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陸水学雑誌
59巻2号，1998，p. 199-206 別刷
Reprinted from
THE JAPANESE JOURNAL OF LIMNOLOGY
Vol. 59, No. 2 p. 199-206
June 1998

Jpn. J. Limnol., *59* : 199-206, 1998

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ABSTRACT

Seasonal and diurnal patterns of emergence were compared in unisexual and bisexual populations of *Ephoron shigae* (TAKAHASHI) from four rivers, including two near the northern and southern periphery of the species range. During the emergence periods in 1991 and 1992 winged mayflies were collected every day in the same way in the four rivers. Seasonal timing and synchrony of adult emergence varied depending on the locality and year. The daily start of emergence gradually became earlier with sunset during the emergence period, except for an unusually early emergence on a heavily rainy day, suggesting that light intensity may affect the time of emergence. In the bisexual populations, males began to emerge earlier than females. Females in the unisexual populations began to emerge as early after sunset as males did in the bisexual populations. Sizes of winged stages gradually decreased during the emergence period : hypotheses of decreasing size for cohorts developing under increasing temperatures cannot be applied to *E. shigae* which spends its later nymphal stages under temperatures fluctuating around the highest level of the year.

Key words : adult size, *Ephoron shigae,* timing of emergence

INTRODUCTION

Mass emergence in mid-September of a burrowing mayfly, *Ephoron shigae* (TAKAHASHI), has been reported almost every year in the mass media from some Japanese rivers, because of its spectacular appearance and its interference with traffic. WATANABE and ISHIWATA (1997) reported that this species is distributed in rivers on Honshu, Shikoku and Kyushu from *ca.* 39°N (Kitakami-gawa) to *ca.* 33°N (Banjo-gawa), and includes unisexual (no or few males) and bisexual populations. To elucidate the factors affecting the seasonal and diurnal timing of emergence, we compare two bisexual and two unisexual populations of *E. shigae* in a latitudinally and longitudinally broad range.

MATERIALS AND METHODS

Winged stages of *E. shigae* were collected every day from the end of August to the beginning of October 1991 and 1992 in the same way in the four rivers ; the Abukuma-gawa (Fukushima ; 37°45′N, 140°29′E), the Shonai-gawa (Nagoya ; 35°15′N, 137°02′E), the Asahi-gawa (Okayama ; 34° 41′N, 133°56′E) and the Oita-gawa (Oita ; 33°12′N, 131°35′E) ; the rivers are arranged from north to south in the tables and figures that follow. The Abukuma-gawa and the Oita-gawa are located near the northern and southern periphery, respectively, of the geographical range of the species. The populations in the Abukuma-gawa and the Asahi-gawa are bisexual, and those in the Shonai-gawa and the Oita-gawa are unisexual (WATANABE and ISHIWATA, 1997). Imagos and subimagos swarming over the water surface were collected by sweeps through the air with an net 40 cm in diameter at a point about 50 cm deep in each of the four rivers. A twenty-stroke sweep was made every 5 min throughout the duration of swarming each night (quantitative sampling). When the daily emergence was scarce, samples were supplemented by careful searching of the air. The specimens of *E. shigae* were preserved in 5 % folmalin solution and were sexed and counted in the laboratory. Head widths of specimens from the Asahi-gawa, *i.e.*, male imagos, male subimagos and female subimagos (females of *Ephoron* lay eggs and die as subimagos), were measured to the nearest 0.01 mm using a binocular microscope with an objective micrometer. When the daily quantitative samples were very large, about fifty specimens for each sex were subsampled for the measurement. When samples were much fewer than fifty, the supplementary samples, when available, were also measured.

RESULTS AND DISCUSSION

The total number and sex ratio of mayflies caught by the quantitative samplings during the emergence periods in 1991 and 1992 are shown in Table 1. The populations in the Shonai-gawa and Oita-gawa had highly female-biased sex ratios, whereas this was not the case in the Abukuma- and Asahi-gawa.

Table 1. Total numbers and sex ratios of *E. shigae* caught by quantitative samplings during an emergence period in the four rivers.

