

Effect of water temperature on the mass emergence of the mayfly, *Ephoron shigae*, in a Japanese river (Ephemeroptera: Polymitarcyidae)

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SUMMARY

1. Winged stages of *Ephoron shigae* were collected every day during their emergence period during a 6-year period from 1989 to 1994, by net sweeps or a light trap along the Asahi-gawa River in western Japan. Emergence occurred mainly in September.
2. Coefficients of determination (r^2) were calculated for the regression of the mean date of emergence against cumulative degree-days during various periods from late March to early September.
3. In both sexes the highest values of r^2 were obtained for regression with degree-days from late June to late August. This indicates that thermal conditions during the late instars affected the emergence timing most strongly. The timing of emergence can be well predicted from the cumulative degree-days during summer.

Keywords: mayfly, emergence timing, water temperature, degree-days, Japanese river

Introduction

The relationship between the growth or development of terrestrial insects and degree-days has long been used to predict the timing or abundance of emerging pest species (e.g. Andrewartha & Birch, 1954). For aquatic insects also, the degree-days required for embryonic development or nymphal growth have been studied in the laboratory (e.g. Wright, Mattice & Beauchamp, 1982; Lillehammer *et al.*, 1989). In addition, the influence of temperature on the life cycle phenology of aquatic insects in the field has often been recognized (Ban & Kawai, 1986; Perry, Perry & Stanford, 1986; Peters, Peters & Fink, 1987; Newbold, Sweeney & Vannote, 1994). However, the application of a degree-days approach to field data has been limited to a few studies. Tokeshi (1985) demonstrated a high correlation between mean body length on each

sampling occasion and degree-days above a minimum threshold temperature. Takemon (1990) explained the timing and synchronicity of emergence of *Ephemera strigata* Eaton by the effective degree-days experienced in the last instar stage in a Japanese stream.

The burrowing mayfly, *Ephoron shigae* (Takahashi), is distributed in many Japanese rivers on the islands of Honshu, Shikoku and Kyushu (Watanabe & Ishiwata, 1997). Mass emergences of this species are reported almost every September from some Japanese rivers because of their spectacular appearance and interference with traffic. Therefore, the emergence timing of *E. shigae* has attracted the attention of people living along rivers as well as that of road-management officials and entomologists. Factors affecting the emergence timing have, however, never been studied. In the present study the effect of water temperature in the nymphal stage on the emergence timing of *E. shigae* was investigated.

Materials and methods

The emergence of *E. shigae* was investigated in the

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lower reaches of the Asahi-gawa River near the center of Okayama City, Honshu (long. 133°56'E, lat. 34°40'N) where the river is about 130 m wide. The emergence of *E. shigae* occurs about an hour after sunset mainly in September and, at its peak, the entire river surface is covered by the mayfly swarm. Swarming ends by 21.00 h at the latest, and the mayflies fall onto the water surface and die (Watanabe, Yoshitaka & Mori, 1989; Watanabe *et al.*, 1998). Imagos and subimagos of *E. shigae* were collected daily during the emergence period from 1989 to 1994. From 1989 to 1992, mayflies swarming over the surface were collected with a sweep net (40 cm in diameter) from a fixed point in the river (usually 0.5 m water depth). Sweeps were made about 1 m above water surface. A 20-stroke sweep was made every 5 min during the swarming, and the daily sum of the number caught was regarded as the abundance of mayflies for that day. During the emergence periods in 1993 and 1994, a portable lamp with a fluorescent black light (6 W) was used to collect the winged mayflies. A polyethylene bottle with a funnel in its opening was put beneath the light suspended from a support stand. Winged stages of *E. shigae* attracted by the light fell onto the slanted wall of funnel. Unable to take flight again, they were trapped in the bottle since their legs are generally very weak. The bottle was changed once it was filled with mayflies. The specimens were preserved in 5% formalin solution, and sexed and counted in the laboratory.

Hourly water temperature on the bottom (usually ≈ 1.5 m water depth) was automatically measured by the Okayama River Management Office of the Ministry of Construction at a point about 100 m downstream of the study site. Daily mean temperatures from mid-March to September 1989–94 were used in this study.

