

# Reports

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## TERRESTRIAL–AQUATIC LINKAGES: RIPARIAN ARTHROPOD INPUTS ALTER TROPHIC CASCADES IN A STREAM FOOD WEB

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**Abstract.** Dynamics of headwater stream ecosystems are generally regarded as occurring at the interface of aquatic and terrestrial ecosystems. Terrestrial arthropod inputs can provide an energy subsidy and increase the abundance of predatory fish, and the ensuing effects potentially can cascade through the food web and ultimately affect primary producers. Nevertheless, the community-based effects of such inputs on stream food web dynamics are still poorly understood. We present experimental evidence that terrestrial arthropod inputs have an indirect but prominent effect on a stream benthic community by altering the intensity of fish predation in the food web. Two key elements of the stream food web, terrestrial arthropod inputs and the presence of predatory fish, were experimentally manipulated by using greenhouse-type covers and enclosures (or exclosures) in a forest stream located in northern Japan. When terrestrial arthropod inputs to the stream were experimentally reduced, fish predation pressure shifted dramatically from terrestrial to aquatic arthropods. The ensuing depletion of aquatic arthropods resulted in a subsequent increase in periphyton biomass. This field experiment revealed that terrestrial arthropod inputs were a primary factor controlling cascading trophic interactions among predatory fish, herbivorous aquatic arthropods, and benthic periphyton. These results provide empirical support for the perspective that transfers of energy and biomass from donor systems are frequently significant for the maintenance of biotic communities in recipient systems.

**Key words:** fish predation; food webs; forest stream; periphyton; stream arthropods; terrestrial arthropod; trophic cascades.

### INTRODUCTION

Ecosystems are rarely bounded by the area selected for study, and external factors have the potential to substantially affect the patterns and dynamics of a focal system. The effects of these across-habitat influences can often exceed internal factors (Polis and Hurd 1996, Polis et al. 1996, 1997). Food web dynamics occurring in a focal habitat, in particular, are often influenced strongly by trophic linkages, the movements of nutrient, detritus, and prey organisms across contiguous habitats (Polis et al. 1996, 1997). For example, allochthonous inputs of prey species can allow consumer populations in recipient habitats to increase, and these subsidized consumers in turn can depress in situ prey

items (Polis and Hurd 1996). Few experimental studies, however, have tested for the effects of allochthonous prey inputs on trophic cascading interactions in natural habitats with the direct manipulation of prey flux at the habitat interface.

Dynamics of headwater stream ecosystems are generally regarded as occurring at the interface of aquatic and terrestrial ecosystems (i.e., the stream ecotone) where food web dynamics are influenced in complex ways by both in situ primary productivity and allochthonous inputs from the terrestrial landscape (Vannote et al. 1980, Naiman and Décamps 1997). In particular, inputs of particulate organic matter from terrestrial ecosystems represent an important energy source of production in most headwater streams of temperate deciduous forests. Most studies, however, have focused on the input of terrestrial plant matter, which is only indirectly available to top consumers such as predatory fish via invertebrate secondary production (Cummins

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et al. 1995, Wallace et al. 1997). Terrestrial arthropods that accidentally fall into stream channels represent a high-quality (i.e., low C:N ratio) food resource that is directly available to fishes (Mason and MacDonald 1982, Garman 1991, Garman and Moring 1992, Edwards and Huryn 1996, Wipfli 1997). This allochthonous input, which often exceeds total in situ aquatic secondary productivity (Cloe and Garman 1996), can provide a tremendous energy subsidy and can increase the abundance of predatory fish; the ensuing effects on consumers can cascade through the food web and ultimately affect resident primary producers. Nevertheless, the community-based impact of such allochthonous inputs via a cascading trophic interaction are poorly understood. We present experimental evidence that terrestrial arthropod inputs have an indirect but prominent effect on a stream benthic community by altering the intensity of fish predation in the stream's food web.

