

TIMING AND SYNCHRONICITY OF THE EMERGENCE OF *EPHEMERA STRIGATA*

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ABSTRACT

Emergence and recruitment periods of the last instar nymphs of the burrowing mayfly *Ephemera strigata* were investigated by emergence trap sampling and quadrat sampling of a small Japanese stream in two seasons, from January to May 1982 and 1984. The developing zero (DZ) and the thermal constant (TC) of the last instar, estimated by a new method, were 8.8°C for males, 9.0°C for females and 151°C day for males, 154°C day for females, respectively. Simulation of the emergence curve based on a range of DZ revealed that the emergence timing delays and its synchronicity increased according to the ascent of DZ. A model of the emergence synchronicity for *E. strigata* was proposed. It was characterized by the necessity of the last instar stage to emerge, by the last instar recruitment period in which the synchronization of development is increased and by a supposition of the proportional relation of the development rate to effective degree-days. Seasonal size reduction of adults was explained by the seasonal difference of the development period and effective degree-days for growth experienced by nymphs.

INTRODUCTION

Many species of aquatic insects have short and synchronous emergence periods, especially spring-emerging species, high latitude inhabitants and parthenogenetic species (Macan 1958, Corbet 1964, Sweeney and Vannote 1982). Several models have been proposed as mechanisms of timing and synchronicity of these species (Ward and Stanford 1982, Butler 1984). Corbet (1957, 1964) attributed ascending temperature as influencing the spring emerging species of Odonata that overwinter in the last instar, and an ascending series of lower temperature thresholds for progressively later instars of summer species. Vannote (1978) and Vannote and Sweeney (1980) suggested single temperature thresholds for emer-

gence, and these have been empirically reported for chironomidae (Danks and Oliver 1972) and for several mayfly species (Humpesch 1971, Sweeney 1978, Sweeney and Vannote 1981). Although photoperiod interacting with temperature has also been considered to be a regulating factor for some species of Odonata and Ephemeroptera (e.g. see Sweeney 1984), thermal regulation can act alone in many species of Ephemeroptera based on examples of shifts in the emergence period corresponding to shifts in the thermal regime (Harper and Magnin 1971, Sweeney and Vannote 1981, Ward and Stanford 1982, Brittain 1982).

While the model of the temperature threshold for emergence (Sweeney and Vannote, 1981) seems to be reasonable theoretically and has some

empirical support, there have been no estimates of the threshold values for the timing and synchronicity of an emergence period. Britt (1962) found that the seasonal timing of the emergence of *Ephemera simulans* correlated more closely with degree-days in the spring than to the total degree-days, indicating that both a temperature threshold and sufficient degree-days are required for development before emergence. Thus the effective degree-days approach (Réamur 1735, cited in Allee *et al.* 1949) seems to be requisite to explain the emergence timing and synchronicity.

The present study was carried out on the mayfly *Ephemera strigata* Eaton which inhabits the middle reaches of Japanese streams (e.g. Kuwata 1955, Hisai and Arai 1973, Watanabe 1985). The species has a univoltine life cycle with synchronous emergence in spring (Gose 1970a). A new method is used to estimate the threshold temperature for emergence, defined as the developing zero (the minimum threshold temperature for development) in the last instar, and also to evaluate the thermal constant (effective degree-days required for development) in the last instar. Emergence curves obtained by the simulation against various values of the developing zero are analyzed in order to estimate the effects of the threshold temperature on the timing and syn-

chronicity of the emergence period. A model of the emergence synchronicity for *E. strigata* and its relationship to the seasonal reduction of adult size within an emergence period are also discussed.

