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Differences in distribution patterns among some species of caddisfly larvae of the family Rhyacophilidae in the Ohta River, Japan

Koichiro KAWAI[1)], Masahiro NISHI[2)] and Hiromichi IMABAYASHI[1)]

Abstract The distribution pattern was compared among the caddisfly larvae of the family Rhyacophilidae by examining the various larval communities covering a total basin of the Ohta River, Japan. A total of 15 species were collected, among which the distribution range and the mean was remarkably different for any environmental parameter.
and . sp. RF showed a narrow range and small standard deviation for distance from riverhead, river width and valley area. Each parameter was standardized, and cluster analysis was performed on the basis of the means of 8 parameters for distribution of each species. A cluster, involving
and . sp. RK, all primitive, was estimated to have adapted to high altitude, steep riverbed slope, small-scale, oligotrophic and low-temperature waters. Another cluster, involving
and , both derivative, was estimated to have adapted to low altitude, loose slope, large-scale, eutrophic and high-temperature waters. Besides, , a species of Nigrocephala group, participated in an -cluster whereas , another species of the same group, constructed a -cluster. These suggest that the original habitat of the ancestral species be headwaters, that strongly restricting factors be different among species and that there be some habitat-partitionings among the sibling species.

Key words: Rhyacophilidae, environmental factor, evolution, habitat-partitioning

INTRODUCTION

The family Rhyacophilidae is a large family of the order Trichoptera. More than 40 species of 3 genera, and , were recorded from Japan and most species belong to the genus (Tanida, 1992). The genus alone comprizes more than 500 species in the northern Hemisphere and is the largest genus in the order (Wiggins, 1996). The family Rhyacophilidae is the most primitive in the Trichoptera and the larvae usually adapt to the boreal areas, live freely in the lotic waters without case building, dwell in the bottom of rapid and is usually carnivorous (Ross, 1956). Among them,
and are reported to be distributed in montaneous rivers whereas and are reported to be distributed in montaneous to flatland rivers (Morishita, 1975; Tsuda, 1981; Tanida, 1992). Besides,
has been reported to be a pest for power plant (Tsuda and Hiro, 1955). Ito (1999) reported the life cycles of 3 species of Rhyacophilidae in Hokkaido, Japan. Recently, life cycle of a

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giant species, , was also reported (Tsuruishi, 2003). On the other hand, only few studies have been extensively conducted on differences in distribution pattern among the species of the family. Kagaya et al. (1998) reported the distributions of 11 species in the Tama River in relation to drainage basin area and altitude.

In this study, the distribution was compared among the species with respect to 8 environmental factors by quantitatively examining the larval communities covering a total basin of a large river in the Chugoku Region, the Ohta River. Species were clustered on the basis of the weighted means of factors for distribution and the relationships between the clustering pattern and evolution of the species were discussed.

MATERIALS AND METHODS

A total of 21 sampling sites were set covering almost all basin of the Ohta River, Hiroshima Prefecture (Fig. 1). The Ohta River originates from Mt. Kammuri (1339 m) of the Western Chugoku Mountains and has 110 km of stretched main flow length and 1690 km^2 of catchment area.

A total of six quadrats (50×50 cm) was collected in a topographic unit at a site and taken as a single sample. Two quadrats were each collected at the center and the littoral of the flow at rapid (‘Hayase’) and at the center of the flow of the intermediate zone (‘Hirase’) between rapid and pool. Sampling was performed 3 times in summer and autumn 1998 and in spring 1999.

Identification of species was performed according to the key provided by Tanida (1992).

Altitude, distance from riverhead, riverbed slope and valley area were calculated on the basis of maps (1/50,000). River width was measured with a tape measure at the rapid. Electric conductivity was measured with a salinometer (YSI, Model 33, Yellow Springs Instrument Co. Inc., OH, USA) as an indicator of water quality. The lowest temperature in February and the highest temperature in

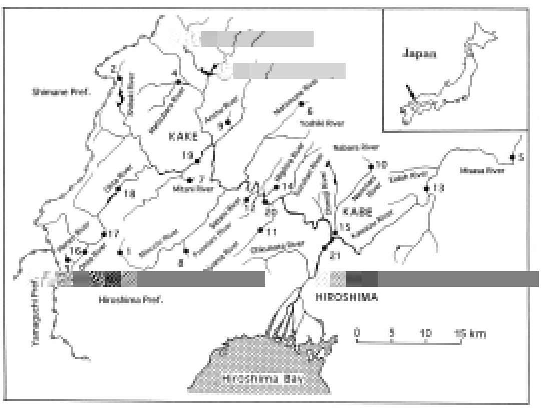

Fig. 1. Map of the Ohta River Basin, showing the locations of 21 sampling sites.