		Abukuma-gawa		Shonai-gawa		Asahi-gawa		Oita-gawa	
		female	male	female	male	female	male	female	male
1991	Nos.	181	289	2604	21	5472	7235	869	7
	ratio	0.63	1	124.00	1	0.76	1	124.14	1
1992	Nos.	383	479	2742	38	3065	1592	1617	10
	ratio	0.80	1	72.16	1	1.93	1	161.70	1

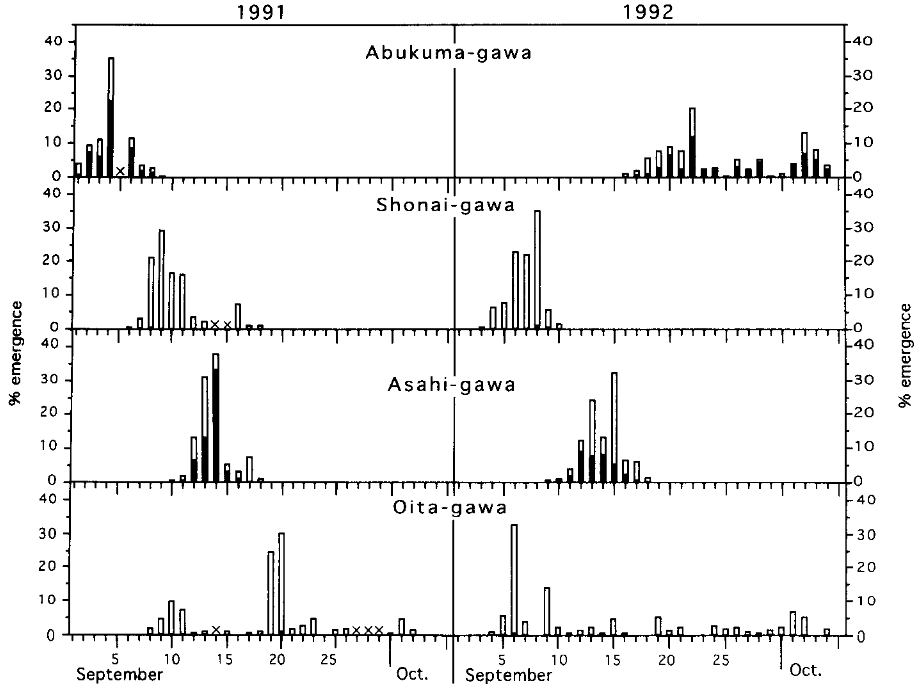

Fig. 1. Seasonal patterns of emergence of *E. shigae* in the four rivers in 1991 and 1992. Open and solid bars show females and males, respectively. No samplings were made on the days shown by cross marks.

Figure 1 shows the seasonal patterns of emergence of *E. shigae* in 1991 and 1992 in the four rivers. In the Shonai-gawa and the Asahi-gawa, emergence occurred for about ten days in both years, whereas in the Oita-gawa it extended over almost a month. In the Abukuma-gawa, emergence occurred synchronously in 1991, but it continued for a considerably longer period in 1992. The peaks of emergence in 1991 occurred later on a north-to-south gradient, but peaks in 1992 did not show such a tendency. Thus, the timing and degree of synchrony varied depending on the locality and year, with no general tendency becoming apparent based on two years of data. Moreover, no difference between unisexual and bisexual populations was observed in the emergence pattern. Despite the analysis of available information on environmental conditions, any factors evidently affecting the daily abundance of emerging mayflies have not yet been found.

Figure 2 shows seasonal changes in the start and the end of daily swarming of *E. shigae* in the four rivers in 1991 and 1992. The start and the end of swarming were defined as those times when 5 % and 95 %, respectively, of the daily captures were collected. The start of swarming (=the start of emergence) gradually became earlier with sunset during the emergence period, except in the Abukuma-gawa in 1991 where the emergence period was very short. Thus, the time of emergence seemed to be determined mainly by decreasing light intensity, as was suggested for *E. album* by BRITT