METHODS

Study site

The study was conducted in the Kurama Stream (35°0'N, 130°0'E and elevation 150 m), a tributary of the River Kamo which runs through the city of Kyoto. The sampling site for nymphs was a pool of length 29 m, width 12 m, and a maximum depth of 85 cm. The flow velocity ranged between 0 and 58 cm sec⁻¹ at the bottom under normal flow conditions. Emergence traps for subimagines were established at an adjacent pool of length 20 m, width 9 m, and maximum depth of 65 cm, in which the flow velocity ranged between 0 and 22 cm sec⁻¹ under normal conditions. Water temperatures were recorded continuously through a year by an automatic thermograph and a remote sensor (Fig. 1). The average temperature at two hourly intervals was used for the calculations of thermal constant. The stream was described in detail by Takemon (1985).

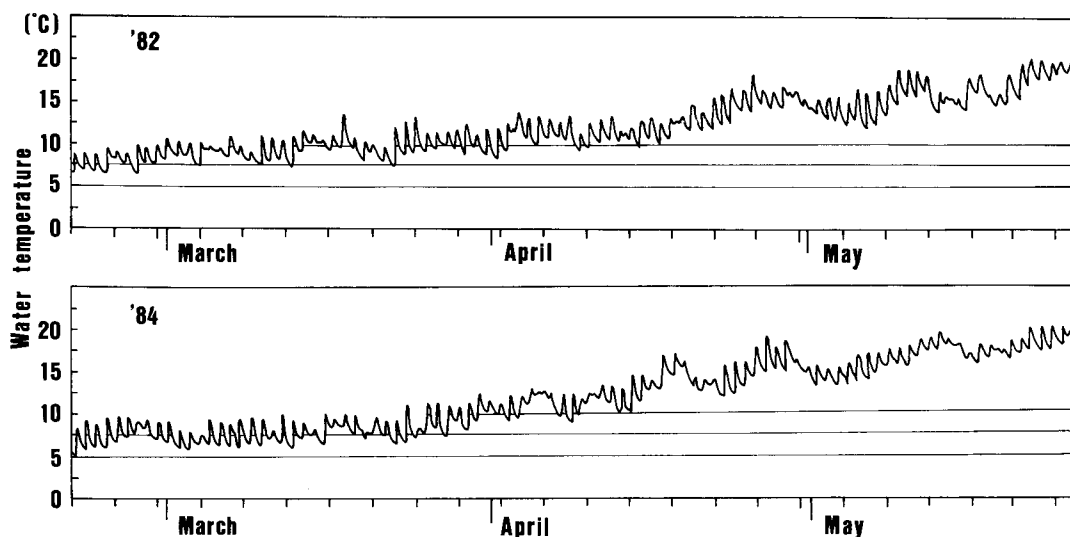


Fig. 1. Daily change of water temperature in spring seasons.

Sampling

Nymphs of *E. strigata* were collected at irregular intervals from 13 January to 21 April 1982, and from 25 January to 16 May 1984, using a box sampler which enclosed a sample area of 25 × 25 cm at silt and sand substrate areas in the lentic parts of the pool, and a Surber net of mesh size 0.47 mm and a sample area of 25 × 25 cm over sand and gravel substrate areas in the lotic parts of the pool. The sampling days and the number of quadrats taken are shown in Table 1. The quadrat site was chosen in order that all substrate types i.e. silt, sand, and sandy gravel were sampled on each sampling day. The samples were sorted live in the laboratory and preserved in alcohol. Measurements were made of head capsule length to the nearest 0.05 mm and of wing bud length to the nearest 0.01 mm. The last instar nymphs were distinguishable by a wing bud length of over 2.00 mm (Fig. 2). Nymphs exceeding 0.95 mm in head capsule length were sexed by the appearance of the genitalia on the ninth abdominal segment.

