Geographic Distribution of the Mayfly, *Ephoron shigae* in Japan, with Evidence of Geographic Parthenogenesis (Insecta : Ephemeroptera : Polymitarcyidae)

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ABSTRACT

The geographic distribution of *Ephoron shigae* in Japan was surveyed based on questionnaires and selected information from publications as well as collections. This species is distributed in rivers on Honshu, Shikoku and Kyushu from *ca.* 39°N to *ca.* 33°N in latitude. Temperature regimes from autumn to spring seem likely to be the main factor limiting distribution to this area. No or few males were found in some populations (unisexual populations), whereas many males as well as females were collected in some other populations (bisexual populations). The distributions of both populations broadly overlapped. The unisexual populations evidently reproduce parthenogenetically.

Key words : *Ephoron shigae,* geographic distribution, geographic parthenogenesis, mayfly

INTRODUCTION

Mass emergence of *Ephoron shigae* (TAKAHASHI) has been reported by the mass media almost every September from some Japanese rivers. The bodies of huge numbers of mayflies attracted by street lights accumulate on roads, interfering with traffic and sometimes causing car accidents. Although the emergence of this species has often been reported on local journals or scientific magazines (*e.g.,* SHIOYAMA, 1978; SHIRAKI *et al.,* 1993), its geographic distribution has not yet been described. Information on the distribution of *E. shigae* can be usefully obtained from people working along rivers and from various kinds of local and governmental publications, because the emergence is noticeable and both adults and nymphs are rather easily identified.

In the present study, the geographic distribution of *E. shigae* in Japan is surveyed based on questionnaires and the selected information from various publications as well as collections. Evidence of geographic parthenogenesis is then presented.

MATERIALS AND METHODS

One of the authors (N.C.W.) sent a questionnaire in mid-September 1991 to all the Regional River Management Offices of the Japanese Ministry of Construction except for Hokkaido and the Ryukyu Islands where *E. shigae* is not distributed based on previous information. He asked the offices to reply to the questionnaire and to send some specimens of dead mayflies that had accumulated under street lights when the mass emergence was observed. Seventy-one of 88 offices replied to the questionnaire. The specimens received were then identified. Similar questionnaires were sent to about 60 entomologists in 1992 to gather additional information and to reconfirm the replies from river management offices that did not send specimens. Another author (S. I.) collected specimens from many localities based partly on information supplied by the questionnaires.

Recently, two species, *Ephoron eophilum* ISHIWATA and *E. limnobium* ISHIWATA, were newly described from Japan (ISHIWATA, 1996), and their morphology apparently resembles that of *E. shigae. E. eophilum*, however, was easily distinguishable in that it emerges at dawn whereas *E. shigae* emerges after sunset. Although *E. limnobium* has so far been found only in Lake Biwa and is probably endemic to the lake, it may possibly be distributed in other areas. Information without specific identification, therefore, is distinguished in the list of localities of *E. shigae* below.

RESULTS

The rivers and localities where *E. shigae* is distributed are listed in Table 1 and plotted on a map of Honshu, Shikoku and Kyushu in Figure 1. *E. shigae* was found at 54 sites of 47 water systems covering an area from *ca.* 39°N (the Kitakami-gawa) to *ca.* 33°N (the Banjo-gawa) in latitude, although some of the information forwarded was not confirmed. The questionnaire responses of eight Regional River Management Offices north of the Kitakami-gawa and seven south of the Banjo-gawa showed no evidence that *E. shigae* had occurred in those districts. As of this writing, we have not obtained any information for its occurrence beyond the *ca.* 33-39°N area. Therefore, the distribution of *E. shigae* seems to be limited to this area. The only occurrence reported in northwestern Honshu was from the Agano-gawa.

No or few males were found in some populations (hereafter referred to as unisexual populations), whereas many males as well as females were collected in some other populations (bisexual populations). The percentage of males in the Shonai-gawa and the Oita-gawa, for example, was around or less than 1%, whereas that in the Asahi-gawa and the Abukuma-gawa reached 50% in 1991 and 1992 (WATANABE *et al.*, unpublished). Furthermore, no males were collected in the Kinu-gawa (NAKAMURA, 1985), the Sagami-gawa (NOZAKI, 1983) or the Yahagi-gawa (BAN *et al.*, 1994). The distributions of unisexual and bisexual populations of *E. shigae* broadly overlapped.