Results

Annual variation in daily mean temperatures was greatest in summer (Fig. 1). The average of daily mean temperatures in July and August was lowest in 1993 (22.4 °C) and highest in 1994 (29.8 °C).

Annual variation in the emergence period was very minor from 1989 to 1992 although the peak shifted slightly from year to year (Fig. 2). Emergence occurred somewhat later in 1993 and much earlier

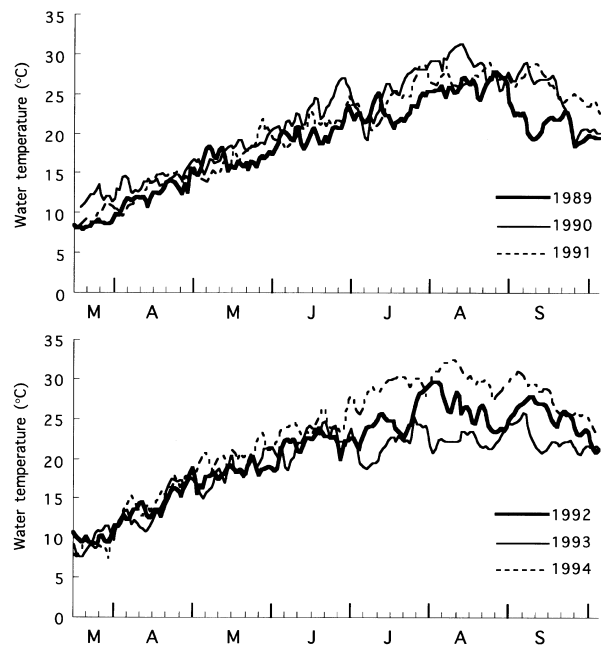


Fig. 1 Daily mean temperatures in the Asahi-gawa River, March–September.

than usual in 1994. Males generally emerged earlier than females ($P < 0.001$ for every year; Mann–Whitney U -test), except for 1989 and 1993. The proportion of males varied from 0.34 in 1992 to 0.76 in 1989.

The mean time of emergence, together with the dates at which 5% and 95% of emergence had occurred, and the length of the emergence period (5–95% emergence) from 1989 to 1994 are shown in Table 1. According to the sweep net samples (1989–92), the main emergence periods lasted about a week. The emergence period determined from the light trap was longer (1993 and 1994), probably because mayflies were attracted from a wider area.

Fig. 3 shows the relationship between cumulative degree-days (> 0 °C) in the nymphal stage and the mean emergence time. Temperature summation started on 25 March, because the mean date of egg hatching in the study area was estimated to be in late March (Watanabe & Ohkita, in press). The closing date was taken as 31 August. Mean emergence time was significantly related to cumulative degree-days in the nymphal stage ($P < 0.05$ for both sexes). The coefficients of determination (r^2) show that $\approx 80\%$ of the variation in the mean date of emergence can be accounted for by the cumulative degree-days from 25 March to 31 August.

