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Species composition and distribution patterns of baetid nymphs (Baetidae: Ephemeroptera) in a Japanese stream

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Abstract

Species composition and distributional patterns among nymphs of five baetid genera (Ephemeroptera), *Baetis, Tenuibaetis, Labiobaetis, Nigrobaetis* and *Alainites* were investigated in Yura Stream, Kyoto Prefecture. I collected 13 species: *B. sahoensis*, *B. thermicus*, *B.* sp. F, *B.* sp. J, *B.* sp. M1, *B.* sp. S1, *T.* sp. E, *T.* sp. H, *L.* sp. G, *N. chocoratus*, *N.* sp. D, *N.* sp. I and *A. yoshinensis*, among which *B. thermicus*, *B.* sp. S1 and *T.* sp. E were dominant, whereas *B. sahoensis*, *B.* sp. F, *B.* sp. M1 and *N.* sp. I were scarce. Based on their longitudinal distribution patterns, the 13 species were classified into upper species, upper-middle species, middle species, middle-lower species and lower species. *Baetis thermicus* and *A. yoshinensis* showed long downstream tails. *Baetis* sp. J and *N.* sp. D extended their longitudinal distribution upstream in summer. With regard to habitat preference, *Alainites* and *Labiobaetis* were restricted to riffle and vegetated zones, respectively. *Tenuibaetis* consisted of riffle-vegetated zone species, whereas *Baetis* and *Nigrobaetis* contained both riffle species and ubiquitous species. Habitat partitioning (‘*sumiwake*’) along the watercourse (macro-*sumiwake*) was evident in *Tenuibaetis*, and that between habitat types (micro-*sumiwake*) in *Labiobaetis* vs. *Baetis* (*rhodani* group species) and *Labiobaetis* vs. *Alainites*.

Introduction

Kobayashi (1987) classified the nymphal stages of 18 Japanese species within the genus *Baetis* Leach 1815 (s.l.) and provided provisional names to the 13 newly-recognized species. Although these latter taxa remain undescribed, Kobayashi (1987) provided sound and practical diagnostic characters which facilitate species-level discrimination. Ongoing studies (Fujitani et al., unpublished) have proposed to assign some of the 13 Japanese ‘*Baetis*’ species to *Tenuibaetis*, *Labiobaetis*, *Nigrobaetis* and *Alainites*.

Yamasaki (1987) examined species composition and distribution patterns of benthos, including *Baetis* (s.l.), in Tama Stream, Honshu Island, Japan, but his study did not cover all seasons and was insufficient to reveal the seasonal dynamics. Kobayashi (1989) provided a schematic presentation of distribution patterns of Japanese *Baetis* (s.l.) species along a watercourse and in relation to current speed. Outside Japan, longitudinal distribution (Dodds & Hisaw, 1925; Macan, 1957; Kamler, 1969; Allan, 1975; Ward & Berner, 1980; Ward & Stanford, 1990) and habitat use (Ulfstrand, 1967; Dudgeon, 1982; Jenkins et al., 1984; Ormerod, 1988) of *Baetis* (s.l.) have been well studied. However, there exists little comparable data for Japanese species.

Herein, I describe the species composition of *Baetis*, *Tenuibaetis*, *Labiobaetis*, *Nigrobaetis* and *Alainites* in Yura Stream, Honshu Island, Japan, over

