EMERGING BEHAVIOUR OF *EPHEMERA STRIGATA* AND *E. JAPONICA* (EPHEMEROPTERA: EPHEMERIDAE)[1]

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SYNOPSIS

TAKEMON, Yasuhiro (Dept. Zool., Fac. Sci., Kyoto Univ., Kyoto). 1985. Emerging behaviour of *Ephemera strigata* and *E. japonica* (Ephemeroptera: Ephemeridae). *Physiol. Ecol. Japan*, 22:17-36.

The emerging behaviour of subimagines of two ephemeran mayflies is described. Subimagines of the spring-emerging species *E. strigata*, an inhabitant of the middle reaches of streams, emerged on the water surface during the late afternoon, whereas those of the summer-emerging species *E. japonica*, an inhabitant of the upper reaches of streams, emerged on partially submerged objects after crawling out of the water during the night time. These results showed that the emerging behaviour may vary between congeneric species whose nymphs have the same life form. Comparisons of the emerging behaviour with the stream type habitat of each species showed that the water surface emergence occurred in Kani's(1944) Bb stream type and that the crawling out emergence in his Aa stream type. These relationships are supposed to be a consequence of the adaptation of emerging subimagines to the stream topography and seemed to be generally applicable not only to the species of burrowing mayflies but also to the perching and swimming mayflies.

INTRODUCTION

The subimagines of mayflies show a great variety of emerging behaviours (Kimmins, 1972), a trend not seen in other orders of aquatic insects: e.g., dragonflies, stoneflies and caddisflies (Ward & Whipple, 1918; Pennak, 1953; Corbet, 1962; Hynes, 1970; Wiggins, 1977). Considering the vulnerability of the emerging stage of mayflies, this stage is crucial for their survival.

Imanishi (1938) divided the emerging behaviour of mayflies into three types and related them to the nymphal life form as follows: emergence on the water surface to the burrowing life form such as *Ephemera* and *Potamanthus*, emergence after crawling out of water to the perching and swimming life form such as *Ameletus*, and emergence under water to the gliding (on the surface of stones and rocks) life form such as *Epeorus* and *Ecdyonurus*. He insisted that the emerging behaviour is not variable among species within the same nymphal life form. However, little reliable information on the emerging behaviour of mayflies has existed until now.

Three species of the genus *Epehmera*, *E. strigata*, *E. japonica* and *E. orientalis*, have been recorded from the main island of Japan (Gose, 1981) and the nymphs of these species are all known to have a burrowing life form in the sandy or muddy bottom of rivers (Imanishi, 1940; Kuwata, 1955, 1958; Mizuno &

Table 1. Comparison of the stream features of the three stations. Stream types were determined according to Kani (1944, 1981).

	Jadani-bashi	Kibune-guchi	Ichihara
Elevation (m)	230	190	150
Stream type	Aa-Bb	Bb	Bb
Stream width (m)	4-7	5-11	5-13
Length of pool (m)	4-10	7-18	9-29
Max. depth of pool (cm)	60	65	85
Length of rapid (m)	4-14	8-32	12-56
Mean gradient of the stream (%)	6.0	3.4	1.8
Artificial modification of the stream	small rock dams	small rock dams	none

Gose, 1972; Hisai & Arai, 1973, 1974). The emerging behaviour of only *E. strigata* has been documented as the water surface type (Imanishi, 1938; Kani, 1940). The emerging behaviour of European and American species of this genus has also been described as the water surface type (Harris, 1956; Britt, 1962).

In 1981, during the sampling of emerging stream insects with emergence traps at the study area, I observed a mature nymph of *E. japonica* which was slowly climbing up the wall of the trap from the water's edge. Several minutes later it moulted the nymphal skin on the wall in a leisurely manner. I was suspicious about this behaviour since it was inconsistent with the opinion of Imanishi (1938).

In this paper, the emerging behaviour, the diel pattern of emergence and the emerging site will be compared between *E. strigata* and *E. japonica*. The relationship among the emerging behaviour, the stream types of the respective habitats and nymphal life forms will also be discussed.

DESCRIPTION OF STREAM AND STATIONS

The Kibune Stream (35°0'N, 130°0'E) runs off a low mountain (elevation 750m) in the north of Kyoto City. It joins the Kurama Stream at Kibune-guchi (elevation 190m) and forms one of the branches of the Kamo River which runs through the city area (elevation 55m). Two main stations, Jadani-bashi and Ichihara, and a supplement station, Kibune-guchi, were situated along these two streams (Fig.1(a)). The general features of these streams have been previously described (Kani, 1944, 1952; Tanida, 1980).

Topographical characters of these 3 stations are shown in Table 1 and the arrangement of rapids and pools in Ichihara and Jadani-bashi is shown in Figs.2 and 3 respectively. The stream topography in these two stations showed a marked
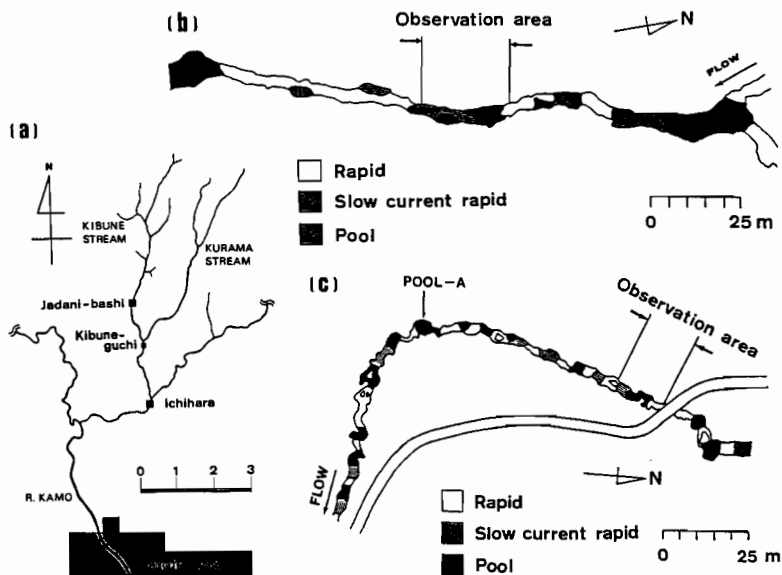
Fig. 1. Map of the study area. (a):The location of the main stations, Jadani-bashi and Ichihara (black square) and the supplementary station Kibune-guchi (small black square). (b):The arrangement of rapids and pools at Ichihara. The slow current rapid means the transitional parts from pool to rapid, which has slower current than rapids and shallower depth than pools. The observation area (25m long) is shown by arrows. (c):The arrangement of rapids and pools at Jadani-bashi. The observation area (15m long) is shown by arrows. At pool A, the emergence trap survey was carried out.

difference in the length of rapid and pool: i.e. Ichihara had much longer rapids and pools than Jadani-bashi. As the gradient in Jadani-bashi was steeper, there were several rapids and pools in one reach (the stretch of water between bends in a stream), whereas in Ichihara, as the stream gradient was so gentle there were no pools between meanders, resulting in a single set of rapid and pool in one reach. The rapid configuration also differed between these two stations. Although the rapid in Jadani-bashi sometimes formed a small waterfall, that in Ichihara had no waterfalls but had a wavy flow sometimes partially with a foaming one. Therefore, Jadani-bashi belonged to an Aa-Bb stream type, and Kibune-guchi and Ichihara to a Bb stream type, according to Kani (1944, 1981).

