

# Drifting plankton from a reservoir subsidize downstream food webs and alter community structure

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**Abstract** Subsidy between ecosystems has been considered in many natural ecosystems, and should alter food webs and communities in human-impacted ones. We estimated how drifting plankton from a reservoir contribute to downstream food webs and showed that they alter community structures over a 10-km reach below the dam. To estimate the contribution of the drifting plankton to macroinvertebrates, we used C and N isotopes and an IsoSource mixing model. In spring and autumn, contributions of plankton to collector-filterer species were highest 0.2 km downstream of the dam, and clearly decreased from 0.2 to 10 km. At 0.2 km, the contribution of plankton to a predator stonefly was remarkably high. These results indicated that drifting plankton from a dam reservoir could subsidize downstream food webs and alter their energy base, but the importance of this subsidy decreased as distance from the reservoir increased. The general linear models indicated that the abundance of collector-filterers and predators was related positively to zooplankton density in stream water.

Thus, food source alteration by drifting plankton also influenced the community structures downstream of the dam.

**Keywords** Stable isotope · IsoSource mixing model · Macroinvertebrates · Dam reservoir · Functional feeding groups

## Introduction

Subsidy between ecosystems has been a central organizing theme in food web ecology (Polis et al. 1997). Many studies have demonstrated subsidies between ecosystems (e.g., Polis and Hurd 1996; Nakano and Murakami 2001; Schindler et al. 2005). Subsidies maintain food web structures, but also abundance of species and community composition in the recipient habitats (e. g., Rose and Polis 1998; Iwata et al. 2003; Kawaguchi et al. 2003; Kato et al. 2003; Matthews and Mazumder 2006). To date, subsidies between ecosystems have mainly been considered in natural ecosystems, but subsidization could alter food webs and communities in human-impacted ecosystems, such as rivers regulated by artificial reservoirs.

Drifting plankton from lake and reservoir outflows are thought to be a high-quality food source for river organisms (Elliot and Corlett 1972; Malmqvist and Bronmark 1984; Richardson 1984; Richardson and Mackay 1991), and could subsidize downstream food webs. Previous studies have found that drifting plankton from reservoirs caused an alternation in the energy base of downstream food webs (e.g., Armitage and Capper 1976; Voelz and Ward 1996). However, the importance of the drifting plankton to downstream food webs in the regulated rivers was not quantitatively estimated in these studies. Thus, we hypothesized that a reservoir would subsidize downstream food webs,

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and alter the downstream macroinvertebrate community structure. Because significant food subsidies change the communities in the recipient systems (Iwata et al. 2003; Kawaguchi et al. 2003; Kato et al. 2003), they can also lead to changes in the distributions of species (Kawaguchi et al. 2003; Matthews and Mazumder 2006) in natural systems.

C and N stable isotope ratios have been increasingly used to analyze food web structures in aquatic ecosystems (e.g., Finlay 2001; Finlay et al. 2002; Doi et al. 2006; Delong and Thorp 2006). Stable isotope analysis should be a useful tool to estimate the contribution of drifting plankton to food webs. In streams, the C isotope ratios of primary producers, benthic microalgae in periphyton, terrestrial plant litter, and also drifting phytoplankton from reservoirs would differ because of their different photosynthetic mechanisms and activity (France 1995; Finlay et al. 2002). Thus, we could estimate the contribution of many food sources for consumers in a stream, which is subsidized by a reservoir. Many isotope studies have been restricted to the use of C and N isotopes, and previous mixing models (e.g., Phillips 2001) for two isotope values have required that there be no more than three important food sources. However, in rivers there are many food sources, including periphyton, plant litter, and particulate organic matter (e.g., Thorp and Delong 2002; Delong and Thorp 2006), and in this study, we treat drifting plankton as an additional source. Phillips and Gregg (2003) developed IsoSource software for an isotope mixing model that is designed for situations in which two isotopes are used and more than three food sources are likely to be contributing to a consumer.

In this study, we investigated the food webs and community structures of macroinvertebrates at increasing distances downstream from dams (0.2–10 km from a dam) in two different seasons (spring and autumn). We mainly focused on macroinvertebrates, since functional feeding groups (FFGs) of macroinvertebrates are well known (Merritt and Cummins 1996), and high mobility of fish would make it difficult to estimate their food sources within the spatial scale of this study. To estimate the contribution of the drifting plankton to the food webs, we employed an IsoSource mixing model using C and N isotope data of the potential food sources and macroinvertebrate consumers. Also, we used general linear models (GLM) to estimate the distribution of FFGs by subsidy availability and environmental factors.

## Materials and methods

### Study sites

The present study was conducted in the Hiji River, downstream of the Kanogawa Dam reservoir on Shikoku Island,

Japan (33°27′–33°N, 132°37′–41°E). The Kanogawa Dam, which was completed in 1958, is a concrete gravity dam (61 m height) with a catchment area of 456 km<sup>2</sup> and a storage volume of 48.2 million m<sup>3</sup>. We had four sampling stations in the river: stations 1, 2, 3, and 4 were 0.2, 1.4, 6.2, and 10.0 km downstream from the dam. We also sampled zooplankton and seston in the reservoir (station D; approximate depth of 35 m and 50 m upstream of the dam gate). In the section under study, there was no large confluence of a tributary with the main river. Samples were collected from riffles at station 1–4 at a depth of 5–30 cm. All samples were taken in May (spring) and November 2005 (autumn).