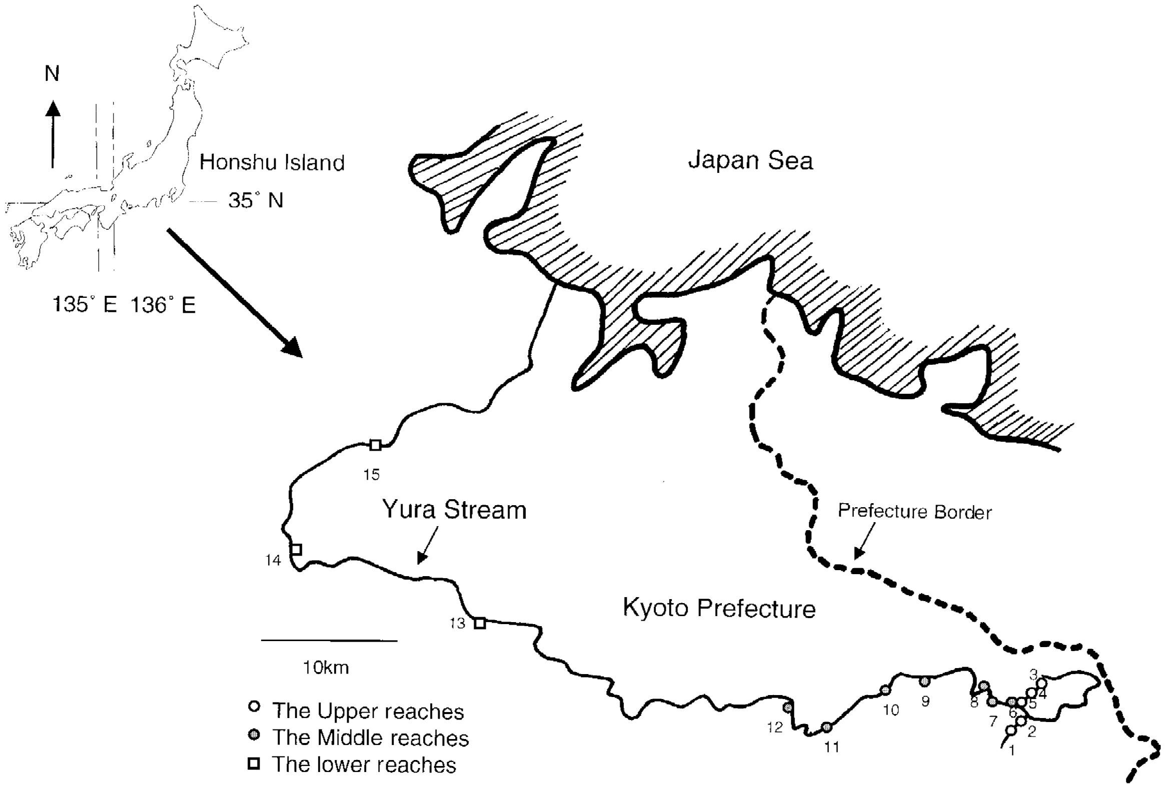

Figure 1. Location of sampling sites in Yura Stream. Sampling sites 1–2 were located in Haidani Creek, sites 3–5 in Onokodani Creek and sites 6–15 in the main channel.

four seasons and examine their longitudinal distribution and habitat preference. I compare their distribution patterns on the basis of the '*sumiwake*' (habitat partitioning) hypothesis (Imanishi, 1941; Kani, 1944; Tanida, 1989).

Material and methods

Study site

Originating at Mt. Mikunigadake (959 m a. s. l.), Yura Stream runs through the northern part of Kyoto Prefecture and flows into Japan Sea (Fig. 1). The main watercourse is 146 km long. About 89% of the 1880 km^2 catchment area is forested. Virgin forests of beech (*Fagus crenata* Blume) remain in the headwaters, but planted forests appear on the stream terrace along the main channel. In the lower reaches, the main channel drains into a basin accounting for about 11% of the catchment area. The natural levee and riparian vegetation remain in the lower reaches. Near the mouth, the main channel flows through a gorge and does not widen. Although there are two reservoirs between Sites 12 and 13 (Fig. 1), I chose this stream since it remains relatively natural condition, compared with other streams and rivers in central Japan.

Environmental variables

I conducted surveys every season from spring 1997 to summer 1998 at 15 sampling sites located along the length of the watercourse. Some sites were not examined on every occasion due to high floods or heavy snow. In October 1999, I recorded maximum current speed (cm s^{-1}), water depth (cm), substrate types, water temperature (°C), specific conductance (μs cm^{-1}), channel width (m), riffle-pool length (m), and canopy index at each sampling site. Maximum current speed was measured just beneath the water surface with a portable current meter (Tanida et al., 1985). Water depth was measured and substrate types were visually classified in type I riffle (RI), type II riffle (RII) and calm zone (CZ) (habitat types are explained hereafter). To calculate Bottom Score (BS; an index of substrate type), I assigned scores to substrate types as follows: loose stones (>50 mm) = 5, embedded stone (>50

Table 1. Environmental variables of sampling sites. BS refers to bottom score. RI, RII, and CZ are abbreviations of type I riffle, type II riffle, and calm zone, respectively.

Site no.		The upper reaches					The middle reaches							The lower reaches		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Altitude	(m)	430	390	400	385	370	355	335	300	255	235	200	170	38	10	4
Channel slope	(%)	16.7	12.1	8.6	7.8	3.8	0.9	0.0	2.0	0.0	2.0	1.0	0.0	0.0	0.0	0.0
Valley slope	(%)	75	80	83	78	90	78	58	38	50	63	50	13	1	6	1
Distance from mouth	(m)	116.0	115.8	116.4	115.8	115.1	114.2	112.2	108.1	102.4	97.0	92.1	86.5	50.2	35.9	23.3
Catchment area	(km^2)	0.5	0.8	2.1	3.0	3.3	32.8	43.2	74.0	113.3	120.7	136.1	149.8	727.5	1039.9	1727.5
Maximum current speed	($cm\ s^{-1}$)	87.0	99.1	103.3	65.9	82.6	148.9	108.1	176.2	131.4	100.0	118.7	150.2	119.2	122.1	132.3
Water depth	(cm)	4.7	11.0	10.7	7.3	7.7	31.0	38.7	32.0	39.3	43.7	30.7	34.7	16.7	20.0	22.7
BS in RI		17	17	15	13	15	15	15	15	15	15	15	15	15	15	13
BS in RII		11	8	11	11	13	10	13	13	13	15	14	13	13	15	14
BS in CZ		12	13	8	6	13	8	8	9	12	11	10	13	13	8	11
Water temperature		11.8	12.0	12.6	12.7	12.6	12.7	13.6	13.7	14.8	14.6	13.9	14.2	17.2	17.6	18.3
Specific conductance	(10^{-6} S cm^{-1})	48	48	42	82	52	55	46	49	50	59	58	60	106	138	139
Channel width	(m)	2.1	1.8	3.4	2.3	5.5	7.1	7.5	27.5	27.5	25.0	20.0	2.5	24.5	100.0	50.0
Riffle-Pool distance	(m)	3.0	2.3	10.0	8.2	10.5	500.0	475.0	175.0	375.0	500.0	425.0	137.5	1250.0	725.0	275.0
Canopy cover		1	1	1	1	1	0.5	0	0.5	0	0.5	0.5	0.5	0	0	0

mm) = 4, gravel (4–50 mm) = 3, sand (0.125–4 mm) = 2, mud (>0.125 mm) = 1; the score of the most dominant type was then doubled and added to that of the second most dominant type (Tanida, 1990). I recorded water temperature and specific conductance in RI by a portable thermometer (SC51, Yokogawa Electric Works) and a portable conductivity meter (B-173, HORIBA), respectively. Channel width and riffle-pool length were measured at tributary brooks and mountain streams, but determined on topographic maps (1: 25,000; Geographical Survey Institute, Japan) for the lower reaches. Canopy index was determined as follows: 1 = channel was covered with canopy (more than 50% above channel margin), 0.5 = channel was covered with canopy (less than 50% above channel margin), 0 = channel was completely open.

