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Variation in trophic pathways and food web characteristics revealed by stable isotopes in an intermittent stream system of the Inukami River, Japan

Hyun-Seon Shin*, Nozomi Amahashi, Lan Ao and Osamu Mitamura

Limnological Laboratory, Environmental Science Graduate School, University of Shiga Prefecture, Hassakachou 3165, Hikone 522–0057, Japan

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To examine variation in trophic pathways and the characteristics of food webs from organic matters to aquatic insects, we used stable isotopes to study an intermittent stream system of the Inukami River, Japan. The aquatic insects, including *Glossosoma* spp., Chironominae spp., *Stenelmis* spp., *Rhyacophilla nigrocephala*, and *Hexatoma* spp., were characterized by different feeding strategies. The $\delta^{13}C$ values for these species indicated that *Glossosoma* spp. graze upon periphyton; Chironominae and *Stenelmis* spp. mainly feed on benthic particulate organic matter, and *R. nigrocephala* and *Hexatoma* spp., which were identified as predators, feed upon *Glossosoma*, *Stenelmis*, and/or Chironominae spp. This suggests that the trophic position of consumers at each station may be determined by the trophic position of basal food sources in situ. For trophic pathways, the $\delta^{13}C$ values for both organic matter and aquatic insects tended to gradually decrease, whilst the $\delta^{15}N$ values increased from the upper reach to the lower reaches, relative to the physicochemical and geographical conditions. These parameters indirectly influence the flow of energy from organic matter to consumers within food web in an intermittent stream system.

Keywords: aquatic insects; intermittent stream system; Inukami River; stable isotope; trophic pathways

Introduction

Rivers and streams are spatially and temporally variable in their biological communities, physical characteristics, and ecosystem processes (Winemiller et al. 2010). Lotic ecosystems and intermittent stream system environments involve a dynamic hydrological system, characterized by a period of water flow and followed by drought, leading to environmental heterogeneity (Simões et al. 2008). The dynamics of these rivers are related to local and regional influences of seasonality, such as infiltration, evaporation, precipitation, runoff, hydroperiod, and exchanges with groundwater (Boulton and Lake 1992; Schwartz and Jenkins 2000).

River food webs typically depend on two main carbon energy sources: inorganic carbon fixed by algae or other aquatic plants, and particulate organic matter derived from terrestrial plant matter (e.g. Vannote et al. 1980; Thorp and Delong 1994; Doucett et al. 2007; Ishikawa et al. 2010). In view of these major energy sources, recent studies based on intermittent stream systems have reported the origin of allochthonous or autochthonous organic matter as food sources within stream ecosystems (Bunn et al. 2003; Reid et al. 2008; Dekar et al. 2009). In order to understand the carbon dynamics of stream ecosystems, many studies have used carbon and nitrogen stable isotope ratios to examine trophic pathways (e.g. Finlay 2001; Finlay et al. 2002; Delong and Thorp 2006; Doi et al. 2006; Ishikawa et al. 2010). The carbon stable isotope ratio ($\delta^{13}C$) is slightly enriched in the route of consumption and assimilation, whilst the nitrogen stable isotope ratio ($\delta^{15}N$) in the tissues of consumers is enriched relative to their diet (Vander Zanden and Rasmussen 2001; Post 2002). Information regarding how factors such as climate, land use, and physical and hydrological properties interact with other abiotic processes to influence the structure of, and energy flow within, aquatic communities is required (Reid et al. 2008). Understanding the trophic basis of stream food webs is crucial for conserving ecosystems exposed to harsh conditions, including drought and intermittent stream drying (Dekar et al. 2009).

In this study, we aimed to identify trophic pathways, from organic matter to aquatic insects (including primary consumers and predators), using stable isotopes (carbon and nitrogen), and to characterize food webs in an intermittent stream system of the Inukami River in Japan. To compare relationships between aquatic insects and their food sources, we classified functional feeding groups (FFGs) based on

*Corresponding author. Email: o10yshin@ec.usp.ac.jp

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the origins of the food items and the mechanisms of food acquisition (Merritt and Cummins 1996).