The riverside vegetation at the stations was mainly artificial forest of Japanese cedar, *Cryptomeria japonica*, with secondary deciduous trees. The natural canopies frequently covered the stream around Jadani-bashi, but were not so thick near Ichihara which was surrounded by houses.

METHODS

The data of the emerging behaviour, the diel pattern and the emerging sites were taken by direct observation at the stations. Information of the latter two aspects were also obtained from emergence traps (Takemon, unpublished).

An observation area for each species was established at Ichihara and Jadani-
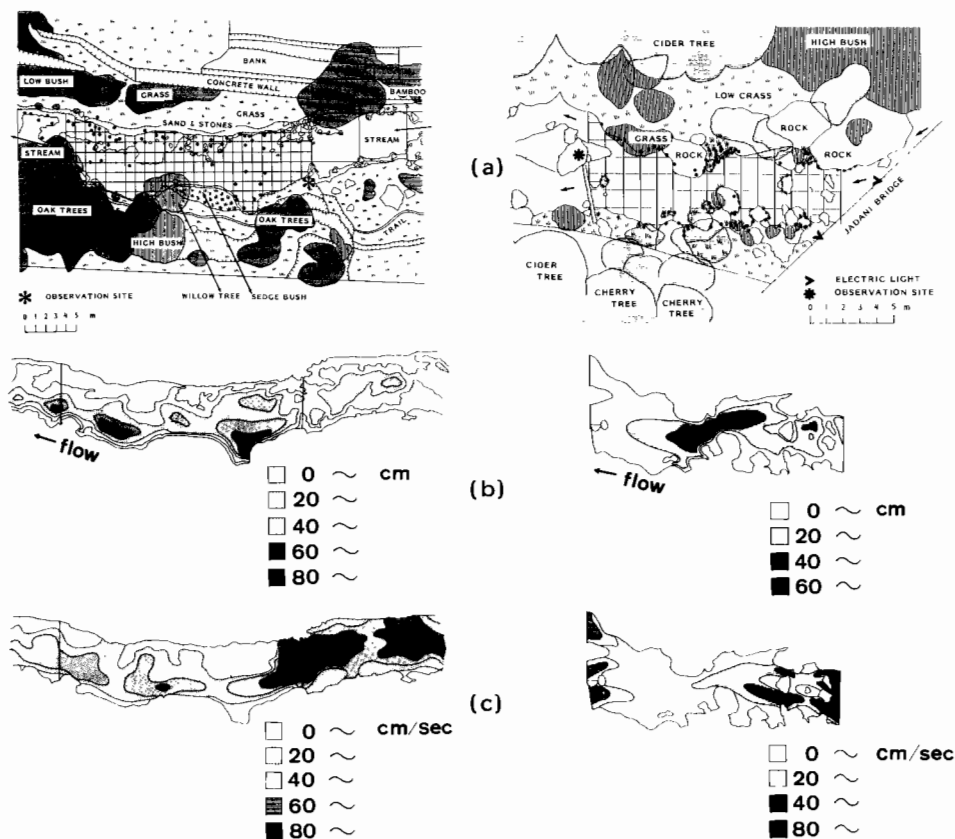
Fig. 2. Map (a), water depth (b) and current velocity of water surface (c) of observation areas at Ichihara (left) and Jadani-bashi (right). The map was made on 18th and 21th April, 1983 at Ichihara and on 9th and 10th June at Jadani-bashi. The solid circles show 59 emerging sites observed on 29th April.

bashi.　Each area was selected so as to consist of a whole pool and a part of a rapid (Fig. 1(b) and (c)).　Observation sites were situated near the dhore from where most of the water surface in the study area was visible (Fig. 2).　The length of the observation area was 25m at Ichihara and 15m at Jadani-bashi.　In order to plot the emerging sites on a map, the grid crossings were marked with stalks, projecting stones and painted or taped branches of shrubs and trees.　The water depth and current velocity of the water surface were also measured at 1m x 1m latticed intersections in each observation area (Fig.2).

The emergence of *E. strigata* was observed daily at Ichihara from 24th April to 26th May, 1983.　Although the daily duration of observation time was varied, the late afternoon period between 14:00 to 18:30, was always surveyed as most of the emergence occurred at this time.　Subimagines emerging in the study area were counted and observed by naked eye or by ×9 power binocular.　The emerging time, site and flight path of the subimago were recorded individually on the map copies

which were renewed at intervals of several minutes.

More detailed observation on the emerging behaviour of *E. strigata* were also made at Kibune-guchi on 5th May, 1981. At this station, 35 mature nymphs, which had black wing-buds and had a complete subimaginal body inside the nymphal skin, were collected with hand net between 15:00 and 15:30 and released in a temporary pool beside the stream at 15:40. Seventeen subimagines emerged between 15:40 and 17:30. In this experiment, 12 emergences were observed fully from nymph to subimago.

The emergence of *E. japonica* was observed at Jadani-bashi during the nights of 11th, 14th, 23rd and 25th June, 9th, 13th and 28th July and 25th and 27th August, 1983. Each daily observation time was 7-8 hrs: more than two hours after sunset, in the mid-night and before sunrise respectively. During the night time, the study area was illuminated by two electric lights (300W × 2) powered by generators, positioned as shown in Fig.5. Luminosity on the water surface in the centre of the area was about 10-20 lux at the moonless midnight. Although subimagines emerging near the lights sometimes flew to them, the emerging behaviour in itself did not seem to be affected. The emerging time, site and flight path of each individual was recorded as soon as possible in the same way as for *E. strigata*. When the emerging site was overlooked because of visual obstruction, the flying path of the subimago was recorded from the point at which it was first observed. Afterwards, the nymphal exuviae were collected along the water margin of the observation area. The emerging sites of overlooked individuals were determined from both the site of the exuvium in behind any obstruction and the flight path record.