### Collection and measurement for isotope samples

Dominant macroinvertebrates and their potential food sources, periphyton, benthic particulate organic matter (BPOM), and suspended particulate organic matter (SPOM) were collected at each station of the river. Dominant macroinvertebrates were collected randomly at each station by hand and tweezers. Three to four replicates of each species were collected in each station. Periphyton was removed from stones using a toothbrush and filtered onto precombusted Whatman GF/F glass filters (Whatman, Clifton, USA). BPOM was collected from 0- to 5-cm depth of riverbed using the Surber sampler, and SPOM was collected using a plankton net (250- $\mu$ m mesh) which was dipped in the stream for at least 5 min. The samples of BPOM and SPOM were sieved by 250- $\mu$ m mesh and samples <250  $\mu$ m was used for isotope analysis. Plant litter was collected on the riverbed at station 1 by hand and washed by river water. For food sources from the dam reservoir, zooplankton and dam seston, we collected the zooplankton samples by vertical tows of a 200- $\mu$ m plankton net from 0- to 25-m water depth, and 500 ml of surface water by bottle. The water samples were filtered by a 200- $\mu$ m plankton net, then onto precombusted Whatman GF/F filters to measure isotopic signature of dam seston. Four replicates were collected of these potential food sources. Periphyton, BPOM, SPOM, plant litter and dam seston were acidified with 1 mol HCl l<sup>-1</sup> to remove carbonate before isotope measurement.

All samples were dried at 50°C for at least 24 h, and stored in desiccators until the isotope ratios were analyzed. C and N isotope ratios of the samples were measured with a continuous flow isotope mass spectrometer (Integra CN, Sercon, UK). All isotopic data are reported in the conventional  $\delta$  notation where  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$  (%).  $R$  is the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratio for  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ , respectively. Pee Dee Belemnite and N<sub>2</sub> in air were used as international standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. The overall analytical errors were within  $\pm 0.2\%$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

## Collection and preparation of macroinvertebrates for community composition

Macroinvertebrates were taken randomly by three individual samples in a riffle of each station using a Surber sampler ( $0.25 \times 0.25 \text{ m}^2$  quadrat area, 250- $\mu\text{m}$  mesh, 1 m long), and fixed with formalin (final concentration of 4–5%). Macroinvertebrates were sorted from detritus and sediment debris, identified to the lowest possible taxonomic level ( $\times 40$  magnification), and assigned FFG designations using Merritt and Cummins (1996) and Kawai and Tanida (2005). We calculated the composition of FFGs (%) in the communities based on density data. To consider the alteration of the community structures by subsidies, we evaluated responses of FFGs of macroinvertebrates to environmental factors including availability of subsidies. FFGs would be influenced directly by food subsidies, since FFGs were classified by the main food sources and feeding habits of the species (Merritt and Cummins 1996; Kawai and Tanida 2005).

## Measurement of environmental factors

We measured randomly current velocity at each site with five replicates using a current meter (VP-201; Kenek, Tokyo). For chlorophyll *a* measurement on stones, we randomly collected three pebbles from each riffle. To determine chlorophyll *a*, each pebble was dipped into the *N,N*-dimethylformamide to extract chlorophyll *a*. Chlorophyll *a* concentration was determined using a fluorometer (AU-10; Turner Designs, Sunnyvale). The chlorophyll concentration of periphyton was calculated according to Fukuda et al. (2004).

Substrate coarseness was measured according to the method of Bisson et al. (1982) and Inoue and Nakano (1998). In each Surber sampler grid, we visually estimated each of the following categories of substrate: particles  $< 2 \text{ mm}$  = sand, 2–16 mm = gravel, 17–64 mm = pebble, 65–256 mm = cobble, and 256–1,024 mm = boulder. These categories were then coded as follows: sand = 1, gravel = 2, pebble = 3, cobble = 4, and boulder = 5. Substrate coarseness of a grid was obtained following the equation: substrate coarseness =  $\sum$  (the code of the material category  $\times$  the proportion of the category). We used mean substrate coarseness with three grids for the analysis.

We investigated the drifting zooplankton density to estimate availability of subsidies for macroinvertebrates. Zooplankton in the river were collected using a bucket at the study sites. A total of 10 l of the river water was filtered through the plankton net (60  $\mu\text{m}$ ) and fixed with formalin (final concentration of 4–5%).