#### MATERIALS AND METHODS

A manipulative field experiment was conducted in the Horonai Stream in the Tomakomai Experimental Forest of Hokkaido University (TOEF; 42°43' N, 141°36' E) in Hokkaido, the northernmost island of the Japanese archipelago. The riparian zone of this small, cold, spring-fed stream (15.4 km<sup>2</sup> in drainage area, 14 km in total length, 2–5 m width, gradient <1%) is covered with a secondary-growth deciduous forest dominated by oak (*Quercus crispula*), ash (*Fraxinus mandshurica*), and maple (*Acer mono*). Approximately 95% of the entire width of the stream is covered by forest canopy. In the Horonai Stream, discharge usually remains stable throughout the year (annual average discharge, 0.24 m<sup>3</sup>/s), with major disturbances rarely occurring. Three common fish species inhabiting the water column are Dolly Varden (*Salvelinus malma*), white-spotted char (*S. leucomaenis*), and rainbow trout (*Oncorhynchus mykiss*), all of which consume both terrestrial and aquatic arthropods. Terrestrial arthropod inputs to the stream measured from early July 1995 to late July 1996, varied considerably among seasons, peaking during summer (June to August; S. Nakano, unpublished data). These fishes consumed, on average, 60% of the total terrestrial arthropod input during the summer, which contributed ~56% of their annual energy (S. Nakano, unpublished data).

Terrestrial arthropod inputs and the presence of predatory fish were experimentally manipulated at the reach scale in the stream during four weeks of early summer (June–July) in 1995. The four experimental treatments (reduced arthropod inputs with fish present, natural arthropod inputs with fish present, reduced arthropod inputs with fish absent, and natural arthropod inputs with fish absent) with two replications of each, were ran-

domly assigned to eight 25 m long reaches (100-m<sup>2</sup> surface area) over a 1.3-km stretch of the stream. Each experimental reach was separated from those immediately adjacent by at least 100 m long unmanipulated reaches. The greenhouse-type covers (5 m wide, 2.5 m high, and 50 m long), which were made of transparent plastic sheets supported by aluminum frames, were constructed so as to cover the entire experimental reach plus 25 m upstream (Fig. 1). Both ends of the cover were blocked to the water surface with 1-mm mesh linen to prevent flying insects from entering the greenhouse. Two roof windows (1 m long and 4 m wide; Fig. 1) at both ends of the cover allowed emerging aquatic insects to escape. The average air temperatures under the covers were ~1°C higher than outside, but water temperatures did not differ. Although light attenuation by the covers averaged 13.2%, such effects were within the natural range of variation in natural lighting conditions due to canopy cover differences among the reaches. Consequently, relative photon flux density above the water surface did not differ among the four treatments (Table 1). Other physical characteristics, depth, current velocity, and discharge, of the stream habitat did not differ among the four treatments (Table 1).

Predatory fish were controlled with enclosures or exclosures of 10-mm mesh walls, which allowed passage of all aquatic arthropods but not fish, excepting fry. Only two to five small salmonid fry (<3 cm in fork length), however, were captured in each study reach during the experiment. The mesh walls were cleaned every 6 h during the experiment. All fish were first removed from all of the experimental reaches by nine-pass electrofishing and four reaches were stocked with 40 Dolly Varden, after 2 wk. The fork length of fish did not differ among the two fish-present treatments (Table 1). Fish density in the enclosures (0.4/m<sup>2</sup>) was about average for stream salmonids in the Horonai Stream, as well as in other forested streams in Hokkaido (Fausch et al. 1994, Kitano et al. 1995; S. Nakano, unpublished data).

The daily input of terrestrial arthropods in each experimental reach was estimated by measuring both falling and drifting inputs once per week during the experiment (totaling four times). The daily input of falling terrestrial arthropods was estimated from samples collected by five pan traps (100 × 100 cm area, 15 cm depth). The traps were filled with water plus 2–3 drops of surfactant, and set across the entire length of the experimental reaches. The pan contents were sieved (with 250-μm mesh) after a 3-d deployment. The drifting inputs into the reaches were censused at three locations across the upstream end of each reach with Nitex drift nets (Shiga-Konchuu Incorporated, Tokyo, Japan; 20 × 20 cm opening, 80 cm long, 250-μm