For each sampling site, I read altitude (m), channel slope (m km^{-1}), valley slope (m), distance from mouth (km), and catchment area (km^2) from topographic maps by using a software NIH-image. Channel slope and valley slope were presented as percentage, calculated by elevation drop divided by channel length within 200 m of sampling sites, and by that within 200 m distance from the highest point to sampling sites, respectively. Distance from mouth and catchment area were measured by using a digitizer (WACOM, SD-420A) connected to a personal computer.

Distinction of habitat types

At each site, I distinguished four habitat types: RI, RII, CZ and vegetated zone (VZ). In tributary brooks, RI referred to step defined by water flow occurring as jets between boulders or falling over them (Petts & Calow, 1996). RII comprised a riffle between an upper pool and a lower step in which current speed was slower than in RI. VZ was root mass of sedge (*Carex* sp.) along the channel margin. CZ referred to pools just downstream of steps. In contrast, in the main channel, RI referred to fast riffle, RII to slow riffle, and VZ to the root mass and submerged portion of reed stems (*Phragmites japonica* Steud.) along the channel margin. CZ included pools, lateral-scour pools, and backwaters.

I recorded surface current speed (SC) and bottom current speed (BC) with a portable current meter (Tanida et al., 1985) each time I conducted sampling. SC and BC were measured just beneath the water surface in each habitat type and just above the bottom in RI, RII, and CZ, respectively, but BC was not recorded at times the water was too shallow to permit measurement.

Collection and identification of nymphs

I collected baetid nymphs semi-quantitatively by kick-sampling in three sets of 10 kicks at each habitat type. For a single sample from RI, RII and CZ, a D-flame net (mesh size: GG40) was held against the streambed and oriented perpendicular to the flow direction, and a total substrate area of about 5 m^2 was sampled. Large root masses in the same area were disturbed in VZ. Collected benthos and organic matter were preserved in 4% formalin. Baetid nymphs were sorted from other materials by eye and identified to species. Species identification followed Kobayashi (1987), and generic assignment followed the unpublished work by Fujitani et al. (submitted). The identification was conducted mostly under a binocular (Nikon, SMZ-10, ×6.7-40), but microstructures, such as the mandibles, labrum and labial palpi, were examined under a biological microscope (OLYMPUS, CH-2, ×40-1, 000).

Data analyses

I performed standardization on environmental variables (Table 1) and log$_{10}$ (n+1) transformation on abundance of each species. For statistical analysis, I used software SRISTAT Ver. 1.0.2. for Microsoft Excel Ver. 5.0.

The centre of longitudinal distribution (CLD) was calculated as average of altitude weighted by abundance of individuals in each site. I compared CLDs between seasons by t-test if variance of the pair was equal, otherwise by Welch test. Before examining whether there was a seasonal shift of longitudinal distribution, I compared CLDs of spring and of summer between 1997 and 1998. If they were different significantly between the 2 years, I did not pursue further examination of the seasonal shift of the species. I analyzed relationships between distribution patterns and four habitat types by One-way Anova and a pairwise Fisher's LSD method. When a significant difference of abundance was found between the four habitat types by One-way Anova, I used a pairwise test to analyze the difference of abundance between pairs of habitat types. For the analysis of habitat preference, I combined data of spring and summer for 2 years, respectively.

Results

Classification of sampling sites by PCA

The first axis accounted for 57% of the total variation, explaining the environmental gradient along the watercourse. Altitude (EV=0.33), valley slope (EV=0.31), distance from mouth (EV=0.31), water temperature (EV=−0.33), channel width (EV=−0.29), and catchment area (EV=-0.29) represented the first axis. The second axis accounted for 16% of the total variation. Water depth (EV=0.56), channel slope (EV=−0.32), and specific conductance (EV=−0.34) represented the second axis (Fig. 2).

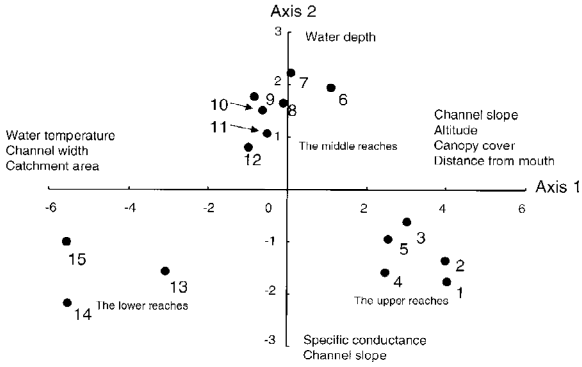

Figure 2. Ordination of the first axis against the second one by PCA of 15 study sites based on 15 environmental variables. Numbers represent the sampling sites. Sites 1–5, 6–12 and 13–15 were grouped as the upper reaches, the middle reaches and the lower reaches, respectively.

Based on the PCA results, I divided sampling sites into three groups (Fig. 2): the upper reaches, the middle reaches, and the lower reaches (Fig. 1). The upper reaches included five sites (Site Nos. 1–5) in two tributary brooks, Haidani and Onokodani, the middle reaches included seven sites (Site Nos. 6–12) on the main channel, and the lower reaches included three sites (Site Nos. 13–15) on the main channel running through the basin.

Environment in each habitat type

In RI, SC mostly exceeded 100 cm s^{-1} and BC was 40–60 cm s^{-1}. In RII, SC and BC were mostly 40–70 cm s^{-1} and 20–40 cm s^{-1}, respectively. In VZ, SC was mostly less than 30 cm s^{-1}. At sampling sites 1 and 2, sedge was not abundant and VZ was not recognized. In CZ, SC and BC were mostly less than 20 cm s^{-1}.