Materials and methods

Study stations

This study was conducted in the Inukami River (35°0′N, 136°0′E), located in the north–eastern region of Shiga prefecture. The Inukami River runs through farmlands, villages, and a town, and flows into the eastern Lake Biwa region of Japan (Figure 1). The Inukami River is 27 km long and has a catchment area of approximately 105 km^2. It has a temperate monsoon climate, and the mean annual precipitation in this watershed is 1571 mm (Hikone Regional Meteorological Office). In addition, the Inukami River has typical limestone geological features and habitat structures such as riffles, runs, and pools. The stream bed of the Inukami River is mainly composed of cobbles and pebbles. Although the river runs through an agricultural area and a town, it is relatively well preserved in its natural state. However, during the dry season (August and November–December), the Inukami River has a dried-up channel approximately 4–9 km from the river mouth (Figure 1C). We expected this to alter the quality of the stream water. Therefore, we established one station upstream (Station 1) and two stations downstream (Stations 2 and 3) of this channel area.

Sample collection and preparation

Benthic macroinvertebrates were collected at the three stations in July 2008. We conducted sampling with three replicates, using a square Surber sampler (250-μm mesh) 0.25 m^2 in size. All biota were separated from other material and were then sorted in the laboratory. Identification was mostly performed using a stereoscopic microscope. Aquatic insects were identi-