## Data analyses

To determine which of the potential food sources were assimilated by macroinvertebrates, we estimated the feasible

contributions for each food source by isotope mixing models using IsoSource version 1.3.1 software (Phillips and Gregg 2003). Essentially, the model iteratively creates all possible combinations of source proportions (with each combination equaling 100%) at preset increments (1% in this study) to create a set of predicted mixtures of sources (see Phillips and Gregg 2003 in detail). For the model, the potential food sources were periphyton, BPOM, SPOM, plant litters, and zooplankton. We used zooplankton as total plankton food source, since isotopic values of zooplankton represent a composite of seston isotopic ratios because they consume the seston in the reservoir, and the isotope turnover time of zooplankton would be longer than that of the dam seston. Tolerance was initially set at 0.1‰; if mixture isotope values were out of bounds, we incrementally increased the tolerance value by 0.1‰ up to a maximum of 0.8‰. The C and N isotope enrichments of macroinvertebrates were +0.4 and +3.4‰ (McCutchan et al. 2003 for C; Post 2002 for N). For secondary consumers, we calculated the contribution according to Delong and Thorp (2006). Trophic positions (TP) of stoneflies *Neoperla* spp. and *Oyamia* spp. were determined by differences between their  $\delta^{15}\text{N}$  and the mean  $\delta^{15}\text{N}$  of *Hydropsyche orientalis* and chironomids as the long-lived dominant primary consumers. Once TP was determined separately for each stonefly, expected levels of fractionation for a single trophic level were multiplied by TP–1, and these expected fractionation values were used for determining the basal source contributions to stoneflies.

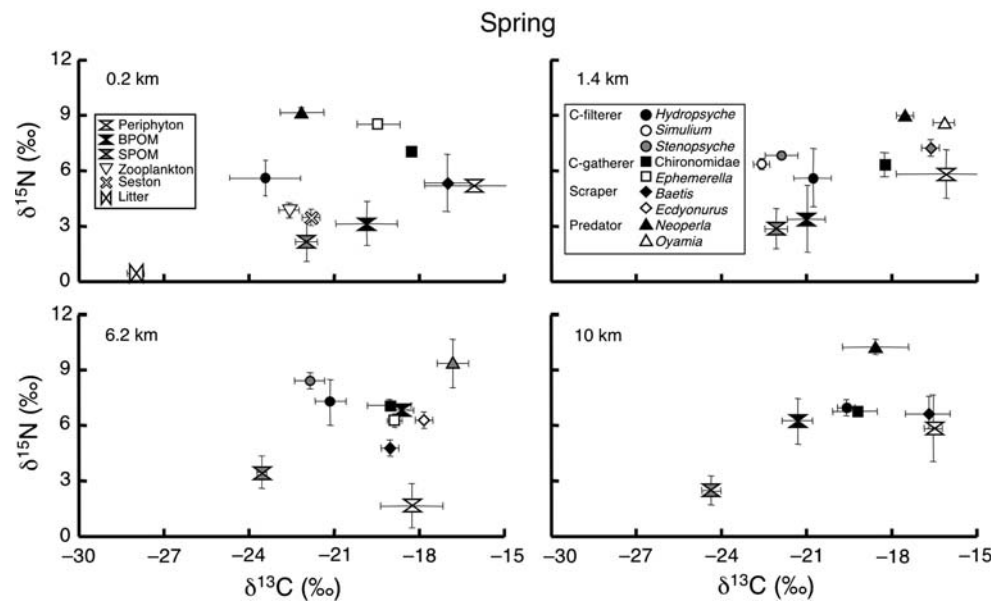
To analyze relationships between environmental factors and FFG composition, we used a GLM. We used the pooled dataset of factors for the two seasons and FFG composition in all the seasons and stations to fit a GLM, and the model was selected stepwise based on Akaike information criterion (AIC) to determine the best model for the relationships. The GLM was (relative abundance of the each FFG) =  $X_v C_v + X_c C_c + X_s C_s + X_z C_z + b$ , where  $C_v$ ,  $C_c$ ,  $C_s$ , and  $C_z$  were mean current velocity, periphytic chlorophyll *a* on stones, substrate coarseness, and zooplankton density (i.e., availability of subsidies), respectively, and  $X$  and  $b$  indicate their parameter coefficients and the constant. We used Pearson's correlation coefficients to estimate the correlation between the distance from the dam and zooplankton density. We performed the statistical analyses using R version 2.5.0 software (R Development Core Team 2007).

## Results

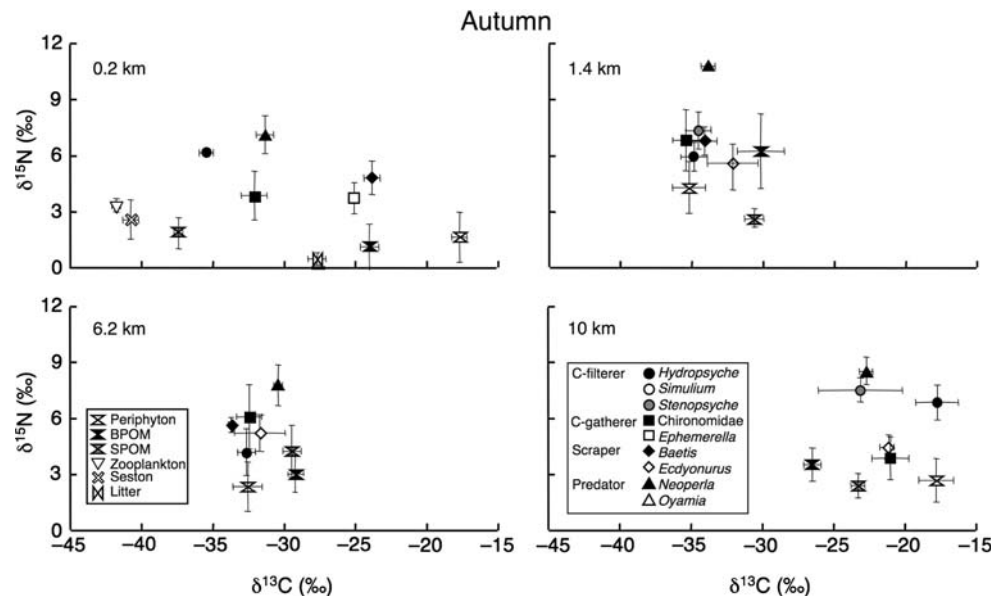
### Contribution of potential food sources to macroinvertebrates