More detailed observations were made at the night of 25th June, 1983. Swimming and climbing nymphs were individually observed from 21:45 to 22:45 and from 2:00 to 3:00. Eleven cases of the emergence were observed fully and the duration of each behavioural process was monitored by stop watch.

The climbing-up distance of emerging nymphs of *E. strigata* was also recorded at Jadani-bashi daily in June and July, 1981. The moulting site was determined by the presence of the thorax of exuvium left after emergence on the emergence traps (Takemon, unpublished) which were established on the water surface in pool-A (Fig.3). In this paper no further data obtained by the emergence traps are given.

Water temperature at each main station was recorded by thermograph and remote sensor. This measurement was carried out from 26th April to 20th June, 1983 at Ichihara and from 9th June to 10th September, 1983 at Jadani-bashi. Air temperature was recorded daily at Ichihara and at a few days interval at Jadani-bashi through each emerging season by a maximum and minimum thermometre concealed at the stream bank. During observations, air temperature was recorded at 30 minute intervals. The weather and temperature conditions during the emergence census at each station is shown in Fig.3.

RESULTS

Behavioural Process of Emergence

The behavioural processes of the emergence of *Epehmera* mayflies may be divided into three stages : I) The behaviour of the fully mature nymphs which leave their nymphal habitats for the emerging sites, II) The moulting behaviour to the subimagines and III) The behaviour of the subimagines until they complete their emerging flight to the resting sites. The characteristics of the species
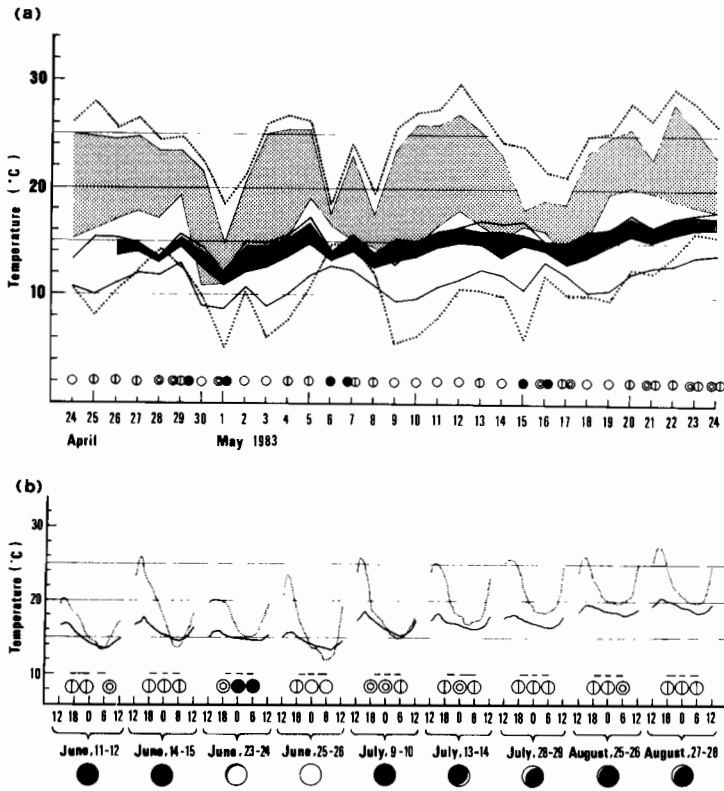
Fig. 3. Weather and temperature conditions at Ichihara (a) and those at Jadani-bashi (b). (a) Upper and lower dotted line is the daily max. and min. air temperature respectively. Shaded zone with dots shows the air temperature between 15:00 and 19:00. Upper and lower solid line is the daily max. and min. water temperatur respectively. Shaded zone with vertical lines shows the water temperature between 15:00 and 19:00. (b) Dotted and solid line represents the air and the water temperature respectively. The three circles in each day show the weather conditions in the morning, around noon and afternoon. Open circle means clear fine, circle with a vertical line fine, double circles cloudy and solid circle rain. Broken line above the weather symbols shows the observation time for the counting of emergence. Solid circle on the bottom shows new moon and open one full moon.

Table 2. Emerging behaviour of *E. strigata* and *E. japonica*

		E. strigata	*E. japonica*
I)	Nymphal behaviour	Floating	Swimming and climbing
II)	Emerging site	On the water surface	On stones or plants
	Time for molting	Less than 2''*	From 25'' to 57''**
III)	Time from molting to flight	Immediately fly up	Stay for some time***

* The value was based on the impression in the field observation.
** The rage of 11 data counted in the night on 25th June. The mean ± S.E. was 42.6'' ± 2.6''.
*** Its length varied with temperature. See Fig. ~~12.~~ 5

in each stage are compared in Table 2 and are described as follows.

E. strigata

I) Just before emergence the mature nymphs of *E. strigata* were found on the substratum, crawling out of the sand. They swimmed actively when they were touched. The body colour appeared a metallic black due to the gas gathered inside the nymphal skin. The nymph floated to the water surface when it emerged. On the way to the water surface, none of the 12 nymphs observed showed any swimming behaviour.

II) The moulting occurred almost instantaneously on the water surface as soon as the nymph floated up. The moulting usually took less than a second or two to occur. The nymphal skin continued to float by the water surface tension on which the brim of the fissure splitting on the mesothorax is hanging.

III) After the moulting, the subimago stood on the water surface by its legs for a second or longer until it flew up. When air temperature exceeded 16°C, the duration from the moulting to flight was less than a few seconds in the 12 examples observed, but on cold days, the moulted subimago showed difficulty in flying up and drifted stream down (See the next section, Diel Pattern of Emergence). Once the subimago had taken off, it flew up vertically if there was no wind. When it had reached several metres above the water surface, it flew towards the tree canopies or any object on the bank of the stream and perched, hanging on the underside of a leaf or a twig.

E. japonica

I) The emerging mature nymph of *E. japonica* also had gas inside the cuticle and floated to the water surface. However, on the way to the surface, the nymph showed actual swimming behaviour. After reaching the surface it swam directly ahead along the surface with it's fore-legs stretching forward until it came into contact with a partially submerged object like a rock or plant. The nymph then slowly climbed up such an object to several centimetres above the water level. The mean distance from the water's edge to the moulting site was 5.9 cm, but some nymphs climbed as far as 30 cm (Fig.4). Table 3 shows an example of the time budget of these behavioural processes and it may be seen that the climbing speed was as slow as 7 cm/min.

n : 450
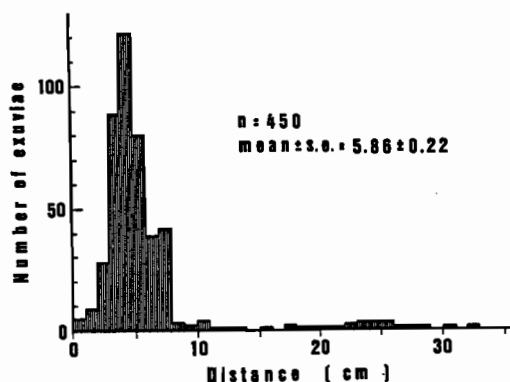mean ± s.e. : 5.86 ± 0.22

Fig. 4. The climbing up distance of emerging nymphs of *E. japonica*. See Methods in text for the explanations of measuring way.