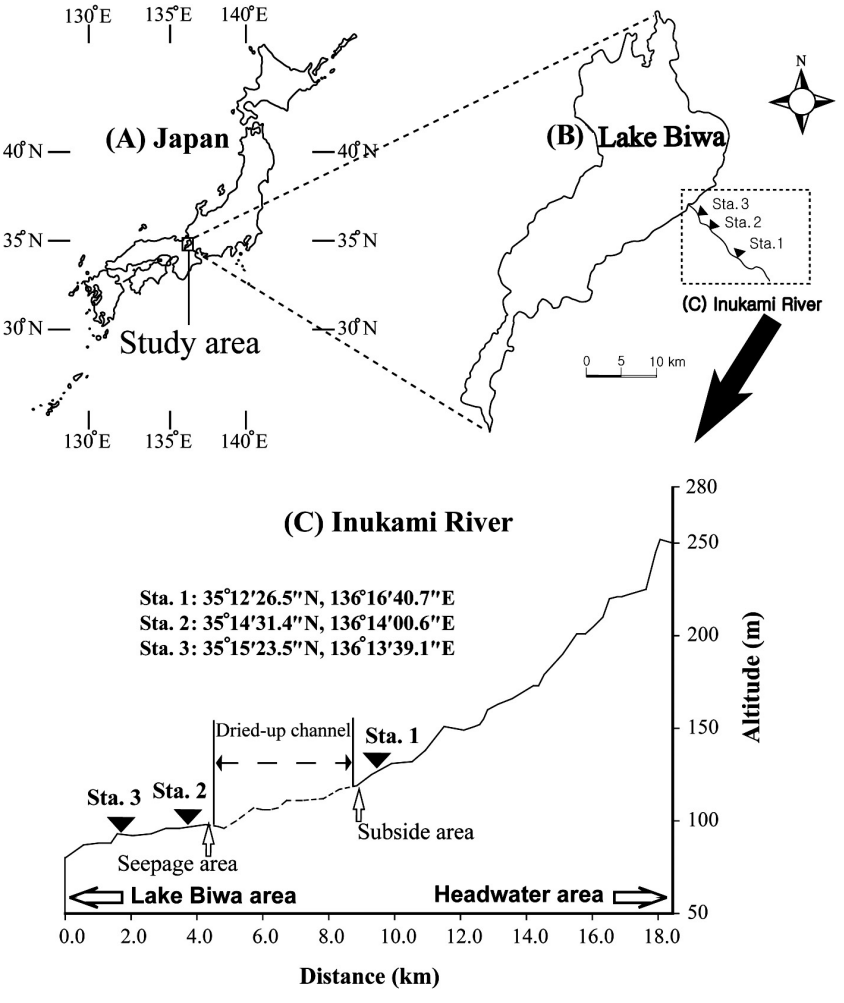

Figure 1. (A) Map of the study area in Japan. (B) Map of the study stations along the Inukami River and in Lake Biwa. (C) A longitudinal section of the Inukami River, including Station (Sta.) 1 in the upper reach, and Stations 2 and 3 in the lower reaches of the dried-up channel. The arrows indicate the locations and characteristics of stations along the Inukami River.

fied to the lowest feasible classification level (mostly to the genus level). Overall, 94 species were identified from the various samples. Among the collections from sampling stations were aquatic insects from different feeding groups (scrapers: *Glossosoma* spp.; scrapers or collectors: *Stenelmis* spp. and Chironominae spp.; predators: *Rhyacophilla nigrocephala* and *Hexatoma* spp). Based on their relatively high abundance, these insects were selected for following analyses.

Analysis of environmental factors

Current velocity was measured at all sampling stations, with a digital current meter (Model–3631, Yokogawa Co.), at 1-m intervals from the right to the left bank. Water temperature (WT) and electric conductivity (EC) were measured using a multiple water quality sensor (U–22, Horiba Co.), and pH was measured by colorimetry. The concentration of dissolved oxygen (DO) was determined using the methods described by Winkler (1888). The water samples to be used for the measurement of major cations (Na^+, K^+, Mg^{2+}, and Ca^{2+}) and anions (Cl^- and SO_4^{2-}) were filtered through filter paper (Toyo No. 5C; pore size 1.0 μm), and were stored in a refrigerator. The concentrations of major ionic elements and nitrate were analyzed using an ion chromatographic analyzer (Dionex DX–120). Water samples to be used for the analyses of nutrients and dissolved organic carbon concentrations were filtered through a glass-fiber filter (Whatman GF/F; pore size 0.7 μm), after combustion at 420°C for 3 h. The ammonium concentration was determined using the methods reported by Sagi (1966); nitrite concentration was determined using the methods reported by Bendschneider and Robinson (1952); phosphate, using the methods reported by Mullin and Riley (1962); and silicate, using the methods reported by Mullin and Riley (1955). The dissolved organic carbon (DOC) concentration was measured by a high-temperature oxidation technique using a total organic carbon analyzer (Shimadzu Model 5000). We collected the matter attached to the surface of stones in a quadrant (5 cm × 5 cm) by scouring the surface of the stones with a brush, and then measured its dry weight. We considered that most of the attached matter consisted of periphyton, and therefore the term 'attached matter' is used to represent periphyton. The chlorophyll *a* (chl. *a*) concentration was determined using a fluorometer (Turner Designs 10–AU).

Analysis of stable isotope ratios

Aquatic insects and their potential food sources were collected from all of the sampling stations. The aquatic insects were maintained in filtered river water at 5°C for 24 h to allow them to eliminate their gut contents, and then the samples were freeze-dried. The potential food sources included suspended particulate organic matter (SPOM), benthic particulate organic matter (BPOM), and periphyton.

For the analysis of stable isotopes, SPOM was collected by filtering the river water through GF/F glass-fiber filters, BPOM was collected from the streambed using sieves with mesh sizes < 250 μm, and attached matter (periphyton and chl. *a*) was collected by scouring stones in a quadrant (5 cm × 5 cm) using a brush. SPOM, BPOM, and periphyton samples were acidified with 1 mol·L^{-1} HCl to remove carbonates. All of the samples were freeze-dried and stored in a freezer at -20°C until the stable isotope ratios were analyzed.

