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Life History and Photoperiodic Responses of a Giant Water Strider, Aquarius elongatus Uhler (Heteroptera: Gerridae) 【Research report】

大水黽的生活史及光週期反應【研究報告】

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Abstract

The aims of this study were, first, to clarify the life history including voltinism of the giant water strider, Aquarius elongatus with field sampling and rearing experiments under quasi-natural conditions; and, second, to examine, with a laboratory experiment, the effects of photoperiods on the growth and reproductive characteristics of this species.
Two peaks in the number of collected adults were shown by overwintered adults in April to May and by the first generation adults in July and August. Larval growth occurred over a long period from May to September. The diapause posture was initially adopted by overwintering adults 3 months after emergence, from 22 October to 20 December. The diapause posture was discontinued during the end of March and the first half of April 2004. Adopting and discontinuing the diapause posture were synchronized with moving from the water surface to the diapause site underneath leaves and vice versa. The entire larval period under a short-day photoperiod of 12L: 12D was 40.0 days, and this was significantly shorter than that under a long-day photoperiod of 15.5L: 8.5D (of 49.5 days), because of the smaller size of the adults. Most of the adults which were kept under the short-day photoperiod, began to adopt the diapause posture within 100-160 days of emergence, which was 10-20 days earlier than those under the long-days.

摘要

本研究的目的，首先以野外取樣及在近似自然環境下飼養試驗的方法釐清水黽的生活史，包括一年幾個世代，其次用室內試驗去檢驗光週期對生長及生殖特性的影響。採集的成蟲呈現二個高峰，4月至5月是過冬的成蟲，而第一代的成蟲則出現在7月及8月。若蟲生長則經過一段長時間從5月至9月。休眠狀態發生在越冬的成蟲羽化後3個月後，從10月22日至12月20日。休眠會在2004年3月底及4月中結束，休眠狀態的開始是與從水面上移至在葉片下的休眠地點同步，而結束則剛好相反。整個若蟲期在12小時短日照的光週期環境下是40天，這比在15.5小時長日照下的49.5天顯著較快，原因可能是成蟲體型較小之故。大部分成蟲在短日照下，在羽化後100～160天內會開始進入休眠，比在長日照下早了10至20天。

Key words: Life history, reproduction, diapause posture, photoperiod, Aquarius elongatus
關鍵詞: 生活史、生殖、休眠狀態、光週期、大水黽

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Life History and Photoperiodic Responses of a Giant Water Strider, *Aquarius elongatus* Uhler (Heteroptera: Gerridae)

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ABSTRACT

The aims of this study were, first, to clarify the life history including voltinism of the giant water strider, *Aquarius elongatus* with field sampling and rearing experiments under quasi-natural conditions; and, second, to examine, with a laboratory experiment, the effects of photoperiods on the growth and reproductive characteristics of this species.

Two peaks in the number of collected adults were shown by overwintered adults in April to May and by the first generation adults in July and August. Larval growth occurred over a long period from May to September. The diapause posture was initially adopted by overwintering adults 3 months after emergence, from 22 October to 20 December. The diapause posture was discontinued during the end of March and the first half of April 2004. Adopting and discontinuing the diapause posture were synchronized with moving from the water surface to the diapause site underneath leaves and vice versa. The entire larval period under a short-day photoperiod of 12L: 12D was 40.0 days, and this was significantly shorter than that under a long-day photoperiod of 15.5L: 8.5D (of 49.5 days), because of the smaller size of the adults. Most of the adults which were kept under the short-day photoperiod, began to adopt the diapause posture within 100-160 days of emergence, which was 10-20 days earlier than those under the long-days.

Key words: Life history, reproduction, diapause posture, photoperiod, *Aquarius elongatus*

Introduction

Many insects inhabiting the temperate zone overwinter in the adult stage (Tauber *et al.*, 1986; Danks, 1987). They enter reproductive diapause and show several correlated characteristics like behavioral changes, heat shock protein levels related to higher survival in winter, lipid deposition on the skin cuticle, metabolic depression, cold and drought hardiness, and changes in flight

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propensity which is the so-called "diapause synme" (Danlinger *et al.*, 1972; Tauber *et al.*, 1986; Hodkova and Hodek, 1997; Yucum *et al.*, 1998; Harada, 2003a; Harada *et al.*, 2003). For insects living in the cool temperate zone, the summer season is short for reproduction and growth of the second offspring generation, and it can be advantageous for the offspring to automatically enter diapause after emergence (obligatory diapause). On the other hand, for other insect living in the warm temperature zone, a relatively long summer season is experienced, and the insect decides whether it reproduces or enters diapause, alternatively, based on seasonal information such as photoperiod, temperature. and precipitation (facultative diapause).