Table 1. Rivers and localities where *Ephoron shigae* occurred.

No.	River	Locality	Latitude	Longitude	References
1	Kitakami-gawa	Esashi, Iwate	39° 11' N	141° 10' E	present study
2	Eae-gawa	Wakuya, Miyagi	38° 32' N	141° 08' E	Ishiwata (1996)
3	Abukuma-gawa**	Fukushima City	37° 45' N	140° 29' E	Hoshi (1986)
4	Agano-gawa	Yasuda, Niigata	37° 45' N	139° 14' E	Ishiwata (1996)
5	Naka-gawa**	Gozenyama, Ibaraki	36° 33' N	140° 20' E	Nakamura et al. (1986)
6	Kinu-gawa*	Utsunomiya, Tochigi	36° 34' N	139° 53' E	Shioyama (1978)
7	Ara-kawa**	Ageo, Saitama	35° 56' N	139° 32' E	Ishiwata (1996)
8	Tama-gawa	Hino, Tokyo	35° 40' N	139° 24' E	Ibid.
9	Yoro-gawa	Ichihara, Chiba	35° 29' N	140° 07' E	Ibid.
10	Obitsu-gawa**	Kimitsu, Chiba	35° 19' N	139° 55' E	Ibid.
11	Isumi-gawa**	Ootaki, Chiba	35° 17' N	140° 15' E	Ibid.
12	Sagami-gawa*	Atsugi, Kanagawa	35° 25' N	139° 23' E	Nozaki(1983)
13	Nagara-gawa	Hozumi, Gifu	35° 23' N	136° 43' E	Hatta, pers. com.
14	Kiso-gawa	Sobue, Aichi	35° 15' N	136° 42' E	Ibid.
15	Shonai-gawa*	Nagoya, Aichi	35° 15' N	137° 02' E	Ibid.
16	Yahagi-gawa*	Toyota, Aichi	35° 04' N	137° 11' E	Shiraki et al. (1993)
17	Oto-gawa*	Okazaki, Aichi	34° 56' N	137° 12' E	Ban et al. (1994)
18	Toyo-gawa	Shinjo, Aichi	34° 53' N	137° 29' E	Ban pers. com.※
19	Kumozu-gawa	Onoki, Ichishi, Mie	34° 39' N	136° 24' E	Ishiwata (1996)
20	Miya-gawa	Watarai, Mie	34° 26' N	136° 37' E	Yamashita (1981)※
21	Uji-gawa	Uji, Kyoto	34° 53' N	135° 49' E	Ishiwata (1996)
22	Yodo-gawa**	Takatsuki, Osaka	34° 49' N	135° 38' E	Ibid.
23	Yura-gawa	Fukuchiyama, Kyoto	35° 18' N	135° 08' E	Kusakabe et al. (1978)※
24	Takeda-gawa	Fukuchiyama, Kyoto	35° 14' N	135° 09' E	Ishiwata (1996)
25	Muko-gawa**	Takarazuka, Hyogo	34° 47' N	135° 22' E	Tanaka (1993)
26	Maruyama-gawa	Hidaka, Hyogo	35° 29' N	134° 43' E	Nishimura et al.(1975)※
27	Kako-gawa	Kakogawa, Hyogo	34° 47' N	134° 54' E	Morishita (1979)※
28	Yumesaki-gawa**	Himeji, Hyogo	34° 52' N	134° 40' E	present study
29	Ibo-gawa	Ibo-gun, Hyogo	34° 55' N	134° 33' E	Morishita (1979)※
30	Yoshii-gawa	Yoshii, Okayama	34° 55' N	134° 06' E	present study
31	Asahi-gawa**	Okayama City	34° 41' N	133° 56' E	Watanabe et al. (1989)
32	Takahashi-gawa	Souja, Okayama	34° 43' N	133° 39' E	present study
33	Hino-gawa	Mizoguchi, Tottori	35° 20' N	133° 27' E	Ishiwata (1996)
34	Hii-gawa	Kisuki, Shimane	35° 18' N	132° 54' E	Nishimura et al. (1979)※
35	Kando-gawa	Izumo, Shimane	35° 17' N	132° 44' E	Ibid. ※
36	Gono-kawa	Miyoshi, Hiroshima	34° 48' N	132° 51' E	present study
37	Gono-kawa	Sakurae, Shimane	35° 58' N	132° 20' E	Ibid.
38	Ota-gawa	Asaminami, Hiroshima	34° 30' N	132° 31' E	Ishiwata (1996)
39	Furu-kawa	Hiroshima City	34° 28' N	132° 29' E	present study
40	Saba-gawa	Houfu, Yamaguchi	34° 04' N	131° 34' E	Ibid.
41	Fushino-gawa	Yamaguchi City	34° 09' N	131° 28' E	†※
42	Koto-gawa	Takamatsu, Kagawa	34° 18' N	134° 01' E	present study
43	Yoshino-gawa	Ishii, Tokushima	34° 06' N	134° 27' E	Ibid.
44	Katsuura-gawa	Tokushima City	33° 58' N	134° 48' E	Ibid.
45	Monobe-gawa	Noichi, Kochi	33° 35' N	133° 42' E	Ishiwata (1996)
46	Hiji-kawa*	Ohzu, Ehime	33° 31' N	132° 33' E	Ibid.
47	Shimanto-gawa	Nakamura, Kochi	33° 01' N	132° 51' E	Furuya (1990)
48	Yamakuni-gawa	Nakatsu, Oita	33° 35' N	131° 11' E	present study
49	Kamimutsuro-gawa	Kamimutsuro, Saga	33° 27' N	130° 13' E	Ishiwata (1996)
50	Tabuse-gawa	Saga City	33° 18' N	130° 17' E	†※
51	Chikugo-gawa	Hita, Oita	33° 19' N	130° 57' E	†※
52	Oita-gawa*	Akegawara, Oita City	33° 12' N	131° 35' E	present study
53	Ono-gawa	Shirataki, Oita City	33° 09' N	131° 39' E	Sato (1987)
54	Banjo-gawa	Saiki, Oita	32° 57' N	131° 51' E	Ibid.