Generally 6 to 140 individuals of the same species were compiled in each sample. The value of all species were measured as an average of compiled individuals. Three replicate measurements of the carbon and nitrogen isotope ratios were taken for each sample, using an elemental analyzer EA1108 (Fisons), which was connected to a mass spectrometer (Delta S, Finnigan MAT), with an interface (Conflo II, Finnigan MAT). The results were reported using the delta notation and have been calculated as follows: $\delta^{13}C$ or $\delta^{15}N$ $(‰) = (R_{sample}/R_{standard} - 1) \times 1000$, where R is the $^{13}C/^{12}C$ ratio for $\delta^{13}C$ and the $^{15}N/^{14}N$ ratio for $\delta^{15}N$. The standards used for $\delta^{13}C$ and $\delta^{15}N$ were Pee Dee Belemnite (PDB) and atmospheric nitrogen, respectively. The analysis errors for $\delta^{13}C$ and $\delta^{15}N$ were within $\pm 0.2‰$.

Statistical analysis

A one-way analysis of variance (ANOVA) was used to test for significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values of aquatic insects and their food sources. We used SPSS (SPSS Inc.) and Sigma Plot (Systat Software Inc.) to compare the $\delta^{13}C$ and $\delta^{15}N$ values of aquatic insects between stations. For descriptive purposes, the mean ± standard deviations (SDs) are displayed.

Results

River environmental parameters

The environmental parameters recorded at the sampling stations are displayed in Table 1. These included river width, water depth, current velocity, discharge, WT, EC, pH, and the concentrations of DO and the major ions (Na^+, K^+, Mg^{2+}, Ca^{2+}, Cl^-, and SO_4^{2-}). The water temperature at Station 1, characterized by stagnant water formed as a result of the sub-flow process, was 33.2°C ± 0.3°C and was higher than that at the other stations. The pH value at Station 1, which was located in

Table 1. Physicochemical parameters and stream water quality at each sampling station (mean (SD), $n = 3$).

Parameter	Station 1	Station 2	Station 3
River width (cm)	610	680	890
Water depth (cm)	13.0 (1.0)	19.0 (1.0)	34.0 (17.0)
Current velocity (cm s^{-1})	24.2 (3.7)	24.6 (8.0)	34.0 (17.0)
Discharge (m^3 s^{-1})	0.15	0.26	0.52
WT (°C)	33.2 (0.3)	23.6 (0.0)	23.0 (0.0)
pH	8.4	7.2	7.4
DO (mg L^{-1})	9.7	8.3	9.9
EC (μs cm^{-1})	185 (5)	214 (0)	207 (2)
Na^+ (mg L^{-1})	5.4 (0.0)	11.0 (0.2)	11.0 (0.2)
K^+ (mg L^{-1})	1.0 (0.0)	1.2 (0.0)	1.0 (0.0)
Mg^{2+} (mg L^{-1})	2.3 (0.0)	2.5 (0.0)	2.7 (0.0)
Ca^{2+} (mg L^{-1})	27.0 (0.0)	28.0 (0.1)	27.0 (0.3)
Cl^- (mg L^{-1})	5.9 (0.0)	12.0 (0.0)	11.0 (0.1)
SO_4^{2-} (mg L^{-1})	7.8 (0.0)	14.0 (0.0)	14.0 (0.0)

the upper reach of the dried-up channel, was 8.4 and was also higher than those of the lower reaches (Stations 2 and 3). The DO concentrations (8.3–9.9 mgL^{-1}) and EC (185–214 μScm^{-1}) did not differ among the stations. The chloride, sulfate, and sodium ion concentrations differed between Station 1 and Stations 2 and 3. However, the concentrations of the other major ions were relatively similar for all the stations.