However, even in the warm temperate zone, half-voltinism or monovoltinism is shown by several insects. For example, a complex 2-year life cycle with three types of diapause was reported in a subtropical cockroach, *Symploce japonica* Shelford: a winter diapause in mid-nymphal instars, a summer diapause in later nymphal instars, and a reproductive diapause in the adult stage were reported (Tanaka and Zhu, 2003). Five common species of water striders in the Gerridae inhabit Kochi, Japan (33°N) which is located in a critical area between warm temperate and subtropical zones. Even in such a warm place, *Gerris graciricornis* Horváth and 70-80% of individuals of *G. latiabdominis* Miyamoto automatically enter reproductive diapause after adult emergence in June or July, irrespective of the photoperiod and temperature in the larval and adult stages (Harada and Taniguchi, 2001; Harada, 2003b). *Aquarius paludum* Motschulsky and *G. nepalensis* Distant enter diapause only when they are grown under a short-day photoperiod (i.e., they exhibit facultative diapause) (Harada, 2003b).

The remaining common species in Kochi is a giant water strider, *Aquarius elongatus* Uhler. This species prefers to inhabit storage ponds near hills and mountains (Harada, unpublished data). Water temperature in these storage ponds is relatively stable at around 20°C, because groundwater derived from the hills and mountains is supplied to the ponds. Individuals of *G. gracilicornis* also prefer such storage ponds and share the habitat with *A. elongatus* (Harada and Taniguchi, 2001).

Hayashi (1985) observed the mating behavior of *A. elongatus* and pointed out alternative strategies of territorial and non-territorial reproductive behaviors according to individual densities, i.e., reproductive males adopt a "territory" when the population density is low; while no territory is adopted under a high population density. Two different kinds of wave signals by males were also reported, one to attract females inside his territory, the other to lead to the ovipositing substratum such as leaves on water surface (Hayashi, 1985). However, there has been no detailed research on the life history of *A. elongatus* so far.

The monovoltine water strider, *G. gracilicornis,* does not respond to photoperiod and temperature for diapause induction (Harada and Taniguchi, 2001). However, diapause development of this species was effectively accelerated by exposure to a short-day photoperiod of 10L: 14D and 1 week exposure to a low temperature of 7°C during the long obligatory diapause period of 220-240 days (Harada and Taniguchi, 2001).

The aims of this study were, first, to clarify the life history including voltinism of the giant water strider, *A. elongatus,* with field sampling and rearing experiments under quasi-natural conditions; and, second, to examine, using laboratory experiments, the effects of photoperiod on the growth and reproductive characteristics of this species.

Materials and Methods

Field samplings

Timed-catch samplings were conducted every week in April to October 2004 with a round net (30 cm in diameter) with a handle 1.5 m long to survey the entire water surface of a small storage pond (165 m^2) on the campus of Kochi University located in Kochi (33°N), Japan. This pond was filled with groundwater derived from the Kagami River and the water temperature was relatively stable at 20 ± 3°C throughout the year. The round net was used to sweep the water surface 80 times in 10 min at every sampling. The number of larvae in each instar and the adult number were counted, and all adults collected were marked with different colored pens on their back for individual identification. All adults marked or identified were immediately released back at the original place on the pond.

Rearing experiment under quasi-natural conditions

Two pairs of overwintered females and males of *A. elongatus* were collected from another storage pond in Kochi, at the beginning of May 2003 and kept under quasi-natural conditions. The first 214 eggs from many eggs laid by these two females were used for the rearing experiment there. Hatching out and growth were recorded under quasi-natural conditions. The first instar larvae were kept at a density of 40-50 individuals per aquarium (65 × 35 × 30 cm) filled with water. Density was controlled by gradually decreasing the number to 10 individuals per aquarium by the the last instar stage. After emergence, each of paired female and male was moved to another aquarium (35 × 25 × 18 cm). Adults of the offspring generation which survived were reared to the next summer under quasi-natural conditions. Adults of *Lucilia illustris* (Meigen) were supplied as food, at a rate of one fly per five first and second instars, one fly per three third and fourth instars, one fly per two fifth (last) instars and one fly per one adult water strider per day. Growth of larvae and whether adults reproduced or not were recorded till the beginning of October.

