky Mountain – Great Plains

- stream: biotic zonation and additive patterns of community change. – *Trans. Am. Fish. Soc.* 120: 319–332.
- Rice, S. P., Greenwood, M. T. and Joyce, C. B. 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. – *Can. J. Fish. Aquat. Sci.* 58: 824–840.
- Rosenfeld, J. 2000. Effects of fish predation in erosional and depositional habitats in a temperate stream. – *Can. J. Fish. Aquat. Sci.* 57: 1369–1379.
- Siler, E. R., Wallace, J. B. and Eggert, S. L. 2001. Long-term effects of resource limitation on stream invertebrate drift. – *Can. J. Fish. Aquat. Sci.* 58: 1624–1637.
- SPSS Inc. 1997. *SPSS Advanced Statistics 7.5*. – SPSS Inc.
- Stone, M. K. and Wallace, J. B. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. – *Freshw. Biol.* 39: 151–169.
- Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. – *Oikos* 47: 75–82.
- Usio, N. and Townsend, C. R. 2004. Roles of crayfish: consequences of predation and bioturbation for stream invertebrates. – *Ecology* 85: 807–822.
- Vannote, R. L., Minshall, G. W., Cummins, K. W. et al. 1980. The river continuum concept. – *Can. J. Fish. Aquat. Sci.* 37: 130–137.
- Walton, O. E. 1980. Invertebrate drift from predator-prey associations. – *Ecology* 61: 1486–1497.
- Wooster, D. and Sih, A. 1995. A review of the drift and activity responses of stream prey to predator presence. – *Oikos* 73: 3–8.