Table 3. An example of the emerging behaviour of *E. japonica* observed in the night on 25th June in 1983. At this time the air temperature was 15.1° C.

Climbing	3'14"	21:45'05"	Reached the water's edge Started climbing on the rock
		48'19"	Stopped climbing after 23 cm walking Started the peristalsis of the abdomen
Molting	0'50"	48'44"	The fissure was appeares on the dorsal thorax Started the molting
		49'34"	Accomplished the molting Shook the body (The wings were a bit rumpled and the tails were curled)
Before flight	1'17"	50'16" 50'38" 50'47"	The wings became flattened The tail became straightened Started walking
Flight	0'06"	50'51" 50'57"	Took off Pearched under a leaf (3.5 m high from the water level)
		51'04"	Closed the three tails into a straight line Became stationary at the underside of the leaf

II) The moulting itself was much slower than that of *E. strigata*. The mean duration was 42.6 seconds, ranging from 25-57 seconds in 11 observations. It was little influenced by air temperature in the range between 12.9°C and 15.1°C (Fig.5). The subimago just after moulting had slightly rumpled wings and curled tails.

III) After moulting, the subimago remained at the emerging site for some time. This duration varied from 0.75 min. to more than 80 min. in relation to
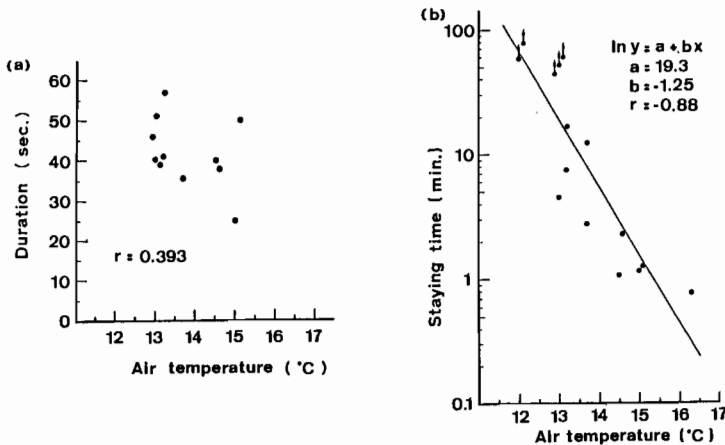

Fig. 5. Relationship of the duration of the moulting of *E. japonica* to the air temperature (a) and relationship of the staying time of *E. japonica* after moulting till flight to the air temperature (b).(a) The moulting duration was defined by the time after the fissure appeared on the mesothorax of nymph till the tails of subimago were pulled out.

the air temperature (Fig. 5). During this time, wings become flat and each tail straightened (Table 3). The subimago then flew up vertically to several metres above the water surface and flew toward the surrounding vegetation and perched under a leaf. The resting subimago shut the three tails in a straight line.

Diel Pattern of Emergence

E. strigata

Hourly change of the emergence number of *E. strigata* counted at Ichihara through the whole emerging season is shown in Fig. 6. In general, the emergence
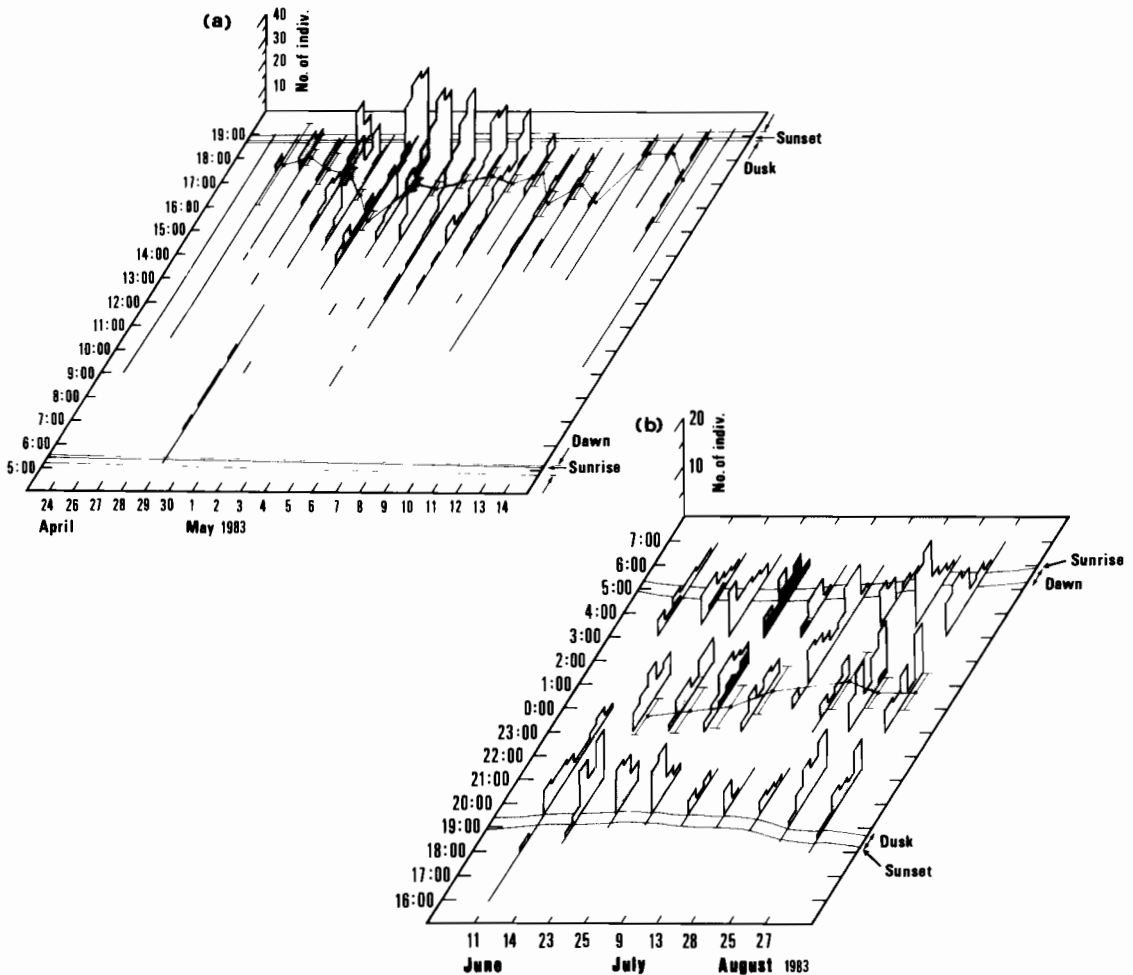

