

Longitudinal changes in zooplankton distribution below a reservoir outfall with reference to river planktivory

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Abstract The fate and interactions with river organisms of zooplankton as they drift downriver from a reservoir on a fourth-order mountain stream (Hiji River, Japan) were investigated. Monthly samples were collected at the reservoir and six river sites, simultaneously, from May 2005 to May 2006. Aquatic macroinvertebrates and fish were collected, and their stomach contents were analyzed in April and May, 2006, respectively. Drift from the reservoir was the primary source for the river plankton community; the abundance of zooplankton, particularly those of cladocerans and large rotifer, rapidly decreased within several kilometers of the dam. Analysis of the contents of fish stomachs showed that drifting zooplankton was the main food for fish, with strong food selectivity for cladocerans and large rotifers. However, fish and insect planktivores showed longitudinally different stomach contents, with progressively fewer zooplankton found in the stomachs at the downriver sites. The results suggest that the outflow of zooplankton from the reservoir is an important food source for the downstream predators, especially fish, but the drift of zooplankton and consequent food availability for the predators at lower sites are strongly limited by concentrated fish predation just below the reservoir dam.

Keywords Small river · Zooplankton drift · Reservoir–river interaction · Fish predation · Cladocerans

Introduction

Factors controlling the seasonal dynamics of zooplankton community structure and productivity have been a major research theme in lentic freshwater studies. Although they can be functionally inter-connected, these factors can be loosely categorized into biotic and abiotic ones for discussion. Biological factors, such as predation and food quality and quantity, have been considered as important factors controlling the temporal and spacial distribution of zooplankton in lake ecosystems (Hassett et al. 1997; Chang et al. 2004). Compared with lentic waters, the physical environment of lotic systems is thought of as unfavorable, because individual zooplankton can hardly maintain position and is transported downstream (Richardson 1992; Walks and Cyr 2004). Thus, physical factors such as discharge and water retention time have been thought of as the most powerful environmental factors limiting zooplankton production and distribution in rivers (Pace et al. 1992; Basu and Pick 1996). However, those river studies have focused on large lowland rivers, and relatively little is known about temporal and spacial distribution of zooplankton in small river ecosystems.

River systems incorporate a diverse spectrum of pelagic habitat of interdependent ecosystems, from headwaters to estuaries (Garnier et al. 1995). Within this spectrum, natural flow-through lakes and artificial reservoirs can induce physically serial discontinuities and other physical/hydrological heterogeneity in the pelagic zone along the river, thus impacting on rates of transport downriver. In particular, lakes and reservoirs can foster the establishment of plankton by providing temporary low-flow lentic environments (Armitage and Capper 1976; Akopian et al. 1999). Through the construction of reservoirs, many river ecosystems have experienced serious physical modification,

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including increases in these lentic characteristics. The upstream presence of lentic habitats, such as natural fluvial lakes and artificial reservoirs, provides a source of organic matter, including phytoplankton and zooplankton (Akopian et al. 1999), with the potential to influence downriver plankton development and the subsequent production of fish and aquatic macroinvertebrates too. Thus, zooplankton introduced from the upstream reservoir to the downstream river, and their interactions with river organisms, are important for our understanding of the role and ecological impact of an upstream reservoir on downriver ecosystems.

Since Japan is a mountainous country, part of an archipelago along the north western margin of the Pacific Ocean, its rivers are short and steep, and they exhibit flashy flow regimes (Yoshimura et al. 2005). Japan is located in the East Asian monsoon region, having heavy rainfall during summer. Because of the need for flood control, water supply, and the generation of hydroelectric power, construction of dams and accompanying reservoirs in the upper reaches of rivers is extensive (Nakayama et al. 2002). Such physical modifications are known to have serious ecological impact on river organisms, especially fish and benthic fauna in Japanese rivers (Yoshimura et al. 2005). We hypothesized that the zooplankton produced in a reservoir and advected downstream may also have a large impact on the diet and productivity of downriver planktivorous fish and invertebrates. In this study, we assessed the longitudinal distribution and fate of zooplankton from an upriver reservoir to 30 km downstream.

Materials and methods

Hiji River is a small fourth-order river (river width approximately 20 m), located in the Shikoku area of the southern island of Japan (33°27′–33′ N, 132°37′–41′ E). The total length of river is 103 km, and its catchment area covers 1,210 km². The Kanogawa Reservoir (maximum depth ca. 35 m) was constructed in 1958 for flood control, water supply and hydroelectric power. The storage volume of the reservoir is 48.2 million m³, and the catchment area is ca. 456 km². Its main outflow to Hiji River is controlled by the main flood gates of the dam during the flood, while constant discharge from the reservoir to the river is carried out through the outlet gate. The reservoir is eutrophic, and water bloom of blue-green algae is often observed during summer.