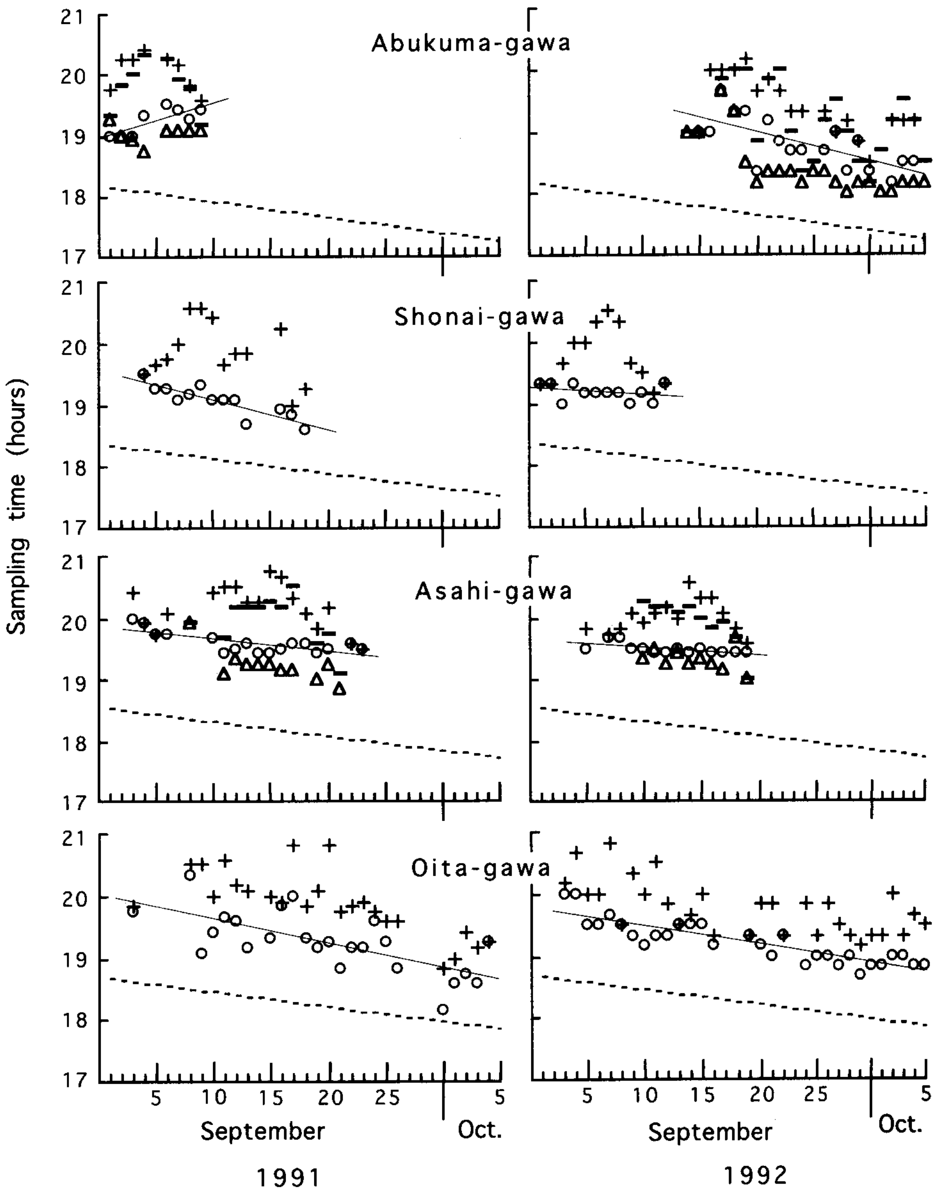

Fig. 2. Seasonal changes in the diurnal timing of *E. shigae* swarming in the four rivers. Open circles/plus marks and open triangles/bars represent the start/end of swarming of females and males, respectively. The start and the end of swarming were defined by the times when 5% and 95%, respectively, of the daily captures were collected. The broken lines indicate the sunset. Regression lines are shown only for the start of female emergence. See the text for further explanation.

(1962). This might be supported by the unusually early emergence in the Oita-gawa on 30 September 1991 when it rained heavily all day from the effect of a typhoon (78-mm daily rainfall). On days with heavy rain, light intensity on the bottom of rivers should decrease earlier in the evening than on fine days, because of weak light incidence and of absorption by increased water depth and turbidity. The end of swarming also came earlier toward the end of emergence period in both years in the Oita-gawa and in 1992 in the Abukuma-gawa where emergence periods were relatively long. In the other cases where emergence occurred rather synchronously, daily swarming ended later at the middle of the emergence periods in general, affected by the daily abundance of mayflies. The swarming always ended before 21.00 hrs, and no difference between the uni- and bisexual populations was recognized.