Emerged subimagines were collected daily from 1 April to 23 May 1982, using seven floating-type emergence traps, each of which enclosed a water surface area of 50 × 60 cm, and from 20 April to

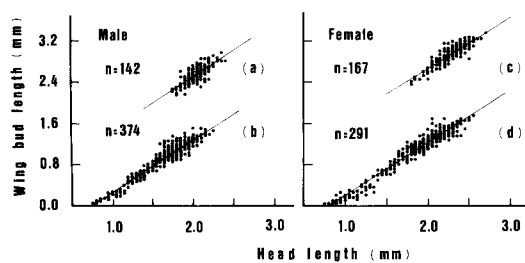


Fig. 2. Relationship between head length (HL) and wing bud length (WBL) of the nymphs collected through the study period. Clusters (a) and (c) are identical with the last instar. Regression equations are: (a) $WBL = 1.017HL + 0.464$, $r = 0.806$, $P < 0.005$ (T-test); (b) $WBL = 1.019HL - 0.765$, $r = 0.969$, $P < 0.005$; (c) $WBL = 1.018HL + 0.618$, $r = 0.902$, $P < 0.005$; (d) $WBL = 1.034HL - 0.853$, $r = 0.988$, $P < 0.005$. Gradient parameters were not different significantly among regressions ($P > 0.05$).

16 June 1984, using eleven traps of the same type. As the peak of the emergence of *E. strigata* occurs in the late afternoon (Takemon 1985), sampling was carried out early the next morning. In 1982, measurements of fresh weight to the nearest 0.1 mg and of fore-wing length to the nearest 0.1 mm were made on the day of sampling.

Estimates of the developing zero and the thermal constant of the last instar nymphs

The recruitment period of the last instar nymphs was determined by the increased percentage of the last instar during a sampling interval. Nymphs recruiting early or late in the period were assumed to emerge early or late, respectively. The date of early or late recruitment and emergence were represented by the date one standard deviation prior to or after the mean date of recruitment and emergence, respectively, and the duration of the last instar of each nymph type was then defined from the date of each recruitment to that of emergence. Both nymph types were also assumed to have the same value of the developing zero (DZ) and of the thermal constant (TC). Total effective degree-hours were calculated separately for each nymph type by summing the effective degree-hours at two hour intervals using each assumed value of DZ, which was set at 0.5°C intervals between 5°C and 14.5°C. Under a thermal regime that is ascending gradually, if an assumed DZ is too low, the early recruit would experience more effective degree-hours than the late recruit, and vice versa if an assumed DZ is too high. Therefore, the relationship curve between DZ and the total effective degree-hours for the early recruit should cross with the curve for the late recruit. The values of the co-ordinates at the crossing point were assumed to be the true DZ and TC. To determine the crossing point, each curve was assumed to be a straight line between the two plots nearest the crossing point. Separate analyses were carried out for each sex.

Simulation of emergence curves

For the simulation of emergence curves, the normal distribution curve of the same mean date and

Table 1. Number of nymphs in each stage of *Ephemera strigata* obtained by quadrat sampling before emerging seasons. wb: wing bud length (mm). The values of (%) are percentages of the last instar nymphs within nymphs which wb > 1.0 mm

