

## Reproduction by Overwintering Adults of Water Strider, *Aquarius paludum* (Fabricius)

TETSUO HARADA<sup>1</sup>

Department of Biology, Faculty of Science, Osaka City University,  
Osaka 558, Japan

**ABSTRACT**—Overwintering adults of a water strider, *Aquarius paludum* having the macropterous and brachypterous wing forms continued to lay eggs for about 35 days in spring. The oviposition occurred at a high and constant rate under quasi-natural conditions. There was no significant difference between the two wing forms with respect to the number of eggs throughout their most reproductive period. Some of the second generation adults which had overwintered after reproduction in the previous autumn also became reproductively active in the following spring together with the third and diapause generation adults. In early spring, macropterous adults appeared on the water surface later than brachypterous adults, demonstrating the longer distance between diapause sites on land and breeding sites on the water surface in macropterous adults than brachypterous adults.

### INTRODUCTION

Among insects, there are many species that are in diapause and overwinter as adults, and the diapause in the adult stage (adult diapause) means that post-emergence development in ovaries does not occur in the female and the ovaries remain small [2]. In most cases of adult diapause, diapause occurs in young and nonparous adults, and the adults became reproductively active after overwintering [2]. Even in reproductive adults, diapause can be induced by suitable cues (e.g., a short-day photoperiod) in a few species of bugs and beetles [6, 9, 11, 16]. However, reproduction after overwintering has never been reported to be induced twice in the same individuals which normally live for less than one year. In some coleopteran species living for several years, adults overwinter in diapause and reproduce repeatedly in successive years in nature, e.g., *Agonum assimile* [10].

*Aquarius paludum* (Fabricius) is trivoltine and shows alary dimorphism in Kochi, Japan [4, 5]. Although reproductive activity in the first genera-

tion continued until death in summer, the females of the second generation entered diapause after a reproductive period in September and October [4]. It is unclear whether the adults of the second generation became reproductively active again in the following spring together with the adults of the third generation.

The present work aims, first, at making this point clear and, second, at studying the appearance on the water surface and the oviposition process by overwintering brachypterous and macropterous adults of *A. paludum* under quasi-natural conditions in spring.

### MATERIALS AND METHODS

Overwintering adults of *Aquarius paludum* were collected from a pond in Kochi City (33.3°N, 133.3°E), Japan on the 1st, 4th, 16th, 17th, and 24th of April, and in late September, 1988. The collected water striders were released back into the pond after measurement of wing lengths. Wing length was expressed in terms of the index as per Harada and Taneda [5]. When it was difficult to distinguish macropterous from brachypterous adults by fore-wing lengths, the distinction was made by reference to hind-wing lengths because the two wing forms showed more clear differences

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<sup>1</sup> Department of Biology, Faculty of Science, Kochi University, Kochi 780, Japan