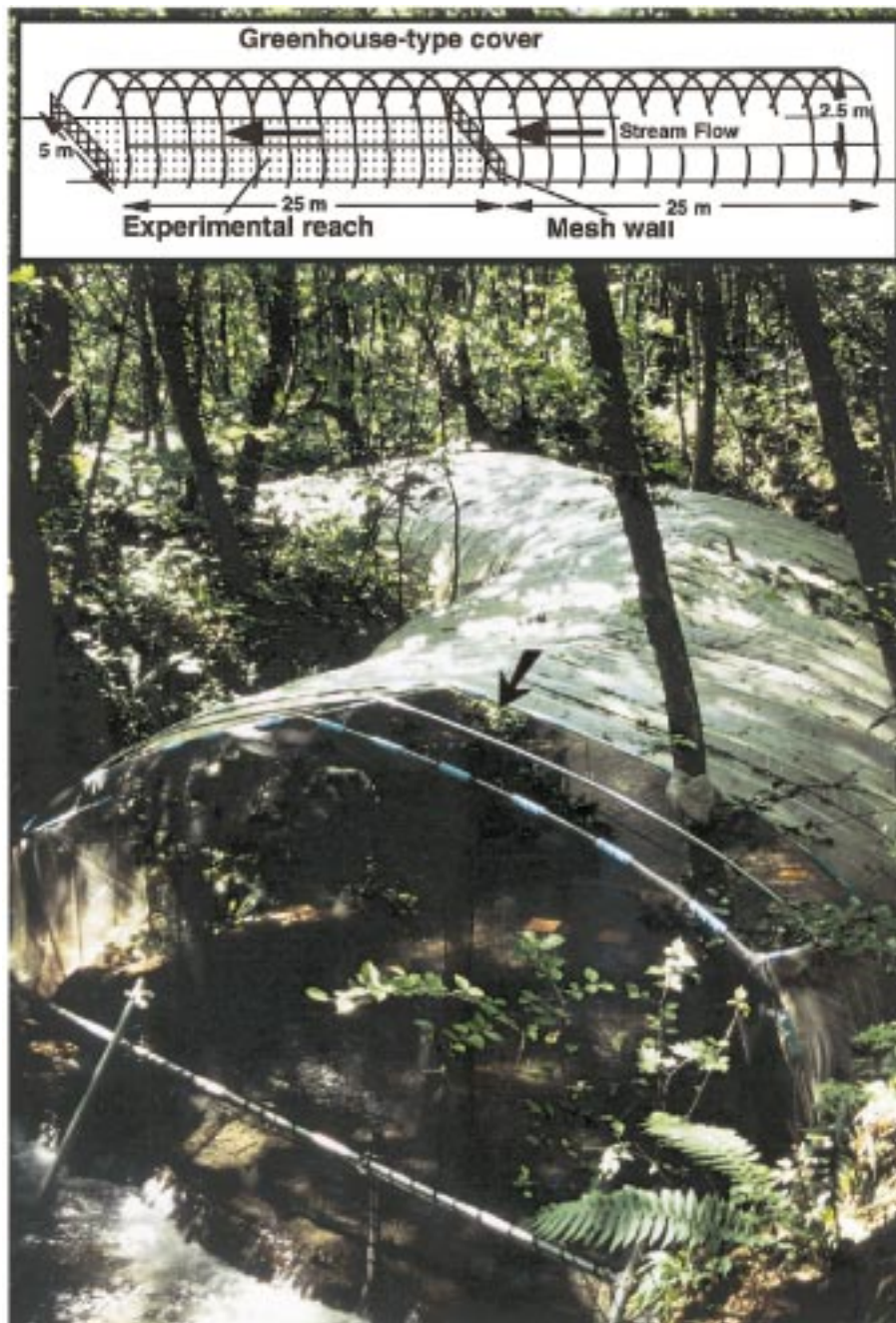


Fig. 1. A photograph and a diagram showing a study reach and the greenhouse-type cover used for experimental reductions of the terrestrial arthropod input from the canopy. An arrow in the photograph points to a roof window, which allowed emerging aquatic insects to escape from the cover.

mesh). The nets were deployed for 30 min two times per day (between 0600 and 0800, and 1800 and 2000) concurrently with their openings extending above the water surface to capture the floating terrestrial arthropods. Water volume sampled was estimated from the

current velocity measured at the center of each net opening using a portable current meter (Model CR-7, Cosmo-Riken Incorporated, Kashihara, Japan; Tanida et al. 1985). All samples were preserved in 70% ethanol until analyzed.

TABLE 1. Habitat characteristics (mean  $\pm$  1 SE) of stream reaches with the four experimental treatments.