Fig. 6. The diel pattern of emergence of *E. strigata* (a) and that of *E. japonica* (b). Total counted number of *E. strigata* and *E. japonica* was 712 and 524 individuals respectively. Solid circle is the mean emergence time with the width of 95% confidence limit. Solid histogram represents the number of flightless emergence.
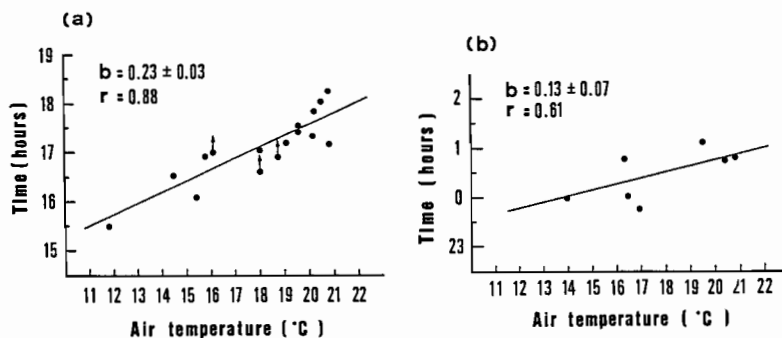
Fig. 7. Relationship of the mean emergence time of *E. strigata* (a) and *E. japonica* (b) to the mean air temperature during four hours before sunset. (a) The mean air temperature is the average of five measurements taken at 16:00, 17:00, 18:00 and 19:00. The mean emergence time of three solid circles with arrow, the data on 2nd, 3rd and 4th May, might be underestimated a little because of the stop of counting at 18:00 in those days.

started around 15:00 and attained it's peak between 17:00 and 19:00. As 5 emergences were noted on the morning of 29th April (8% of the total emergences of this day), the emergence is evidently not restricted to the late afternoon.

The variation of the mean emergence time was related to the temperature conditions. There is fairly high correlation (r=0.88) between the mean air temperature and the mean emergence time (Fig. 7). A lower correlation was observed between the mean water temperature and the mean emergence time (r=0.79). The fact that the emergence ceased rather early on 30th April and on 1st May (Fig. 6) seems to have been caused by the low temperature conditions on these two days. Rain did not effect the emergence: e.g. on 29th April and on 6th May the emergence period was not abbreviated, in spite of rainfall in the afternoon.

On 30th April and on 1st May, it was also found that some completely-moulted subimagines had drifted down the stream or drifted to the shore or partially submerged stones without flying up. Although the same behaviour was also observed in other days, such examples were very rare(Fig. 6). In contrast, in the late afternoon on 30th April and on 1st May, some subimagines were found drifting through the study area in addition to the number shown in Fig. 6. The two cases of flightless subimagines on 1st May and further examples on 4th and 6th May were evidently caused by a failure in moulting (e.g. by leaving a wing or another part inside the nymphal skin), but other cases appeared to be complete subimagines.

This inability to fly was also related to the low temperature conditions. The ratio of subimagines performing a successful emerging flight decreased when the air temperature fell below to 15°C and at around 10.5°C flight became impossible (Fig. 8).

Although no night time observations were made for *E. strigata*, the emergence trap survey at Ichihara indicated that the emergence of this species was restricted to the daytime:i.e. 23 subimagines were caught between 13:10 and 19:05 but none between 19:15 and 9:10 on 29-30th April, 1983(Takemon, unpublished).

E. japonica

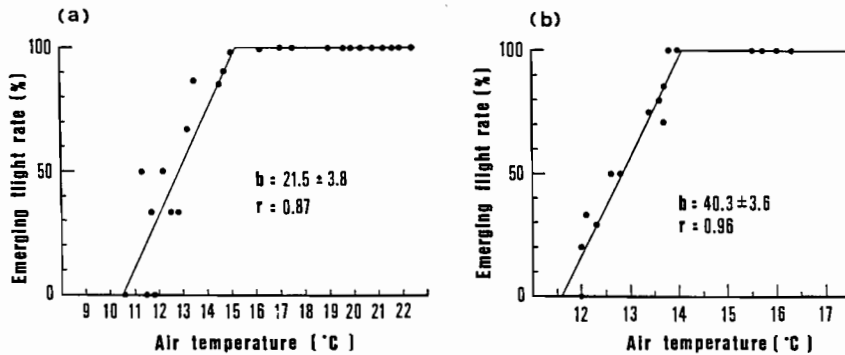Hourly changes in the emergence number of *E. japonica* counted at Jadani-

Fig. 8. Relationship of the emerging flight rate of *E. strigata* (a) and *E. japonica* (b) to the air temperature. (a) Each value of the plot was taken by the average of each thirty minutes' data on 30th April, 1st and 2nd May, when the decreasing of the air temperature happened. (b) The value was taken in the same way as above on the data on 25th June.

bashi is shown in Fig.6. In general, the emergence of this species started just after dusk and continued sequentially until the next morning, without any clear peak. Comparing the beginning of emergence after dusk with the ending around dawn, the former showed a more sudden increase and the latter showed a more gradual decrease, persisting until after dawn. This trend was more evident in June than in July and August.

The relationship between the temperature conditions and the mean emergence time was less clear than for *E. strigata* (Fig. 7). A rather low correlation was observed between air temperature (r=0.61) and water temperature (r=0.66) respectively. The effects of the weather conditions or moonlight were not detected (Figs. 3 and 6).

Twenty subimagines which were flightless after emergence were found in the night on 25th June and a few specimens also on other days (Fig. 6). On this occasion subimagines stayed at the moulting site near the shore. At 6:10 on the morning of 26th, 22 subimagines remained stationary beside their moulted skins. Only one of them was due to a failure in moulting and the others appeared to be complete subimagines. However, when picked up and released into the air, flight proved impossible and the subimagines fell to the ground.

This inability to accomplish the emerging flight was also related to the low temperature conditions. The ratio of subimagines performing the emerging flight decreased when the air temperature fell to less than $14°C$ and flight became impossible at around $11.5°C$ (Fig. 8).