The sampling was conducted at the reservoir (near the dam) and at six sites (St. 1–6) in Hiji River, the distances of which from the dam were 0.2 km, 1.4 km, 6.2 km, 10 km, 18 km, and 30 km, respectively, from May 2005 to May 2006, on a monthly or bimonthly basis (Fig. 1). Water temperature and current velocity at each river site were

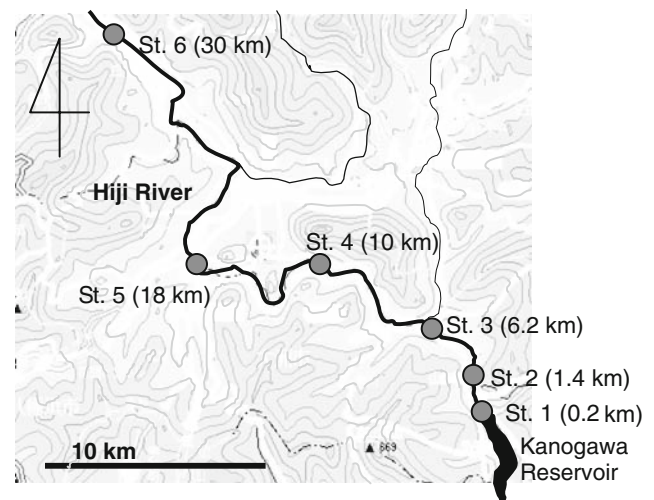


Fig. 1 Map of study sites. Only major tributaries are shown on the map

measured with a thermistor (ABT-1, ALEC Electronics Co. Ltd., Kobe, Japan) and a current meter (VP-201, Kenek Co. Ltd., Tokyo, Japan), respectively. At the reservoir, water was sampled from depths of 0 m, 1 m, 3 m, 5 m, 10 m, 20 m, and 30 m with a Van Dorn sampler and collected into a 20 l bucket from the surface at the river sites. The collected water was used for the measurement of phytoplankton biomass (chlorophyll *a* concentration) and nutrient concentrations [dissolved inorganic nitrogen (DIN); soluble reactive phosphorus (SRP); dissolved silica], and zooplankton numbers. Concentrations of chlorophyll *a* (Chl. *a*) and nutrients were measured with a 10-AU fluorometer (Turner Designs, Sunnyvale, USA.) and TRAACS-800 autoanalyzer (Bran + Luebbe, Tokyo, Japan), respectively. For zooplankton counting, collected water (10–20 l) was filtered through a plankton net (60 μm) and fixed with neutral buffered formalin (final concentration of approximately 4–5%).

For the comparison of species composition at each site, a similarity matrix was constructed, using the Bray–Curtis measure of similarity (Clarke and Warwick 2001), for the average number of zooplankton collected from each site during the study period (fourth-root-transformed). The differences in composition among sites were analyzed by cluster analysis and displayed by multidimensional scaling (MDS) ordinations using PRIMER 5 (Primer-E Ltd., Plymouth, UK). The longitudinal changes in zooplankton species composition were determined using the Bray–Curtis similarity between St. 1 and St. 4. The relationship between seasonal variations of river discharge and similarity between St. 1 and St. 4 was determined with linear correlation using StatView 5.0 (SAS Institute Inc.). Site 4 was selected for the comparison with the reservoir inflow site (St. 1) because it represented the impact of inflow from

the main tributary (Fig. 1) and still contained enough drifting zooplankton individuals for the comparison (Fig. 3). The mean distance that the zooplankton persisted from the initial point (at the reservoir) was calculated from the equation of weighted mean depth (WMD), with distance replacing the depth representing the midpoint of each depth stratum (Frost and Bollens 1992):

$$\text{WMD} = \frac{(\sum n_i d_i)}{\sum n_i},$$

where n_i is the abundance (individual number per liter) at distance d_i . Water discharge at the dam outflow site was obtained from the management office of the Kanogawa Dam, Ehime Prefecture.

To examine whether the zooplankton individuals that had drifted from the reservoir and reached the site below the dam (St. 1) were alive or dead, we conducted a zooplankton sedimentation experiment using a chamber designed for collecting the animals settled on the bottom. The chamber had a polyethylene body (2 l volume) with a sloping bottom connected to a tube, which enabled the extraction of any settled material. Two liters of the river water, including zooplankton, was gently poured into the chamber and left for 30 min. After 30 min, a sample of bottom water (50 ml) containing any sedimented materials was collected through a valve at the bottom of the chamber and separated from upper water containing living organisms. The remaining upper water was filtered through the 60 μm plankton net. The sedimented particles (presumed to include dead zooplankton) and filtered material from the upper column (presumed to be live zooplankton) were fixed with neutral buffered formalin, separately, and the individual numbers of zooplankton contained in each sample were counted. The experiment was conducted in triplicate at St. 1 in June 2005.