Date	Number of Quadrats	MALE			FEMALE			SEX UNIDENTIFIED		TOTAL	
		wb < 1.0	1.0 ≤ wb < 2.0	2.0 ≤ wb (%)	Total	wb < 1.0	1.0 ≤ wb < 2.0	2.0 ≤ wb (%)	Total		wb < 0.05
1982 Jan 13	5	19	16	0 (0.00)	35	31	17	0 (0.00)	48	7	90
Feb 18	6	19	29	0 (0.00)	48	27	23	0 (0.00)	50	4	102
Feb 19	5	21	20	0 (0.00)	41	20	14	0 (0.00)	34	10	85
Feb 21	12	71	104	1 (0.95)	176	52	79	0 (0.00)	131	19	326
Mar 4	6	2	44	6 (12.00)	52	8	46	10 (17.86)	64	5	121
Mar 17	5	0	15	32 (38.46)	47	5	36	15 (29.41)	56	1	104
Mar 21	6	2	7	27 (79.41)	36	4	15	18 (54.54)	37	4	77
Apr 2	4	0	1	20 (95.24)	21	0	2	20 (90.91)	22	3	46
Apr 17	4	0	1	25 (96.15)	26	0	1	21 (95.45)	22	5	53
Apr 21	5	1	2	31 (93.94)	34	2	2	28 (95.23)	32	5	71
Total	68				516				496	63	1075
1984 Jan 25	10	32	108	0 (0.00)	140	38	86	0 (0.00)	124	14	278
Mar 9	8	21	28	0 (0.00)	49	29	25	0 (0.00)	54	19	122
Mar 25	10	6	57	2 (3.39)	67	14	52	0 (0.00)	66	11	144
Apr 2	5	3	16	14 (46.67)	33	5	22	9 (29.01)	36	2	71
Apr 14	5	4	10	34 (77.27)	48	3	16	34 (68.00)	53	4	105
Apr 20	4	0	0	26 (100.00)	26	0	4	13 (76.47)	17	4	47
Apr 24	4	1	0	31 (100.00)	31	1	4	32 (88.89)	37	2	70
Apr 27	4	0	1	22 (95.25)	23	0	0	28 (100.00)	28	6	57
May 2	5	0	0	29 (100.00)	29	0	1	25 (96.15)	26	5	60
May 11	5	1	0	9 (100.00)	10	0	1	18 (94.74)	19	4	33
May 16	6	1	0	1 (100.00)	2	1	0	4 (100.00)	5	9	16
Total	66				458				465	80	1003

standard deviation as the last instar recruitment was used as the initial date value of the last instar stage. The effective degree-hours based on the estimated DZ were summed at two hourly intervals from each initial day until the accumulated value became equal to the estimated TC. As the greater part of the emergence of *E. strigata* occurs in the late afternoon before 19:00 (Takemon, 1985), when the simulated point of the emergence fell after 19:00 the date of emergence was assumed to be the next day. This calculation was repeated for each initial date of the last instar stage, and the daily emergence curve was obtained.

This simulation was also repeated for a range of given values for DZ, at 1°C intervals between 5°C and 14°C. The relations of the value of DZ to the timing and synchronicity of the emergence period were then analysed.

RESULTS AND DISCUSSION

The last instar recruitment and emergence period

Seasonal changes of the nymphal stage composition of *E. strigata* showed that the last instar appeared in March and its relative proportion increased by April (Table 1). However, tiny individuals less than 0.05 mm in wing bud length were always found, even in April and May. The fact that nymphs around 1.00 mm in wing bud length disappeared abruptly at the beginning of the last instar recruitment suggested that nymphs which had grown over 1.00 mm in wing bud length would develop into the last instar, whereas nymphs which had not attained this size would not.

On average the last instar recruitment in 1984 was later (male: 19 days, female: 22 days later) and over a shorter period than in 1982 (Fig. 3). The delay may have been due to the unusual coldness in the winter of 1984 (Fig. 1). Snowdrift remained until early April in 1984, though it usually disappears by mid-March. However, the timing of emergence was not so delayed, and the emergence peak showed only 8 days difference between the years in both sexes. Therefore the last

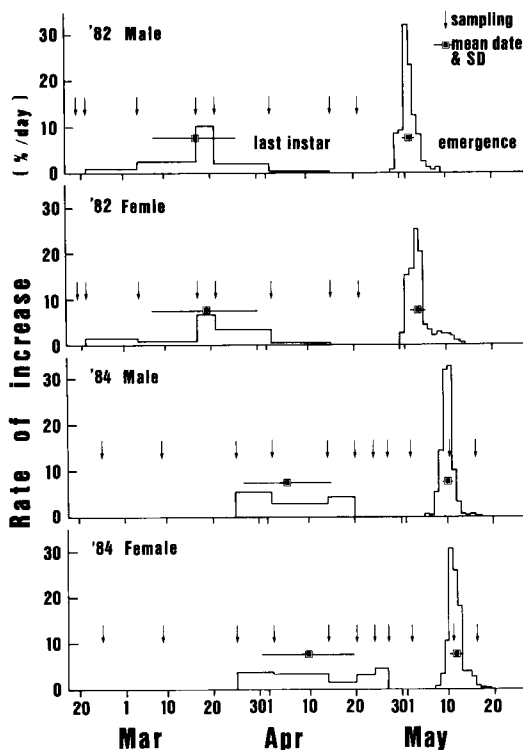


Fig. 3. Rate of increase per day of the last instar recruitment and of the subimaginal emergence.

