

## Life history of *Potamanthodes kamonis* in a stream of central Japan (Ephemeroptera: Potamanthidae)

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With 5 figures in the text

### Introduction

UENO (1928) reported the occurrence of nymphs of Potamanthidae in central Japan, and identified them to be *Potamanthus luteus* LINNÉ. IMANISHI (1940), however, concluded on the basis of the adult characteristics that these potamanthids belonged to a new species, *Potamanthus (Potamanthodes) kamonis*. Recently, YOU (1984) placed this species into the genus *Potamanthodes*; this is the only species of Potamanthidae in Japan.

Life history information for *Potamanthodes kamonis* (IMANISHI) is very limited although this species is widely distributed in Japanese streams. GOSE (1973) reported a prolonged emergence period over four months for *P. kamonis*. He interpreted the monthly occurrence data of adults and nymphs as indicating a univoltine life cycle. However, my preliminary survey suggested that the long emergence period of this species could not be assigned to a single cohort. In this paper, I describe and discuss the life history of *P. kamonis* including the voltinism and the nymphal size difference among habitats.

### Materials and methods

The study area was located in the upper reach of the Hatsukagawa Creek (35°01'N, 135°17'E, 340 m in altitude), a tributary of the Muko River which flows southward to Osaka Bay (Fig. 1). Four sampling sites were selected along the stream length of about 40 m; P, R-1, R-2 and R-3 from upstream to downstream. Site P was an area shallower than 0.5 m at a lower part of a pool. The current velocity there was nearly zero and the substratum consisted of sand and embedded rubble. The area just below the pool was Site R-1, a riffle, whose current was relatively slow (0.23–0.32 m/s) and whose dominant type of substratum was loose rubble. Site R-1 was followed by a fast current riffle (0.50–0.97 m/s), Site R-2. Below Site R-2, there was a wider, medium current riffle (0.30–0.52 m/s), Site R-3.

Mayfly nymphs were collected monthly in the cold season, from November to March, and twice a month in the other period, when possible, from August 22, 1978 to October 11, 1979 at Sites P and R-1, and from July 10, 1978 to July 16, 1979 at Sites R-2 and R-3. In addition, samples were collected at Site P weekly or semimonthly from June 11 to September 17, and October 16, 1980.

At Site P, a box sampler was used which was made of a steel frame (30 × 30 cm base; 53 cm height) with sides covered in canvas. The sampler was pushed down onto the substratum. The enclosed area was stirred and floating organisms were collected with a hand net of 15 mesh · cm<sup>-1</sup> (0.471 mm pore opening). The stirring and sweeping were repeated until no organism was found. At Sites R-1, R-2 and R-3, samples were collected with a SURBER sampler which covered a 30 × 30 cm area of the bottom, and which had a net of 15 mesh · cm<sup>-1</sup>. Four samples at each of the sites were randomly taken on every sampling occasion except the samplings in 1980 when more than 100 nymphs were randomly collected by the hand net.

*P. kamonis* nymphs collected were preserved immediately in 5% formalin solution and transferred to 70% ethanol solution in the laboratory. Their head widths were measured to the nearest 0.1 mm using a binocular microscope with an objective micrometer. Nymphs larger than 1.2 mm head width were sexed.

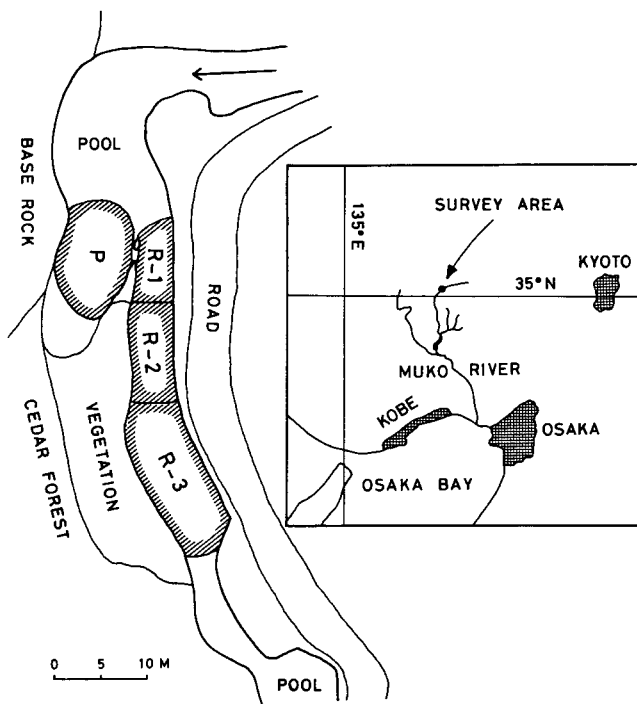


Fig. 1. Sketch map showing the four sampling sites. Site P is a pool and the other three sites are riffles.