The isotope data of macroinvertebrates and potential food sources are shown in Figs. 1 and 2. In both sampling sea-

**Fig. 1** Mean C and N isotope values of potential food sources and consumers in spring. *Upper left-hand panel* Zooplankton and dam seston collected at the dam and plant litter collected only at station 1. *Bars* indicate  $\pm 1$  SE. *BPOM* Benthic particulate organic matter, *SPOM* suspended particulate organic matter



**Fig. 2** Mean C and N isotope values of potential food sources and consumers in autumn. *Upper left-hand panel* Zooplankton and dam seston collected at the dam and plant litter collected only at station 1. *Bars* indicate  $\pm 1$  SE. For abbreviations, see Fig. 1



sons, the isotope values of food sources were almost separated (Figs. 1, 2). The high variations among C isotope values of the food sources, including zooplankton and seston in the reservoir (0.2 km panel in Fig. 2), were observed in the autumn, especially, at 0.2 and 10 km. In the spring, the variations in isotope values of food sources were smaller than those in autumn. The isotope values of macroinvertebrates ranged within those of food sources, except for some grazer species in spring.

The contribution of potential food sources varied among species (Table 1). The percentiles contribution shown following different FFGs represent the range of first percentile and 99th percentile outputs from IsoSource for the species representing that FFG (Figs. 3, 4). In spring, periphyton constituted a major proportion of the food source for scrapers and collector-gatherers (first percen-

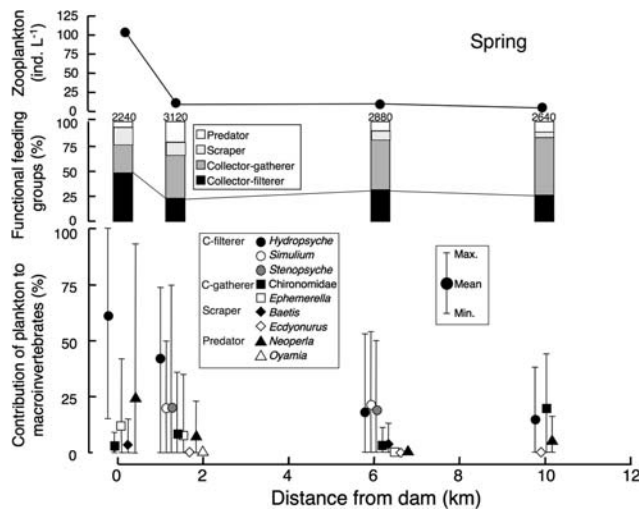
tile, 29–69%; maximum percentile, 65–95%), but we could not calculate the contribution using IsoSource software for several scraper species, since their C isotope values were higher than those of periphyton. Thus, the scrapers probably fed mainly on periphyton. The contributions of BPOM for collector-gatherers were higher than for the other FFGs (first percentile, 0–29%; maximum percentile, 11–93%), and those of SPOM for collector-filterer were higher than for the other FFGs (first percentile, 0%; maximum percentile, 34–78%). While the potential contributions of BPOM and SPOM for scrapers were smaller than for the other FFGs (first percentile, 0–5%; maximum percentile, 10–26%).

The contribution of plankton varied among species (Fig. 3). For collector-filterer species including *Hydropsyche*, *Simulium* and *Stenopsyche*, the maximum percentile of

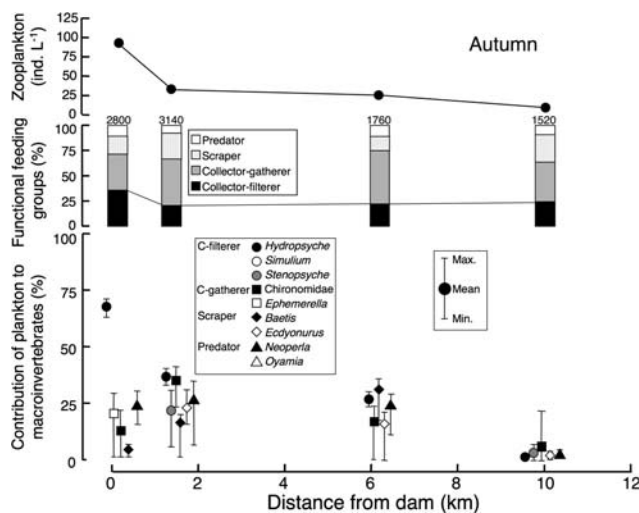
**Table 1** Means and ranges of feasible contribution of the potential food sources to macroinvertebrates determined using the IsoSource mixing model. *BPOM* Benthic particulate organic matter, *SPOM* suspended particulate organic matter, *FFGs* functional feeding groups, *CF* collector-filterer, *CG* collector-gatherer, *SC* scraper, *PR* predator