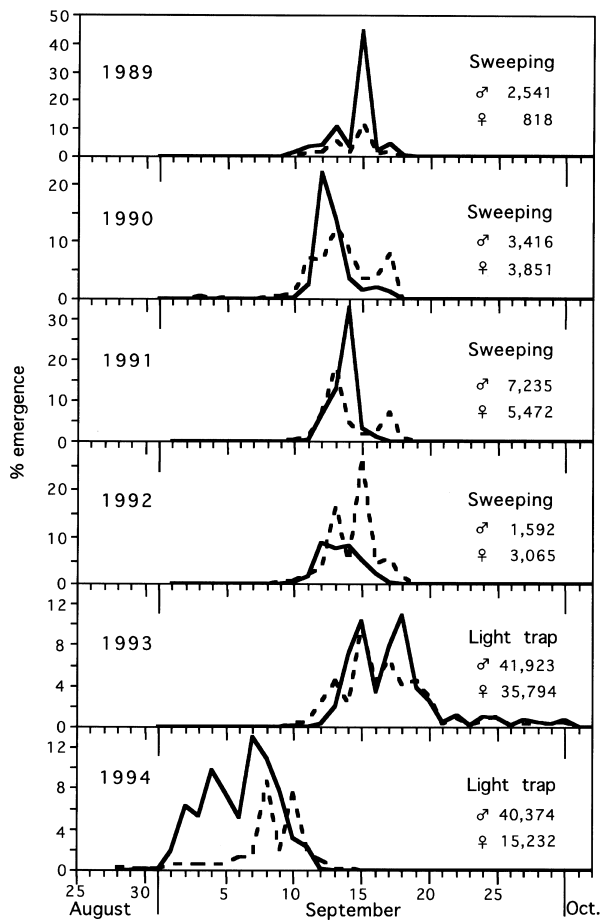


Fig. 2 Seasonal patterns of emergence of *E. shigae* 1989–94. Solid and broken lines indicate males and females, respectively. Numbers of males and females collected during the emergence periods are shown in the figure.

To examine the period when temperature most strongly affected the seasonal timing of emergence, the highest coefficient of determination was sought in

the regression of mean date of emergence on cumulative degree-days during various periods, using an approach resembling the 'maximum likelihood method' (Tokeshi, 1985). The starting point of summations was fixed, as before, at 25 March. The r^2 value in the regression of the mean date of emergence against cumulative degree-days from 25 March until a given day, from 1 April to 5 September, are shown in Fig. 4(a). The highest r^2 value was obtained for the summation from 25 March to 28 August for males and to 26 August for females. Next, the dates obtained above were fixed as the close of summations. The highest r^2 value was sought again in the regression of the mean date of emergence against cumulative degree-days from a given day to 28 August for males and to 26 August for females. The highest value was obtained for the summation from 28 June for males and 27 June for females (Fig. 4b). Therefore, the sum of daily temperatures during the periods from 28 June to 28 August for males and 27 June to 26 August for females best explains the observed seasonal timing of emergence. The regression equation and r^2 value for each sex for the respective period are indicated in Table 2. Ninety percent or more of the variation in the mean date of emergence can be accounted for by cumulative degree-days during the respective periods for both sexes.

The period when temperatures affected emergence timing most strongly was slightly different between the sexes. For the purposes of prediction, Fig. 5 indicates the regression of the mean date of emergence for both sexes combined together against the degree-days from 1 July to 31 August. Although the r^2 value is slightly lower than those in Table 2, almost 90% of the emergence timing was explained by degree-days.

Table 1 Timing of emergence and the length of emergence period (5–95% emergence). Mean emergence time is indicated by the date in September with time expressed by a decimal system taking 0–1 for a day

| Emergence | | Year | | | | | |
|-----------|-------------------------------------|-------|-------|-------|-------|-------|------|
| | | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 |
| Male | Mean emergence time in September | 14.39 | 12.79 | 13.63 | 13.38 | 17.35 | 6.07 |
| | 5–95% emergence (date in September) | 11–17 | 11–16 | 12–15 | 11–16 | 14–25 | 2–10 |
| | Emergence period (days) | 7 | 6 | 4 | 6 | 12 | 9 |
| Female | Mean emergence time in September | 14.26 | 13.48 | 13.91 | 14.32 | 16.78 | 8.18 |
| | 5–95% emergence (date in September) | 11–17 | 10–17 | 12–17 | 11–17 | 12–25 | 2–12 |
| | Emergence period (days) | 7 | 8 | 6 | 7 | 14 | 11 |

Discussion

Seasonal timing of the emergence of *E. shigae* was closely related to cumulative degree-days in the nymphal stage, especially during the period from late June to late August. This indicates that the thermal conditions in late instars most strongly affect emergence timing. Late August corresponds to the time when almost all nymphs have reached the final instar (Watanabe & Ohkita, in press). Britt (1962) also reported that the controlling factor in the emergence of *Ephemera simulans* Walker appeared to be the degree-days in spring just before emergence in May to June rather than the total degree-days to which the eggs and nymphs were exposed. Takemon (1990) proposed a model explaining the emergence timing and its synchronicity for *E. strigata* based on the effective degree-days in the last instar.

The mass emergence of *E. shigae* is not only a spectacular phenomenon attracting the attention of many people but is also often a nuisance to traffic. In the Abukuma-gawa River in the northern part of Honshu, for example, traffic control by police officers and the removal of accumulated mayflies on the road have been necessary during the emergence periods.