Fish for diet analysis were collected in May 2006 at sites 2, 4, and 5 by a cast net and a hand net. Aquatic macroinvertebrates (caddisfly and stonefly larvae) were collected in April 2006 at sites 2, 3, 4, and 5 by hand-sampling of rocks. The collected fish and invertebrates were fixed with 10% formalin and preserved in the refrigerator until required for the stomach and gut analyses. Cladocerans and copepods including their body parts in the stomach of fish (four individuals for each site) and intestine of invertebrates (three individuals for each genus and site) were counted. For the examination of rotifers, commercial bleach was added to the isolated gut to dissolve the organic matter, and rotifer trophi were identified and counted (Schoeneck et al. 1990). Food selectivity of the fish at St. 2, where they consumed enough zooplankton species for the calculation, was calculated using Chesson's selectivity index (α), $\alpha = (r_i/p_i)/(r_i/p_i + r_j/p_j)$, where r_i is the proportion of prey class i in the stomach and p_i is the

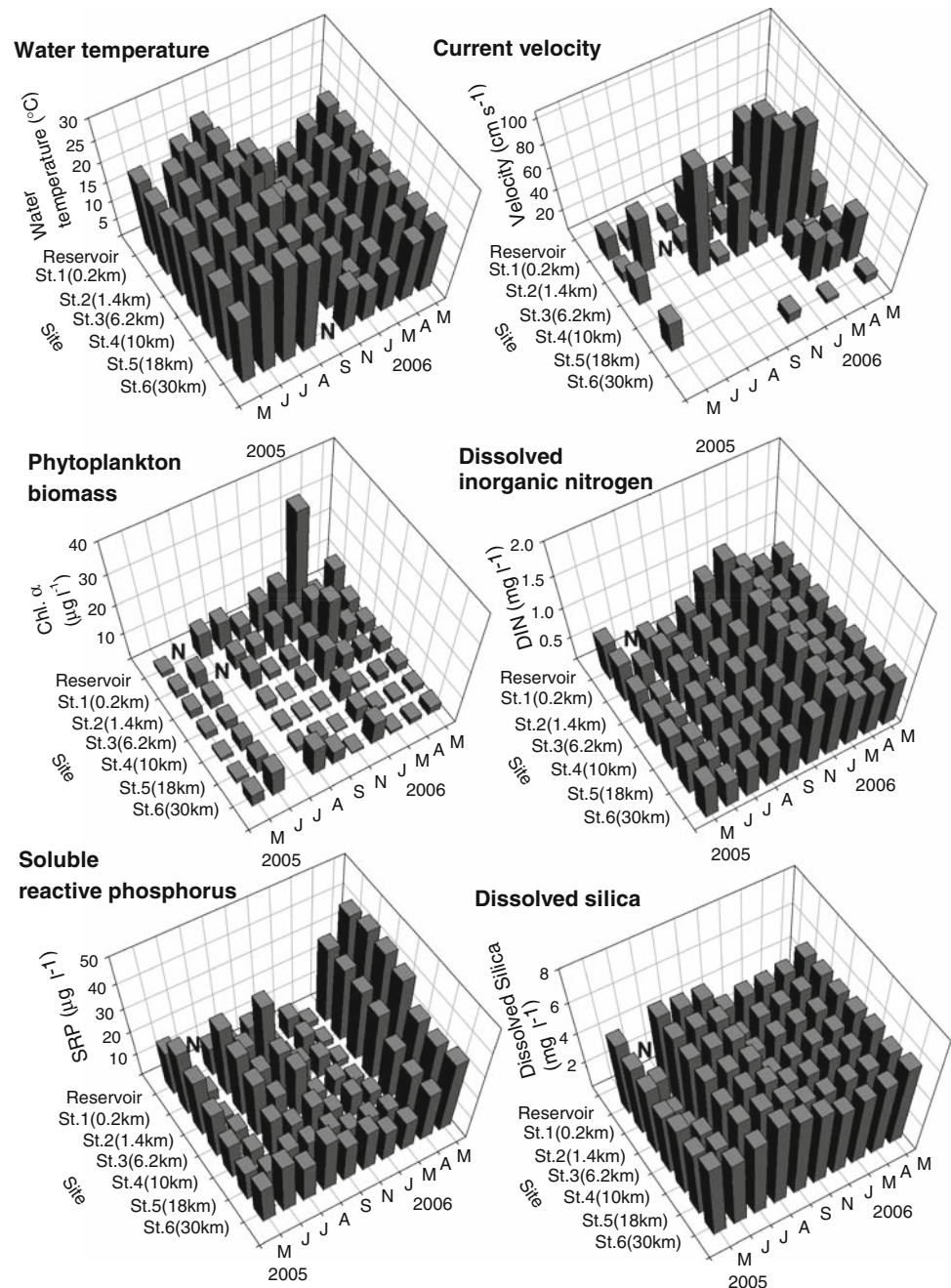
proportion in the environment, while r_j and p_j are the proportion of other prey classes in the stomach and environment, respectively (Chesson 1978). Selectivity index ranged from 0 (negative selection) to 1 (positive selection), and non-selectivity was 0.5.