*no or very few males were found. **many males were found. Insufficient information in the other rivers. † Based on photographs or circumstantial evidences. The information from river management offices has not been reconfirmed. ※There is a little possibility of being *E. limnobium* because the specimens were not checked.

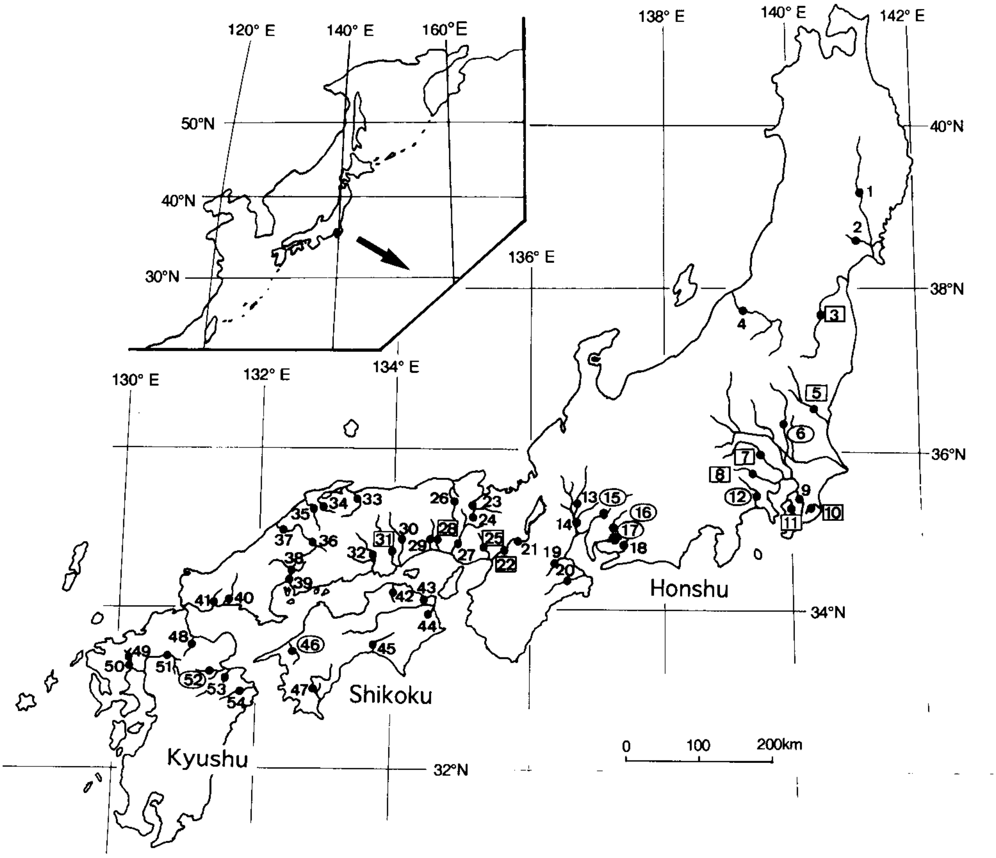

Fig. 1. Map showing the distribution of *Ephoron shigae* in Japan. The number of each locality corresponds to that in Table 1. Ovals and rectangles indicate unisexual and bisexual populations, respectively.

DISCUSSION

Factors limiting geographic distribution of *E. shigae*

It has been known that eggs of the genus *Ephoron* develop effectively by going through a period of cold temperature (EDMUNDS *et al.,* 1956 ; BRITT, 1962 ; GIBERSON and GALLOWAY, 1985 ; NAKAMURA, 1985). Experimental studies on *E. shigae* have shown that the eggs have to experience relatively high temperatures after oviposition for pre-diapause development. After that, they almost stop developing at an advanced embryonic stage characterized by the appearance of dark eyespots, and require a period of low temperature for diapause development. After the diapause period, the eggs further require relatively high temperatures for post-diapause development to hatching (NAKAMURA *et al.,* 1987 ; WATANABE and TAKAO, 1991). Therefore, the egg diapause is induced obligatorily, and its termination depends on temperature. The