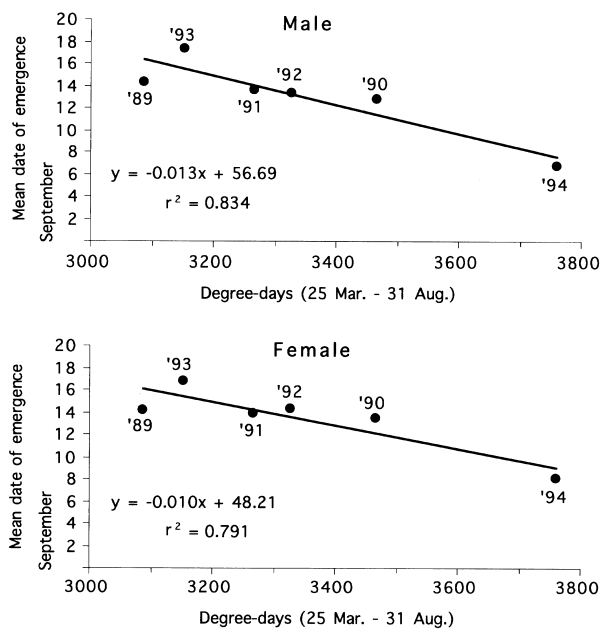


Fig. 3 Regressions of mean dates of emergence for both sexes of *E. shigae* against degree-days during the period from 25 March to 31 August.

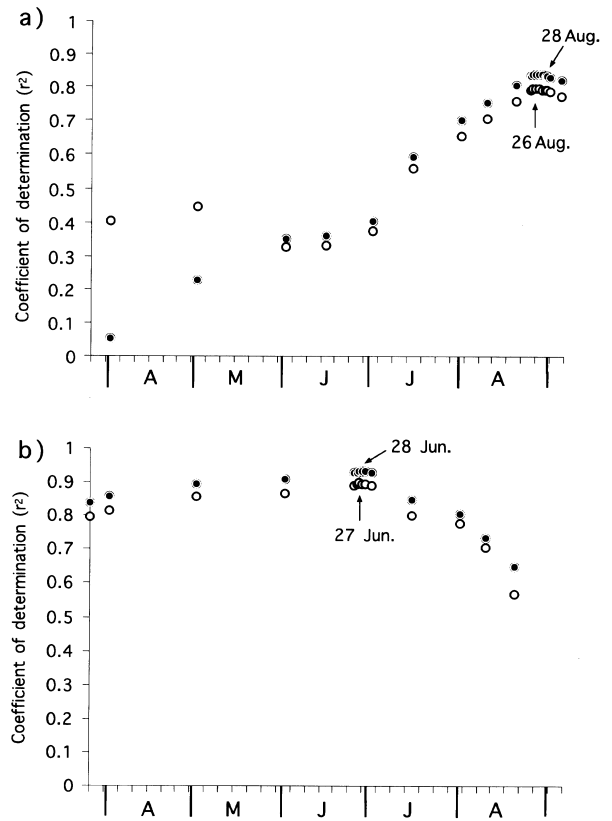


Fig. 4 (a) Coefficient of determination (r^2) in the regression of mean date of emergence of *E. shigae* against cumulative degree-days from 25 March to a given day from 1 April to 5 September (abscissa). (b) Coefficient of determination in the regression of mean date of emergence against cumulative degree-days from a given day (abscissa) to 28 August for males and to 26 August for females. Solid and open symbols are males and females, respectively.

Accurate prediction of their emergence period is therefore of practical importance.