In October, adults were moved to another aquarium (35 × 25 × 18 cm) into which soil was placed on one half and water on the other half of the bottom of it. On the soil portion, one fallen leaf (17 × 12 cm) was placed for an overwintering site. Locations (on the water, on the open land, or under the leaf) where the striders were seen, and whether they adopted the diapause posture (Harada, 1994) were recorded. When all adults which overwintered under the leaves, began to appear on the water surface the next spring, they were transferred back to the former aquaria filled with water. One paired female and male were kept in the aquarium. The number of eggs laid by each female was counted every day.

The number of surviving individuals was recorded throughout the rearing period from egg to reproductive stage the following spring and summer.

Rearing experiment to examine the photoperiodic response

The remaining eggs laid by the two pairs of overwintering adults were used for the laboratory experiments. First instars which hatched out from these eggs were transferred to one of two photoperiodic conditions of either 15.5L: 8.5D or 12L: 12D, at 20 ± 2ºC within 24 h of hatching. Survival and the larval instar were recorded every day. Survival, mating behavior, and oviposition were recorded every day after adult emergence. Whether they adopted the diapause posture was recorded every 10 days for each adult.

Statistical analysis

Data were statistically analyzed using

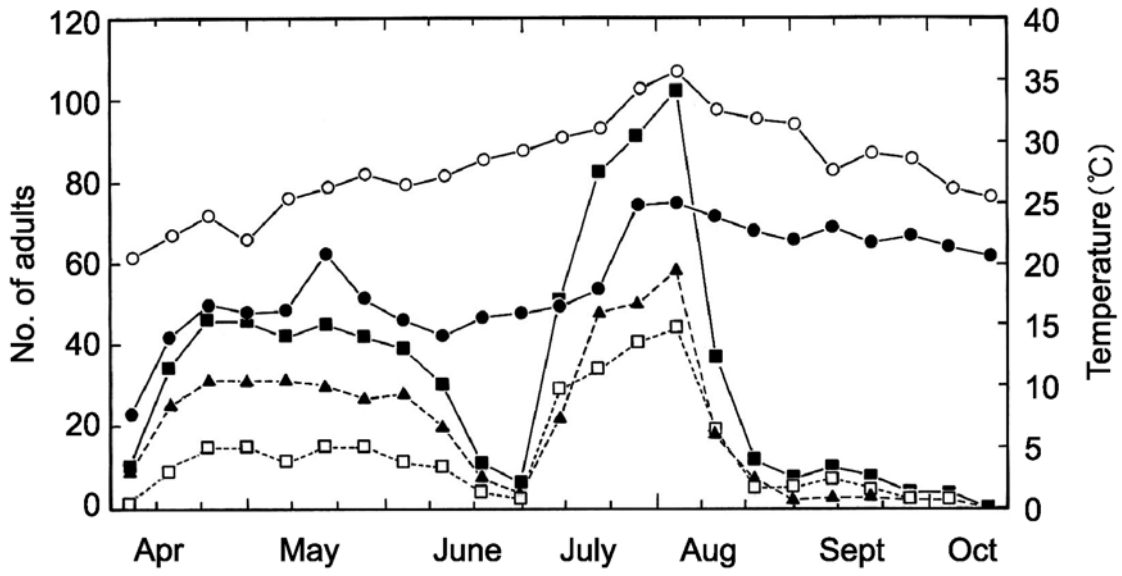

Fig. 1. Seasonal variation in the collected number of adults of the giant water-strider, *Aquarius elongatus.* The X- and left Y-axes show the number of adults collected. The X- and right Y-axes show the air temperature (°C). Open and solid circles, maximum and minimum daily temperatures in a given seasonal day, respectively; solid triangles, females; open squares, males; solid squares, total number of individuals.

SSPS version 11.0 for personal computers. Pearson's analysis and the Mann-Whitney U-test were used for the data from the field samplings. Pearson's correlation test was performed for the data from the rearing experiment under quasi-natural conditions. The Mann-Whitney U-test and two-way or one-way ANOVA were administered for analysis of the data from the rearing experiment to examine the photoperiodic response.

Results

Field samplings

Two peaks in the number of collected adults were shown by overwintered adults in April to May (Pearson's analysis, r = -0.970, p = 0.001, n = 6, from June 23 to July 30) and by first generation adults in July and August (Peason's analysis, r = 0.954, p = 0.012, n = 5, from June 23 to July 30) (Fig. 1). Overwintered adults and firtst generation adults newly inhabited the small pond in April and July, respectively (Fig. 2). Larval growth occurred over a long period from May to September (Fig. 3). Adult emergence occurred mainly in the latter half of June and in July (Figs. 1, 3). The number of times each individual was collected was 4.71 on average (SD = ± 2.74) for the overwintered generation adults which was significantly more than that for the first generation adults (2.52 ± 1.33, Mann-Whitney U-test, Z = 6.002, p < 0.001) (Fig. 4).