Variables	<i>n</i>	Treatment			
		Fish		No fish	
		Reduced input	Natural input	Reduced input	Natural input
Fish fork length (mm)	80	130 $\pm$ 2	132 $\pm$ 2	...	...
Depth (cm)	100	20.6 $\pm$ 0.9	21.5 $\pm$ 1.0	21.4 $\pm$ 0.6	21.9 $\pm$ 0.7
Current velocity (cm/s)	100	30.9 $\pm$ 1.2	31.7 $\pm$ 1.0	31.1 $\pm$ 0.9	34.6 $\pm$ 1.2
Discharge (m <sup>3</sup> /s)	4	0.27 $\pm$ 0.01	0.26 $\pm$ 0.02	0.27 $\pm$ 0.01	0.27 $\pm$ 0.02
Relative photon flux (%)	20	3.2 $\pm$ 0.2	3.0 $\pm$ 0.2	2.9 $\pm$ 0.3	3.1 $\pm$ 0.3

Note: Experimental treatments were: reduced terrestrial arthropod input with predatory fish; natural input with fish; reduced input with fish absent; and natural input with fish absent. Sample sizes (*n*) are the same for all the treatments.

On days 14 and 28 of the experiment, biomass of aquatic arthropods and periphyton was measured from samples collected from bricks in each of the eight reaches. Forty-eight bricks (20  $\times$  20  $\times$  5 cm high) had been placed on the streambed of each study reach for 2 mo before the onset of the experiment so that the bricks were sufficiently colonized by benthic organisms at the beginning of the experiment. On each sampling date, all aquatic arthropods were collected with a 100- $\mu$ m mesh Surber net sampler (Miura-Rika Incorporated, Sapporo, Japan; 25  $\times$  25  $\times$  100 cm long) from 16 bricks randomly chosen from the entire length of the study reaches. These samples were preserved in 70% ethanol until analyzed. In addition, periphyton was removed from the entire top surface of the bricks with a steel brush, and preserved in 2% formalin solution until analyzed.

Stomach contents of 17–42 (26 on average) fish (Dolly Varden) stocked in the experimental reaches were examined just after each benthic organism sampling procedure. On days 14 and 28 of the experiment, fish were captured between 1600 and 1900 with a backpack electrofishing unit (Model 12, Smith-Root Incorporated, Vancouver, Washington, USA). Captured fish were anesthetized (with 2-amino-4-phenylthiazole hydrobromide) and the stomach contents were examined using a stomach pumping method, which employed a 2-mL pipette to flush prey items from the entire stomach region (Giles 1980). Captured fish were then released into the original experimental reaches. Stomach contents samples were preserved in 70% ethanol until analyzed.

Pan trap, drift, benthos, and stomach contents samples were first sorted as terrestrial and aquatic arthropods, which were identified to species when possible at 10 $\times$  magnification under a binocular microscope. The biomass of each category was measured as dry mass to the nearest 0.01 mg after drying at 60°C for 24 h. Aquatic insect adults, which contributed to <3% of the total biomass in each sample, were excluded from all the analyses. For analyses of fish diets, all aquatic arthropods were grouped into families. The per-

centage of dry mass contributed by each prey category was determined for each individual fish, and averaged for each experimental reach. Drift biomass (g/m<sup>3</sup>) was calculated by dividing the total mass of terrestrial arthropods retained in each net by water volume sieved. Daily input of drifting arthropods was then estimated by multiplying by daily stream discharge. Subsamples of the well-mixed periphyton suspension were collected on glass fiber filters, which had been precombusted at 450°C for 2 h. The filters were then 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 periphyton ash-free dry mass (AFDM).

During the experiment, five taxa of mayflies, *Epeorus latifolium*, *Cinygmula* spp. (Heptageniidae), *Baetis thermicus* (Baetidae), *Paraleptophlebia chocorata* (Leptophlebiidae), and *Drunella* spp. (Ephemereillidae), two stone flies, *Protonemura* spp. (Nemouridae) and *Alloperla* spp., a midge, *Diamesa* spp. (Chironomidae), and an amphipod, *Jesogammarus jesoensis* (Gammaridae), were dominant components of the aquatic arthropod assemblage on the bricks. Seven of these nine taxa, which contributed to 80.6% of the total biomass when all the samples were combined, were herbivorous arthropods (grazer-scraper or collector-gatherer), which can graze on periphyton. Two omnivorous insects, *Drunella* spp. and *Alloperla* spp., accounted for 6.5% of the total biomass, the remaining 12.9% was composed of other trophic guilds. In the present study, only the herbivorous arthropods were examined.