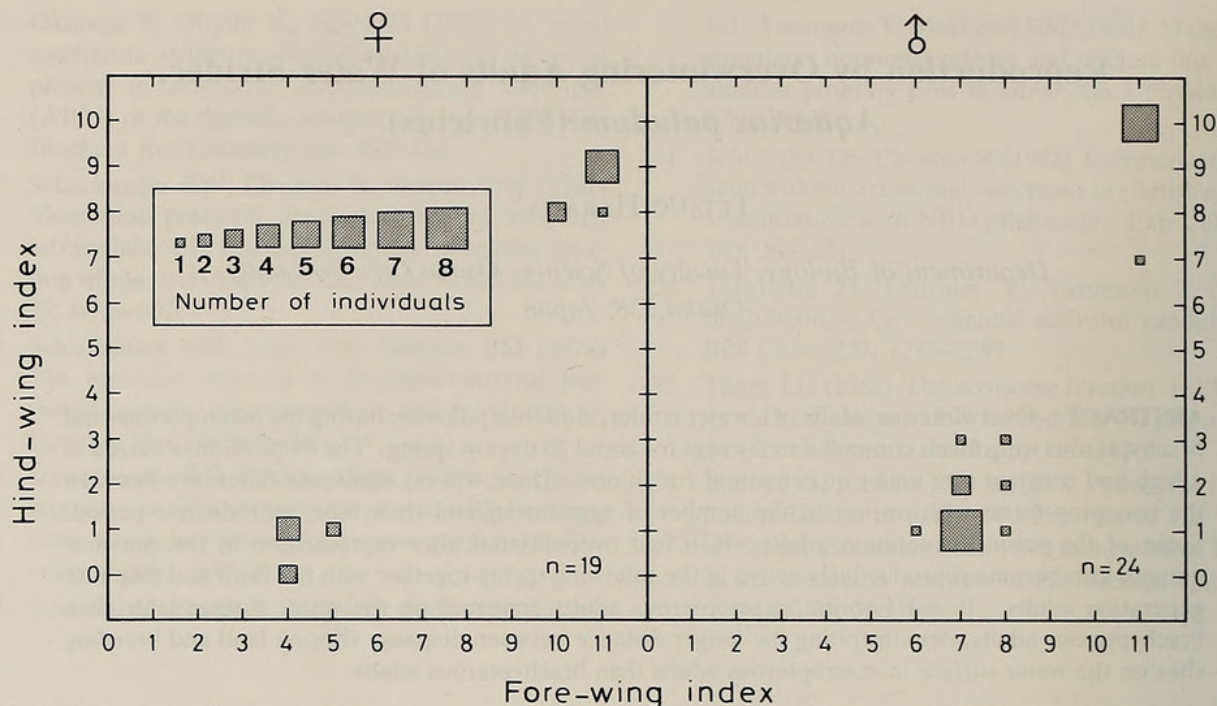


FIG. 1. Fore- and hind-wing lengths of the adults collected from a water way in Kochi in late September, 1988.

in the hind-wing lengths than in the fore-wing lengths (Fig. 1).

Overwintering adults of *A. paludum* were collected in early April, 1991, from the pond. In 1990, fifth instar nymphs of the second generation were collected just before adult emergence from two small canals (A- and B-canal). The water temperature in the A- and B-canal had been higher than 27°C and lower than 22°C, respectively, in the daytime in July and August. Fifth instar nymphs belonging to the third generation were collected from A-canal in mid-October, 1991. Pairs consisting of one male and one female with the same wing form were put just after collection or adult emergence in individual plastic pots, 14 cm in diameter and 5 cm in depth, and reared under quasi-natural conditions in Osaka City (35.0°N, 135.5°E), Japan. Longevity was examined in each pair and the number of eggs was counted every 1–2 days in September, 1990 to May, 1991, and in October, 1991 to May, 1992. The plastic pots were filled with water to a depth of 5–10 mm. A wooden stick, about 10 cm in length and about 1 cm in diameter, was put in each pot for oviposition and resting sites. Water in the pots was replaced daily. Water striders were fed on adult specimens of *Fannia canicularis* or *Lucilia illustris* which were

supplied daily at a rate of one fly per two adults.

## RESULTS

Overwintering females (mainly the third generation) with either of the two wing forms continued to lay eggs for an average of 36.0 days in spring and then died. Eggs were laid at a constant and high rate (about 60 eggs per 5 days per female) throughout the reproductive period for both wing forms (Fig. 2). The average total number of eggs per female was 386.0 in brachypterous females and 396.7 in macropterous females. Difference in numbers of eggs laid per five days was not significant between the two wing forms (*t*-test,  $P > 0.05$ ) except a period between 16th and 21st May ( $P < 0.05$ ). Furthermore, no significant difference was observed between the two wing forms with respect to longevity (*t*-test,  $P > 0.05$ ).