In Figure 2, the time intervals from sunset to the start of female emergence in the unisexual populations (the Shonai- and the Oita-gawa) are apparently shorter than those in the bisexual populations (the Abukuma- and Asahi-gawa). This was tested by the following method : For regression analysis, the daily starting time of emergence was weighted depending on the daily abundance of mayflies by being multiplied by 1 for 1-10 individuals collected, by 2 for 11-50 and by 3 for over 51 (if weighted by daily abundance itself, the regression would be affected too strongly by a few days of mass emergence). Then, regression equations (Eqs. 1 in Table 2) for the relationships between the daily start of emergence based on the weighted data and the date counted from August 31 (t=0) were calculated ; the regression lines for females are shown in Figure 2. The interval of time from sunset to the start of emergence was obtained by subtracting the sunset time calculated by Eqs. 2 from the starting time of emergence by Eqs. 1 on a given day. On 15 and 20 September, for example, when emergence was possible

Table 2. Regression equations of daily start of emergence (SE) on date (Eqs. 1) and sunset on date (Eqs. 2). The intervals between sunset and SE on 15 and 20 September are shown in the column on the far right. Data in 1991 on the Abukuma-gawa are omitted because the emergence period was far from 15 or 20 September. See the text for further explanation.

Rivers			SE y=bx+a (Eqs. 1)			sunset y=bx+a (Eqs. 2)		sunset → SE on September	
			a	b	r^2	a	b	15	20
Abukuma-gawa	♀	1992	0.8387	-0.0023	0.545**	0.7574	-0.0011	1 : 31	1 : 22
	♂	1992	0.8089	-0.0018	0.473**			0 : 59	0 : 54
Shonai-gawa	♀	1991	0.8149	-0.0020	0.664**	0.7654	-0.0010	0 : 49	0 : 42
	♀	1992	0.8039	-0.0008	0.205*			0 : 59	1 : 01
Asahi-gawa	♀	1991	0.8245	-0.0007	0.348**	0.7731	-0.0010	1 : 20	1 : 22
	♀	1992	0.8173	-0.0005	0.373**			1 : 14	1 : 18
	♂	1991	0.8200	-0.0013	0.303**			1 : 01	0 : 58
	♂	1992	0.8172	-0.0009	0.149*			1 : 05	1 : 06
Oita-gawa	♀	1991	0.8312	-0.0015	0.473**	0.7790	-0.0010	1 : 04	1 : 00
	♀	1992	0.8238	-0.0012	0.774**			1 : 00	0 : 58

* $p \leqq 0.05$; ** $p \leqq 0.01$.

in all the rivers, females in the Shonai-gawa and the Oita-gawa began to emerge nearly an hour after sunset (Table 2). These times of female emergence were significantly earlier than those in the Abukuma-gawa and the Asahi-gawa (MANN-WHITNEY U-test; $p=0.05$ for each day), and agree approximately with the times of male emergence there. WATANABE *et al.* (1989) reported for *E. shigae* in the Asahi-gawa that male subimagos emerged synchronously and molted to imagos in a 25 min period (by sampling intervals of 5 min) immediately prior to an abrupt increase in female emergence. It is an interesting phenomenon that females in the unisexual populations began to emerge as early as males in the bisexual populations. Determining the mechanism and ecological or evolutionary significance of this phenomenon must await future studies.

Seasonal changes in the head width of imagos and subimagos in the Asahi-gawa are shown in Figure 3. Females were much larger than males, and male imagos were slightly smaller than male subimagos. Sizes of winged stages gradually decreased during an emergence period.