Mean values for herbivorous arthropod and periphyton biomass recorded in each reach on days 14 and 28 of the experiment were first analyzed with a repeated-measures ANOVA, with treatments as the main effect. Both daily inputs of terrestrial arthropods and the mean percentage of each dietary category for fish captured were analyzed with a repeated-measures ANOVA, with the presence of greenhouse-type cover as the main effect. When all within-subject effects were not significant for each of the above, differences among treatments were assessed by Fisher's least significant



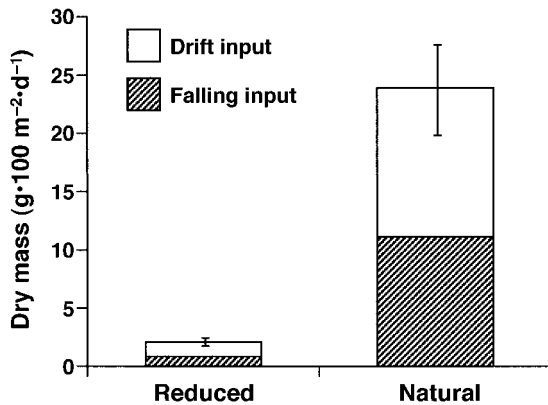


FIG. 2. Comparison of total terrestrial arthropod inputs (mean  $\pm$  1 SE,  $n = 8$ ) to experimental reaches in treatments with reduced vs. natural terrestrial arthropod inputs in the Horonai Stream. Fish present and absent treatments were combined in each of the reduced and natural inputs treatments.

difference (LSD) multiple contrasts with the within-subject effects being dropped. Log<sub>10</sub>-transformations of exact values and arcsine square-root transformations for percentage data were performed in order to standardize variances and improve normality.

### RESULTS

In the natural input treatment, the mean falling input of terrestrial arthropods was 11.2 g·100 m<sup>-2</sup>·d<sup>-1</sup>. The terrestrial arthropod input was effectively reduced by a greenhouse-type covering over the entire channel width (Fig. 2). The total of the falling and drifting inputs in the natural input treatments was far greater than those in the reduced input treatments, as revealed by a highly significant between-subject effect ( $F_{1,6} = 397.36$ ,  $P < 0.001$ ). Both within-subject effects, however, were also significant (period,  $F_{3,18} = 24.34$ ,  $P < 0.001$ ; period by treatment,  $F_{3,18} = 3.80$ ,  $P = 0.029$ ), revealing the temporal fluctuation of the inputs.

The diet composition by dry mass of Dolly Varden largely differed between the reduced and natural input treatments (Fig. 3). In the latter treatment, more than half of the fish diet comprised terrestrial arthropods. In contrast, terrestrial arthropods comprised a very small portion of the diet in the reduced input treatment, with the proportion of midge larvae being considerably higher. The main effect was significant for both the percentages of midge larvae ( $F_{1,2} = 123.27$ ,  $P = 0.008$ ) and terrestrial arthropods ( $F_{1,2} = 295.60$ ,  $P = 0.003$ ), but not for those of any other categories ( $F_{1,2} < 2.69$ ,  $P > 0.242$  for all). No within-subject effects were significant for any of the prey categories (period,  $F_{1,2} < 2.30$ ,  $P > 0.269$ ; period by treatment,  $F_{1,2} < 8.58$ ,  $P > 0.099$  for all).