Rearing experiment under quasinatural conditions

Overwintered adults laid eggs during May 7-22, and the first instars hatched out of eggs over the following 2 weeks (Fig. 5). Larval development occurred mainly in June and the first half of July, then adults of the first generation

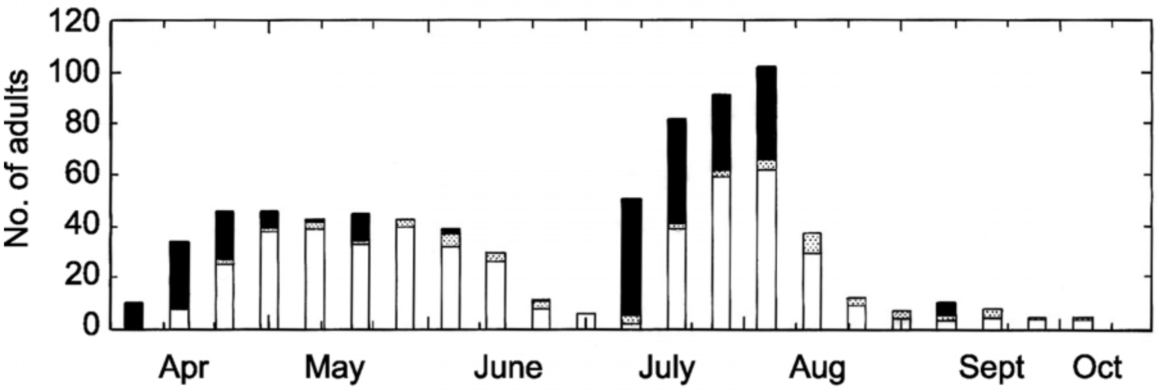

Fig. 2. Seasonal variation of newly inhabited adults of *Aquarius elongatus* in a small pond. From the beginning of April, individuals newly caught were marked with paint for individual identification. Black columns, the number of individuals newly caught; white ones, caught currently and also 10 days before; columns with dots, caught once 20 days previous or before and once again currently.

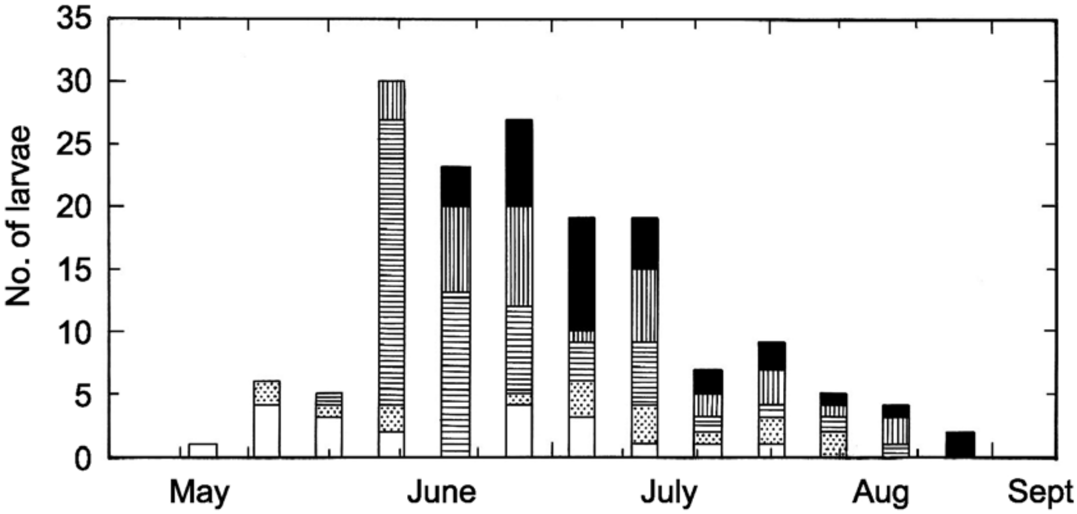

Fig. 3. Seasonal variation in the number of collected larvae of *Aquarius elongatus* with timed-catch samplings. First instars, white columns; second instars, columns with dots; third instars, columns with horizontal lines; fourth instars, columns with longitudinal lines; and fifth instars, black columns.