Results

Both reservoir and river water temperatures fell below 10°C in January but exceeded 25°C during summer (June–August). The water temperatures were higher at river sites, and increased downstream (Fig. 2). Water current velocities in the river were highly variable, depending on the sites as well as the seasons. The water current became markedly slow at the lower sites (St. 5 and St. 6), but neither longitudinal nor seasonal trend was observed between St. 1 and St. 4. Current velocity at St. 5 was negligible and not detected by our measuring instrument. Phytoplankton biomass (Chl. *a*) was highest in March 2006, reaching a vertical mean of approximately 34 $\mu\text{g l}^{-1}$ at the reservoir. However, it hardly exceeded 10 $\mu\text{g l}^{-1}$ in other seasons. In the river, Chl. *a* concentration rapidly decreased after the reservoir water had flowed into the river, and it continued to decrease downstream except at site 6, the lowest sampling point, where it showed rather higher concentration than at the upstream sites. Nutrient concentrations showed no marked longitudinal trend during the study period.

The zooplankton community of the reservoir showed the typical seasonal succession pattern usually observed at lakes with high densities of rotifers and cladocerans from spring to summer, while there were low densities during winter (Fig. 3). The primary rotifers in most samples were *Polyarthra* spp. and *Keratella cochlearis*, but additional common taxa included *Diurella stylata* and *Ascomorpha* sp. Among those taxa, *Polyarthra* spp. dominated the rotifer community in most seasons. *Daphnia galeata* was dominant in May 2005, but *Bosmina longirostris* dominated the cladoceran community thereafter. Other genera such as *Ceriodaphnia* and *Bosminopsis* showed lower densities than *Daphnia* and *Bosmina* throughout the study period (maximum densities in the reservoir were 28.4 individuals (ind.) per liter for *Ceriodaphnia* and 6.1 ind. per liter for *Bosminopsis*). Although copepod nauplii were frequently observed, adult and late copepodid stages of copepod were rarely found in the samples. In the river, their abundance rapidly decreased, and the density at St. 1 (0.2 km from the dam) showed less than half of the initial zooplankton abundance at the reservoir. The zooplankton abundance continued to decrease downstream, and few zooplankton individuals were detected after St. 4, which was located 10 km from the outlet dam.

Fig. 2 Seasonal changes in environmental variables from Kanogawa Reservoir to Hiji River (*N* no data). Water temperature in September, and current velocity and phytoplankton biomass in July, were not measured



The species composition of zooplankton in the river sites was similar to that of the reservoir from St. 1 to St. 3; however, few cladocerans were detected from the samples thereafter, and species composition continued to diverge (Fig. 4a) from the upper sites. Similarities between St. 1 and St. 4 during the study period, representing the degree of modification of zooplankton composition within a 10 km stretch of river from St. 1, was significantly and positively correlated to river discharge (Fig. 4b). During the higher discharge period, the zooplankton species composition was rather steady until St. 4. The calculated mean distances of dominant zooplankton species showed that rotifer species

persisted for longer distances than did cladoceran species (Fig. 5). They persisted for longer distances during higher discharge seasons from January to May 2006. However, such a relationship between mean distance and river discharge was not observed for *B. longirostris*, the dominant cladoceran species.

In the sedimentation experiment, most zooplankters did not sink and remained in the water column (Fig. 6). As we assume that the individuals that had settled on the bottom were ones that had died due to physical disturbance during the transportation from reservoir to river through the out-flow channel of the dam, the mortality (the percentage of

Fig. 3 Seasonal changes of longitudinal distribution of zooplankton from Kanogawa Reservoir to Hiji River (N no data)