instar period in 1984 (male: 35 days, female: 33 days on average) was shorter than in 1982 (both sexes: 46 days on average). The shortness of the last instar period in 1984 seems to have been affected by the high water temperature in April 1984, indicating the requirement of cumulative degree-days for development.

Synchronicity of the emergence period was much higher than that of the last instar recruitment in both years (Fig. 3). At the peak of the emergence curve, about 30% of the whole daily emergence was observed for each sex. The mean date of emergence of males calculated from the emergence curve preceded that of females by two days in both years. The mode of the emergence curve was located early in the emergence period.

A size reduction in subimagines through the emergence period was observed (Fig. 4a), as also known for other species of mayflies (Gledhill 1959, Sweeney 1978, Clifford *et al.* 1979, Sweeney and Vannote 1981). The fresh body

weight of subimagines in the last period was about half that in the initial period, a similar size reduction to that found for *Ephemerella subvaria* by Sweeney and Vannote (1981). The mean size of the last instar nymphs also decreased seasonally (Fig. 4b). In the latter case, as the mean values included the size of individuals which recruited before the sampling date, size reduction through the recruitment period must have occurred more

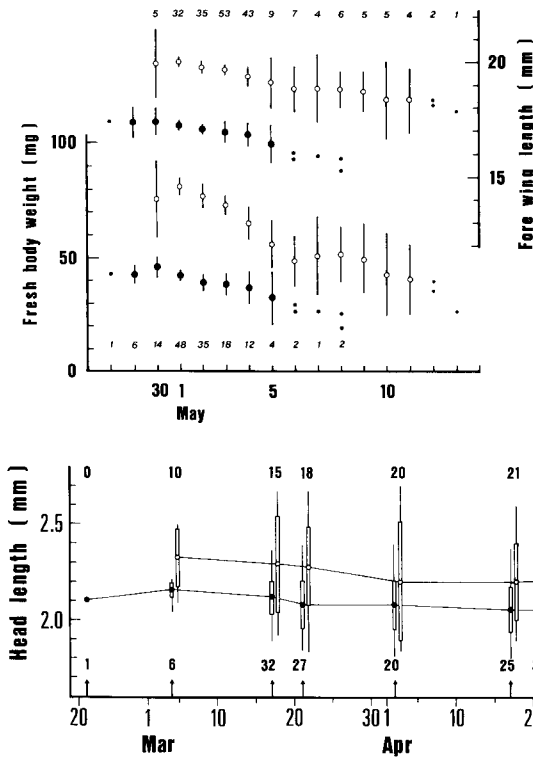


Fig. 4. Seasonal size reduction in the subimagines of fore wing length and fresh body weight (a) and in the last instar nymphs of head length (b). (a): Open and closed circles indicate the means values of females and males, respectively. Each vertical line shows the standard deviation. Top and bottom numbers are sample sizes of females and males, respectively. Significant differences ($P < 0.005$, T-test by Cochran-Cox Method) are detected both in forewing length and fresh body weight between females between 1st and 11th May and males between 30th April and 5th May. (b): Circle symbols and numbers are same as of (a). Vertical lines and open boxes show the range and the standard deviation, respectively. Significant differences are detected for females ($0.01 < P < 0.05$) and for males ($0.005 < P < 0.01$) between 4th March and 21st April.

distinctly. Together, these facts indicate that the early or late recruits emerged early or late, respectively, unless the late recruits showed a higher growth rate than the early ones.