emerged July 8-22 (Fig. 5). The diapause posture began to be adopted 3 months after emergence, on October 10-December 28 (Pearson's correlation test between % behavioral diapause and days past, r = 0.991, $p < 0.001$, n = 8) (Fig. 6). The diapause posture was discontinued between March 17 and the first half of April, 2004 (Pearson's correlation test between % diapause posture and days past, r = -0.993, p = 0.007, n = 7) (Fig. 6). Adopting and discontinuing the diapause

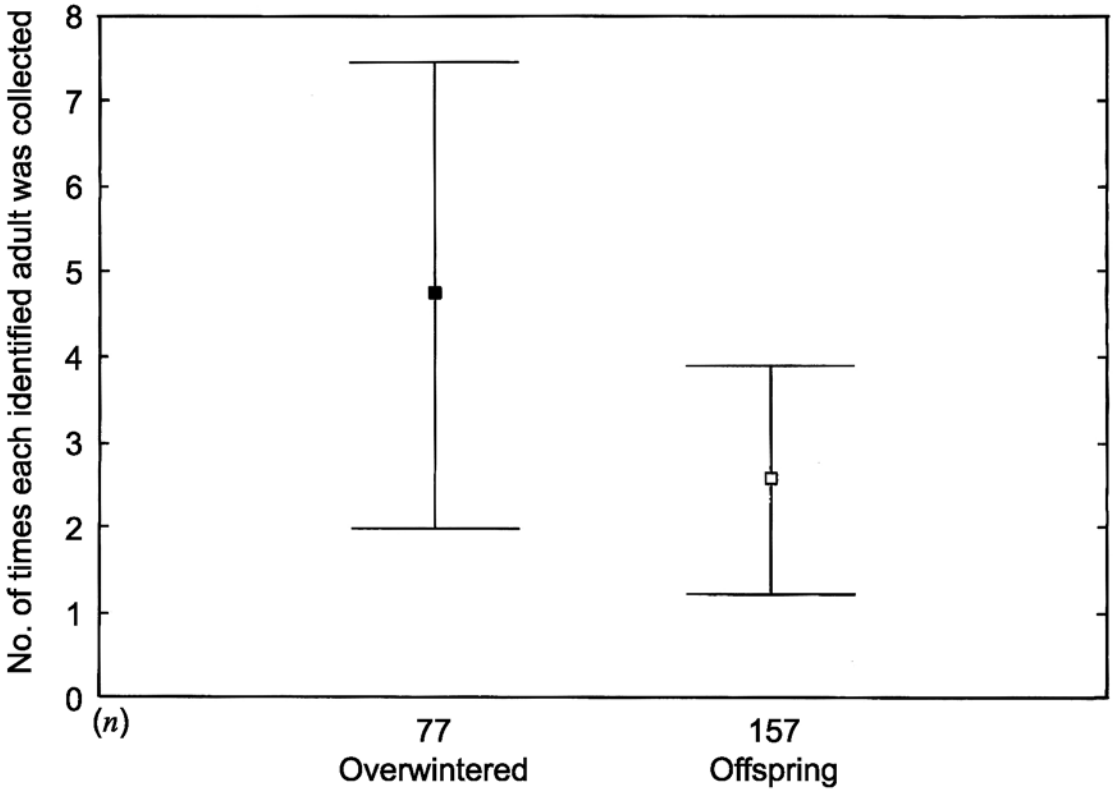

Fig. 4. Times when each identified adult of the overwintered and offspring generations were caught. Mean ± SD (*n*), 4.71 ± 2.74 (77) times for overwintered adults; 2.53 ± 1.33 (157) for offspring adults.