August were measured by a maximum-minimum thermometer (push type, Ishihara Thermometer Manufactures, Tokyo) set on the bottom. The mean value of a parameter for the distribution of a species was weighted by the number of individuals. The measurements of each parameter were standardized (mean 0, standard deviation 1), and the weighted, standardized mean and the weighted, standardized standard deviation was calculated for each parameter and each species.

Euclidian distance was calculated between each combination of species on the basis of the weighted, standardized means for 8 parameters, and a dendrogram was constructed by the Ward method (Ward, 1963).

RESULTS

The measurements of environmental factors at the sampling were listed in Table 1. Altitude was in the range of 0-780 m. Distance from the riverhead was in the range of 2.0-88 km. River width was in a wide range of 1.3-150 m. Riverbed slope was also in a wide range of 0.5-133 (×1/1000). Valley area was in an extremely wide range of 1.5-1496 km^2. Electric conductivity was usually low and in a rather narrow range of 33-143 µmhos/cm. The lowest water temperature in February was in a narrow range of -0.5-4.0℃ and the highest water temperature in August was in a wide range of 16.5-35.0℃.

Species collected and the abbreviations were listed in Table 2. A total of 1,034 individuals belonging to 15 species were collected. RN was the most abundant. RBr and RY were also abundant. In contrast, RI, RRC, RRD and RRF were rare.

Ranges, weighted means and weighted, standardized standard deviations were shown for distribution of each species with respect to each parameter in Table 3.

The range of altitude was relatively narrow for RKi whereas it was quite wide for RBr, RN, RT and RY. The weighted mean was the highest for RS and the lowest for RY. The weighted, standardized standard deviation was the smallest for RS and the largest for RY.

The range of distance from riverhead was narrow for RBi and RRF whereas it was quite wide for RBr, RN, RT and RY. The weighted mean was the smallest for RS and the largest for RN. The weighted, standardized standard deviation was the smallest for RBi and the largest for RN.

The range of river width was narrow for RS and RRF whereas it was quite wide for RN and RT. The weighted mean was the narrowest and the weighted, standardized standard deviation was the smallest for RS whereas they were the widest and the largest for RN, respectively.

The range of riverbed slope was narrow for RKi whereas it was quite wide for AS, RBr, RN and RS. The weighted mean was the steepest for RBi and the loosest for RN. The weighted, standardized standard deviation was the smallest for RKi and the largest for RBi.

The range of valley area was narrow for RBi, RS and RRF whereas it was quite wide for RBr, RN, RT and RY. The weighted mean was the smallest for RS and the largest for RN. The weighted,

Table 1. Environmental conditions at 21 sampling sites.

Site	Altitude (m)	River width (m)	Riverbed slope (X1/1000)	Valley area (km^2)	Electric conductivity (μmhos/cm)	Lowest water temp. in Feb.(℃)	Highest water temp. in Aug.(℃)
1	780	1.3	40	2.9	38	0.6	19.5
2	760	4.2	3.6	22	39	-0.5	26
3	730	1.6	80	1.5	33	0	16.5
4	520	4.8	15	32	41	ND	24.5
5	460	2.2	40	2.6	34	3.5	22
6	450	3.1	40	8.9	75	1	22
7	370	1.3	67	3.2	37	0.6	19
8	300	2.1	20	7.5	62	3.5	21.5
9	290	3	133	5.2	57	0	18
10	290	2.8	40	8.4	49	3.2	23
11	260	4.4	20	8.7	53	3	22
12	130	2.5	80	1.8	56	1.8	21
13	120	25	4	274	88	3	30
14	100	4.5	50	3.6	62	4	27
15	10	14	10	89	143	ND	25
16	620	7	27	22	41	1	18
17	560	13	5.7	72	47	ND	ND
18	380	25	16	148	36	0.3	ND
19	210	75	10	351	59	1	24
20	70	50	7.1	966	66	3.2	24
21	0	150	0.5	1496	65	3.7	35

Table 2. A list of collected species and the abbreviations.

Species	Abbreviation	No. indiv.
	AS	73
	RBi	11
	RBr	164
	RC	23
	RI	1
	RKa	24
	RKi	10
	RN	458
	RS	21
	RT	21
	RY	135
. sp. RC	RRC	1
. sp. RD	RRD	1
. sp. RF	RRF	5
. sp. RK	RRK	86
Total		1034

Table 3. Ranges, weighted means and weighted, standardized standard deviations of 8 environmental parameters for distribution of 15 species. Top, range ; middle, weighted mean ; bottom,weighted, standardized standard deviation.