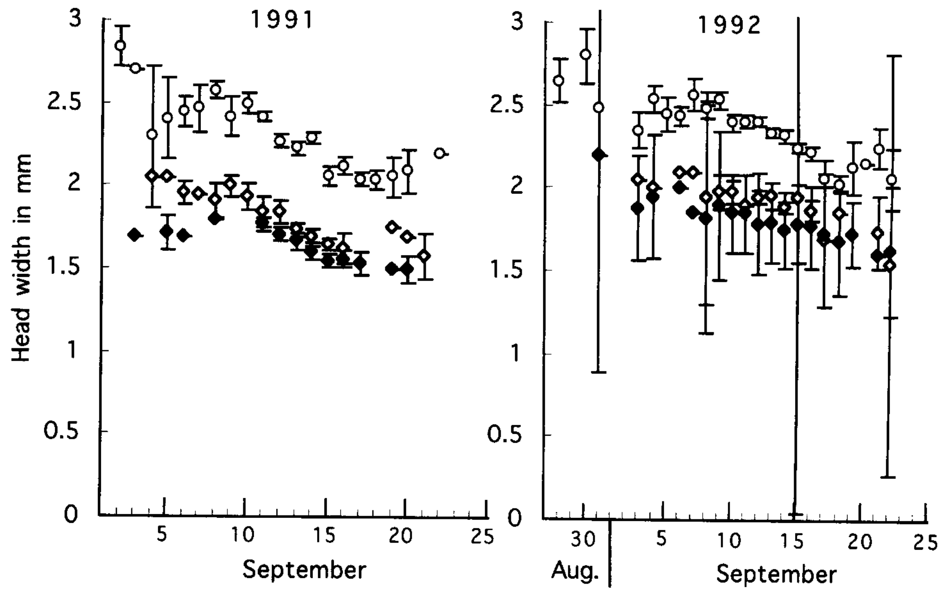

Fig. 3. Seasonal changes in the head width of imagos and subimagos of *E. shigae* in the Asahi-gawa. Open circles, open diamonds, and solid diamonds with vertical lines indicate the mean head width with 95 % confidence limits of female subimagos, male subimagos and male imagos, respectively. Circles and diamonds with a tail on the right indicate that only one sample was measured. Numbers of male subimagos measured were sometimes very few because they molted to imagos soon in collecting nets.

Similar seasonal reduction in adult size has been reported for many aquatic insects. SWEENEY and VANNOTE (1981) and TAKEMON (1990) suggested hypotheses explaining the seasonal size reduction in species whose larvae grow during their final phase under increasing temperatures. However, during the period from mid-July to early September when *E. shigae* is in its later nymphal stages (nymphs recruit to the last instars in mid- or late August ; WATANABE, unpublished data), water temperature fluctuates around the highest level of the year. Furthermore, the adult emergence occurs in September when water temperature generally begins to decrease. Therefore, it seems difficult to apply the hypotheses mentioned above to the size reduction in *E. shigae* adults. An alternative explanation is needed for 'autumn species' which spend summer as later instars.

ACKNOWLEDGEMENTS

We wish to thank Dr. A. SUGIYAMA (Nagoya Women's University), Mr. I. YOSHITAKA (Kanzei High School), Miss I. MORI (Okayama Prefectural Nature Conservation Center) and all the other collaborators for their assistance with the field surveys. We also thank Dr. R. W. FLOWERS (Florida A & M University) for his helpful comments on an earlier version of the manuscript. This study is supported by the Nissan Science Foundation.

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(*Received 12 September 1997 ; Accepted : 12 December 1997*)

4河川におけるオオシロカゲロウの羽化期および羽化時刻の比較

渡辺　直・八田耕吉・久枝和生・星　一彰・石綿進一

摘　　要

種の分布域の北限および南限近くの川と，単性および両性個体群とを含んだ4河川で，オオシロカゲロウの羽化の季節的・日周期的パターンを比較した。1991年と1992年の羽化期に毎日，4河川とも同一の方法で，成虫・亜成虫を採集した。羽化の時期とその集中性は，川によって，また年によって異なっており，一定の傾向は認められなかった。1日の羽化開始時刻は，日没時刻の変化につれてしだいに早くなったが，大雨の降った日には例外的に早く羽化した。これらのことは，羽化時刻に照度が影響することを示唆している。単性個体群における雌の羽化時刻は両性個体群の場合よりも早く，両性個体群での雄にほぼ相当する時刻に羽化が始まった。羽化個体のサイズは，羽化期の後になるほどしだいに小さくなった。羽化期間中のサイズ減少の原因について，後期幼虫の発育が春の水温上昇期に起こることを前提とした仮説がこれまでに提出されているが，オオシロカゲロウは水温が年間の最高値付近で変動している夏期に後期幼虫期を過ごすので，これまでの仮説では説明出来ない。