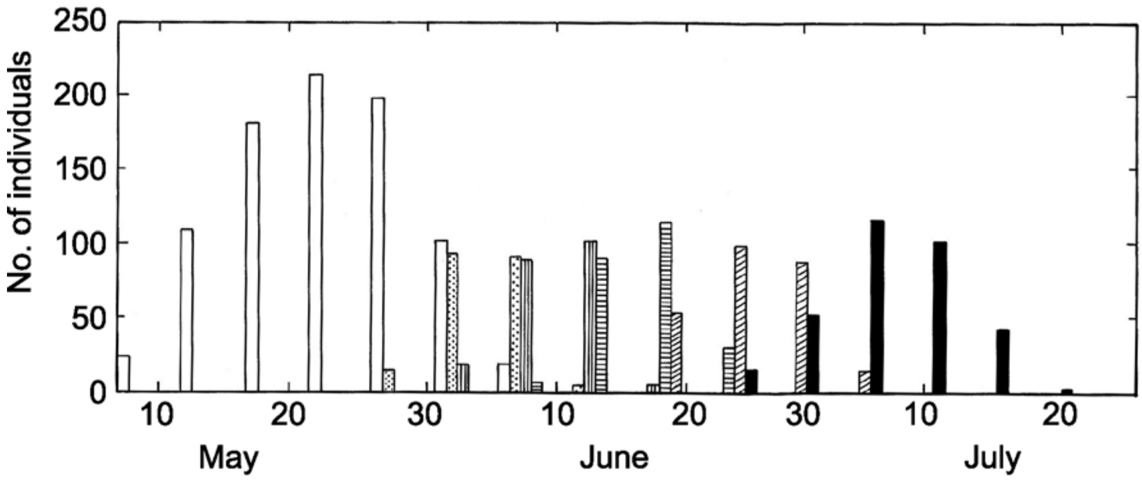

Fig. 5. Embryonic and larval development of the offspring generation of *Aquarius elongatus* under quasi-natural conditions. Embryos, white columns; first instars, columns with dots; second instars, columns with longitudinal lines; third instars, columns with horizontal lines; fourth instars, columns with slanted lines; and fifth instars, black columns.

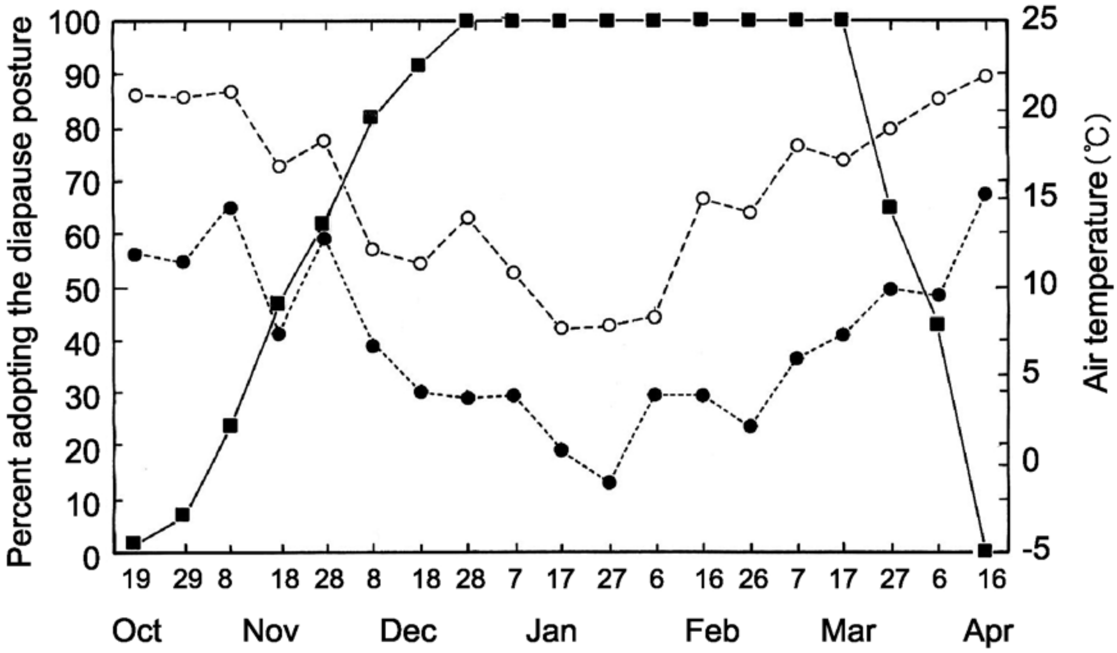

Fig. 6. Seasonal process of adopting and discontinuing the diapause posture by *Aquarius elongatus* during October 2003 to April 2004, under quasi-natural conditions. Squares, percent adopting the diapause posture; open and solid circles, daily maximum and minimum air temperatures in a given seasonal day, respectively.

posture were synchronized with moving from the water surface to the diapause site underneath leaves and vice versa, respectively (Pearson's correlation test between % diapause and % on water bodies, r = -0.98, $p < 0.001$, n = 8 in October 19 to December 28, r = -1.00, p = 0.001, n = 4, in March 15 to April 15) (Figs. 6, 7). During overwintering from mid-December to the end of the following March, 80% of overwintering adults had died (Fig. 8). Four females survived and laid 420.5 eggs on average during the next spring and summer.