In the second generation, all the reproductive females laid the fertilized eggs in fall. The reproductive females stopped laying eggs between the 21st September and the 31st October, and entered diapause (Fig. 3). None of the pairs in the third generation reproduced in autumn, and all entered diapause (Fig. 3). In early December, the diapause adults of the second and third generations



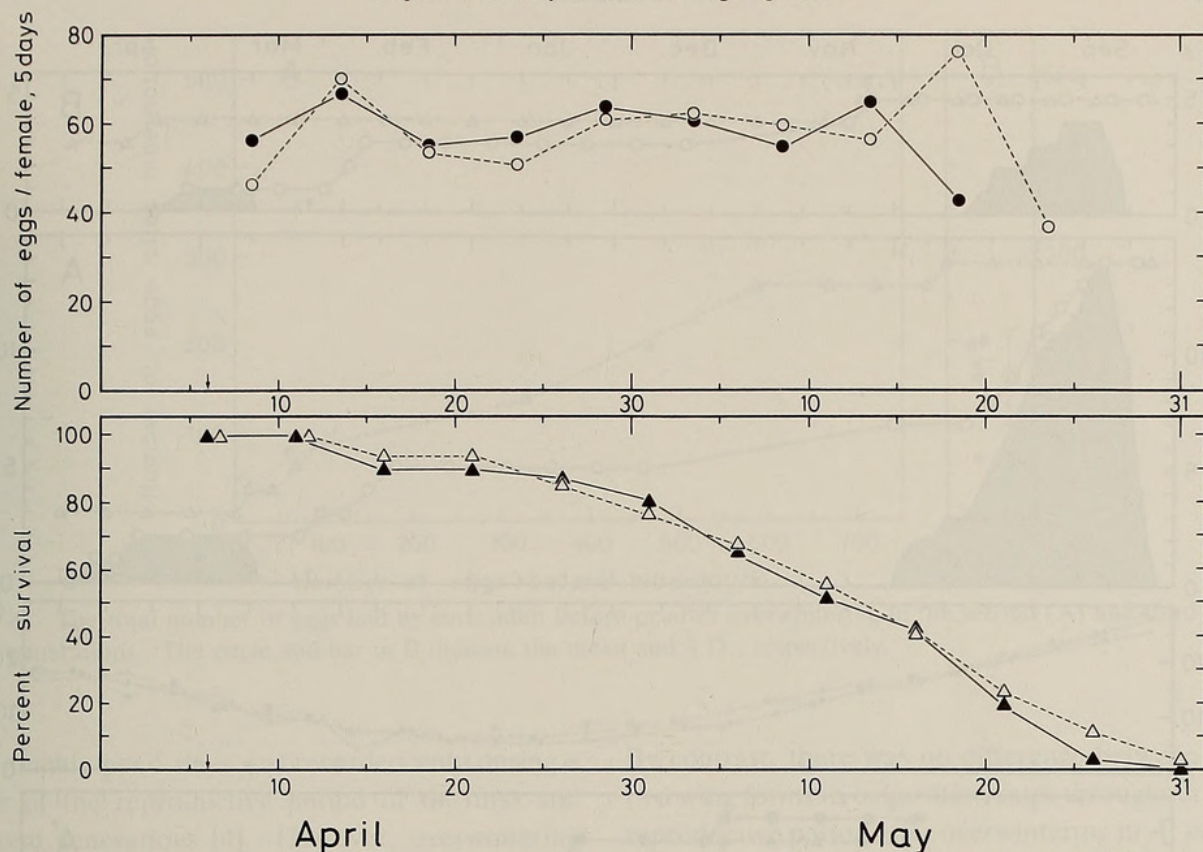


FIG. 2. Survival curves and rates of oviposition for overwintering females (mainly the third generation). Open and solid symbols show brachypterous and macropterous groups, respectively. Arrows show the day on which adults were collected from the pond in Kochi, Japan, 1991.  $n=34$  for brachypterous pairs;  $n=29$  for macropterous pairs.