overwintering of eggs and spring hatching were verified by the fact that the eggs collected in the Asahi-gawa in March and transferred to warmer conditions in the laboratory hatched successfully (WATANABE, unpublished). In the streams where *E. shigae* is distributed, thermal regimes from autumn to spring must satisfy the above conditions required for egg development.

Figure 2 shows the seasonal changes in water temperature in the Kitakami-gawa (the northern periphery of the species range), the Banjo-gawa (the southern periphery), and the Asahi-gawa (shown for reference). In the Banjo-gawa, the temperature in winter rarely fell below 10 °C, although temperatures below *ca.* 15 °C continued for nearly three months. WATANABE and TAKAO (1991) demonstrated that the longer eggs from the Asahi-gawa were subjected to colder temperatures, the more effectively and more synchronously they hatched after the cold period ended. For instance, more than 80% of the eggs hatched quickly and synchronously after 75 days at 0–8 °C, while only about 20% hatched rather sporadically during one

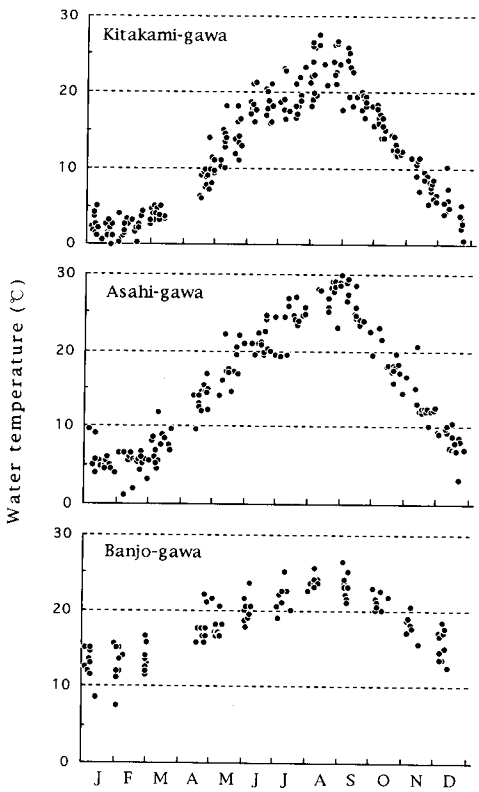

Fig. 2. Seasonal changes in water temperature in the Kitakami-gawa, the Asahi-gawa and the Banjo-gawa during the ten years from 1984 to 1993. Temperature measurements at the point nearest to the site where *E. shigae* occurred in each river were selected from the Annual Report of Water Quality (River Bureau, 1984–1993) and averaged.