Subimagos and imagos were collected by a light trap using butane gas light on every sampling occasion from May 29 to October 11, 1979 and from June 11 to October 16, 1980.

An attempt at artificial fertilization was made in the laboratory. Some eggs from subimagos were mixed with extract of male abdomen in water and kept between 23 °C and 26 °C. Some eggs hatched after about two weeks, but the rest did not hatch after a month when the experiment was stopped because of the rapid growth of aquatic fungi. The hatching time and the head widths of the 1st instar nymphs were recorded.

## Results

Nymphal density at Sites P, R-1 and R-3 are shown in Fig. 2. Site R-2 is excluded from the figure because only a few nymphs were collected there on every sampling occasion. The nymphal density at Site R-3 was much lower than at Sites P and R-1. The lower densities at Sites R-2 and R-3 indicate that this species lives mainly in pools or slow current riffles.

Figs. 3 and 4 show the frequency distribution of head widths of the nymphs collected on each sampling occasion at Sites P and R-1 in 1978 and 1979 (Fig. 3) and at Site P in 1980 (Fig. 4). The sizes of the final stage nymphs having black wing pads and the sampling occasions when adults were collected are also indicated in the figure.

From the seasonal trend of the size distributions in Fig. 3, two distinct cohorts are recognized. The first cohort (Cohort W1) recruited from August to September 1978, grew in autumn and next spring, and the largest individuals occurred in June 1979. Most of the

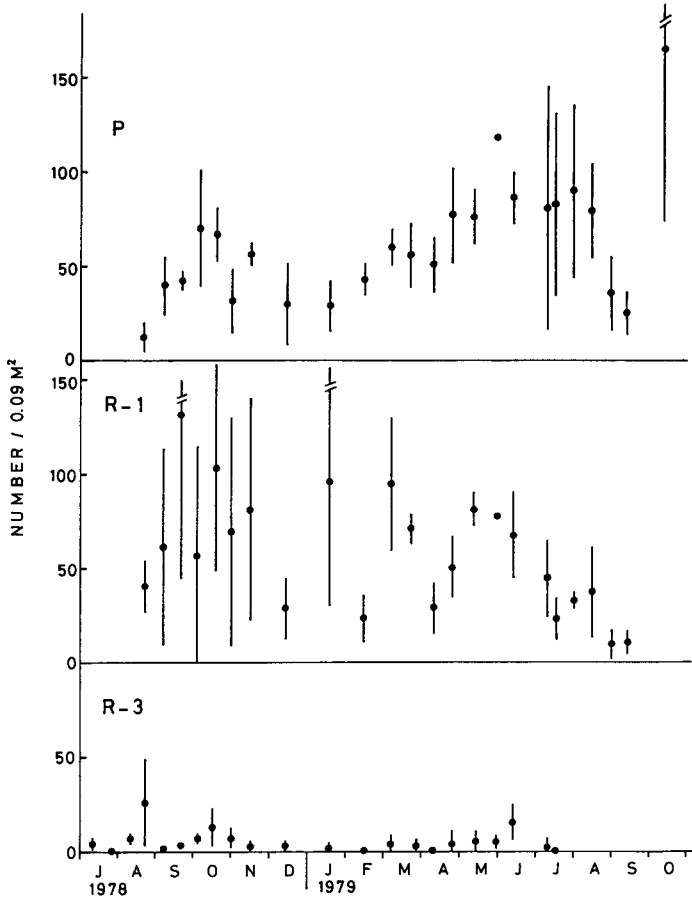


Fig. 2. Density of *P. kamonis* nymphs at sites P, R-1 and R-3. Each data point represents the mean and standard deviation of four replicated samples.

cohort emerged probably between June 12 and July 9, 1979. The second cohort (Cohort S) is a summer generation which was recruited mainly in July, and emerged in late August to early October 1979 (see also Fig. 4).