The dissolved inorganic nitrogenous compounds, phosphate, silicate, chl. *a*, and periphyton biomass concentrations are shown in Table 2. Most of the dissolved inorganic nitrogen (DIN: sum of nitrate, nitrite, and ammonium nitrogen) in the river was composed of nitrate. Although the DIN concentrations were variable, they did not differ between stations. The nitrate concentration at Station 2 (43.8 ± 2.4 μM) and the phosphate concentration at Station 1 (2.3 μM) were relatively higher than those at the other stations. The phosphate concentration at Station 2 (1.3 μM) and the silicate concentration at Station 1 (176 μM) were also comparatively higher than those at the other stations. The DOC concentrations slightly declined from the upper reach (1.5 mgL^{-1}) to the lower reaches (0.8–0.9 mgL^{-1}).

The mean values of periphyton biomass (26–53 gm^{-2}) were not significantly different among stations (one-way ANOVA: df = 4, $F = 0.8$, $P > 0.05$). However, the mean chl. *a* concentrations were significantly different between Station 1 and Stations 2 and 3 (one-way ANOVA: df = 4, $F = 4.4$, $P < 0.04$).

Isotopic signatures of periphyton, SPOM, and BPOM

The $\delta^{13}C$ and $\delta^{15}N$ (‰) values of aquatic insects and their potential food sources at each study station are displayed in Table 3 and Figure 2. The mean $\delta^{13}C$ values of periphyton (-21.6 to -19.1‰) were different among stations (one-way ANOVA: df = 3, $F = 293.6$, $P < 0.01$; Tukey multiple comparison, $P < 0.01$ for all values). The mean $\delta^{13}C$ values of SPOM (-25.4 to -21.4‰) and BPOM (-24.2 to -22.2‰) were significantly different among stations (one-way ANOVA: df = 3, $F = 4.4$ and 22.9, respectively; $P < 0.01$). However, these values did not differ between Stations 2 and 3, which were located in the lower reaches (Tukey multiple comparison, $P > 0.05$). The mean $\delta^{15}N$ values of periphyton (1.8–3.7‰) were also considerably different among stations (one-way ANOVA: df = 3, $F = 114.1$, $P < 0.01$; Tukey multiple comparison, $P < 0.02$ for all values). The mean $\delta^{15}N$ values of SPOM (1.3–3.7‰) and BPOM (2.3–4.4‰) were relatively different among the stations (one-way ANOVA: df = 3, $F = 58.5$ and 76.3, respectively, $P < 0.01$). However, again these values did not differ between Stations 2 and 3 in the lower reaches (Tukey multiple comparison, $P > 0.05$). The $\delta^{13}C$ and $\delta^{15}N$ values of SPOM and BPOM varied in a similar pattern from Station 1 to 3 (Figure 2). Although Stations 2 and 3 had similar values, the $\delta^{13}C$ values of SPOM and BPOM tended to

Table 2. Concentrations of nitrogenous compounds, phosphate, silicate, dissolved organic carbon (DOC), periphyton, and chlorophyll *a,* at the sampling stations. Mean (SD) values of chlorophyll *a,* and periphyton are displayed with the range values in parentheses.

Parameter	Station 1	Station 2	Station 3
Nitrate (μM)	25.2 (0.0)	43.8 (2.4)	39.8 (0.5)
Nitrite (μM)	0.4 (0.0)	0.4 (0.0)	0.2 (0.0)
Ammonium (μM)	2.3 (0.0)	1.1 (0.1)	1.2 (0.1)
Phosphate (μM)	0.5 (0.0)	1.3 (0.0)	0.5 (0.0)
Silicate (μM)	176 (0)	131 (2)	135 (1)
DOC (mg L^{-1})	1.5 (0.0)	0.9 (0.0)	0.8 (0.0)
Periphyton (g m^{-2})	26 (20) (8–60)	43 (18) (19–68)	53 (37) (10–79)
Chlorophyll *a* (mg m^{-2})	56 (39) (15–98)	166 (40) (102–205)	158 (101) (43–263)