Taxon	FFGs	Distance (km)	Plankton		Periphyton		BPOM		SPOM		Terrestrial litters	
			Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Spring												
<i>Hydropsyche orientalis</i>	CF	0.2	61.1 ± 13.9	15–100	2.9 ± 2.7	0–15	11.6 ± 9.7	0–54	10.8 ± 9	0–50	13.7 ± 5.3	0–31
Chironomid	CG	0.2	11.7 ± 9.2	0–42	48.2 ± 5.7	29–61	28.8 ± 15.1	0–71	9.3 ± 8.0	0–45	1.9 ± 1.9	0–10
<i>Ephemerella chinoi</i>	CG	0.2	2.0 ± 2.0	0–9	72.2 ± 1.5	68–76	2.3 ± 2.3	0–11	3.0 ± 2.8	0–13	20.6 ± 1.6	17–25
<i>Baetis</i> spp.	SC	0.2	3.2 ± 0.3	0–15	86.2 ± 3.7	74–95	5.7 ± 4.9	0–26	3.4 ± 3.1	0–16	1.5 ± 1.6	0–8
<i>Neoperla</i> spp.	PR	0.2	26.9 ± 19.6	0–93	8.9 ± 6.2	0–30	23.7 ± 16.0	0–80	28.7 ± 20.7	0–10	11.8 ± 7.7	0–41
<i>Hydropsyche orientalis</i>	CF	1.4	42.0 ± 16.6	0–74	25.1 ± 2.6	18–33	6.9 ± 5.9	0–32	24.4 ± 18.8	0–78	1.6 ± 1.7	0–8
<i>Simulium</i> spp.	CF	1.4	19.9 ± 7.2	0–50	14.8 ± 10.8	0–40	24.5 ± 20.2	0–85	22.2 ± 8.9	0–50	18.6 ± 8.2	0–52
<i>Stenopsyche marmorata</i>	CF	1.4	20.2 ± 14.4	0–75	17.2 ± 9.5	0–47	28.1 ± 19.8	0–93	23.0 ± 16.9	0–88	11.5 ± 7.7	0–40
Chironomid	CG	1.4	8.6 ± 6.8	0–36	68.2 ± 4.7	54–83	10.5 ± 7.0	0–46	8.9 ± 7.2	0–38	3.9 ± 3.4	0–19
<i>Ephemerella chinoi</i>	CG	1.4	7.7 ± 6.4	0–35	61.3 ± 5.9	43–79	15.3 ± 11.5	0–57	9.0 ± 7.5	0–41	6.7 ± 4.7	0–23
<i>Ecdyonurus yoshidae</i>	SC	1.4	n.c. <sup>a</sup>	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
<i>Neoperla</i> spp.	PR	1.4	6.8 ± 5.0	0–23	77.5 ± 2.5	70–85	6.8 ± 5.9	0–30	6.9 ± 5.2	0–25	2.0 ± 2.0	0–10
<i>Oyamia</i> spp.	PR	1.4	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
<i>Hydropsyche orientalis</i>	CF	6.2	17.7 ± 12.5	0–53	56.0 ± 5.3	40–66	6.7 ± 3.7	0–17	12.4 ± 8.9	0–38	7.1 ± 5.1	0–22
<i>Simulium</i> spp.	CF	6.2	21.1 ± 13.8	0–54	9.9 ± 5.8	0–22	12.5 ± 7.6	0–30	28.1 ± 17.0	0–68	27.3 ± 9.8	5–52
<i>Stenopsyche marmorata</i>	CF	6.2	18.6 ± 12.5	0–50	9.8 ± 5.2	0–21	38.0 ± 6.1	23–53	22.1 ± 14.3	0–60	11.5 ± 7.5	0–31
Chironomid	CG	6.2	2.9 ± 2.6	0–11	59.3 ± 2.9	52–67	34.6 ± 2.4	29–40	2.2 ± 2.0	0–9	1.0 ± 1.1	0–4
<i>Ephemerella chinoi</i>	CG	6.2	0.7 ± 0.8	0–2	71.6 ± 1.3	69–74	27.3 ± 1.2	26–29	0.3 ± 0.5	0–1	0.1 ± 0.2	0–1
<i>Baetis</i> spp.	SC	6.2	3.6 ± 3.1	0–13	81.5 ± 3.0	73–89	10.9 ± 2.5	5–16	2.7 ± 2.4	0–10	1.2 ± 1.3	0–5
<i>Ecdyonurus yoshidae</i>	SC	6.2	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
<i>Neoperla</i> spp.	PR	6.2	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
<i>Hydropsyche orientalis</i>	CF	10	14.5 ± 8.6	0–38	65.1 ± 4.9	52–78	3.9 ± 2.9	0–14	9.6 ± 7.3	0–34	7.0 ± 5.3	0–23
Chironomid	CG	10	19.6 ± 9.0	0–44	65.7 ± 4.4	54–79	2.4 ± 2.3	0–13	6.8 ± 5.9	0–32	5.4 ± 4.7	0–22