Estimates of developing zero and thermal constant

The relationship between given values of developing zero (DZ) and calculated values of the total effective degree-days for the early and late recruits is shown in Fig. 5. The estimated values of true developing zero (DZ) and thermal constant (TC) determined by the coordinates of the intersections are also shown in Fig. 5. The average values of two years were as follows: DZ = 8.8°C for males and 9.0°C for females; TC = 3624°C hr (151°C.day) for males and 3706°C hr (154°C day) for females. The estimated value of DZ in the last instar seems to be higher than DZ in previous instars, judging from the fact that, in both years, the last instar recruitment occurred even though water temperatures barely exceeded 9°C before start of the recruitment.

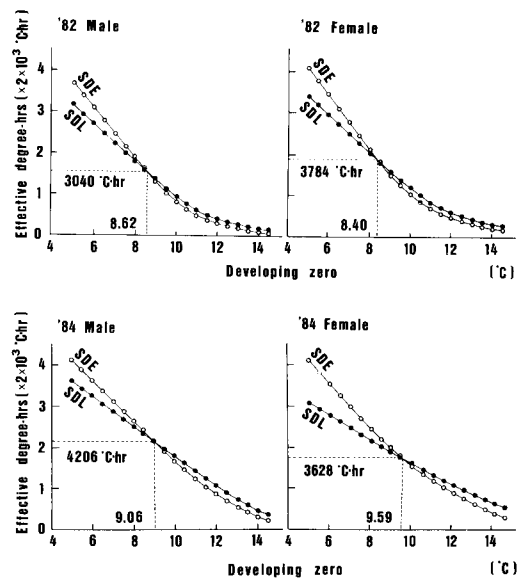


Fig. 5. Relationship between given DZ and the effective degree-hours required for emergence for the early recruit (SDE) and for the late recruit (SDL). True DZ and TC determined by the crossing points are shown in figures. See the text for further explanation.

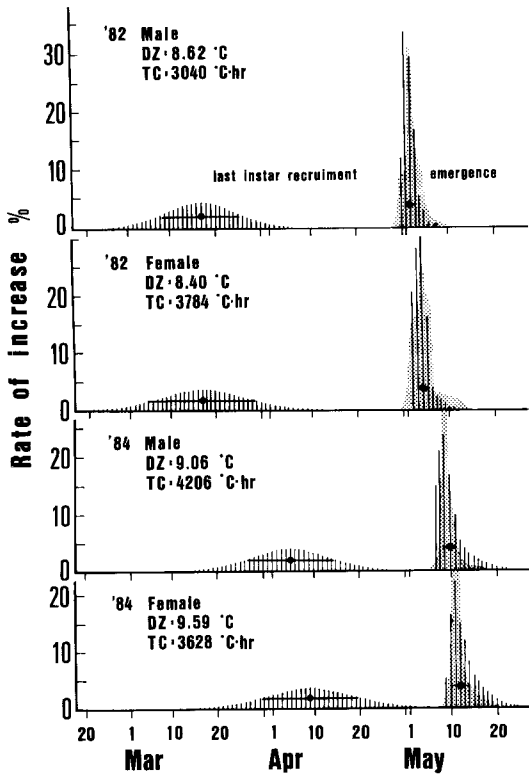


Fig. 6. Simulation of the emergence curves based on the estimated DZ and TC. The normal distribution curve which has the same standard deviations the field sample (shown as horizontal line) is used for the last instar initiation. Shaded curves show the emergence obtained by emergence traps.

Simulation of emergence curves

Simulated emergence curves (Fig. 6) revealed that the distribution of the last instar recruitment spreading over 50 days would synchronize within a maximum of 16 days at the emergence. The shapes of the simulated curves were the same as the field pattern, i.e., the mode of the emergence was located early in the emergence period and the delayed emergence decreased in sequence. The mechanisms of the synchronization and the cause of this shape can be explained as follows. During periods of water temperatures lower than DZ during the last instar recruitment period, the earlier recruits must have delayed development. In fact, these water temperatures occurred before mid-March in 1982 and before late March in 1984

(Fig. 1). As those periods corresponded to the earlier parts of the last instar recruitment period, the synchronization of development arose in the populations, especially in the early recruits. The agreement of the simulation with the field emergence in reference to the timing and synchronicity, even though rough, indicates that the mechanisms mentioned above may also function in the field.