In this species, also based on the emergence trap survey at Jadani-bashi, the emergence was restricted in the night time and just after dawn:i.e. 20 subimagines were caught between 18:25 and 6:30, but none between 6:30 and 18:20 on 25-26th June, 1983 (Takemon, unpublished).

Distribution of the Emerging Sites

E. strigata

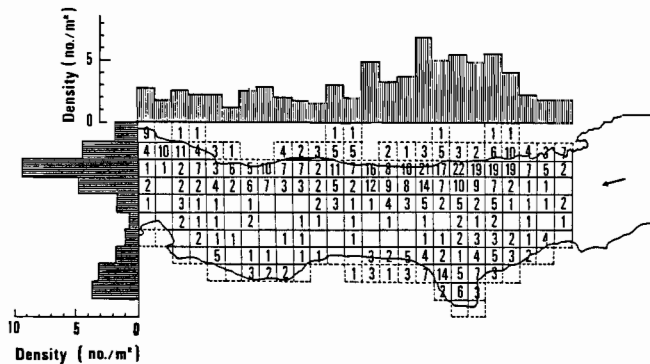Out of 712 observations of emergence of *E. strigata* at Ichihara, the

Fig. 9.   The distribution of the emerging sites of *E. strigata* in 197 grids in
the observation area at Ichihara.   Each grid is 1m £ 1m in size.   The number in
each grid represents the total number of emergence observed throughout the
season.

emerging sites were determined in 657 cases.   Fig. 9 shows the distribution of
these sites presented as the total number of emergences found in each grid.   The
mean density (m) of 195 grids was $3.37/m^2$.   The calculation of Lloyd's (1967)
'mean crowding' ($\overset{*}{m}$) resulted in 7.67 per individual per grid, and the $\overset{*}{m}$ /m was
2.28.   This value indicates that the distribution pattern of the emerging sites
of this species is fairly aggregated according to Iwao (1968).

The changing pattern of the mean density of each cross section and that of
each longitudinal section are also shown in Fig. 9.   The former shows that the
density is comparatively high in the upper parts of the pool, while the latter
shows a more distinctive pattern where the density is highly concentrated near
both shore lines, especially near the shore of the right side.   This side of the
pool was characterized by being shallow and having a slow current (Fig. 2).

Fig. 10 shows that the majority of the species emerged in shallow and slow
current areas than in rapid and deep areas.   The emerging density was notably
higher in still or slow current areas (0-20 cm/sec), where the number of
emergence comprised 64% of the total emergences.   The correlations between
emerging density and the water depth and current velocity, however, were low: r=-
0.21 for the water depth and r=-0.38 for the current velocity.

Consequently, it can be said that the distribution pattern of the emerging
sites of *E. strigata* showed a marked concentration in the shallow and slow
current parts but it can not be said that the shallow and slow current parts
always showed the high density of emergence.

E. japonica

Out of 524 observed emergences of *E. japonica* at Jadani-bashi, the emerging
sites were determined in 467 cases.   Fig. 11 shows the distribution of the
emerging sites presented as the total number of emergences found in each grid.
As this species moults after climbing out of the water as mentioned above, the
emerging density must be defined as the number of emergences per unit length of
the shore line.   Therefore, the emerging density within each grid was calculated
by dividing by the length of shore line inside the grid (Fig. 11).   The mean
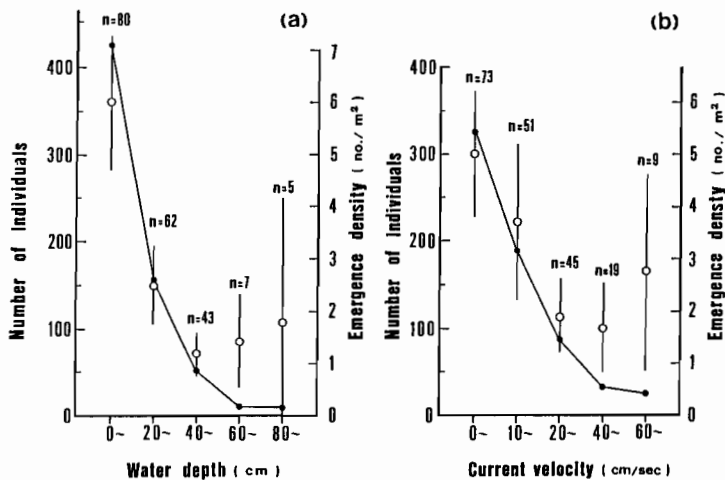
Fig. 10. Total number of emergence (solid circle) and the mean emerging density (open circle with the width of 95% confidence limit) of *E. strigata* within the same range of the water depth (a) and of the current velocity (b).
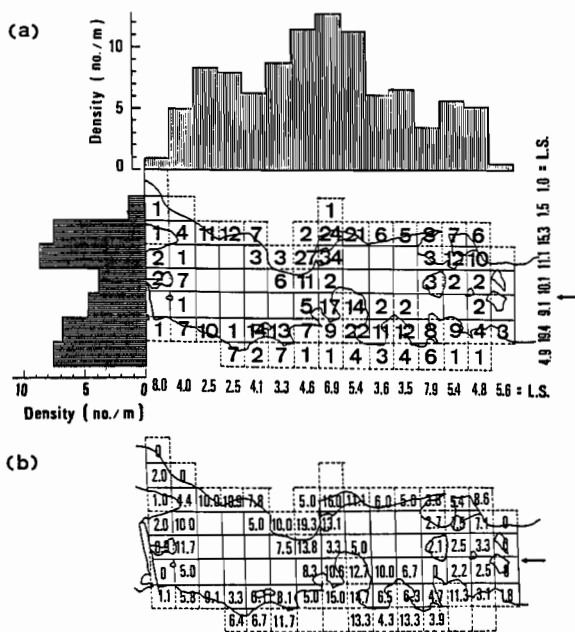
Fig. 11. Distribution of the emerging sites (a) and of the density of the emerging sites (b) of *E. japonica* in 90 grids in the observation area at Jadani-bashi. Each grid is 1m £ 1m in size. (a) The number in each grid represents the total number of emergence observed in the nine nights. The abbreviation L.S. is total length of the shoreline in a cross section and in a longitudinal section of the observation area. Shaded histogram represents the mean emerging density in cross sections (above) and in longitudinal sections (left). The density was given by the number of emergence per unit length of the shoreline. (b) The density of each grid was calculated in the same way.

density (m) of 69 grids was $6.42/m^2$. The 'mean crowding' ($\overset{*}{m}$) was 9.67 per individual per grid, and $\overset{*}{m}$ /m was 1.51: i.e. the emerging sites were rather aggregated in distribution, but as highly as in the case of *E. strigata*.