month following 75 days at 14 °C. Therefore, the thermal condition in winter in the Banjo-gawa seems to be inadequate for the effective diapause development of *E. shigae*. Prolonged and sporadic emergence in the Oita-gawa population near the southern periphery was reported (WATANABE *et al.*, 1993). This may be partly due to temperatures too high for synchronous hatching. The southern limit of the distribution of *E. shigae* seems likely to be determined by the water temperature in winter.

On the other hand, the thermal requirements for pre-diapause development of eggs and for nymphal development may be vital problems in the northern periphery. NAKAMURA *et al.* (1987) reported that most of the eggs from the Kinu-gawa population (36°34′ N ; 139°53′ E) which incubated for 36 days at 16–29 °C for pre-diapause development hatched successfully after chilling, but only about half of the eggs hatched when incubated for 25 days at the same temperatures. Although the emergence period in the Kitakami-gawa was not clear, it occurred mainly in September in four other rivers including the Abukuma-gawa, near the northern periphery, and the Oita-gawa, near the southern periphery (WATANABE *et al.*, 1993). Moreover, Mr. M. TAKEDA of Yamagata University sent us some specimens of female subimagos collected in the Kitakami-gawa on October 3, 1992. This would put the main emergence period in the Kitakami-gawa population as September at the earliest. Because the temperature there falls below 15 °C in mid-October, thermal conditions seem to be rather severe for the eggs to complete their pre-diapause development.

Furthermore, the period of nymphal development may be restricted in the northern periphery. In the Asahi-gawa, eggs hatched from mid-March to early April in 1991 and 1992 when water temperature reached 10–11 °C (WATANABE, unpublished). The stream temperature exceeds 10 °C at the beginning of May in the Kitakami-gawa and from then on it is generally lower than in the Asahi-gawa. Total number of degree-days needed for nymphal development in the Kitakami-gawa population, therefore, must be lower than for the Asahi-gawa population. To complete their nymphal development until emergence in early autumn may be a daunting task for the northern populations. The scarce distribution of *E. shigae* in northwestern Honshu may support the above argument. Because of heavy snowfalls, the vernal increase in river temperature was heavily suppressed by melting snow in this area (ARAI, 1962 ; NISHIZAWA and NANNBA, 1962). The scarce distribution of *E. shigae* there may be due to an insufficient number of degree-days for nymphal development, although the reason for their exceptional occurrence in the Agano-gawa is unknown.

Therefore, the thermal requirements for the development of eggs and nymphs seem to be the limiting factor in the geographic distribution of *E. shigae*, although geographic variations in egg and nymphal development need to be studied.

Evidence of geographic parthenogenesis

Parthenogenesis is widespread in mayflies (DEGRANGE, 1960 ; HUMPESCH, 1980). In most cases, however, the parthenogenesis is occasional or accidental, including that of *Ephoron album* (SAY) in North America (BRITT, 1962). The percentage of hatching success for parthenogenetic eggs was usually much lower than that for fertilized eggs in these cases. On the other hand, obligatory parthenogenesis, where parthenogenesis is the normal mode of reproduction, has been known for unisexual populations of several mayfly species (CLEMENS, 1922 ; FROEHLICH, 1969 ; GIBBS, 1977 ; BERGMAN and HILSENHOFF, 1978 ; SWEENEY and VANNOTE, 1987 ; GILLIES and KNOWLES, 1990). For these populations, the rate of unfertilized eggs hatched was usually above 80% (reviewed by HUMPESCH, 1980). Among them, obvious evidence of geographic parthenogenesis, *i.e.,* unisexual and bisexual populations of the same species existing geographically, has been verified only for an ephemerellid mayfly, *Eurylophella funeralis* (McDUNNOUGH) in North America (SWEENEY and VANNOTE, 1987), except for a few suspected cases. The hatching success of unfertilized *E. funeralis* eggs was inversely related to the proportion of males in the bisexual populations.