were transferred onto fallen leaves as overwintering sites. At the beginning of the following March, surviving adults were moved again onto the water surface. For specimens derived from the A-canal, the survival percentage just prior to the move in March was higher in the third generation (females, 84.6%; males, 76.9%) than that in the second generation (females, 21.4%; males, 42.9%) (Fig. 3). In the second generation, when the surviving adults were transferred to the water surface, three pairs were made and the four remaining males were paired with virgin females which had been reared during the nymphal stage under a long-day (14.5L-9.5D) photoperiod at  $20 \pm 2^\circ\text{C}$ . In the third generation, ten pairs were made in early March. The three females in the second generation and surviving five females in the third generation began to lay eggs on average about 2 weeks after the move to the water surface [second generation,  $13.3 \pm 1.5$  (S.D.) days; third generation,  $15.6 \pm 9.0$  (S.D.) days] (Fig. 3). The number of eggs laid

after diapause was thought to correlate positively with the number of eggs before diapause, although the correlation could not be inferred statistically because of the insufficient number of samples (Fig. 4A). Both the three overwintering females and the reproductive four females that had been paired with the remaining overwintering males in the second generation laid fertilized eggs in addition to 4 out of 5 females of the third generation.

The proportion of brachypterous adults on the water surface was higher at the beginning than the end of April following overwintering ( $\chi^2$ -test between 4th and 24th April,  $P < 0.05$ ; Fig. 5).

## DISCUSSION

Diapause and migration are most closely associated when diapause sites and breeding sites are separated in insects [7]. Water striders are typical examples of this close association. Landin and Vepsäläinen [8] caught many flying long-winged