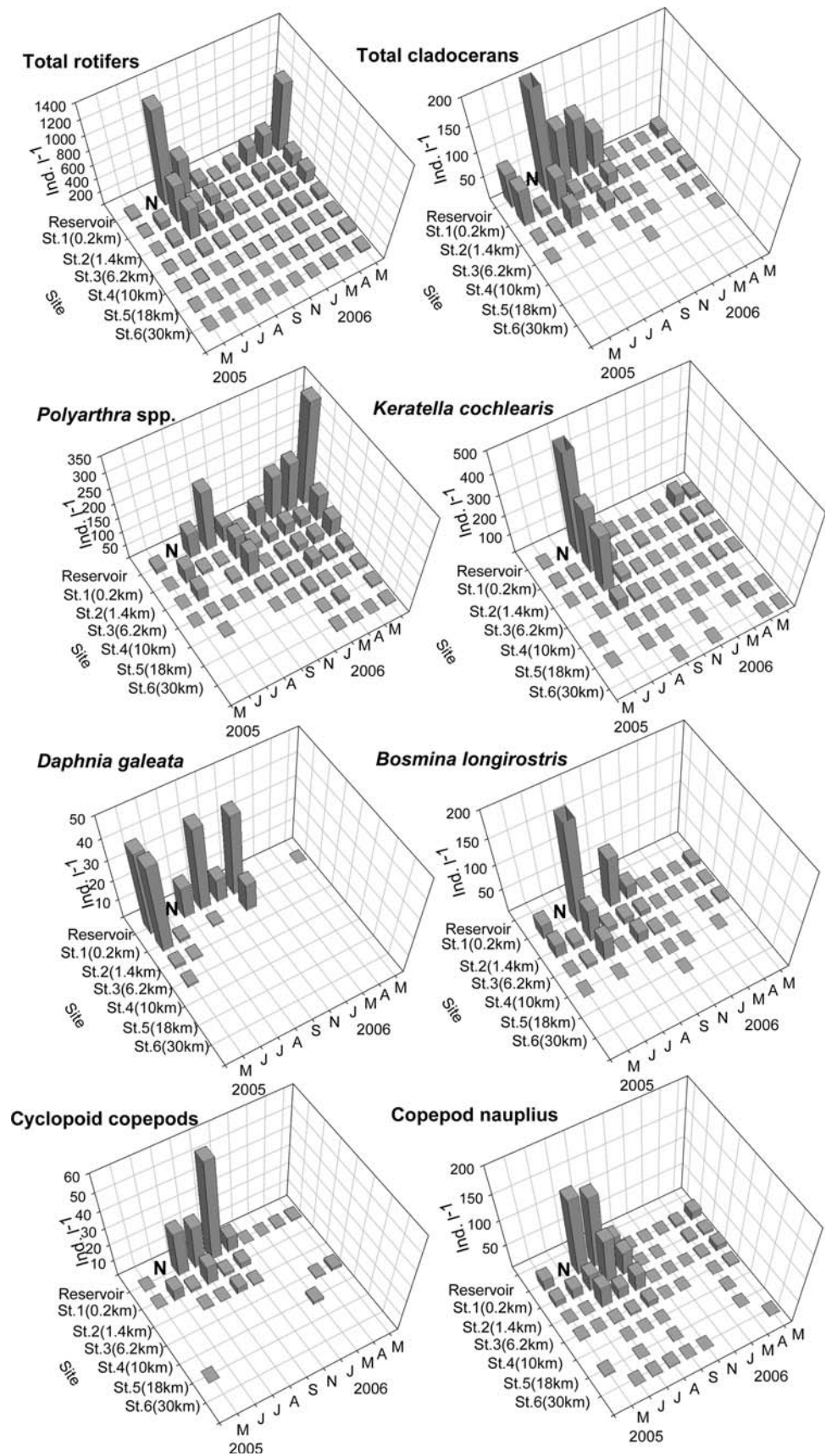
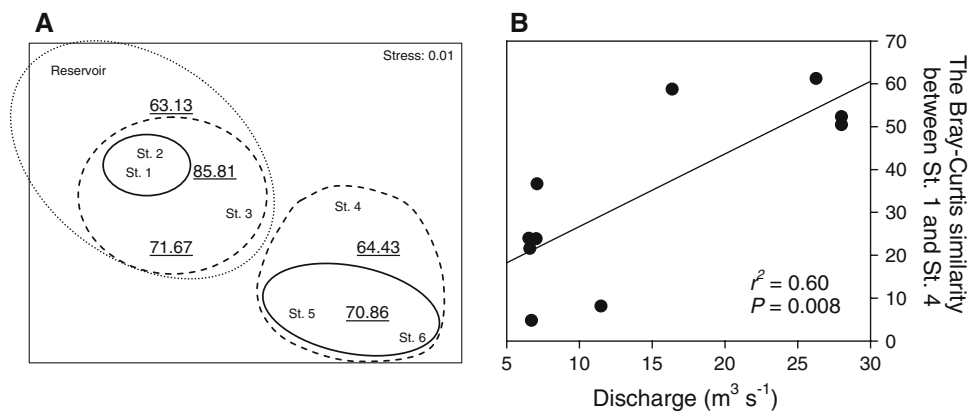


Fig. 4 MDS ordination of zooplankton species compositions of reservoir and river sites (a), and the correlation between river discharge and similarity values between St. 1 and St. 4 (b). The grouping in the MDS ordination was based on the calculation of the Bray–Curtis similarity, and the values between sites and between groups are shown as *underlined numbers*



dead individuals) was lowest for copepod nauplii (only 5.7% of individuals had settled), followed by rotifers (11.6%) and cladocerans (22.2%). However, 47.4% of copepodids were included in the sediment samples.

During the fish sampling in May 2006, juveniles of the pale chub (*Zacco platypus*) were mainly caught in the hand net. Adults of *Z. platypus* and ayu (*Plecoglossus altivelis*) were also caught in the cast net, but they consumed only attached algae, and no zooplankton prey was found in their diets. The analysis of stomach contents showed that the diets of *Z. platypus* juveniles were quite different longitudinally. At St. 2, *Z. platypus* mainly consumed cladocerans (*B. longirostris* and *Bosminopsis deitersi*) and large rotifers, *Asplanchna* spp. (Fig. 7). The mean individual number of cladocerans in a *Z. platypus* juvenile's stomach exceeded 600 individuals. Selective indices for *B. longirostris* and *B. deitersi* were high, indicating strong positive selection (Table 1). Large rotifers, *Asplanchna* spp. were also positively selected, but small rotifers and copepods (copepodids and nauplii) were negatively selected by *Z. platypus*. In contrast, the abundance of zooplankton in fish stomachs markedly decreased after St. 4 with decrease of available zooplankton prey in the river water. Main food items of *Z. platypus* were diatoms and aquatic insects such as chironomids at St. 4 and St. 5.