Besides the above two cohorts, a group of nymphs smaller than Cohort W1 were found in many months beyond the emergence period. These tiny nymphs occurred even in autumn and winter, but became abundant in spring. They are indistinguishable from Cohort S after June in Fig. 3. However, Fig. 4 shows that these nymphs grew in June and July, and are distinguishable from Cohort S because their average size on July 2 is greater than that of Cohort S on July 16 (significant at 1% level). The adult occurrence between those of Cohorts W1 and S suggests that these nymphs grew and emerged successively from July to mid-August; this group is called here Cohort W2.

A further look at Fig. 3 shows the difference in nymphal size between the pool and riffle. Small nymphs of Cohorts W1 and W2 were always more abundant at Site R-1 than at Site P. In addition, the mode of head width of Cohort W1 was generally smaller

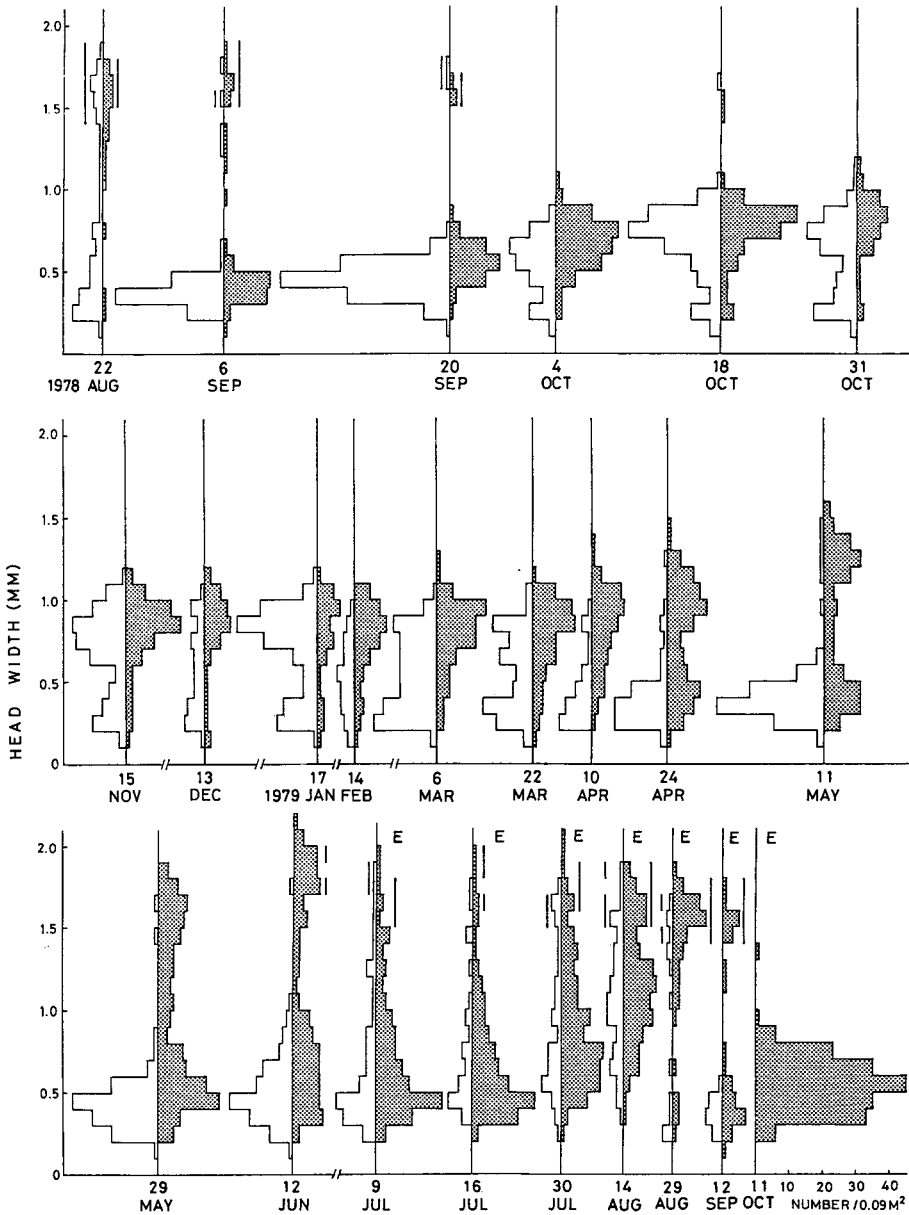


Fig. 3. Seasonal change in the frequency distributions of nymphal head width at Sites P (shaded area) and R-1 (white area). Scale is indicated at the right bottom. Vertical lines from June to September = size ranges of the final stage nymphs, E = the sampling occasions when adults were collected.

at Site R-1 than at Site P until March. Growth of Cohort W1 resumed at Site P in April whereas the corresponding nymphs almost disappeared at Site R-1.