Biomass of both herbivorous aquatic arthropods and periphyton differed significantly between the treatments (Fig. 4). The treatment effect was significant for both arthropod ( $F_{3,4} = 8.50$ ,  $P = 0.033$ ) and periphyton biomass ( $F_{3,4} = 12.27$ ,  $P = 0.017$ ). No within-subject effects were significant for either arthropod (period,  $F_{1,4} = 0.22$ ,  $P = 0.662$ ; period by treatment,  $F_{3,4} = 0.37$ ,  $P = 0.777$ ) or periphyton biomass (period,  $F_{1,4} = 0.27$ ,  $P = 0.630$ ; period by treatment,  $F_{3,4} = 0.71$ ,  $P = 0.594$ ). The biomass of herbivorous aquatic arthropods in the reduced input plus fish treatment was significantly smaller than that in the other three treatments, which were not significantly different (Fig. 4A). Moreover, the smaller herbivore biomass in the reduced input plus fish treatment resulted in a greater periphyton biomass than that in the other treatments, which exhibited no significant differences in periphyton biomass (Fig. 4B). The biomass of both herbivorous arthropods and periphyton in the natural input plus fish treatment did not differ from those in the two fish-absent treatments, indicating that there was no fish-cascading effect on the benthic community when terrestrial arthropods were supplied naturally. In addition, because neither the biomass of herbivorous arthropod nor the periphyton differed between the two fish-absent treatments, irrespective of terrestrial arthropod input rate, the experimental covers did not appear to directly affect the stream benthic community.

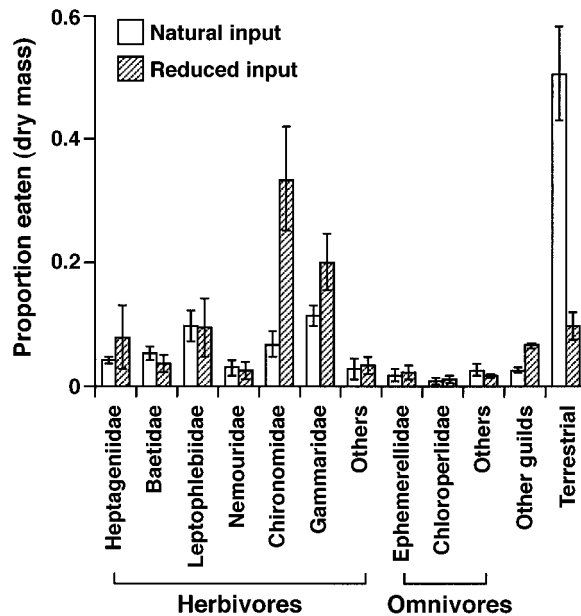


FIG. 3. Differences in dietary composition of Dolly Varden by dry mass (mean  $\pm$  1 SE,  $n = 4$ ) between treatments with reduced and natural terrestrial arthropod inputs in the Horonai Stream.

## DISCUSSION

Under natural conditions, the mean daily input of terrestrial insects from the riparian forest to stream was  $11.2 \text{ g} \cdot 100 \text{ m}^{-2} \cdot \text{d}^{-1}$  (dry mass), a figure comparable to values reported by several previous studies in headwater streams in temperate deciduous forests (Mason and MacDonald 1982, Cloe and Garman 1996). Annual energy contributed by such allochthonous inputs to stream ecosystems may be equivalent to the potentially available energy represented by aquatic arthropod production and an equally important trophic basis for fish production, especially in fully canopied temperate headwater streams (Cole and Garman 1996). Moreover, a greater terrestrial arthropod input during summer, when aquatic arthropod biomass in streams is generally at its lowest, may be an important seasonal subsidy for fishes. Although terrestrial plant detrital material is generally believed to support the basis for consumer

production via bottom-up trophic cascades (Wallace et al. 1997), the input of terrestrial arthropods, which are directly available to predatory fish, represents a potentially more energy-efficient linkage of food webs at the interface between terrestrial and aquatic ecosystems (Garman 1991, Cloe and Garman 1996).