The mean density of each cross section was comparatively high in the middle parts of the pool. Moreover, a markedly high density was found at the upper stream side of rocks which were projecting into the moderate current or at sheltered bays in stagnant parts. The high emerging density at the upper stream side of the rocks seemed to be caused by the drift of emerging nymphs, and field observations of a nymph landing on the rock after drifting would support this hypothesis.

DISCUSSION

The extreme vulnerability of the emerging stage of mayflies to predation by various kinds of animals (Traver, 1925; Percival & Whitehead, 1926; Needham, et.al., 1935; Edmunds & Edmunds, 1979; etc.) and the high incidence of failure to accomplish the emerging flight on cold days (Imanishi, 1945; Harris, 1956; etc.) have long been noted. So far, however, there have been few works which discuss the detailed process of the emerging behaviour of mayflies in relation to the season, the diel pattern and the features of the water basin in which the species is distributed.

Relation of the Emerging Behaviour of E. strigata and E. japonica to the Stream Type

Members of the genus *Ephemera* have been reported to emerge mainly on the water surface. *E. simulans*, living in North America, was reported to swim or float to the surface and moult (Kennedy, 1925, 1926; Spieth, 1936; Britt, 1962). *E. danica*, living in Europe, was said to moult on the water surface (Percival & Whitehead, 1926; Harris, 1956) or moult after climbing up stalks of vegetation in rare cases (Percival & Whitehead, 1926). Among the other genera of Ephemeridae, only emergence on the water surface has been reported: e.g., *Ephoron album* (Britt, 1962), *Ephoron leukon* (Ide, 1935), *Afromera evae* (MaCafferty & Gillies, 1979) and *Hexagenia limbata* (Neave, 1932). Thus the crawling out emergence of *E. japonica* is a distinctive exception.

The genus *Ephemera* has been termed a stream-adapted genus when compared with the other genera of Ephemeridae, most of which live in lakes and the lower reaches of rivers (McCafferty & Gillies, 1979). However *E. simulans* is common in lakes and in the slow-flowing streams and rivers (Britt, 1962; McCafferty, 1975) and *E. danica* inhabits both lakes and rivers (Maccan, 1979) usually of the less hilly districts (Percival & Whitehead, 1926). Although *E. strigata* is also distributed in the middle stream, *E. japonica* is restricted to the upper stream of hilly or mountainous districts (Imanishi, 1940; Kuwata, 1955, 1958; Hisai & Arai, 1973, 1974; Takemon, unpublished) and is thus also exceptional in its distribution pattern. Therefore the differences in the emerging behaviour of the two species may be related to differences in the stream features and accompanying ecological conditions between the distribution areas of each species.

Kani(1944, 1981) classified streams by the rapid/pool distribution and the rapid/pool configuration. His classification is convenient when comparing differnces in the stream feature between the distribution area of *E. strigata* and *E. japonica*. Earlier work has stated that the longitudinal distribution of each species corresponds to Aa-Bb or Bb stream type and Aa stream type respectively (Kani, 1944; Kuwata, 1958). In case of Kurama and Kibune Streams, Imanishi(1941)

stated that E. strigata was found from the upper region of Kibune-guchi(Aa-Bb) to the Kyoto City area(Bb) and that *E. japonica* was found from headstreams(Aa) to Kibune-guchi(Aa-Bb)(The stream type of each area is quoted from Kani(1944)).

The Aa type stream is characterized by more than two rapids and pools in one reach, a stair like configuration by a series of rapids and pools, small waterfalls of rapids and the short length of a rapid and a pool. The Bb type stream is characterized by a single rapid and pool in one reach, long pools at the bends of meanders and wavy or foaming rapids without waterfalls. The Aa-Bb type stream is characterized by more than two rapids and pools in one reach and wavy or foaming rapids without waterfalls (Kani, 1944, 1981).

E. strigata

What kind of characters of Bb type can relate to the water surface emergence of *E. strigata*? The first process of the emerging behaviour is the nymphal ascent in the water to the surface. As this species emerges in the daytime, any delay in the emerging process due to the ambient temperature conditions will increase the danger of predation by fish. In order to minimize this potential danger, the shallow and stagnant area is utilized.

The second process of the emerging behaviour is the moulting on the water surface, which the subimago completes while being supported by the surface tension. The surface turbulence at the waterfalls and the foaming rapids is likely to submerge the subimago and probably prevent further emerging. In this respect, there are less problems in the Bb type river system as the rapid has no waterfalls.

The third process is the period spent at the moulting site until take-off to the resting site. Remaining on the water surface results in the danger of drift and predation. The drifting subimago is liable to stick its wing or other body part to the surface film due to the break waves in rapids. Moreover, a subimago remaining on the surface will be vulnerable to predation. Sweeney and Vannote (1982) have reported that the predation rate on the subimagines of *Dolania americana* by aquatic beetles (mainly *Dineutes discolor*) on the water surface was more than 20%, even at the peak of the emerging season. Considering these perils, the low air temperature which makes the subimago flightless is unsuitable for the water surface emergence. However, when it happens to be too cold to fly quickly as on 1st May, 1983, the Bb type stream is relatively safer owing to the presence of long pools and rapids without waterfalls.

In terms of the whole process of the emerging behaviour, it may be said that the Bb type is more suitable for water surface emergence than the Aa type, because it has a greater proportion of shallow and slow current areas in a pool and has no waterfalls in a rapid. In this respect, the high concentration of emerging sites in the shallow and slow current parts found in *E. strigata* might promote the safe emergence.

E. japonica

What characteristics of the Aa type stream can be related to the crawling out emergence of *E. japonica*? The first process is the horizontal swimming to the landing site and the climbing to the moulting site. When the nymph is distributed in areas not adjacent to the bank, the danger of predation in this process will be increased. The nymph of *Leptophlebia cupida* is eaten by fish and stonefly during the migration before the emerging season (Traver, 1925). Therefore the nighttime emergence of *E. japonica* might be related to the

avoidance of predation. However, in the stream, this process also has the inherent danger of drifting for *E. japonica*, and the high density of emerging sites observed at the upper stream side of the shoreline in the moderate current would seem to indicate that this is a usual occurrence for emerging nymphs. The following characters of the Aa type stream would facilitate the crawling out of the water within a short distance: i.e., a stagnant area appears repeatedly along the stream, the water course meanders and the shore lines are intricate and thus the drifting nymph comes across the shore in the moderate current frequently.

The second and the third processes of the emerging behaviour are the moulting and remaining stationary until take-off. As the moulting site of E. japonica is on the shore or on partially submerged objects, the insect can support its body weight by holding on to a solid surface during the moulting until take-off. However, although there is no danger of drowning or predation by fish, the subimago will be vulnerable to terrestrial predators. In this respect, the nighttime emergence of *E. japonica* must be advantageous against visual searching predators such as birds and dragonflies. Consequently the stream features do not seem to be restrictive for these processes.