The mean date of emergence of *E. shigae* can be practically estimated from water temperatures in July and August. The main emergence period will fall within a week of the mean date. The prediction of emergence timing of *E. shigae* may also be possible in other rivers after records of emergence have been kept

Table 2 Regression equation ($y = a + bx$) of the mean date of emergence against cumulative degree-days ($>0^\circ\text{C}$) during the period with the highest r^2 value for each sex

| Sex | Period | r^2 | a | b |
|--------|-------------------|-------|-------|--------|
| Male | 28 June–28 August | 0.934 | 48.19 | -0.022 |
| Female | 27 June–26 August | 0.899 | 41.59 | -0.018 |

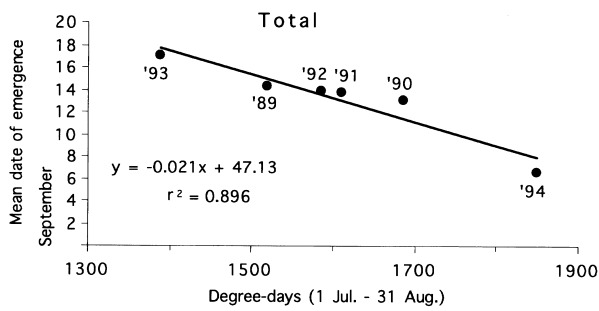


Fig. 5 Regressions of mean dates of emergence for both sexes of *E. shigae* against degree-days from 1 July to 31 August.

for some years. Temperature data recorded by the Ministry of Construction or local governments may be available since the mass emergence of *E. shigae* usually occurs in major rivers.

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References

- Andrewartha H.G. & Birch L.C. (1954) *The Distribution and Abundance of Animals*. The University of Chicago Press, Chicago.
- Ban R. & Kawai T. (1986) Comparison of the life cycles of two mayfly species between upper and lower parts of the same stream. *Aquatic Insects*, **8**, 207–215.
- Britt N.W. (1962) Biology of two species of Lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. *Bulletin of the Ohio Biological Survey*, **1**, 1–70.
- Lillehammer A., Brittain J.E., Saltveit S.J. & Nielsen P.S. (1989) Egg development, nymphal growth and life cycle strategies in Plecoptera. *Holarctic Ecology*, **12**, 173–186.

- Newbold J.D., Sweeney B.W. & Vannote R.L. (1994) A model for seasonal synchrony in stream mayflies. *Journal of the North American Benthological Society*, **13**, 3–18.
- Perry S.A., Perry W.B. & Stanford J.A. (1986) Effects of stream regulation on density, growth, and emergence of two mayflies (Ephemeroptera: Ephemerellidae) and a caddisfly (Trichoptera: Hydropsychidae) in two Rocky Mountain rivers (U.S.A.). *Canadian Journal of Zoology*, **64**, 656–666.
- Peters J.G., Peters W. & Fink T. (1987) Seasonal synchronization of emergence in *Dolania americana* (Ephemeroptera: Behningiidae). *Canadian Journal of Zoology*, **65**, 3177–3185.
- Takemon Y. (1990) Timing and synchronicity of the emergence of *Ephemera strigata*. *Mayflies and Stoneflies* (ed I.C. Campbell), pp. 61–70. Kluwer Academic Publishers, Dordrecht.
- Tokeshi M. (1985) Life-cycle and production of the burrowing mayfly, *Ephemera danica*: a new method for estimating degree-days required for growth. *Journal of Animal Ecology*, **54**, 919–930.
- Watanabe N.C., Hatta K., Hisaeda K., Hoshi K. & Ishiwata S. (1998) Seasonal and diurnal timing of emergence of *Ephoron shigae* (Ephemeroptera: Polymitarcyidae) from four Japanese rivers. *The Japanese Journal of Limnology*, **59**, 199–206.
- Watanabe N.C. & Ishiwata S. (1997) Geographic distribution of the mayfly, *Ephoron shigae* in Japan, with evidence of geographic parthenogenesis (Insecta: Ephemeroptera: Polymitarcyidae). *The Japanese Journal of Limnology*, **58**, 15–25.
- Watanabe N.C. & Ohkita A. Life cycle and synchronization of nymphal development of the mayfly *Ephoron shigae* in Japan (Ephemeroptera: Polymitarcyidae). *Aquatic Insects*, in press.
- Watanabe N.C., Yoshitaka I. & Mori I. (1989) Timing of emergence of males and females of *Ephoron shigae* (Ephemeroptera: Polymitarcyidae). *Freshwater Biology*, **21**, 473–476.
- Wright L.L., Mattice J.S. & Beauchamp J.J. (1982) Effect of temperature and sex on growth patterns in nymphs of the mayfly *Hexagenia bilineata* in the laboratory. *Freshwater Biology*, **12**, 535–545.

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