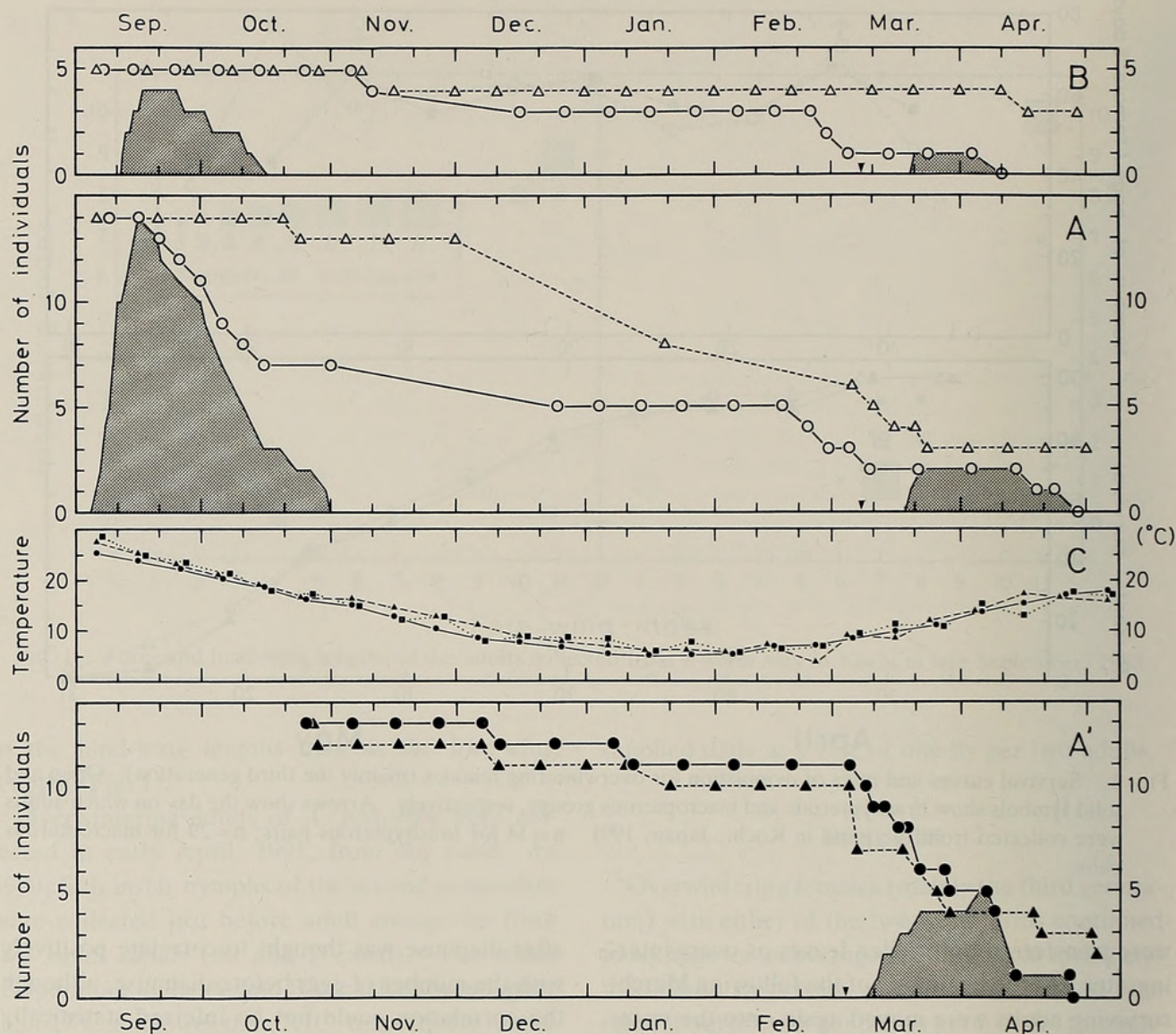


FIG. 3. Survival curves for adults in the second (A, B) and third (A') generations derived from A- (A, A') and B-canal (B). All individuals: macropterous. Circles, females; triangles, males. Shaded area shows the number of females which were laying eggs. Arrows indicate the days on which the water striders were transferred from fallen leaves to the water surface in 1991 (A, B) or 1992 (A'). The mean date of adult emergence was 29 August and 15 October in the second and third generations, respectively. C, Seasonal variations in air temperature in Kochi (circles) and Osaka (triangles, squares). The triangles and squares show the means for the first, middle, or last ten days of each month in 1990–1991 and 1991–1992, respectively. The circles indicate the means of the values for 30 years (1961–1990). The data of air temperature were gained by Osaka and Kochi Meteorological observatories.

adults of *Gerris argentatus* on the way from their diapause sites to water surfaces in a meadow on the shore of a lake in Finland. Their capture suggests that the macropterous adults of *G. argentatus* overwintered at sites far from water surfaces. In early spring, no late-awakening from diapause but the long distance between diapause and breeding sites is demonstrated in the case of macropterous adults of *A. paludum* by the following: macropterous adults appear on water surface later than

brachypterous adults (Fig. 5), macropterous adults show similar reproductive and survival processes to brachypterous adults (Fig. 2). Moreover, the two facts, the earlier appearance of brachypterous adults (Fig. 5) and the lack of flight ability in the brachypterous having very short hind-wing (Fig. 1), suggest that their diapause sites are near water surface, e.g. under logs or stones on the banks as is the case with *Aquarius remigis* [13].