Therefore it can be said that the Aa type stream is suitable for the crawling out emergence, especially, as for reaching the moulting site.

If the crawling out behaviour of *E. japonica* is a consequence of an adaptation to the physical features of an Aa stream type, other torrent-living species of *Ephemera* would also be likely to show the same behaviour. *E. guttulata* (Kennedy, 1925, 1926) and *E. blanda* (McCafferty, 1975) are both found in mountain torrents in North America. While *E. lankensis* occurs in mountainous areas in Sri Lanka (Hubbard, 1983). Unfortunately, however, there is no information on the emerging behaviour of these species and further observation is needed.

Relationship between the Moulting Site and the Moulting or Staying Duration

There seems to be a relationship between the moulting duration or the staying time after moulting and the moulting site of the species: i.e., species which moult on solid objects out of the water seem to show a slow moulting and a comparatively long staying time until flight, whereas species which moult on or under the water seem to show a rapid moulting and immediate flight.

The moulting of *E. japonica* takes as long as 40 seconds, and the subimago then remains stationary as long as 1 minute until take-off, even in moderate temperature conditions. A rather prolonged stationary period after moulting was also reported for members of the genera *Siphlonurus* and *Leptophlebia* (Illies, 1968). *Leptophlebia cupida* has been reported as remaining stationary for as long as 6 minutes (Traver, 1926), but this record cannot be regarded subjectively due to a a lack of temperature data. Members of the genera *Siphlonurus* and *Leptophlebia* are also known for their crawling entirely out of the water before moulting (Needham *et al.*, 1935; Edmunds *et al.*, 1976).

Conversely, a rapid moulting and a very short staying time as seen in *E. strigata* were noted in following species which moult on or under the water surface: *Cloeon dipterum* (Illies, 1968; Edmunds *et al.*, 1976), *Cloeon simile* (Harris, 1956), *Stenonema modestum* (Kondratieff & Voshell, 1980), *Ephoron album* (Britt, 1962), *Hexagenia* orlando (Edmunds *et al.*, 1976) and some members of the genera *Baetis, Pseudocloeon, Stenonema, Epeorus, Choroterpes, Ephemerella* and *Tricorythodes* (Edmunds *et al.*, 1976). The rapid moulting and the quick take-off seem to facilitate the safer emergence from the water surface against the

peril of the predation and drowning.

Relationship between the Emerging Behaviour and the Nymphal Life Form

Kimmins (1972) noted the four general types of emerging behaviour of mayflies: i.e., 1) moult after crawling out of water, either partially or entirely, 2) moult under water before crawling out, 3) moult under water before floating up to the water surface, 4) moult on the water surface after floating up.   Imanishi (1938), Harris (1956), Britt (1962), Illies (1968) failed to distinguish types 2) and 3) and stated there were three types in general.

Imanishi (1938) regarded each type of emerging behaviour as being attributable to the nymphal life form (the typology of the mayfly nymphs by the body form which reflects the nymphal habitat and the way of living) as mentioned earlier.   Certainly is it likely that the behavioural ability at the emergence is restricted by the morphological structure of the nymph, as mayflies are hemimetabolous insects.   For example, Imanishi (1938) stated that species of the genus *Epeorus* moult under water and then float up to the water surface.   He attributed this behaviour to the gliding life form of this genus: as the nymph has a flat body shape suitable for clinging onto stone surfaces in the a current, the nymph cannot swim nor walk across irregular substrates and thus is obliged to moult at the site of nymphal habitat.

The nymphs of the genus *Ephemera*, which have the burrowing life form, would be expected to emerge on the water surface, according to Imanishi's(1938) hypothesis.   However, as the nymphs of each species of this genus are proficient swimmers, they have the potential ability to migrate before emergence. The swimming motion of the nymphs of *E. strigata* and *E. japonica* agreed closely with the observations on *Hexagenia* by Lyman (1943), these species waving the abdomen vertically with the fore-legs stretched forward when swimming.

The mayfly species which is hitherto known for the crawling out emergence belongs to the perching and swimming life form (*Ameletus, Siphlonurus, Isonychia*) or the weakly gliding life form (*Leptophlebia, Paraleptophlebia*) or the reposing life form (*Baetisca*) (Needham, *et al.*, 1935; Edmunds *et al.*, 1976).   And then the ability of skillful swimming is common to them all.

While the species of *Baetis, Cloeon* and *Callibaetis* which also have the perching and swimming life form are reported to emerge on the water surface (Needham *et al.*, 1935; Edmunds *et al.*, 1976).   Some of the torrent dwelling species of *Baetis* crawl partially out of water when they emerge, though (Takemon, unpublished).

Among these, species which have the crawling out type of emergence, are all inhabitants of the upper or the middle stream or of the edges of lakes where there is some wave action.   Among the species which can swim proficiently, those whose emergence occurs on the water surface are all known as the inhabitants of the middle or the lower stream or of lakes and ponds.   Consequently the suitability of the respective emerging behaviours to the conditions within the distribution area discussed earlier on the two species of *Ephemera* can be applied generally to the species whose nymphs are proficient swimmers.

SUMMARY

1. The emerging behaviour of subimagines of the mayflies, *Ephemere strigata* and *E. japonica* was observed along the Kurama Stream and the Kibune Stream, in Kyoto City, from April to May and from June to August, 1983, respectively.

2. The mature nymph of *E. strigata* floated to the water surface moulted instantaneously. The subimago stood there for less than a few seconds and flew up.

3. The mature nymph of *E. japonica* floated to the water surface, swam directly ahead, came into contact with a partially submerged rock or plant, climbed it up and moulted. The mean climbing distance was 5.9 cm. The moulting took 25-57 seconds. The subimago remained at the emerging site for 0.75-80 min. in relation to the air temperature and flew up.

4. The emergence of *E. strigata* began to increase around 15:00 and peaked between 17:00 and 19:00. That of *E. japonica* started just after dusk and continued without any clear peak until next morning.

5. The subimago of *E. strigata* and *E. japonica* showed the inability to fly at the air temperature less than 15°C and 14°C and became impossible to fly at 10.5°C and 11.5°C, respectively.

6. The distribution of the emerging sites of *E. strigata* showed a marked concentration in the shallow and slow current parts of the stream. That of *E. japonica* was concentrated at the upper stream side of the shoreline in the moderate current and sheltered bays in stagnant parts.

7. The relationship among the emerging behaviour, the stream types of the respective habitats and the nymphal life forms was discussed.

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