Larvae of caddisfly (*Hydropsyche* spp.) and stonefly (*Neoperla* spp.) were mainly collected during the sampling in April 2006. Although they consumed zooplankton, the amount consumed per insect was small, and most of their diet was composed of unidentified organic particles and phytoplankton (mainly diatoms). From their zooplankton prey, *Hydropsyche* spp. mainly consumed copepods and cladocerans at upper river sites (Fig. 8). However, at St. 5, no zooplankton prey was found in the gut, and they mainly consumed other aquatic insects (chironomid larvae). *Neoperla* spp. were not collected at St. 2. Cladocerans were found in their diets at St. 3, but no zooplankton prey were detected at St. 4. At St. 5, chironomid larvae were found in

the gut contents, but *Neoperla* spp. mainly consumed diatoms.

Discussion

The drift from the reservoir may play an important role as a major source of zooplankton for Hiji River. However, densities of drifted zooplankton rapidly fell with increasing distance from the dam. In particular, cladoceran density rapidly decreased in the river, and few individuals remained after St. 2, which was only 1.4 km from the reservoir. Rapid downstream decreases of drifted zooplankton have been often reported in shallow streams (Armitage and Capper 1976; Sandlund 1982; Walks and Cyr 2004).

The distance over which the zooplankton can be transported in the outlet river strongly depends not only on abiotic factors, including discharge and physical damage during downstream transport, but also on biotic factors, such as predation pressure by benthic macroinvertebrates and planktivorous fish (Lair 2006). From the results of the sedimentation experiment, it seems that physical disturbance of the zooplankton when they are being flushed passively from the reservoir to the river has little impact on their mortality. Dilution by the addition of water to the river through tributaries and groundwater is also thought to be a major factor that decreases the density of drifting zooplankton in the river (Walks and Cyr 2004). However, inflow from the major tributary enters Hiji River between St. 3 and St. 4 (Fig. 1), and it is unlikely that dilution by ground water accounting for the rapid decreases of cladocerans was present within such a short distance. Alternatively, the decrease of zooplankton density can be attributed to predation by planktivorous and/or filter-feeding macroinvertebrates (mainly Trichoptera and Diptera). In fact, their predation has often been proposed as a critical factor in the removal of zooplankton from the drift in lake–stream systems (Armitage and Capper 1976; Sandlund

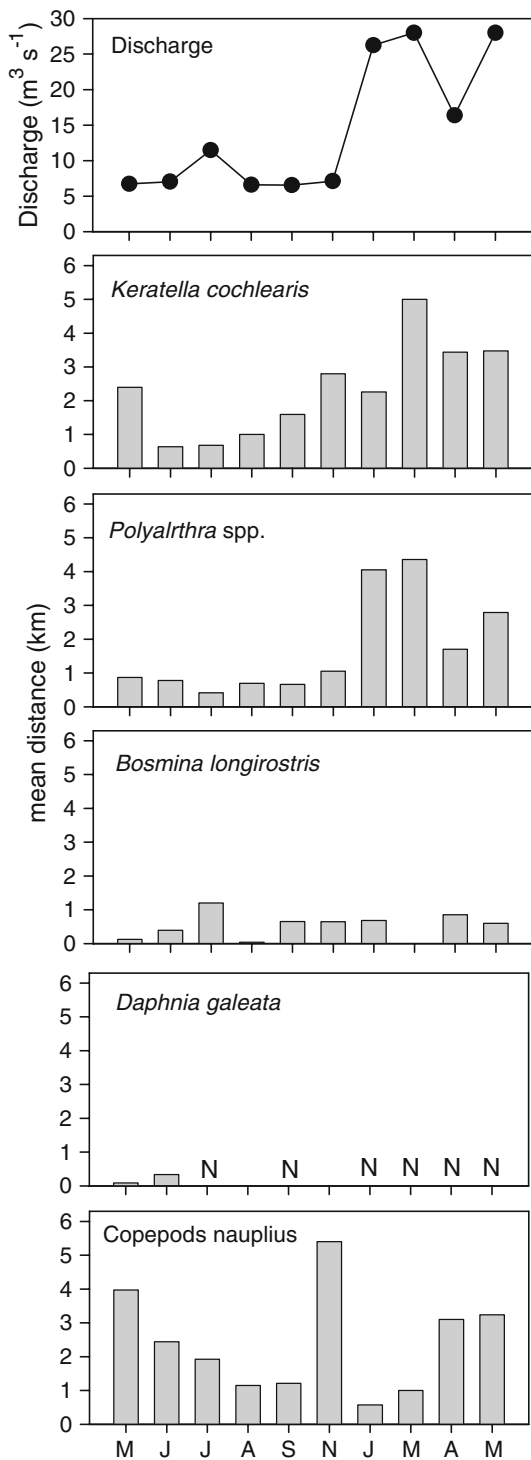


Fig. 5 Seasonal changes in the river discharge and the calculated mean distances of dominant zooplankton species (*N* no individual collected)