The emergence curves simulated on various values of DZ for the males of 1982 are illustrated in Fig. 7. The emergence was later and synchronicity greater with an increase of DZ. The relationship between the standard deviation of each emergence curve and DZ showed that the synchronicity increased abruptly when DZ exceeded the temperatures at the beginning of the last instar recruitment (Fig. 7). If temperature is lower than DZ the early recruits must postpone development until the temperature exceeds DZ, resulting in the synchronization of development with later recruits.

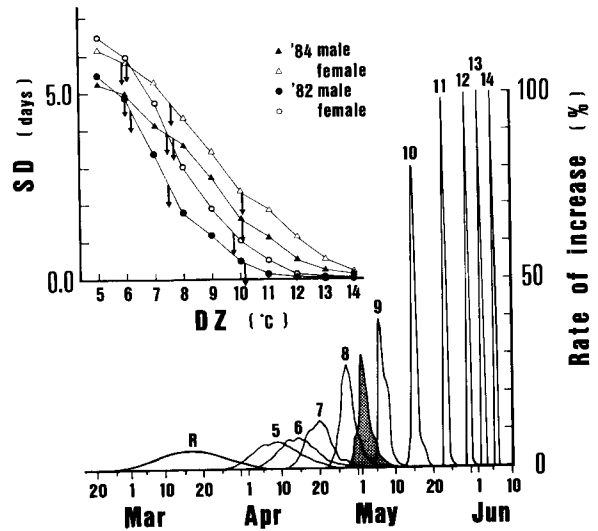


Fig. 7. Emergence curves for males in 1982 simulated by the range of values for DZ (lower graph) and relationship between given values of DZ and the standard deviations of the simulated emergence curves (upper graph). The character R and a number on the top of each emergence curve show the assumed recruitment rate of the last instar and the given values of DZ, respectively. The shaded curve corresponds to the field emergence. Arrows on the lines of the upper graph indicate the max., mean and min. water temperature in the initial week of the last instar recruitment periods for each sex and year.

A model of the emergence synchronicity for *E. strigata*

The distinctiveness of the last instar nymphs with long wing buds (Fig. 2), developed eyes, and lengthened forceps, indicates that the last instar is an indispensable stage to mature the subimaginal tissues. Seasonal timing and synchronicity of the last instar recruitment also affected those of emergence, though the influence of these factors was reduced by the high value of DZ in the last instar. Delay and contraction of the last instar recruitment found under the low temperature conditions in 1984 suggested that there is a different DZ for nymphs in a previous instar to develop the last instar tissues (DZL), and that this value may be lower than DZ for the last instar (DZE). As the relationship between head length and wing bud length was inseparable in the previous instar stages, and as the size ranges of head length of the last and previous instars greatly overlapped (Fig. 2), nymphs seem to have a possibility to develop into the last instar regardless of their size once they reach over 1.00 mm in wing bud length, which corresponds to the minimum head length of the last instar nymph. This is also supported by the results of seasonal change of the nymphal stages already mentioned.

Mechanisms determining timing and synchronicity of emergence of *E. strigata* may be described by two steps: (1) recruitment of the last instar promoted by the temperature exceeding DZL for previous instars; (2) development of subimaginal tissues promoted by the temperature exceeding DZE for the last instar. These steps function to synchronize stages under the conditions of an ascending thermal regime. Although this model agrees with Sweeney and Vannote (1978, 1981) with respect to the existence of a threshold temperature for initiating the development of adult tissues, it differs in three respects: (1) nymphs should pass through the last instar stage to emerge; thus, (2) the initiation of the development is not on, nor near the same date; (3) Sweeney and Vannote regarded the threshold temperature as a switch for the metabolism or production of one or more endocrine compounds and for subse-

quent initiation of adult tissue synthesis, whereas here, the threshold temperature is regarded not only as a switch but also as the DZ by which a period of development is predicted through the effective degree-days summation. However, note that this model is a hypothetical one supposing the proportional relation of the development rate of tissues to effective degree-days.