Species composition

I collected 12,083 individuals and classified them into four genera comprising 13 species following Kobayashi (1987) and Fujitani (unpublished): *Baetis sahoensis* Gose, *B. thermicus* Uéno, *B.* sp. F, *B.* sp. J, *B.* sp. M1, *B.* sp. S1, *Tenuibaetis* sp. E, *T.* sp. H, *Labiobaetis* sp. G, *Nigrobaetis chocoratus* (Gose), *N.* sp. D, *N.* sp. I and *Alainites yoshinensis* (Gose). *Baetis* sp. M1 and *B.* sp. S1 were newly distinguished in this study.

Baetis sp. M1 resembles *B. thermicus*, but can be distinguished from it by the absence of subapical setae on the claws. *Baetis* sp. S1 is similar to *B. sahoensis*, but the shape of the posterior spines and the color pattern on the abdominal terga are different (Fujitani, unpublished).

Baetis thermicus, *B.* sp. S1, and *T.* sp. E were numerically dominant, comprising more than 10% of total baetid abundance, whereas *B. sahoensis*, *B.* sp. F, *B.* sp. M1 and *N.* sp. I were scarce, comprising less than 3% of it.

According to recent generic concept (McCafferty & Waltz, 1997), Japanese *Baetis* species include the *rhodani* group and the *fuscatus* group which were proposed by Müller–Liebenau (1969). For comparing distribution patterns of *Baetis* (s. str.), I used the distribution patterns of the *rhodani* group (*thermicus*, sp. M1) and the *fuscatus* group (*sahoensis*).

Patterns of longitudinal distribution

To examine species-specific patterns of longitudinal distribution, I drew graphs of abundance against altitude, one of the variables representing the first axis in PCA (Fig. 3).

Baetis sahoensis (Fig. 3a) occurred mainly in the middle and the lower reaches, with CLDs in the middle reaches. This species was not recorded in winter. *Baetis thermicus* (Fig. 3b) occurred in all the reaches, with CLDs in the upper reaches or upper part of the middle reaches. Downstream tails, a gradual decrease of abundance with downstream extension (sensu Allan, 1975), were present in all seasons. *Baetis* sp. F (Fig. 3c) was restricted to the upper reaches. *Baetis* sp. J (Fig. 3d) occurred in the middle and the lower reaches. The upper limit of distribution shifted from lower portion of the middle reaches in spring, to the upper portion of the middle reaches in summer and autumn. CLDs were in the lower reaches in spring, but shifted markedly upstream in summer (spring vs. summer: $t = 2.88$, $p < 0.001$). This species was not recorded in winter. *Baetis* sp. M1 (Fig. 3e) was restricted to the upper reaches, where it was recorded only in spring. *Baetis* sp. S1 (Fig. 3f) occurred in the middle and the lower reaches, with CLDs in the middle reaches.

Tenuibaetis sp. E (Fig. 3g) occurred mainly in the middle reaches, where its CLDs were also located. Downstream tails were present in summer, autumn and winter. *Tenuibaetis* sp. H (Fig. 3h) occurred in the lower portion of the middle reaches and the lower reaches, with CLDs located in the lower reaches.

Labiobaetis sp. G (Fig. 3i) occurred mainly in the middle and lower reaches, with CLDs located in the lower reaches and in the lower portion of the middle reaches.

Nigrobaetis chocoratus (Fig. 3j) occurred mainly in the middle reaches, where its CLDs were located. Downstream tails were present in spring, summer and winter. *Nigrobaetis* sp. D (Fig. 3k) occurred in the lower reaches in spring, but its distribution extended to the middle reaches in summer and autumn. CLDs were located in the lower reaches in spring, but shifted markedly upstream in summer (spring vs. summer: $t = 3.37$, $p < 0.01$). This species was not recorded in winter. *Nigrobaetis* sp. I (Fig. 3l) occurred mainly in the middle reaches, where its CLDs were also located. A downstream tail was present in spring.

Alainites yoshinensis (Fig. 3m) occurred mainly in the upper and the middle reaches. Its CLDs were located in the upper reaches or upper part of the middle reaches in spring, summer and winter, but shifted downstream in autumn when the abundance decreased in the upper reaches (spring vs. autumn: $t = 2.39$, $p < 0.05$; summer vs. autumn: $t = 2.63$, $p < 0.05$). Downstream tails were present in spring and winter.

Overall, five patterns of longitudinal distribution were evident, within which species could be conveniently placed: the upper reaches species: *B.* sp. F and *B.* sp. M1; the upper-middle reaches species: *B. thermicus* and *A. yoshinensis*; the middle reaches species: *T.* sp. E, *N. chocoratus* and *N.* sp. I; the middle-lower reaches species: *B. sahoensis*, *B.* sp. J, *B.* sp. S1, *L.* sp. G and *N.* sp. D; the lower reaches species: *T.* sp. H.