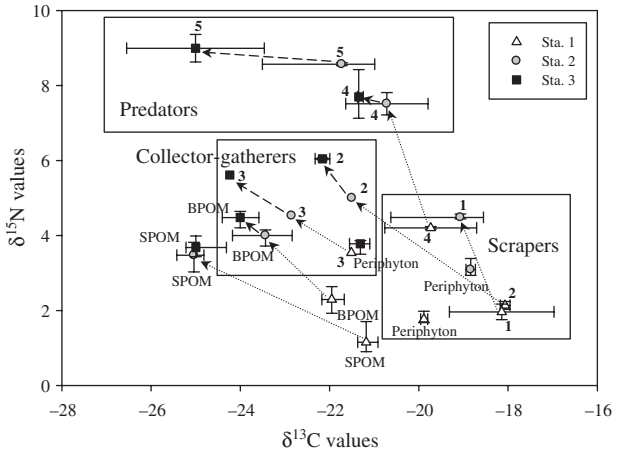

Figure 2. Carbon and nitrogen (mean ± SD) stable isotope plots of aquatic insects and their potential food sources in the Inukami River. The triangles indicate Station 1, gray circles indicate Station 2, and black squares indicate Station 3. SPOM, suspended particulate organic matter; BPOM, benthic particulate organic matter; 1, *Glossosoma* spp., 2, *Stenelmis* spp., 3, Chironominae spp., 4, *Rhyacophila nigrocephala*; 5, *Hexatoma* spp.

gradually decrease from Stations 1 to 3, whilst the $\delta^{15}N$ values of SPOM and BPOM tended to increase from Stations 1 to 3.

Isotopic signatures of aquatic insects

The mean $\delta^{13}C$ and $\delta^{15}N$ values of aquatic insects (ranging from -25.0 to $-18.1‰$ and 2.0 to 9.0‰ respectively) differed among stations and species (Table 3). The $\delta^{13}C$ values of *Glossosoma* spp. ranged between -19.0 and $-18.1‰$, whilst the $\delta^{15}N$ values ranged between 2.0 and 4.5‰. The $\delta^{13}C$ values at Station 1 and the $\delta^{15}N$ values at Station 2 were higher than those at the other stations. The $\delta^{13}C$ and $\delta^{15}N$ values of Chironominae spp. (ranging from -24.2 to $-21.5‰$ and 3.5 to 5.6‰, respectively) were slightly different among stations. The $\delta^{13}C$ values of *Stenelmis* spp. ranged from -22.2 to $-18.1‰$, while the $\delta^{15}N$ values ranged from 2.1 to 6.0‰. The $\delta^{13}C$ and $\delta^{15}N$ values of Chironominae and *Stenelmis* spp. at Station 1 were higher than those at Station 3. Although the $\delta^{13}C$ values of *Hexatoma* spp. and *R. nigrocephala* at Station 2 were higher than those at Station 3, the $\delta^{15}N$ values of these species appeared to be similar among stations.

Discussion

Physicochemical features of the upper and lower reaches of the dried-up channel

Mulholland and Hill (1997) used calcium and sulfate as a means to separate stream discharge into three catchment flow paths. In the present study, the concentrations of a conservative solute (silicate) and some major ions (chloride, sulfate, and sodium ions) differed among the upper reach (Station 1) and lower reaches (Stations 2 and 3) (Tables 1 and 2). These levels may be influenced by water seepage from underground layers in the lower reaches. Furthermore, the pH values in the lower reaches were lower than those in the upper reach (Table 2). These results were likely to be influenced by the water that seeped from Station 2 to 3.

Allan (1995) reported that primary production was relatively high in small spring streams, which are exposed to sunlight, are algae-rich and contain adequate concentrations of nitrogen and phosphate. The chl. *a*, nitrogen, and phosphate concentrations in the lower reaches were higher than those in the upper reach (Table 2). These results were probably influenced not only by water seepage, but also by contaminated groundwater with possible inflow of ions, such as chloride, sulfate, and sodium ions, which may be associated with anthropogenic factors.