According to Britt (1962) the seasonal timing of the emergence of *Ephemera simulans* was controlled by the degree-days in the spring rather than the total degree-days to which the eggs and nymphs were exposed. He compared annual degree-days and the emergence timing and found that there was a higher correlation between the emergence timing and the degree-days in the spring. Although he did not assume the threshold temperature for development, his data seem to support the assumption that the development rate before emergence is proportionally related to effective degree-days, and also support the result that the DZ in the last instar was higher than that in previous stages.

Influence of developing zero and growing zero on size

Growing zero (GZ), the minimum threshold temperature for growth, has been investigated for a few species of Ephemeroptera (e.g. Britt 1962, Wright *et al.* 1982, Tokeshi 1985) and for several species of aquatic Diptera (e.g. Becker 1973, Ross and Merritt 1978) and Trichoptera (e.g. Gose, 1970b). Most works using this approach used the value of GZ for estimating the thermal constant (summation of effective day-degrees) required for a whole life cycle in order to interpret the voltinism of a species. In the case of the genus *Ephemera*, Tokeshi (1985) estimated GZ for *E. danica* to be 2.6°C for males and 3.1°C for females. Although no similar work has been done on *E. strigata*, judging from the nymphal stage progress in winter (Table 1), GZ seems to be much lower than DZE. This difference between the two values is expected to affect the size of nymphs, because intermediate temperatures between them will commence growth but not development. Therefore, when the

last instar recruitment starts at temperature conditions in this range and ends at a higher temperature than DZE, the growing period of earlier recruits becomes longer than that of later ones within the last instar stage. Thus the size variation of the last instar nymphs increases during the recruitment period.

The same processes are supposed to act on the size variations at the initiation of the last instar. If nymphs in previous instars are able to enter the last instar stage provided that they clear the lower size limitation, greater variations will be produced in this period, as recruits result in a mixture of nymphs with a range of size, and even of instars.

The seasonal size reduction found in both subimagines and the last instar nymphs (Fig. 4) seems attributable to two factors: (1) earlier recruits of the last instar experience more effective degree-days for growth than do later ones due to their emergence in ascending thermal conditions; and (2) the later recruits have experienced fewer effective degree-days for growth in the previous instars after clearing the lower size limitation. The presence of small sized nymphs throughout the study period (Table 1) indicates that factors other than thermal conditions affect nymphal growth and development. Therefore, the size variation in itself may derive from factors such as food supply (Sweeney 1984) or the size of original eggs, like the aquatic fire fly, *Luciola cruciata* (Yuma 1986). Consequently, the phenomenon of seasonal size reduction is supposed to originate from size variations produced by several life history factors, and to be attributable to the difference of DZ and GZ in conditions of ascending temperature, which accelerates the size variation and causes the seasonal size reduction in a regular manner.

Sweeney and Vannote (1981) attributed the seasonal size reduction to the nymphal size dependency on the rate and degree of adult tissue synthesis. They also reported a clear cline among six species of *Ephemerella*, where the magnitude of seasonal size reduction of adult females was the highest in the spring species, the lowest in the summer species, and intermediate among species that emerge in May and June. However, there has never been sufficient explanation for the

differences of the degree of size reduction in reference to the seasonal timing of emergence. According to the hypothesis for *E. strigata* proposed here, ascending thermal conditions will produce a wider difference of effective degree-days between early and late recruits, because the developmental period decreases for the latter. In contrast, as the summer thermal condition changes gradually, the developmental period is nearly the same, regardless of the recruitment timing, resulting in less difference between the early and late recruits. These differences in the thermal conditions may also affect the degree of seasonal size reduction among emergence seasons in other species.

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