A high rate of oviposition of more than 60 eggs



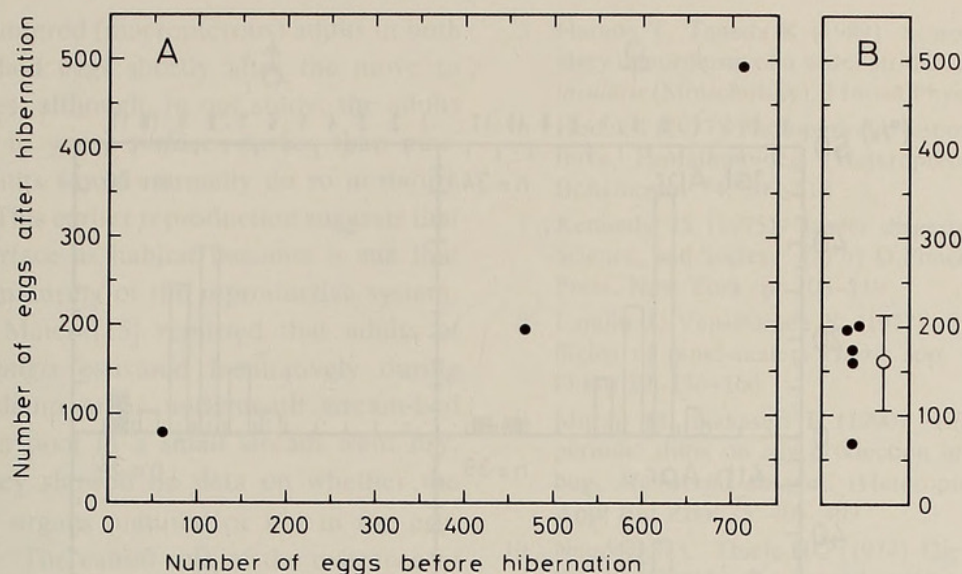


FIG. 4. The total number of eggs laid by each adult before or after overwintering in the second (A) and third (B) generations. The circle and bar in B indicate the mean and S.D., respectively.

per female per 5 days was recorded only during a part of the reproductive period of the first and second generations [4]. However, overwintering adults laid more than 60 eggs per female per 5 days throughout almost their entire reproductive period (Fig. 2). Overwintering adults of *A. paludum* also continue to show strong positive phototaxis for about 50 days in spring [3]. Harada showed experimentally that the experience of overwintering made the adults easy to show the strong positive phototaxis. The overwintering adults of *A. paludum* may be, physiologically, in a specific phase after overwintering. Spence [12] also reported that in some Canadian water striders, *Gerris pingreensis*, *G. comatus*, *G. buenoi*, and *Limnoporus dissortis*, diapause breeders showed higher reproductive rates in spring than direct breeders in summer. The experience of overwintering includes the experience of diapause as an internal condition, as well as exposure to low temperature and other winter-related environmental conditions. It is unclear which of these factors is the major one which induces a constant and high rate of oviposition in *A. paludum*.

Spence [12] reported that overwintered macropterous females of *G. pingreensis* had longer pre-oviposition periods than overwintered apterous females, and that their reproductive rate was lower than that of apterous females in early spring.

By contrast, there was no difference between the two wing forms in oviposition rates throughout the reproductive period after overwintering in *A. paludum* (Fig. 2). Why do macropterous adults of *A. paludum* continue to lay eggs at the same rate as brachypterous adults, even though macropterous adults seem to expend so much energy during their spring dispersal flight? They may histolyze their wing muscles and their resulting nutrients may be used for the maturation of eggs, as shown in *G. odontogaster* [1], and in *G. lacustris*, *G. lateralis*, and *G. argentatus* [14].

A high fecundity during the early adult stage was shown in the second generation and that is advantageous for many nymphs of the third generation who can develop into adults before winter comes [4]. The overwintered females of the second generation participated in the reproduction again in the following spring together with third generation females (Fig. 3). The fecundity of the second generation adults was not smaller than that in the third generation (Fig. 4), and moreover the surviving males in the second generation fertilized the eggs in the following spring. Therefore, it seems that diapause after reproduction in autumn and the resulting second reproduction during the subsequent spring are adaptive tactics for the second generation adults to bequeath a larger number of offspring.