Trophic pathway of aquatic insects and their food sources

Potential food sources for herbivores include periphyton, SPOM, and BPOM. The $\delta^{13}C$ and $\delta^{15}N$ values of SPOM and BPOM differed across the sampling stations. Moreover, the $\delta^{13}C$ values of SPOM and BPOM were not close to those recorded for C3 terrestrial plant litter (-29 to $-26‰$) (Wada et al. 1987). The $\delta^{13}C$ values of SPOM and BPOM were higher than those of C3 terrestrial plant litter, perhaps because SPOM and BPOM contained a greater number of benthic diatoms.

Analysis of trophic relationships using stable isotope ratios is generally based on the premise that $\delta^{13}C$ enrichment during trophic transfer is slight ($0.8 \pm 1.1‰$, mean ± 1 SD), whilst that of $\delta^{15}N$ is substantial ($3.4 \pm 1.1‰$) (Deniro and Epstein 1978; Minagawa and Wada 1984; Post 2002). The $\delta^{13}C$ values of *Glossosoma* spp. were close to those of periphyton *in situ*, indicating that they generally feed upon periphyton. This is consistent with the findings of Merritt and Cummins (1996), who reported that *Glossosoma* spp. belongs to the scraper group. The $\delta^{13}C$ values of Chironominae and *Stenelmis* spp. were similar to those of BPOM at each station (Table 2, Figure 2), indicating that BPOM constitutes the major food source for those species. Merritt and Cummins (1996) reported that Chironominae spp. belong to the collector-gatherer group, whilst *Stenelmis* spp. belong to either the scraper or the collector-gatherer group. However, our results indicate that *Stenelmis* spp. may be closer to the collector-gatherer group than the scraper group.

Table 3. $\delta^{13}C$ and $\delta^{15}N$ (‰) values of aquatic insects and their potential food sources at each station in the Inukami River.

Station	Consumer/Food source		$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)				
			Average	SD	Min	Max	Average	SD	Min	Max	*n*
1	Sccraper	*Gossosoma* spp.	−18.1	–	−19.0	−17.3	2.0	–	1.8	2.1	2
	Collector-gatherer	*Stenelmis* spp.	−18.1	–	−18.1	−18.0	2.1	–	2.1	2.2	2
	Collector-gatherer	Chironominae spp.	−21.5	–	–	–	3.5	–	–	–	1
	Predator	*Rhyacophilla nigrocephala*	−19.7	–	−20.5	−19.0	4.2	–	4.2	4.2	2
	Predator	*Hexatoma* spp.	–	–	–	–	–	–	–	–	–
	Periphyton		−20.1	0.1	−20.2	−20.0	1.8	0.1	1.7	2.0	4
	SPOM		−21.4	0.2	−21.6	−21.1	1.3	0.4	1.0	1.9	4
	BPOM		−22.2	0.3	−22.4	−21.9	2.3	0.4	1.9	2.6	4
2	Sccraper	*Gossosoma* spp.	−19.0	–	−19.1	−18.9	4.5	–	4.5	4.6	2
	Collector-gatherer	*Stenelmis* spp.	−22.2	–	−22.3	−22.0	6.0	–	6.0	6.1	2
	Collector-gatherer	Chironominae spp.	−22.9	–	–	–	4.5	–	–	–	1
	Predator	*Rhyacophilla nigrocephala*	−20.7	–	21.4	20.1	7.5	–	7.3	7.7	2
	Predator	*Hexatoma* spp.	−22.2	1.3	−23.7	−21.3	8.6	0.0	8.5	8.6	3
	Periphyton		−19.1	0.1	−19.2	−19.0	3.2	0.2	3.0	3.5	4
	SPOM		−25.4	0.3	−25.8	−25.1	3.4	0.4	3.0	3.8	4
	BPOM		−23.8	0.7	−24.5	−23.1	3.9	0.2	3.6	4.1	4
3	Sccraper	*Gossosoma* spp.	–	–	–	–	–	–	–	–	–
	Collector-gatherer	*Stenelmis* spp.	−21.5	–	–	–	5.0	–	–	–	–
	Collector-gatherer	Chironominae spp.	−24.2	–	–	–	5.6	–	–	–	–
	Predator	*Rhyacophilla nigrocephala*	−21.3	0.1	21.4	21.2	7.8	0.6	7.2	8.5	3
	Predator	*Hexatoma* spp.	−25.0	–	−26.1	−23.9	9.0	–	8.7	9.4	2
	Periphyton		−21.6	0.2	−21.9	−21.3	3.7	0.2	3.4	3.8	4
	SPOM		−25.0	0.5	−25.4	−24.3	3.7	0.3	3.5	4.2	4
	BPOM		−24.2	0.4	−24.7	−23.3	4.4	0.2	4.1	4.7	4