	AS	RBi	RBr	RC	RI	RKa	RKi	RN	RS	RT	RY	RRC	RRD	RRF	RRK
Altitude	100-780	260-780	10-780	290-780	260	100-780	260-560	0-780	290-780	0-780	10-760	620	730	260-730	130-780
	519	496	374	566		593	362	293	710	524	267			408	622
	0.87	0.93	0.76	0.94		0.77	0.55	1.17	0.54	0.93	1.18			0.82	0.73
Distance from	2.0-21	2.5-5.0	2.0-64	2.2-21	4	2.5-36	4.0-10	2.2-88	2.2-7.0	2.5-88	3.0-64	5	3	3.0-5.0	2.0-36
riverhead	6.7	3.5	7	3.8		8.4	6.3	23	3	12	16			4.2	4.5
	0.3	0.03	0.45	0.17		0.34	0.12	1.05	0.05	0.89	0.63			0.04	0.21
River width	1.3-25	1.3-7.0	1.3-75	1.3-25	4.4	1.3-75	2.1-13	1.3-150	1.3-4.2	1.3-150	2.1-75	7	1.6	1.6-4.4	1.3-75
	7.1	2.9	7.9	3.2		8.8	4.2	31	1.7	16	17			2.7	3.3
	0.24	0.05	0.44	0.14		0.44	0.1	1.15	0.02	1.02	0.58			0.03	0.24
Riverbed	5.7-133	22-133	3.6-133	16-133	22	3.6-80	5.7-22	0.5-133	3.6-133	0.5-80	3.6-50	27	80	20-80	10-80
slope	46	73	35	63		30	18	12	65	38	14			36	57
	0.95	1.34	0.6	1.15		0.91	0.15	0.54	0.85	0.89	0.36			0.8	0.79
Valley area	1.5-148	1.5-22	1.5-966	1.5-148	8.7	1.5-351	7.5-72	1.5-1496	1.5-22	1.5-1496	3.6-966	22	1.5	1.5-8.9	1.5-351
	34	6.5	44	11		44	19	268	3.2	113	127			6.8	13
	0.15	0.02	0.35	0.08		0.2	0.06	1.1	0.01	0.9	0.56			0.01	0.11
Electric	33-75	33-75	33-143	33-75	53	33-59	41-62	33-143	33-57	33-65	39-143	41	33	33-75	33-75
conductivity	41	48	51	43		41	55	74	36	42	87			57	40
	0.39	0.56	0.69	0.45		0.32	0.37	1.54	0.22	0.41	1.86			0.65	0.45
Lowest water	0.0-4.0	0.0-3.2	-0.5-4.0	0.0-3.2	3	-0.5-4.0	3.0-3.5	0.0-4.0	-0.5-0.6	0.0-3.7	-0.5-4.0	1	0	0.0-3.5	0.0-3.5
temp. in Feb.	1.04	0.8	2.33	0.75		0.67	3.36	1.04	0.54	1.09	1.46			2.2	0.53
	0.89	0.8	0.95	0.68		0.92	0.16	0.89	0.22	0.95	1.08			1.07	0.6
Highest water	16.5-27.0	16.5-23.0	16.5-35.0	16.5-23.0	22	16.5-27.0	21.5-24.5	16.5-27.0	16.5-26.0	16.5-35.0	18.0-30.0	18	16.5	16.5-22.0	16.5-24.5
temp. in Aug.	19.5	18.9	22.3	19.2		22.2	22.3	19.5	18.1	21.3	24.5			20.7	19.2
	0.67	0.55	0.6	0.43		0.85	0.32	0.67	0.46	1.03	0.47			0.53	0.62

standardized standard deviation were the smallest for RS and RRF and the largest for RN.

The range of electric conductivity was the narrowest for RKi and the widest for RBr and RN. The weighted mean was the lowest and the weighted, standardized standard deviation was the smallest for RS and they were the highest and the largest for RY, respectively.

The range of the lowest water temperature in February was the narrowest for RKi whereas it was the widest for RBr, RKa, RN and RY. The weighted mean was the lowest for RRK and the highest for RKi. The weighted, standardized standard deviation was the smallest for RKi and the largest for RY.

The range of the highest water temperature in August was the narrowest for RKi whereas it was the widest for RBr, RN and RT. The weighted mean was the lowest for RS and the highest for RN. The weighted, standardized standard deviation was the smallest for RKi and the largest for RT.

Largely 4 clusters were constructed: RC, RRK, RBi, RS and RRD (RC-cluster); AS, RT, RKa and RRC (AS-cluster); RBr, RRF, RI and RKi (RBr-cluster); and RN and RY (RN-cluster). RC and RRK; RS and RRD; AS and RT; RBr and RRF; and RI and RKi each made an intimate cluster. RC-cluster and AS-cluster connected at a relatively short Euclidian Distance whereas RBr-cluster and RN-cluster connected at a relatively long distance. These two large clusters finally connected at a long distance.