The transition of a population from reproduction by fertilization to parthenogenesis requires that : (a) the females must be able to lay eggs without the oviposition-stimulus of mating ; (b) the unfertilized eggs must be able to develop (SUOMALAINEN, 1962) ; (c) the offspring must be able to maintain the population in the midst of or adjacent to their parental source or sources without being eliminated by competition or hybridization (HUMPESCH, 1980). The first of these requirements was satisfied for *E. shigae* after the following observations. All of the *ca.* 30 female subimagos of the unisexual population in the Shonai-gawa caught with a light trap were unfertilized (WATANABE, unpublished data), whereas almost all females were fertilized in the bisexual population in the Asahi-gawa (WATANABE *et al.,* 1989). The female subimagos from the Shonai-gawa population oviposited voluntarily in a way similar to those from the Asahi-gawa population when placed in contact with water or even in dry insect nets (WATANABE, unpublished). The second requirement was fulfilled because the rate of hatching success of unfertilized eggs from the unisexual population in the Kinu-gawa was as high (> 80%) (NAKAMURA, 1985) as that of fertilized eggs from the Asahi-gawa population (WATANABE and TAKAO, 1991). As for the third requirement, some of the unisexual and bisexual populations of *E. shigae* have been maintained for at least ten years according to entomologists who have conducted studies in the following rivers : unisexual populations in the Kinu-gawa (NAKAMURA *et al.,* 1986 ; K. NAKAMURA, personal communication), the Shonai-gawa (K. HATTA, pers. com.), the Yahagi-gawa (SHIRAKI *et al.,* 1993 ; Y. BAN, pers. com.), and the Oita-gawa (K. HISAEDA, pers. com.) ; bisexual populations in the Abukuma-gawa (K. HOSHI, pers. com.) and the Asahi-gawa (WATANABE *et al.,* 1993 ; WATANABE, unpublished). Therefore, unisexual populations seem to mainly reproduce parthenogenetically. The parthenogenesis must be obligatory and thelytokous (female producing). *Ephoron shigae* presents the second demonstrated case of geographic parthenogenesis of mayflies.

There are not a few examples of geographic parthenogenesis in the animal kingdom (reviewed by SUOMALAINEN, 1950, 1962). Parthenogenetic populations tend to occur under severe conditions such as higher latitudes and altitudes, xeric as opposed to mesic conditions (SUOMALAINEN, 1950; GLESENER and TILMAN, 1978), or in habitats where a high ability of dispersal is advantageous to colonization, such as islands and island-like habitats or the periphery of a species range (CUELLAR, 1977). Unisexual populations of the mayfly, *Eurylophella funeralis,* seemed to occur largely at the periphery of their geographic range in North America (SWEENEY and VANNOTE, 1987). For *E. shigae,* however, unisexual and bisexual populations broadly overlapped. Any difference in topographical or hydrological characteristics between rivers with unisexual and those with bisexual populations could not be found in data from the Yearbook of Water Quality in Japanese Rivers (Japanese River Association, 1992), although other environmental differences between these two types of populations are still undetermined. In any case, *E. shigae* may provide good material to investigate both the conditions required for the establishment of parthenogenetic populations and the significance of sexual reproduction. Further comparative studies of unisexual and bisexual populations from ecology and population genetics are needed.

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日本におけるオオシロカゲロウ *Ephoron shigae* (TAKAHASHI) の地理的分布および地理的単為生殖

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摘　　要

直接の標本採集に加えて，アンケート（質問票および一部標本）および文献にもとづいて日本におけるオオシロカゲロウの地理的分布を調査した。この種は，およそ北緯39度（北上川）から33度（番匠川）までの47水系54地点に分布していた。秋から春にかけての水温がこの種の分布を限定する主要因と考えられる。オスがいないか，あるいはきわめて少ない個体群と，メスと同様に多くのオスがいる個体群があり，両者の分布は広い範囲で重複していた。オスのほとんどいない個体群は単為生殖によって維持されているものと思われる。