Distribution patterns in relation to habitat types

Baetis sahoensis (Table 2a) was widely distributed among various habitat types but was scarce in RI and CZ. *Baetis thermicus* (Table 2b) was most abundant in RI in spring, summer and autumn, but extended its habitat to RII and VZ during winter. *Baetis* sp. F (Table 2c) showed a wide distribution, but was scarce in RI. *Baetis* sp. J (Table 2d) was most abundant in RI in summer and autumn, and was not present in CZ. *Baetis* sp. M1 (Table 2e) showed a wide distribution, but was relatively abundant in RI and RII. *Baetis* sp. S1 (Table 2f) was the most abundant in VZ in spring and summer. It extended its habitat range to RII

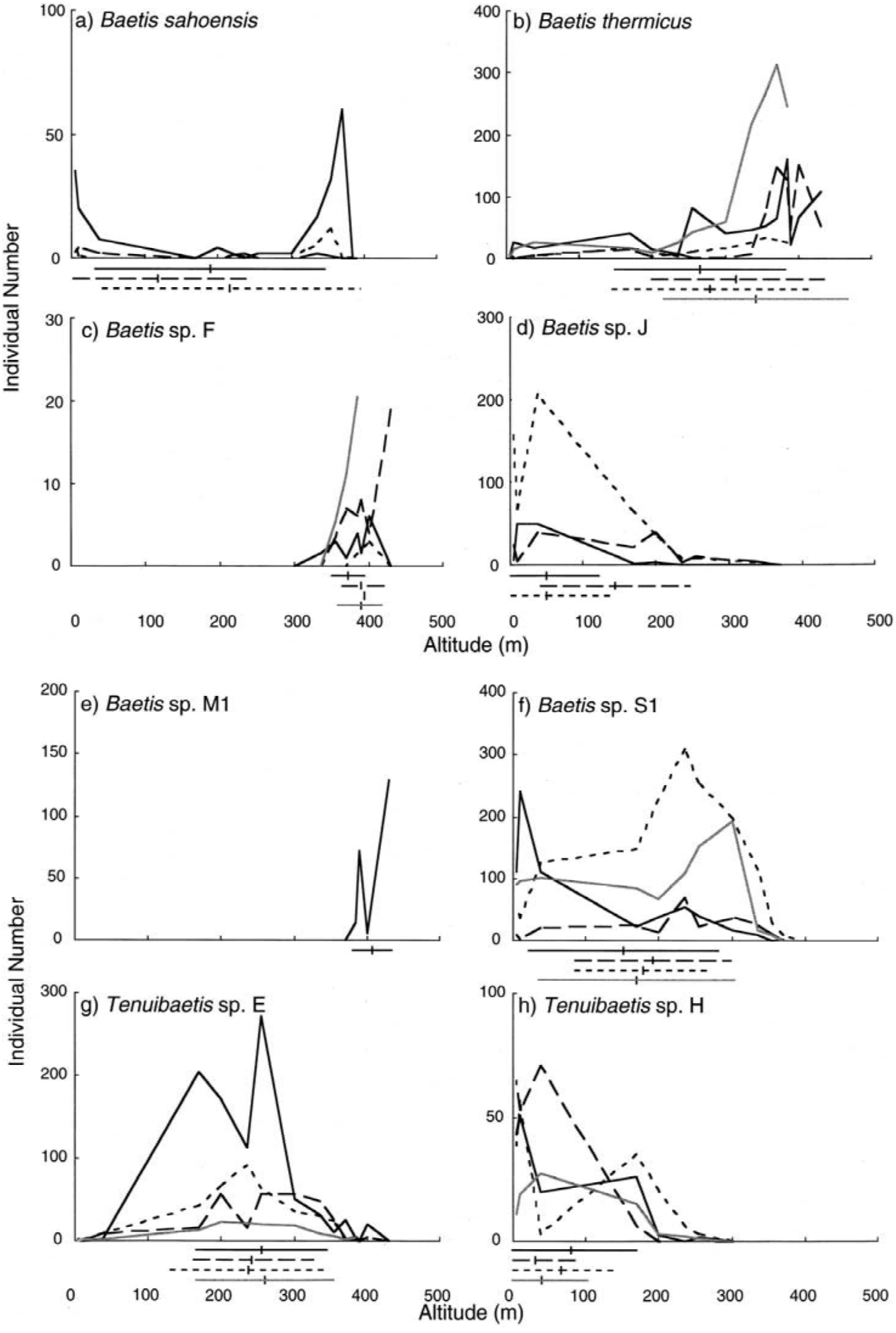

Figure 3. Patterns of longitudinal distribution of *Baetis, Tenuibaetis, Labiobaetis, Nigrobaetis* and *Alainites* species in Yura Stream. Upper graphs show changes of abundance including all habitat types against altitude, and lower bars show centers of longitudinal distribution and their standard deviations. Black solid line shows the abundance in spring, dashed line (- - - - -) in summer, dotted line (·········) in autumn, and gray solid line in winter. The scales of individual numbers are different between species.