Fig. 5 (a) illustrates the growth curves of the respective cohorts. Each cohort was separated from the others in the monthly size distribution by CASSIE's (1954) probability

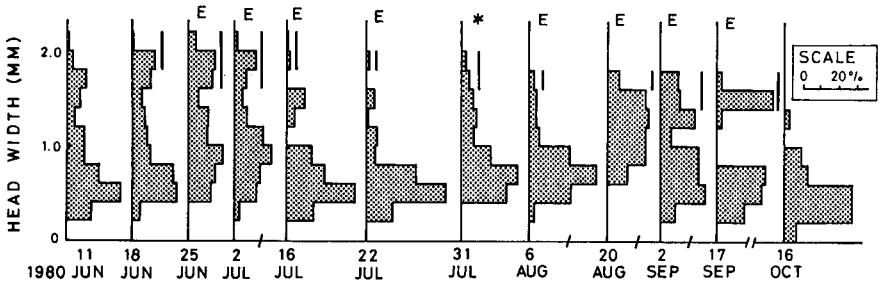


Fig. 4. Change in the frequency distribution (percentage) of nymphal head width at Site P during summer 1980. \* = no data of adults.

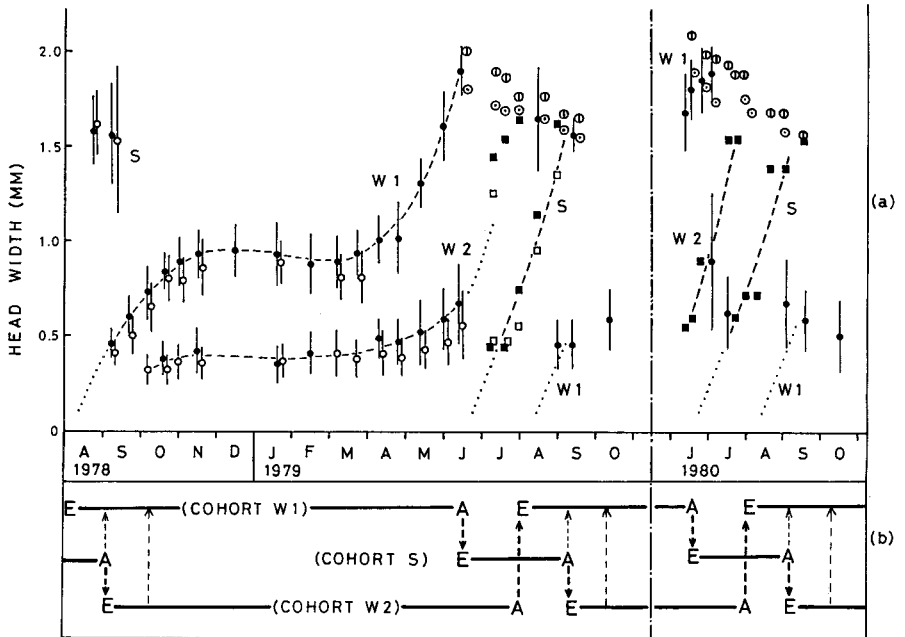


Fig. 5. (a): Seasonal change in nymphal head width. Solid marks = Site P, open marks = Site R-1; circles and bars = means and standard deviations, squares = modes of size distributions; points inside circles and bars inside circles = mean sizes at final nymphal stage of males and females, respectively. (b): Schematic illustration of the life cycle pattern. E = egg, A = adult. Thick lines are fundamental pattern. Broken lines represent the shift of generation.

paper method, and the average head width and standard deviation were calculated. When Cohorts S and W2 were indistinguishable, the modes of the size distributions are shown. The average head widths of final stage nymphs are added in the figure. The hatching date of each cohort was estimated by back extrapolation of the growth curve given the knowledge that all the 1st instar nymphs obtained from artificially fertilized eggs had a head width of 0.1 mm.