Note: *n* indicates the number analyzed.
– indicate item that could not be calculated or measured due to a small number of samples.

Moreover, analysis of their stable isotope ratios revealed that the $\delta^{13}C$ values were gradually depleted and that the $\delta^{15}N$ values were enriched from Station 1 to 3 (Figure 2). The $\delta^{13}C$ values of the predator group, which included *Hexatoma* spp. and *R. nigrocephala*, were lower at Station 3 than at Station 2. The $\delta^{13}C$ values of *R. nigrocephala* were similar to, and particularly appeared to change in parallel with, those of *Stenelmis* and *Glossosoma* spp. This indicates that the larvae of *R. nigrocephala* may feed on *Stenelmis* and *Glossosoma* larvae at each station. The $\delta^{13}C$ values of *Hexatoma* spp. were close to those of Chironominae and *Stenelmis* spp., suggesting that *Hexatoma* larvae may feed on Chironominae and *Stenelmis* larvae at each station. Consequently, the predator groups in our study area appeared to have at least one or more food sources, and shifted in the trophic pathways according to their food sources.

Analysis of the $\delta^{13}C$ and $\delta^{15}N$ values of *Glossosoma* spp. revealed that the $\delta^{15}N$ values tended to get enriched from Station 1 to 2 (Figure 2). The $\delta^{13}C$ values of Chironominae and *Stenelmis* spp. gradually depleted, whereas the $\delta^{15}N$ values were enriched from Station 1 to 3. Moreover, the predator group exhibited depletion in the $\delta^{13}C$ values from Station 2 to 3. Thus, our results revealed that $\delta^{13}C$ values for the upper reach (Station 1) were high, whereas those for the lower reaches (Stations 2 and 3) were low, based on the absence of a water channel in the Inukami River. Presumably, terrestrial DOC does not flow from the upper reach to the lower reaches due to the dried-up channel. Finlay et al. (2002) suggested that transport of particulate organic carbon from tributary streams to the South Fork Eel River may be reduced because of the absence of summer rainfall. Furthermore, our results suggested that the dried-up channel may also be an important factor in preventing the input of terrestrial DOC. At the same time, the $\delta^{15}N$ values tended to increase from the upper to the lower reaches, indicating that the trophic base of organic matter may directly reflect the characteristics of consumers in the upper and lower reaches in terms of habitat, physico-chemical conditions (WT, pH, and the concentration of major ions, DOC, chl. *a,* and periphyton), and geographical conditions (the dried-up channel).

In conclusion, our results revealed that trophic pathways vary considerably according to in situ food

sources, and reflect the flow of energy from organic matter to consumers. Furthermore, our results suggested that basal food sources were influenced by riverine characteristics, such as physicochemical and geomorphological conditions. Consequently, these parameters may represent important factors that indirectly influence consumers and the trophic position of basal food sources and consumers in the river system.

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