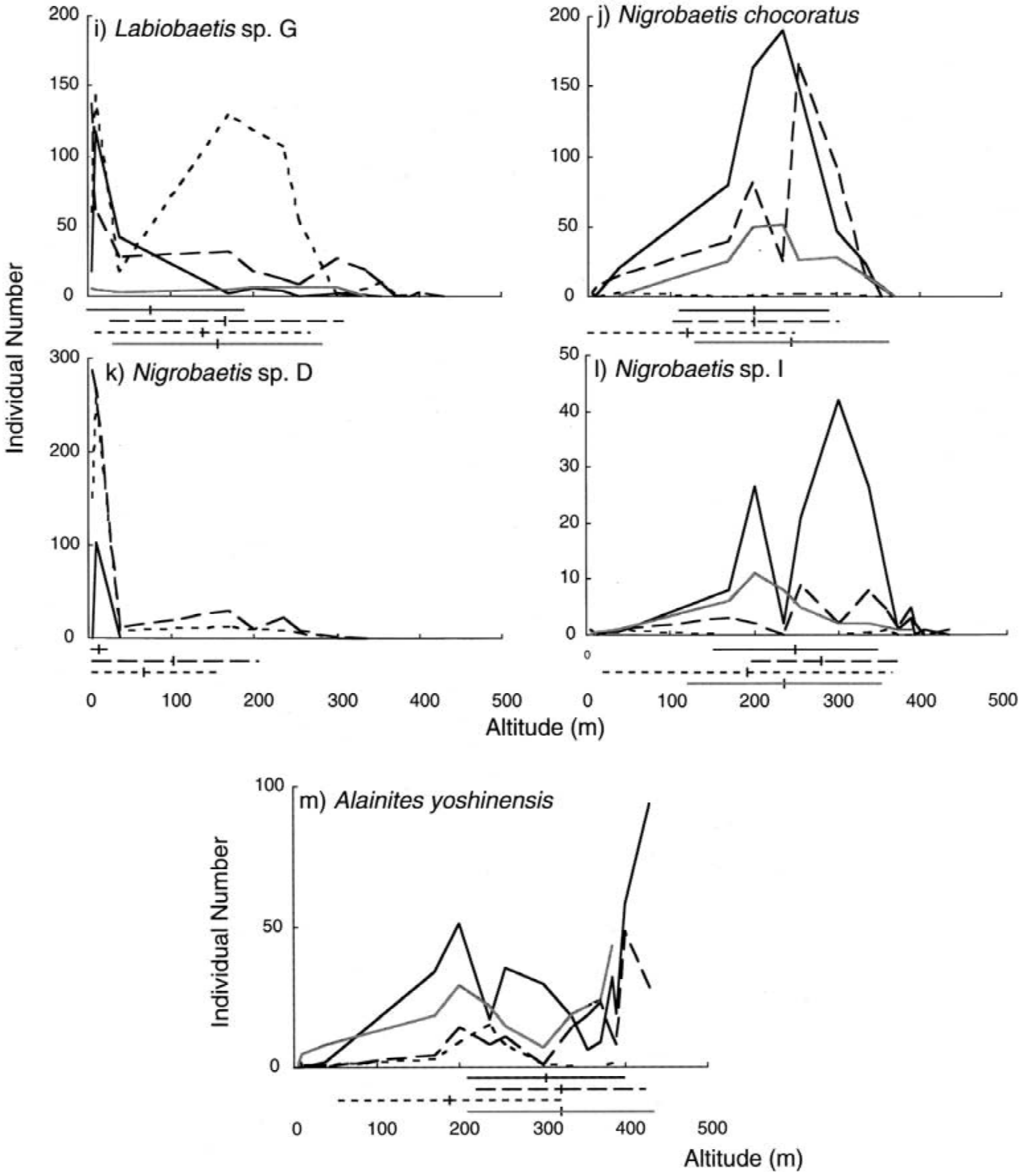

Figure 3. Contd.

and CZ in autumn, and showed a wide distribution in winter.

Tenuibaetis sp. E (Table 2g) was abundant in RI and RII in summer and winter, but extended its habitat range to VZ in spring and autumn. *Tenuibaetis* sp. H (Table 2h) showed no significant habitat preference, but was very scarce in CZ.

Labiobaetis sp. G (Table 2i) occurred almost exclusively in VZ.

Nigrobaetis chocoratus (Table 2j) was more abundant in RI and RII in spring, summer and winter, but did not show any significant difference of abundance in autumn. *Nigrobaetis* sp. D (Table 2k) was abundant in RI and RII in summer but did not show any significant difference of abundance between habitat types in spring and autumn. *Nigrobaetis* sp. I (Table 2l) was widely distributed, but was less abundant in RI.

Alainites yoshinensis (Table 2m) was relatively common in RI and RII in spring, summer and winter. In autumn, however, it became scarce in RII.

Table 2. Distribution patterns of *Baetis* (s.l.) species in relation to habitat types. Averages of individual numbers per sampling site are given. Data of each season were tested by One-way Anova ($^{*}p < 0.05$,$^{**}p < 0.01$,$^{***}p < 0.001$, ns = not significant). Different letters indicate significant difference of average abundance between habitat types (Fisher's LSD method: $p < 0.05$)