Judging from the estimated hatching date, Cohort S must be the offspring of Cohort W1 (W1 → S). Most of the next W1 which starts to appear in early September is probably

the offspring of Cohort W2 (W2 → W1), although the hatching date of the next W1 cannot precisely be estimated because of the continuous recruitment. Since the majority of offspring of Cohort S hatch after early September, they must be smaller than the next W1 and become the next W2 (S → W2), although a few of them may join the next Cohort W1 (S → W1). Accordingly, the fundamental life cycle of *P. kamonis* seems to be a repetition of W1 → S → W2 → W1. The cohort sequence is summarized in Fig. 5 (b).

### Discussion

There are a lot of mayfly species whose tiny nymphs resemble those of Cohort W2 of *P. kamonis* in being found for a long time other than during the emergence period. This phenomenon has been attributed to delayed hatching by many authors (e.g. MACAN 1957, HYNES 1970 a). On the other hand, ELLIOTT & HUMPHESCH (1980) believed that the prolonged occurrence of tiny nymphs is not due to delayed hatching but to the very slow growth of some nymphs after hatching, because the eggs under the same conditions hatch within a remarkably short period in many mayflies. The artificially fertilized eggs of *P. kamonis* hatched in thirteen to fifteen days at 23 °C to 26 °C in the laboratory, and the delayed hatching of *P. kamonis* eggs was not demonstrated. IDE (1935) also reported that the hatching time of two species of *Potamanthus* was fourteen days in the laboratory. In natural conditions, however, the eggs of *P. kamonis* develop under various temperature regimes because of the prolonged emergence period from June to October. The significant effect of water temperature on the time required for egg-hatching has been reported by many authors; the time generally lengthens with decreasing temperature (ELLIOTT 1972, 1978, SWEENEY 1978, ELLIOTT & HUMPHESCH 1980). Besides, ELLIOTT (1972) and FRIESEN et al. (1979) showed that the hatching period was prolonged under low water temperature. In *P. kamonis*, most of the eggs from Cohorts W1 and W2 probably hatch after a relatively short period because of high water temperature. On the other hand, the water temperature gradually decreases from late August to early October when Cohort S emerges and lays eggs. Therefore, a rather small difference in the start of egg development seems to result in a great difference in hatching time and hence in a prolonged hatching period. It is possible for some eggs to overwinter and hatch in spring although I cannot deny to possibility that the occurrence of tiny nymphs (W2) was due to delayed nymphal growth. Egg masses of *P. kamonis* were often collected together with nymphs even in winter and spring although it was not confirmed whether they had been alive or not before formalin fixing.

Simultaneous existence of different nymphal stages is considered to have an advantage in population survival. HARKER (1953) described that the large nymphs of *Ecdyonurus torrentis* were often found dead after floods, but that small dead nymphs were seldom found. WISE (1980) showed that the new recruits of small nymphs took over the population after a great accidental death of the larger nymphs. Moreover, mayfly eggs have been believed to be resistant to unfavourable conditions such as spates, desiccation and low oxygen (BRITT 1962, HYNES 1970 b).

In *P. kamonis*, the life cycle sequence, W1 → S → W2 → W1, proceeds with a time lag of a year, and two different stages of development exist simultaneously at any time. Assuming that survival in unfavourable conditions depends on the developmental stage, if one cohort suffers a heavy accidental mortality, the other cohort can survive to continue the population. In such a case, the life cycle pattern is probably restored to the original

state in a few years because the offspring of Cohort S may partly join the next Cohort W1 as mentioned before, and moreover, some nymphs of Cohort W2 may grow fast enough to catch up with Cohort W1, judging from the fact that the size distributions of Cohorts W1 and W2 partly overlap (Fig. 3).

KOVALAK (1978) reported that the larval sizes of some mayflies and a caddisfly were different between habitats having different current velocities. He gave to the cases of the greater size in a slower current site the explanation that insects in slower current regimes spend less energy maintaining position in the stream and can channel more energy into growth.

In *P. kamonis*, the generally larger size of Cohort W1 before March at Site P than at Site R-1 may be attributable to a greater energy allocation to growth. After April, the larger nymphs (W1) and the smaller nymphs (W2) were both represented in the pool, whereas almost all the riffle samples consisted of the smaller nymphs: this suggests that Cohort W1 migrates with growth from riffles to pools. The cause of such a migration is not clear, but it may be an advantage for the emergence success because *Potamanthodes* emerges onto the surface of open water (IMANISHI 1938).

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