1982; Walks and Cyr 2004). In Hiji River, considering the small amount of cladoceran zooplankton consumed, the impact of predation by macroinvertebrates on downriver

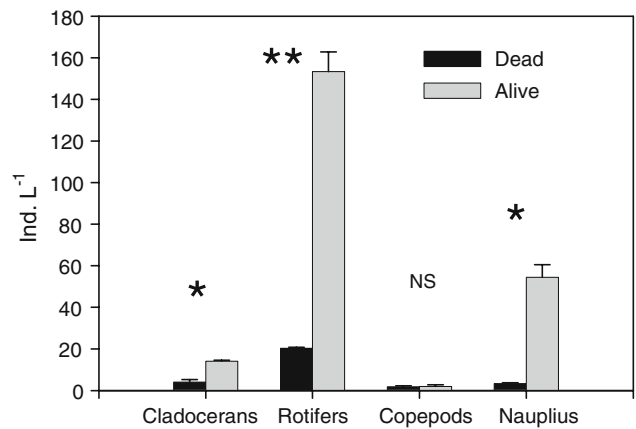


Fig. 6 Densities of dead (settled at the bottom of the chamber designed for the sedimentation experiment) and live (remaining in the water column of the chamber) zooplankton during the sedimentation experiment. Significance of the difference between dead and live zooplankton tested by the *t*-test are shown. (*NS* not significant, * $P < 0.005$, ** $P < 0.0005$)

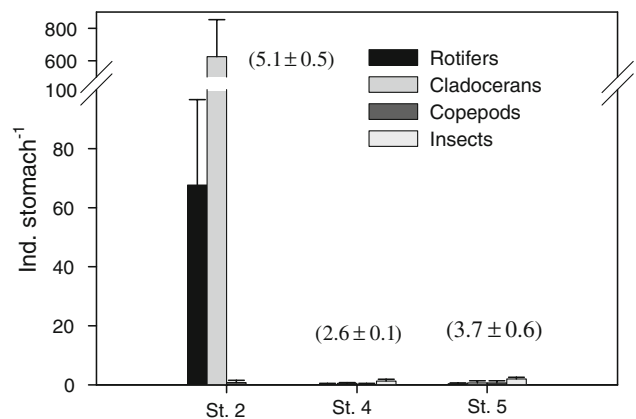


Fig. 7 Stomach contents of *Zacco platypus* collected in May 2006. Mean body sizes of fish (in millimeters \pm SD) are given in parenthesis

drift of zooplankton may be assumed to be small. Their consumption of rotifer was not detected from their gut content analysis.

On the other hand, fish stomach analysis showed that *Z. platypus* collected at St. 2 consumed a large amount of cladocerans. Although adult *Z. platypus*, of which body length exceeds 10 cm, mainly consumed filamentous algae attached to stones, juveniles from 4 cm to 7 cm in size selectively fed on cladocerans, but they consumed only a small amount of small rotifers with negative selection. Only the large genus, *Asplanchna*, was abundantly included in the fish stomach, with a high selectivity index. Removal of large zooplankton species from the drift has often been observed in lake–outlet river systems (Sandlund 1982; Akopian et al. 1999). Although we could not analyze the fish density in the river quantitatively, dense fish schools were observed at St. 1 and St. 2 throughout the

Table 1 Summary of selectivity index (α) of zooplankton prey in the stomach contents of *Zacco platypus* (mean \pm SD, $n = 4$)

| Rotifers | α | Cladocerans | α | Copepods | α |
|-----------------------------|-----------------|-----------------------------|-----------------|-----------------------|-----------------|
| <i>Asplanchna</i> spp. | 0.66 \pm 0.45 | <i>Bosmina longirostris</i> | 0.99 \pm 0.01 | Unidentified copepods | 0.13 \pm 0.27 |
| <i>Keratella cochlearis</i> | 0.20 \pm 0.16 | <i>Bosminopsis deitersi</i> | 0.98 \pm 0.01 | Nauplius | 0.09 \pm 0.18 |
| <i>Trichocerca</i> spp. | 0.36 \pm 0.25 | | | | |
| <i>Pompholix complanata</i> | 0.22 \pm 0.44 | | | | |
| <i>Ascomorpha</i> sp. | 0.14 \pm 0.26 | | | | |

The selectivity index ranges from 0 (negative selection) to 1 (positive selection), and non-selectivity is 0.5