Rearing experiment to examine the photoperiodic response

Larval periods were significantly shortened under the short-day photoperiod from the second instars on (Table 1). During the fourth and fifth instars, larval periods were significantly and extremely shortened under short-days compared with those under long-days (Table 1). The entire larval period under the short day photoperiod was 40.0 days and significantly shorter than the 49.5 days under the long-day photoperiod (Mann-Whitney U-test, Z = -10.92, $p < 0.001$). Molting to fifth instar and adult stage under the short-day photoperiod seemed to occur earlier than that under the long-day photoperiod, because the body sizes of adults grown under the short-days were significantly smaller than those under the long-day photoperiod (two-way ANOVA, effects of photoperiod and sex on body size; photoperiod, df = 1, F = 46.17, $p < 0.001$; sex, df = 1, F = 13.42, p = 0.001; one-way ANOVA, effect of photoperiod: df = 1, F = 32.66, $p < 0.001$) (Table 2).

Most of the adults which were kept under the short-days, began to adopt

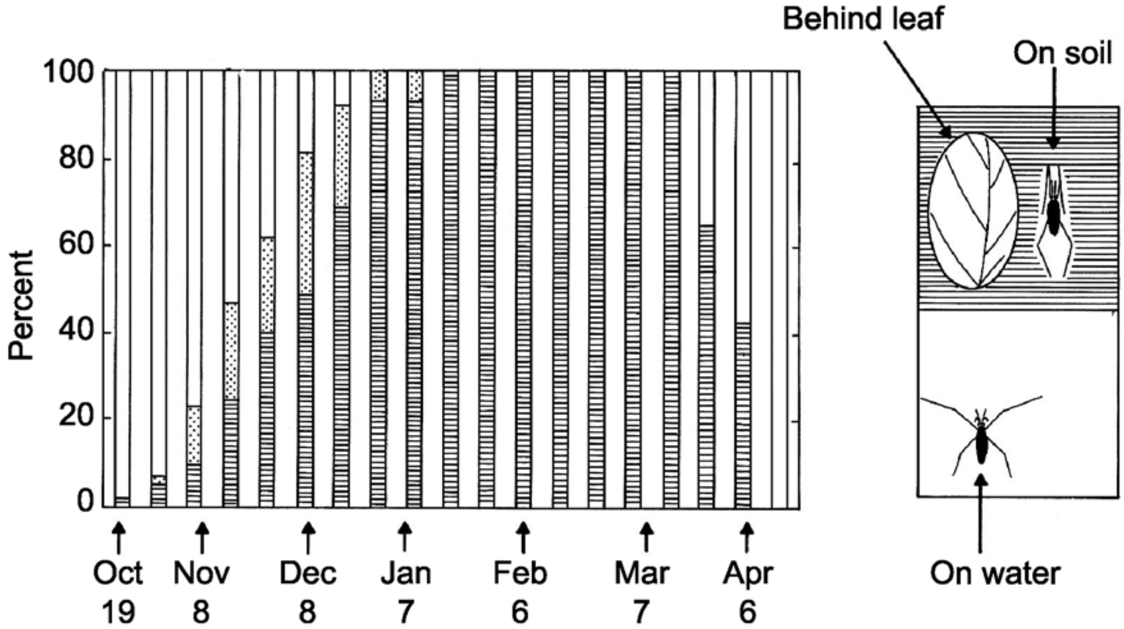

Fig. 7. Moving of adult *Aquarius elongatus* between the water surface and diapause place under a fallen leaf in fall and winter 2003 to the following spring. White bars, percent on water without adopting the diapause posture; bars with dots, percent on open soil adopting diapause posture; bars with horizontal lines, percent adopting the diapause posture under a leave.