<i>Ecdyonurus yoshidae</i>	SC	10	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
<i>Neoperla</i> spp.	PR	10	4.8 ± 4.3	0–22	46.3 ± 2.8	37–52	43.7 ± 6.9	26–63	4.1 ± 3.7	0–19	1.1 ± 2.4	0–6
Autumn												
<i>Hydropsyche orientalis</i>	CF	0.2	67 ± 2.0	61–71	24.0 ± 2.0	18–28	4.0 ± 3.4	0–14	3.1 ± 2.8	0–13	1.7 ± 1.7	0–7
Chironomid	CG	0.2	12.5 ± 8.6	0–32	5.3 ± 3.9	0–18	11.7 ± 8.2	0–38	29.9 ± 14.5	0–56	40.6 ± 11.6	10–70
<i>Ephemerella chinoi</i>	CG	0.2	19.6 ± 9.0	0–44	65.7 ± 4.4	54–79	2.4 ± 2.3	0–13	6.8 ± 5.9	0–32	5.4 ± 4.7	0–22
<i>Baetis</i> spp.	SC	0.2	3.6 ± 2.5	0–11	41.1 ± 10.0	12–61	31.6 ± 20.5	0–86	6.3 ± 4.4	0–19	17.3 ± 9.9	0–42
<i>Neoperla</i> spp.	PR	0.2	21.2 ± 11.8	0–39	14.9 ± 10.1	0–44	19.3 ± 13.4	0–59	26.2 ± 10.4	0–50	18.4 ± 13.3	0–64
<i>Hydropsyche orientalis</i>	CF	1.4	35.9 ± 3.7	26–45	12.6 ± 9.3	0–41	5.2 ± 4.0	0–18	20.0 ± 14.6	0–65	26.4 ± 7.8	2–40
<i>Stenopsyche marmorata</i>	CF	1.4	21.2 ± 8.7	1–39	32.3 ± 20.4	0–83	14.5 ± 8.5	0–36	20.1 ± 12.9	0–51	11.9 ± 6.9	0–28
Chironomid	CG	1.4	34.2 ± 6.1	19–48	22.3 ± 14.4	0–62	9.6 ± 6.1	0–26	20.6 ± 13.5	0–52	13.4 ± 7.2	0–29
<i>Baetis</i> spp.	SC	1.4	15.6 ± 3.6	6–25	12.3 ± 9.1	0–40	5.0 ± 3.9	0–17	19.4 ± 14.2	0–63	47.7 ± 7.6	24–61
<i>Ecdyonurus yoshidae</i>	SC	1.4	22.5 ± 7.6	4–39	28.1 ± 17.9	0–76	12.3 ± 7.6	0–32	22.8 ± 14.8	0–57	14.3 ± 7.9	0–32
<i>Neoperla</i> spp.	PR	1.4	26.0 ± 5.3	8–40	16.2 ± 12.0	0–59	6.8 ± 5.2	0–25	24.2 ± 17.6	0–77	26.8 ± 10.2	0–48
<i>Hydropsyche orientalis</i>	CF	6.2	26.0 ± 3.3	14–31	14.8 ± 11.1	0–53	6.3 ± 4.9	0–22	3.9 ± 3.2	0–14	49.0 ± 4.8	33–60
Chironomid	CG	6.2	15.9 ± 7.0	0–27	35.3 ± 24.3	0–94	17.9 ± 12.5	0–56	11.5 ± 8.0	0–36	19.3 ± 9.4	0–42
<i>Baetis</i> spp.	SC	6.2	30.4 ± 4.6	15–37	21.5 ± 15.7	0–72	9.2 ± 6.9	0–31	5.8 ± 4.5	0–20	33.1 ± 6.3	13–48
<i>Ecdyonurus yoshidae</i>	SC	6.2	15.0 ± 5.2	0–23	24.7 ± 17.9	0–78	10.6 ± 7.9	0–36	6.7 ± 5.1	0–23	43.0 ± 7.1	22–60
<i>Neoperla</i> spp.	PR	6.2	23.6 ± 5.1	3–33	20.9 ± 16.3	0–85	9.0 ± 7.3	0–37	5.7 ± 4.7	0–24	40.8 ± 8.8	12–63
<i>Hydropsyche orientalis</i>	CF	10	0.3 ± 0.5	0–2	94.9 ± 1.9	90–100	2.3 ± 2.3	0–10	1.4 ± 1.5	0–6	1.1 ± 1.3	0–5
<i>Stenopsyche marmorata</i>	CF	10	6.4 ± 4.9	0–23	46.9 ± 11.7	10–80	18.8 ± 14.8	0–75	22.8 ± 12.5	0–63	5.0 ± 4.0	0–20
Chironomid	CG	10	3.0 ± 2.6	0–12	66.6 ± 5.6	53–84	6.8 ± 5.6	0–27	22.1 ± 6.1	0.4–35	1.5 ± 1.5	0–7
<i>Ecdyonurus yoshidae</i>	SC	10	1.8 ± 1.8	0–9	63.7 ± 4.5	51–76	4.4 ± 3.9	0–20	29.3 ± 4.4	17–42	0.9 ± 1.0	0–5
<i>Neoperla</i> spp.	PR	10	1.9 ± 1.8	0–8	63.2 ± 3.9	55–75	4.5 ± 3.9	0–17	29.5 ± 4.3	17–39	0.9 ± 1.0	0–4