	Species name		RI	RII	VZ	CZ	
(a)	*B. sahoensis*	Spring	0.9	3.1	6.4	1.2	ns
		Summer	0.2	0.3	0.4	0.0	ns
		Autumn	0.2	2.1	0.9	0.0	ns
		Winter	–	–	–	–	
(b)	*B. thermicus*	Spring	33.3^{a}	6.3^{a}	4.6^{ab}	0.1^{b}	***
		Summer	25.9^{a}	5.7^{ab}	10.7^{ab}	0.2^{b}	***
		Autumn	9.8^{a}	2.8^{b}	2.3^{b}	0.0^{c}	***
		Winter	48.9^{a}	49.3^{a}	16.4^{b}	0.7^{c}	**
(c)	*B.* sp. F	Spring	0.0	0.3	0.5	0.2	ns
		Summer	0.3	1.5	0.4	0.9	ns
		Autumn	0.0	0.1	0.2	0.0	ns
		Winter	0.1	0.7	1.4	3.6	ns
(d)	*B.* sp. J	Spring	6.7	2.3	0.3	0.0	ns
		Summer	8.8^{a}	2.1^{ab}	0.1^{b}	0.0^{b}	***
		Autumn	48.1^{a}	7.8^{b}	1.3^{c}	0.0^{d}	**
		Winter	–	–	–	–	
(e)	*B.* sp. M1	Spring	4.8	4.1	0.1	2.1	ns
		Summer	–	–	–	–	
		Autumn	–	–	–	–	
		Winter	–	–	–	–	
(f)	*B.* sp. S1	Spring	0.4^{b}	5.0^{ab}	40.8^{a}	3.8^{ab}	**
		Summer	0.3^{b}	2.8^{ab}	12.9^{a}	1.9^{ab}	**
		Autumn	0.8^{c}	32.0^{a}	50.0^{a}	17.8^{ab}	**
		Winter	2.0	8.4	45.6	11.0	ns
(g)	*T.* sp. E	Spring	29.7^{a}	20.0^{b}	13.3^{b}	0.3^{b}	**
		Summer	10.2^{a}	6.0^{ab}	3.1^{ab}	0.3^{b}	**
		Autumn	11.0^{a}	7.8^{a}	3.9^{b}	0.0^{c}	***
		Winter	2.6^{b}	5.3^{a}	0.7^{bc}	0.1^{c}	**
(h)	*T.* sp. H	Spring	2.0	1.6	7.6	0.1	ns
		Summer	5.5	1.9	7.5	0.1	ns
		Autumn	7.6	1.0	9.3	0.0	ns
		Winter	3.1	1.4	1.3	0.0	ns
(i)	*L.*sp. G	Spring	0.0^{b}	0.0^{b}	16.0^{a}	0.0^{b}	***
		Summer	0.0^{b}	0.0^{b}	29.2^{a}	0.1^{b}	***
		Autumn	0.0^{b}	0.0^{b}	51.9^{a}	0.0^{b}	***
		Winter	0.0^{b}	0.0^{b}	3.3^{a}	0.0^{b}	***
(j)	*N. chocoratus*	Spring	25.0	22.9	0.8	0.7	ns
		Summer	19.3^{a}	12.5^{a}	0.0^{b}	0.1^{b}	***
		Autumn	0.3	0.6	0.0	0.0	ns
		Winter	5.1^{a}	8.4^{a}	0.0^{b}	0.0^{b}	**
(k)	*N.* sp. D	Spring	4.5	2.6	0.2	0.1	ns
		Summer	20.5	25.1	0.1	0.1	*
		Autumn	34.2^{a}	13.9^{a}	0.1^{b}	0.0^{b}	*
		Winter	–	–	–	–	
(l)	*N.* sp. I	Spring	0.4	3.6	1.2	2.5	ns
		Summer	0.5	1.1	0.7	0.3	ns
		Autumn	0.0	0.2	0.0	0.0	ns
		Winter	0.0	0.1	0.3	2.1	ns
(m)	*A. yoshinensis*	Spring	16.1^{a}	6.4^{a}	1.8^{ab}	0.3^{b}	***
		Summer	6.3^{a}	4.1^{ab}	2.2^{bc}	0.0^{c}	***
		Autumn	2.6^{a}	0.4^{b}	0.0^{b}	0.0^{b}	***
		Winter	10.3^{a}	10.1^{a}	1.0^{b}	0.0^{c}	***

Baetis and *Nigrobaetis* contained both riffle species and ubiquitous species. Within the genus *Baetis*, the *rhodani* group and the *fuscatus* group contained the riffle species and the ubiquitous species, respectively. All taxa within *Tenuibaetis* were riffle-vegetated zone species, whereas *Alainites yoshinensis* and *Labiobaetis* sp. G were riffle species and vegetated zone species, respectively.

Discussion

Species composition

In the course of this survey, 13 species of mayfly nymphs belonging to five genera, *Baetis, Tenuibaetis, Labiobaetis, Nigrobaetis* and *Alainites* were recorded.

In Japan, the species composition of *Baetis* (s.l.) along an entire watercourse has been investigated in Tama Stream (Yamasaki, 1987) and Shinano River (Kobayashi, 1989), both on Honshu Island. Tama Stream originates at Okutama, Tokyo (about 1500 m a.s.l.). Its main watercourse is 120 km long and catchment area is 1200 km^{2}. Shinano River rises in the Hida Mountains (about 2000 m a.s.l.). Its catchment area is 11 900 km^{2} and main watercourse is 367 km long, making it the longest river in Japan. In Tama Stream, Yamasaki (1987) collected 11 species: *B. sahoensis*, *B. thermicus*, *B.* sp. F, *B.* sp. J, *T.* sp. E, *T.* sp. H, *L.* sp. G, *N. chocoratus*, *N.* sp. D, *N.* sp. I and *A. yoshinensis*. In Shinano River, Kobayashi (1989) collected 13 species: *B. bicaudatus*, 1923, *B. sahoensis*, *B. thermicus*, *B.* sp. F, *B.*sp. J, *T.* sp. E, *T.* sp. H, *L.* sp. g, *L.* sp. Q, *N. chocoratus*, *N.* sp. D, *N.* sp. I and *A. yoshinensis*. Among them, probably *B. bicaudatus,* distinguished as *B.* sp. L in Kobayashi (1987), and *L.* sp. Q were not present in Yura Stream and Tama Stream (Kobayashi, 1989). Within Japan, *Baetis bicaudatus* was recorded from the Japan Alps in Honshu and Mt. Taisetsu in Hokkaido (Kobayashi, 1989; Ishiwata et al., 2000). *Labiobaetis* sp. Q is restricted to the lower reaches of rivers flowing in large alluvial plains, such as Shinano River (Kobayashi, 1989). Yura Stream flows through a gorge near the mouth, and Tama Stream receives polluted water from the metropolitan area in its lower reaches (Yamasaki, 1987; Kobayashi, 1989). Such environmental conditions probably prevent *L.* sp. Q from occurring in Yura Stream and Tama Stream.

The number of species in Yura Stream was similar to that found in Shinano River. However, before meaningful comparison is possible, we first need to examine the materials from Tama Stream and Shinano River, since *B.* sp. M1 and *B.* sp. S1 were not recognized when Yamasaki (1987) and Kobayashi (1989) conducted their studies.