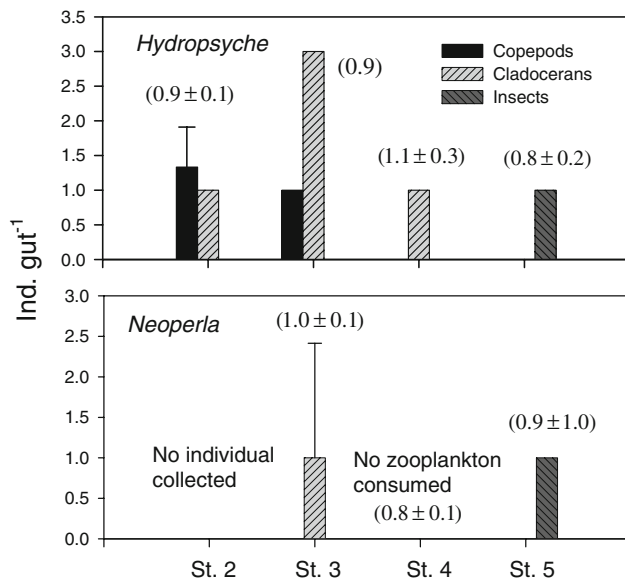


Fig. 8 Gut contents of macroinvertebrates collected in April 2006. Mean body sizes of insects (mm \pm SD) are given in *parenthesis*

study period. Therefore, it seems that fish at the connecting point between the reservoir outlet and the river may be sieving the drifting zooplankters through size-selective predation.

In contrast, even though densities of rotifers declined downriver, their mean distances from the dam showed that rotifers persisted further than cladocerans did. The distances over which rotifers could be found in the outlet river seemed to be related to the river discharge, since, during the higher discharge period, rotifers persisted further downstream, as shown in Fig. 5. The zooplankton composition in the river was dominated by small rotifers after St. 1, and the correlation between the similarity of the two sites (St. 1 and St. 4) and discharge indicated that zooplankton composition was less diverged when the high discharges were recorded.

The effects of discharge on zooplankton community in lake–stream systems are not yet fully understood and vary among habitats (Nielsen et al. 2005). However, it has been suggested that the distance traveled by the animals in the

drift is related to the current speed and the water discharge. The increased current speed makes the animals stay in the drift for a longer distance (McLay 1970). High discharge has also been proposed as a factor leading to the flushing of zooplankton and their transportation further downstream (Sandlund 1982; Campbell 2002). In Hiji River, zooplankton that had drifted from the reservoir and remained in the river was dominated by small rotifers less susceptible to fish predation, and it is likely that high discharge and increased current speed during the high discharge period induced the active downstream transport of rotifers. Since they are not affected by selective predation during the drift, their composition would be maintained more steadily throughout a further distance during the high discharge period.

For zooplankton in large rivers, the hydrology of the river is often considered to be a critical factor determining the internal production of zooplankton during their transport downriver, especially for crustaceans (Basu and Pick 1996; Baranyi et al. 2002; Viroux 2002; Thorp and Mantovani 2005), and biological control such as predation may take place after physical control has happened (Chang et al. 2001; Thorp and Casper 2003; Lair 2006). However, in Hiji River, where the water velocity is too fast for plankton development, the species composition and abundance of plankton totally depend on the transportation from its upper reservoir, and negligible internal production and development of community during the downriver transportation were observed. Their abundance and species composition seem to be determined by the environment at the beginning of the outlet river, where lake zooplankton enters and faces predators dwelling in the river. In narrow and shallow outlet rivers, fish can encounter drifting zooplankton efficiently, and most large zooplankton can be easily removed by the predation within short distances of the reservoir. It is difficult to estimate how fish predation contributes to the mortality of drifting cladocerans, since it is not clear whether live or dead cladocerans are consumed by fish. However, in the river system like Hiji River, where the internal production of cladocerans is strongly restricted by its fast flow, fish predation can be an important factor controlling the absolute abundance of drifting organic

matter. In contrast, the drift of small rotifers that are less susceptible to fish predation is likely to be primarily governed by physical factors such as discharge.

Owing to the rapid decrease of available zooplankton prey near the dam site, the amount of zooplankton consumed by fish also decreased seriously at the lower sites. *Z. platypus* at the lower sites consumed phytoplankton such as diatoms as their main food. Although they were still consuming zooplankton at St. 4, the gut contents of *Hydropsyche* spp. and *Neoperla* spp. had shifted to unidentified organic matter, phytoplankton (diatoms) and other macroinvertebrates at the lowest site. The results indicate that concentrated fish predation at the upper part of outlet rivers may strongly limit the availability of food for downriver fish and macroinvertebrates.

The connection between a productive lake and its less productive outlet river causes spatial subsidies of nutrients, detritus, and prey, and, accordingly, influences the energy, carbon, and nutrient budget of subsidized river habitat (Polis et al. 1997). Particularly, as shown in the present results, the zooplankton produced in the upper reservoir worked as a main food source for fish and invertebrates, and it had a large impact on their diets. However, in the reservoir and its small and steep outlet river systems, the spatial subsidy of prey to river consumers seems to be limited to only several kilometers from the reservoir by the concentrated predation pressure below the dam.

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