<sup>a</sup> The contribution could not be determined using the IsoSource mixing model due to higher or lower isotope values from potential food sources



**Fig. 3** Zooplankton density, functional feeding group (FFG) compositions, and contribution of plankton to macroinvertebrates in spring. *Upper panel* Total zooplankton density in the surface stream water. *Middle panel* FFG compositions of macroinvertebrate community. *White symbols* Mean predators, *striped symbols* mean scrapers, *grey symbols* mean collector-gatherers, *black symbols* mean collector-filterers. *Numbers on bars* Mean total abundance of macroinvertebrates (individuals  $m^{-2}$ ). *Lower panel* Potential contribution of plankton to macroinvertebrates determined using the IsoSource mixing model. *Symbols* indicate means and *bars* the range of the contribution



**Fig. 4** Zooplankton density, FFG composition, and contribution of plankton to macroinvertebrates in autumn. *Upper panel* Total zooplankton density in the surface stream water. *Middle panel* FFG compositions of macroinvertebrate community. *White symbols* Mean predators, *striped symbols* mean scrapers, *grey symbols* mean collector-gatherers, *black symbols* mean collector-filterers. *Numbers on bars* Mean total abundance of macroinvertebrates (individuals  $m^{-2}$ ). *Lower panel* Potential contribution of plankton to macroinvertebrates determined using IsoSource mixing model. *Symbols* indicate means and *bars* the range of the contribution

the contribution of plankton clearly decreased from 0.2 to 10 km. At station 1, the contribution of plankton to the predator stonefly *Neoperla* was much higher than at the

other sites. At station 2, maximum percentiles of some species for contribution of plankton were higher than those at station 1. The contributions of plant litter to macroinvertebrates (first percentile, 0–17%; maximum percentile, 1–52%) were the lowest of the potential food sources.

In autumn, periphyton also constituted a major proportion of the food source for scrapers and collector-gatherers (Table 1; first percentile, 0–54%; maximum percentile, 18–94%). At 10 km, the contributions of periphyton for all FFGs were higher than for the other food sources (first percentile, 10–90%; maximum percentile, 75–100%). The contributions of BPOM and SPOM for all FFGs were intermediate at stations 1–3, while at station 4, the contributions were decreased. Contributions of plankton varied among species (Fig. 4), and were of a similar pattern to those in spring. For the collector-filterer *Hydropsyche*, the maximum percentile and mean values of the contribution of plankton clearly decreased from 0.2 to 10 km. At 10 km, the contribution of plankton was almost 0% for all consumers, and periphyton contributed 90–100% to *Hydropsyche*. The ranges of the contributions in each species in autumn were narrower than those in spring (i.e., smaller differences between minimum and maximum percentile). This is probably because the ranges of the C isotope of food sources in the autumn were higher than in the spring.

#### Downstream patterns of zooplankton and macroinvertebrates

Total zooplankton density of surface water decreased downstream (from 0.2 to 1.4 km) in spring, and few zooplankton remained at stations 3 and 4 (Fig. 3). In autumn, although the density rapidly decreased, a larger number of individuals ( $>20 l^{-1}$ ) remained at stations 2 and 3 (Fig. 4). The zooplankton density was negatively correlated with the distance from the dam ( $r = -0.71$ ,  $P < 0.05$ ). For FFGs of macroinvertebrates, the proportions of collector-filterers decreased markedly from 0.2 to 10 km in both seasons, while the other FFGs tended not to change markedly throughout stations 1–4. Proportions of macroinvertebrate species for isotope analysis were  $76.2 \pm 1.5$  and  $73.5 \pm 4.5\%$  in spring and autumn, respectively (mean  $\pm 1$  SE).

#### Relationships between environmental factors and FFGs

There was variation in the environmental variables used in the GLMs, but relationships were evident between some environmental factors and FFGs (Tables 2, 3). From the best models, the relative abundance of collector-filterers related positively with zooplankton density (i.e., availability of subsidy). Also, scraper relative abundance was related positively to chlorophyll *a* of microalgae on stones,

and predator relative abundance to substrate and zooplankton. However, the full model predicted collector-gatherer relative abundance best, and there was a significant positive relationship between their abundance and the abundance of chlorophyll *a* on stones and substrate coarseness.

**Discussion**

Our mixing model results showed that contributions of plankton to macroinvertebrates were higher closer to reservoirs, being highest at 0.2 km and rapidly decreasing from 0.2 to 10 km as the abundance of drifting zooplankton decreased. These results suggested that drifting plankton from a dam reservoir could subsidize food webs downstream and alter the energy base of food webs.

Collector-filterers, including *Hydropsyche*, *Simulium* and *Stenopsyche*, feed on plankton more than the other FFGs, especially under a dam with a high density of drifting zooplankton. The relationships between drifting plankton and collector-filterers on the riverbed may be strongly controlled by the effective contact between macroinvertebrates and the water column (Bunt et al. 1993; Walks and Cyr 2004). The filtration rate of macroinvertebrates on the drifting plankton is related to the connectivity between flowing water and benthic collector-filterers. Among the

predators, contributions of plankton to stonefly *Neoperla* at 0.2 km were relatively high. Thus, the predatory stonefly may feed mainly on the collector-filterers (probably small ones) at 0.2 km or directly feed on deposited plankton on the riverbed. In fact, high proportions of zooplankton were observed in their stomachs (K. H. Chang, unpublished data). Therefore, the drifting plankton could subsidize the predatory macroinvertebrates indirectly or directly. At 1.4–10 km, plankton became less important, and predators depended mainly on periphyton production. The change in predator resources can be explained by the reduced availability of plankton and reduced abundance of collector-filterers downstream, as well as a shift in the diets of collector-filterers. The GLM showed that the relative abundance of both predators and filterers was positively related to zooplankton densities. Thus, the subsidies altered the abundance of collector-filterers and predators through their availability.