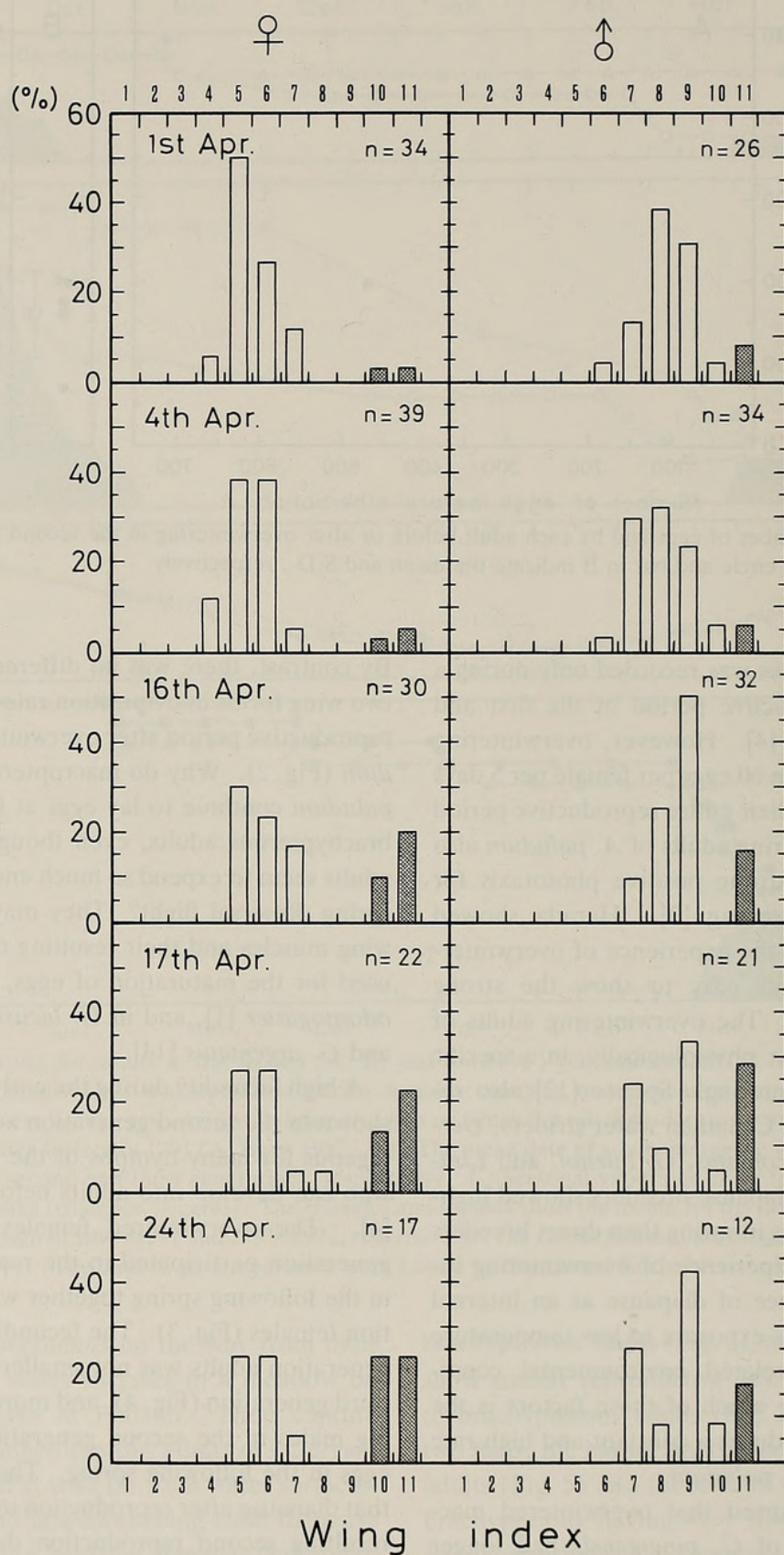


FIG. 5. The appearance of *Aquarius paludum* on the water surface of a pond in Kochi in early spring, 1988. Open bars, brachypterous adults; shaded bars, macropterous adults.



The overwintered (macropterous) adults in both generations laid eggs shortly after the move to water surfaces, although, in our study, the adults were moved to water surfaces earlier than macropterous adults would normally do so in nature (Figs. 3, 5). This earlier reproduction suggests that the water surface as habitat becomes a cue that induces the maturing of the reproductive system. Wilcox and Maier [15] reported that adults of *Aquarius remigis* estivated facultatively during summer in damp areas underneath stream-bed rocks when a pool in a small stream went dry. However, they showed no data on whether the reproductive organs matured or not in the estivated adults. The causal role of the existence of water surfaces in reproductive maturation should be investigated further experimentally on water striders in the future.

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