DISCUSSION

and have been reported to be distributed only in montaneous or small-scale rivers whereas and have been reported to be distributed in montaneous to flatland or small- to large-scale rivers (Morishita, 1975; Tsuda, 1981; Tanida, 1992; Kagaya et al., 1998). These are largely compatible to the results in this study. Although was reported to be distributed only in montaneous rivers (Morishita, 1975; Tsuda, 1981; Tanida, 1992), it was widely distributed in the Ohta River in this study and also in the Tama River (Kagaya et al., 1998).

In the cluster analysis, . sp. RD and . sp. RK constructed a cluster. These species are estimated to have adapted to such an environment that has high altitude, steep riverbed slope, small-scale, oligotrophic and low-temperature waters, judging

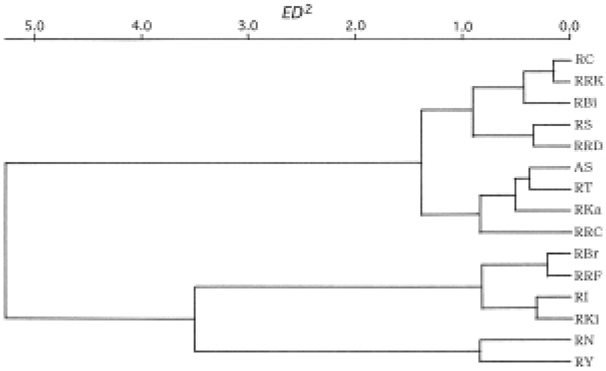

Fig. 2. A dendrogram of 15 species of Rhyacophilidae on the basis of weighted,standardized means of 8 environmental parameters for distribution by Ward method (Ward, 1963).

from the weighted means of these parameters. Headwaters usually possess such a combination of parameters. and constructed another cluster. These are estimated to have adapted to such an environment that has low altitude, loose riverbed slope, large-scale, eutrophic and high-temperature waters. Lower reaches usually possess such a combination. Besides, and . sp. RF constructed another cluster. These are estimated to have adapted to such an environment that has low to middle altitude, low to moderate riverbed slope, small- to middle-scale, mesotrophic and moderate-temperature waters. On the other hand, and . sp. RK were considered to be primitive whereas and were to be derivative (Ross, 1956). Therefore, it might be inferred that the original habitat of the ancestral species to Rhyacophilidae be headwaters and that some derivative species could have successfully advanced to lower and lower reaches.

There seem to be some habitat-partitionings among the sibling species of the same group. For example, , a species of Nigrocephala group, belonged to an AS-cluster whereas , another species of the same group, belonged to a RN-cluster. Indeed, was also reported to incline to be distributed in lower altitude in the Tama River Basin (Kagaya et al., 1998).

A narrow distribution range or small weighted, standardized standard deviation for an environmental factor suggests the strong confinement of the species to the factor for some reason. For example, and . sp. RF showed a remarkably narrow range and an extremely small weighted, standardized standard deviation for distance from riverhead, river width and valley area. It was suggested that there be no habitats involved in the life cycle (e.g., larval microhabitats and sites for reproductive behavior of adults) other than those in narrow range(s) of environmental factor(s).

In this study, only six quadrats of 50 cm×50 cm were collected in a topographic unit and taken as a single sample, and the bottom materials at the center and the littoral parts of the flow at rapid and the center of the flow at the intermediate zone between rapid and pool were collected. However, this method cannot always include all the habitats for Rhyacophilidae larvae at a site. A more inclusive method should be worked out for more strict assessments of distribution.

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太田川水系におけるナガレトビケラ科幼虫各種の分布様式の違いについて

河合幸一郎[1]・西　昌宏[2]・今林博道[1]

[1] 広島大学大学院生物圏科学研究科, 〒739-8528 東広島市鏡山
[2] 株式会社アサムラサキ, 〒714-0062 岡山県笠岡市茂平

要　旨　太田川水系の全体を網羅するいろいろな幼虫群集を調べることによって，ナガレトビケラ科幼虫の分布様式を比較した。合計15種が採集され，どの環境パラメータについても，分布範囲と平均値は種間で著しく異なった。 , . および . sp. RFは，源流からの距離，川幅および流域面積について，狭い範囲と小さな標準偏差を示した。各パラメータを標準化し，8つのパラメータについての分布平均に基づいてクラスター分析を行った。すべて原始的な種である , . と . sp. RKからなるクラスターは，高標高，急な川床勾配，小規模，貧栄養で低温の水域に適応してきたと推定された。共に派生的な種である . と . からなるクラスターは，低標高，緩い川床勾配，大規模，富栄養で高温の水域に適応してきたと推定された。さらに，Nigrocephalaグループの一員である . が . のクラスターを形成したのに対し，同グループの . は のクラスターに加わった。これらの結果は，祖先種の本来の生息地は源流域であること，分布制限要因は種間で異なること，さらに近縁種間で何らかの棲み分けがあることを示唆する。

キーワード：ナガレトビケラ科，環境要因，進化，棲み分け