Patterns of longitudinal distribution

Baetis thermicus and *A. yoshinensis* showed long downstream tails from the middle to the lower reaches. Allan (1975) considered that drift and subsequent colonization of downstream areas was responsible for downstream tails. I recognized downstream decrease of abundance extending from the upper or middle reaches as downstream tails. *Baetis* nymphs are a major component of invertebrate drift in streams and rivers (Waters, 1972; Adamus & Gaufin, 1976; Allan, 1987). Miyasaka & Nakano (2001) confirmed that *B. thermicus* drifted in response to predatory risk by fish. The distinct downstream tails of *B. thermicus* and *A. yoshinensis* suggest that they are actively drifting and subsequently colonizing the lower reaches.

A significant seasonal shift of downstream distribution was evident in *A. yoshinensis, B.* sp. J and *N.* sp. D. *Alainites yoshinensis* showed a significant downward shift of CLD in autumn, reflecting a decrease of abundance in the upper reaches (Fig. 3m). *Baetis* sp. J (Fig. 3d) and *N.* sp. D (Fig. 3k) showed an upstream extension of their distribution and CLDs in summer, while maintaining high abundance levels in the lower reaches. Water temperature is an important determinant of the longitudinal distribution of aquatic insects (e.g., Hynes, 1970; Wise, 1976; Ward & Berner, 1980; Resh & Rosenburg, 1984; Ward, 1992; Allan, 1995). Water temperature also determines the length of egg period (Brittain, 1982). It is known that hatch of mayfly eggs delays in low water temperature (Elliott & Humpesch, 1983; Resh & Rosenburg, 1984), and it is possible that their eggs overwintering in the middle reaches hatch later than those in the lower reaches due to the relative delay in the rise of water temperature during spring and summer.

Distribution patterns in relation to habitat types

This study showed clearly that overlap of habitat preference is frequent between baetid genera. Dudgeon (1982) found four *Baetis* (s.l.) species occurring in different types of habitat among central, marginal and intermediate areas of a channel. Jenkins et al. (1984) showed that two *Baetis* (s.l.) species were abundant in macrophytes or roots of marginal vegetation and that two other species were ubiquitous among riffles, pools and aquatic macrophytes. Ormerod (1988) separated these *Baetis* (s.l.) species into riffle, marginal and general species, and noted the similarity of their gut contents. These authors proposed that habitat partitioning acted to reduce competition between ‘congeneric’ species. In this study, the distribution of species belonging to different genera frequently overlapped. It is necessary to examine if interspecific competition is actually occurring between overlapping species.

Habitat partitioning

The ‘*sumiwake*’ concept was proposed by Imanishi (1941) and Kani (1944). Imanishi (1941) translated *sumiwake* as ‘habitat segregation’, but Tanida (1989) considered that ‘habitat partitioning’ was a more accurate translation. Imanishi (1941) documented habitat partitioning among heptagenid mayfly nymphs from the stream channel margin to the centre, and also found habitat partitioning along the length of a watercourse among heptagenid nymphs utilizing similar habitat types. Kani (1944) recognized three species groups of heptagenid nymphs characterized by their habitat usage and body structure, and found habitat partitioning occurring within a riffle-pool unit between different groups and along a watercourse between species in the same group. In instances where species belonging to the same group co-occurred in the same reaches, they were replaced between seasons. Tanida (1989) proposed two terms for habitat partitioning. ‘Micro-*sumiwake*’ refers to habitat partitioning occurring at a small scale between different taxa (genus or species group), and ‘Macro-*sumiwake*’ refers to habitat partitioning occurring at a large scale within the same taxon. Grant & Mackey (1969) also stressed the importance of examining ecological separation of congeneric species.

Habitat preference was different between *Labiobaetis* vs. *Baetis* (*rhodani*) and *Labiobaetis* vs. *Alainites.* These patterns correspond to micro-*sumiwake*. Distribution of *Baetis* (*f*), *Tenuibaetis* and *Nigrobaetis* overlapped with that of all other genera. In the genus *Baetis*, habitat preference was different between the *rhodani* group and the *fuscatus* group. If the '*sumiwake*' hypothesis is correct, then this suggests that *Baetis* (s. str.) actually includes species of different genera.

To evaluate this possibility, I subsequently examined the macro-*sumiwake* of *Baetis* (*r*), *Tenuibaetis* and *Nigrobaetis* along the watercourse. *Tenuibaetis* sp. E and *T.* sp. H showed clear partitioning of macrohabitat. *Baetis* sp. M1 occurred in the upper reaches in spring and coexisted with *B. thermicus*. *Nigrobaetis* sp. D occurred mainly in the lower reaches, and *N. chocoratus* and *N.* sp. I coexisted in the middle reaches. The distribution patterns of the first case corresponds to macro-*sumiwake.*

Sumiwake was less clear in the baetid genera than in the heptagenid mayfly nymphs studied by Imanishi (1941) and Kani (1944). The mechanism supporting their coexistence is an interesting topic for future research. Coexisting *Ephemerella* nymphs within the same subgenus differ in body size, especially during the maximal growth period (Sweeney & Vannote, 1981). Among aquatic insects, habitat change of nymphs with advancing instar is well known (Malas & Wallas, 1977; Hildrew & Edington, 1979; Holomuzki & Messier, 1993; Collier, 1994; Buffagni et al., 1995). Probably the interaction of different growth periods and habitat shift facilitates coexistence of closely related species of aquatic insects. Detailed studies of the microdistribution and life history of baetid genera may reveal much about mechanism of their habitat partitioning.

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