The potential contribution of basal food sources to the assimilated diet of collector-gatherers and scrapers did not change appreciatively with distance below the dam. This is attributable to a diet that relies directly on benthic sources rather than suspended organic matter (Merritt and Cummins 1996). The GLM showed that the composition of collector-gatherers and scrapers was not affected by zooplankton density, but affected by periphytonic chlorophyll *a*. Thus, these FFGs were not strongly influenced by food subsidies from the reservoir.

Our results showed similar patterns of food-source use by macroinvertebrates in the spring and autumn. The dam is controlled to maintain a relatively constant discharge into the river (K. H. Chang et al., unpublished data). The supply of drifting plankton may be fairly consistent through time, which may explain the lack of importance of seasonal variation to the subsidy.

Zooplankton and phytoplankton can develop in large and long lowland rivers with a sufficiently long retention time (e.g., De Ruyter van Steveninck et al. 1992; Chang et al. 2001). Thus, hydrological retention time in river should influence the production of riverine zooplankton and phytoplankton and also the contribution of plankton to macroin-

**Table 2** Environmental factors for the general linear model (GLM) to predict the distribution of FFGs, means ± 1 SE. *Cur* Current velocity, *Chl* chlorophyll *a* on stones, *Sub* substrate coarseness

Season	Distance (km)	Cur (cm s <sup>-1</sup> )	Chl (µg cm <sup>-2</sup> )	Sub
Spring	0.2	23.0 ± 1.4	5.9 ± 1.6	3.5 ± 0.3
	1.4	10.9 ± 0.3	10.6 ± 2.5	3.2 ± 0.4
	6.2	29.0 ± 1.6	14.7 ± 1.0	3.4 ± 0.3
	10.0	32.0 ± 0.6	1.4 ± 0.5	3.0 ± 0.2
Autumn	0.2	20.8 ± 2.1	8.0 ± 1.2	3.5 ± 0.6
	1.4	15.5 ± 0.5	8.8 ± 2.0	3.0 ± 0.4
	6.2	57.2 ± 3.2	9.2 ± 1.0	3.3 ± 0.3
	10.0	27.6 ± 0.7	12.8 ± 2.1	3.1 ± 0.2

**Table 3** GLM results between FFGs of macroinvertebrates and environmental factors. *AIC* Akaike's information criterion (means), *zoo* drifting zooplankton density; for other abbreviations, see Table 2

FFGs	Best models	AIC (best GLM model)	AIC (full GLM model)
Collector-filterer	<b>0.51zoo + 2.67</b>	55.1	58.9
Collector-gatherer	-0.17zoo + 0.003cur - <b>0.53sub + 0.04chl + 2.68</b>	54.4	54.4
Scraper	<b>0.07chl + 3.36</b>	56.1	58.5
Predator	<b>0.65zoo -0.21sub + 2.70</b>	44.6	47.2

Significant factors in *bold* (*P* < 0.05)

vertebrates. In this study, the total density of zooplankton decreased from 0.2 to 10 km. Hydrological retention time was short; approximately 10–15 h from the dam to 10 km downstream. In fact, there are very few riverine zooplankton species in this river (K. H. Chang, unpublished data). In the other river, especially large and long lowland rivers, we should consider effects of riverine zooplankton on stream food web and community structure.

Our results show that drifting plankton changed the food sources of individual species and altered the macroinvertebrate community structure downstream of the reservoir. The results suggest that drifting plankton play a significant role in determining the downstream community. In fact, many papers have reported high densities of collector-filterers downstream from dams (e.g., McKay and Waters 1986; Richardson and Mackay 1991; Voelz and Ward 1996). In various natural systems, subsidies alter the distribution and abundance of species and the composition of communities (e.g., Rose and Polis 1998; Iwata et al. 2003; Kawaguchi et al. 2003). These studies mainly reported the changes in the distribution of vertebrates (but see Kato et al. 2003 for spiders in a riparian zone). In this study, we suggest that the subsidies also alter the invertebrate community in the stream.

In this study, the drifting plankton from a dam reservoir altered the food web and community structure in the river ecosystem. In stream ecosystems, allochthonous inputs such as plant litter, insects and drifting plankton are important factors determining the stream communities. Dams fragmented the continuous systems of rivers and altered the downstream ecosystems (e. g., Ward and Stanford 1983; Poff and Hart 2002; Nilsson et al. 2005). Dam construction strongly alters not only habitat structures, but also food subsidies for the macroinvertebrate community. Consequently, the alterations due to subsidies in human-impacted systems may have a great impact on the structure and function of the ecosystems. Stable isotope analysis may help future efforts for the assessment and management of subsidies from human-impacted systems, which influence on natural recipient systems.

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