In the present study, the biomass of herbivorous aquatic arthropods was depressed by Dolly Varden predation when terrestrial arthropod input was experimentally reduced. In contrast, no predation effect was evident on the aquatic arthropods when terrestrial arthropods were supplied naturally. The impact of fish predation on stream arthropod assemblages has long been the subject of debate (Power 1990, Wooster and Sih 1995, Dahl and Greenberg 1996). Dolly Varden dramatically shifted their major prey category from terrestrial to aquatic arthropods, partly specializing on midge larvae in the reaches where terrestrial arthropod inputs were experimentally reduced. Because the proportion of midge larvae in the stream drift was much smaller than that found in the diet (S. Nakano, *personal observation*), Dolly Varden were regarded as having shifted from drift interception to active foraging on the stream benthos in response to the decline in drift prey, in order to maximize their energy gain (Nakano and Furukawa-Tanaka 1994, Fausch et al. 1997, Nakano et al. 1999). A difference in foraging modes (foraging on drift or benthos) adopted by predatory fish has been hypothesized as a determinant of impacts that predatory fishes have on benthic arthropod assemblages (Dahl and Greenberg 1996). Benthic-foraging fish are considered to have significantly larger impacts on stream arthropods than are drift foragers, if the amount of terrestrial arthropod input is large enough to subsidize the drift foragers. The shifts in foraging mode shown by Dolly Varden can be an important element in the alteration of predation pressure on aquatic arthropod assemblages. In addition, the consequent depletion of herbivorous aquatic arthropods resulted in an increase in periphyton biomass, as found by Power (1990, 1992) and McIntosh and Townsend (1996). We thus concluded that in summer the trophic cascading effects of predatory fish in the stream food web were controlled by the supply rate of terrestrial arthropods from the riparian forest canopies.

In the present study, we showed that experimental reductions of terrestrial arthropod inputs had a strong indirect effect on a stream benthic community by altering the effects of fish predation on the stream food web. Although such an across-habitats transfer may be a very minor event for the terrestrial arthropod assemblage and far smaller in mass than other components of allochthonous inputs (e.g., plant litter), its community-based function is prominent in stream ecosystems. This result provides empirical support for the

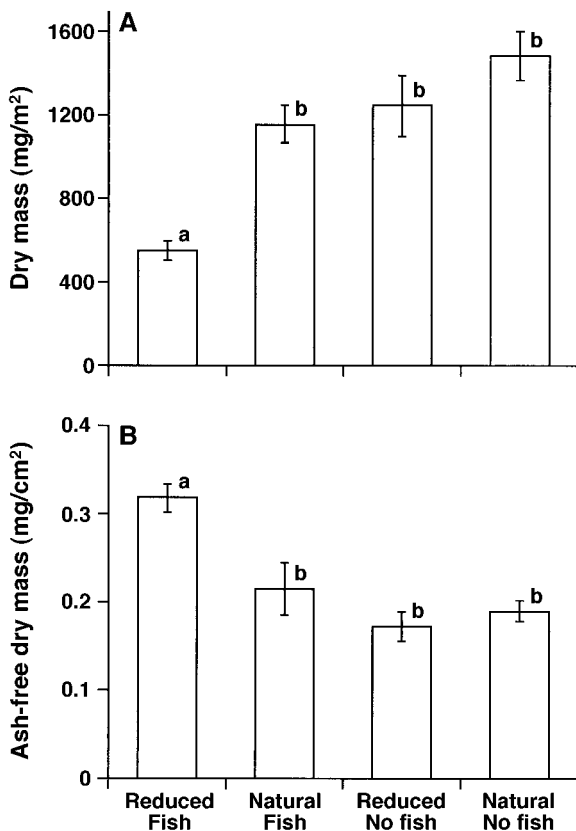


FIG. 4. Biomass (mean  $\pm$  1 SE,  $n = 4$ ) of (A) aquatic herbivorous arthropods and (B) periphyton in the four experimental treatments: reduced terrestrial arthropod input with predatory fish; natural input with fish; reduced input with fish absent; and natural input with fish absent. Different letters indicate significant differences ( $P < 0.05$ ) among treatments as assessed by Fisher's least significant difference (LSD) multiple contrasts.

general perspective that transfers of energy and biomass from more productive donor systems are frequently significant for the maintenance of communities in less productive recipient systems (Polis and Hurd 1996, Polis et al. 1996, 1997). The development and maintenance of diverse stream communities are largely dependent upon the degree of trophic connectivity between terrestrial landscapes and stream ecosystems (Vannote et al. 1980, Malason 1993, Naiman and Décamps 1997, Wallace et al. 1997). However, recent worldwide changes in riparian land-use regimes, e.g., loss and degradation of riparian forests, have potentially detrimental influences not only on terrestrial litter input but also on that of arthropods (Mason and MacDonald 1982, Edwards and Huryn 1996). Our results emphasize the need for greater concern regarding the significance of terrestrial arthropod input as a trophic linkage across a forest–stream interface when stream ecosystems management strategies are developed.

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