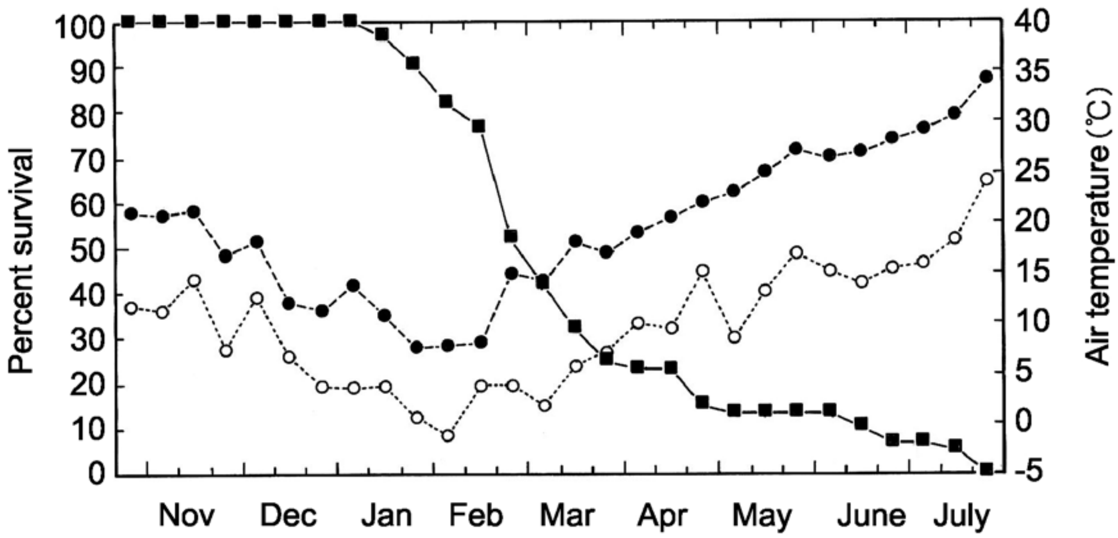

Fig. 8. Survival process of adult *Aquarius elongatus* during overwintering under quasi-natural conditions in Kochi, Japan from mid-October 2003 to the following July. Squares, percent survival; solid and open circles, daily maximum and minimum air temperatures in a given seasonal day, respectively.

Table 1. Effects of photoperiod on the larval period in the giant water strider, *Aquarius elongatus*

Larval stage	Photoperiod	Larval period (days)		
		Mean ± SD (*n*)	Mann-Whitney	U-test (LD vs. SD)
			z	*p*
1st instar	15.5L: 8.5D	5.98 ± 1.19 (177)		
	12L: 12D	5.80 ± 0.54 (138)	-0.643	0.52
1st -2nd instars	15.5L: 8.5D	11.55 ± 1.97 (168)		
	12L: 12D	10.59 ± 1.31 (110)	-4.143	< 0.001
1st -3rd instars	15.5L: 8.5D	18.33 ± 1.54 (145)		
	12L: 12D	17.76 ± 1.46 (95)	-3.568	< 0.001
1st -4th instars	15.5L: 8.5D	31.27 ± 1.67 (116)		
	12L: 12D	26.32 ± 1.81 (82)	-11.268	< 0.001
1st-5th instars	15.5L: 8.5D	49.52 ± 1.75 (88)		
	12L: 12D	39.96 ± 1.37 (70)	-10.922	< 0.001

Table 2. Effects of photoperiod during the larval period on adult body lengths in the water strider, *Aquarius paludum*

Photoperiod	Mean ± SD (*n*) of body lengths (mm)	
	Females	Males
15.5L: 8.5D	23.64 ± 0.64 (8)	22.81 ± 0.48 (8)
12L: 12D	22.15 ± 0.47 (8)	21.43 ± 0.79 (8)

diapause-posture in 100 to 160 days after emergence, earlier by 10-20 days than those under the long-days (Mann-Whitney U-test, $p < 0.001$) (Fig. 9).

Discussion

Monovoltine life history of *A. elogatus*

Based on the field sampling and rearing experiment in this study, *A. elongatus* is obviously monovoltine in Kochi (33°N), Japan. They enter a long reproductive diapause after emergence, and it lasts from July to the following March. However, they do not leave the water surface until late October to the beginning of December in Kochi. On average, they stay on the water surface for 4 months in reproductive diapause. Overwintering adults of *A. elongatus* mainly left the sampling pond in August (Fig. 1). However, they moved from the water surface to the diapause site 3 months later in November (Fig. 7). What is the ecological meaning of this gap of 3 months? It can be speculated that overwintering adults migrate to another water surface at a higher elevation in order to avoid high temperatures and stay there for 3 months before moving to the overwintering sites on land.

Comparative life history of *A. elongatus* with other monovoltine species of *Gerris gracilicornis* Harváth and *G. latiabdominis* Miyamoto

Three common monovoltine species, *A. elongatus, G. gracilicornis and G. latiabdominis* inhabit Kochi, Japan (Taneda and Harada, 1987; Harada and Taniguchi, 2001; Harada, 2003b). Adults of the first offspring generation of the two relatively small species, *G. gracilicornis* (10.5-14.5 mm long) and *G. latiabdominis* (8.5-11 mm) emerge in June (Taneda and Harada, 1987; Harada and Taniguchi, 2001), while adults of the new generation of the giant water strider, *A. elongatus*

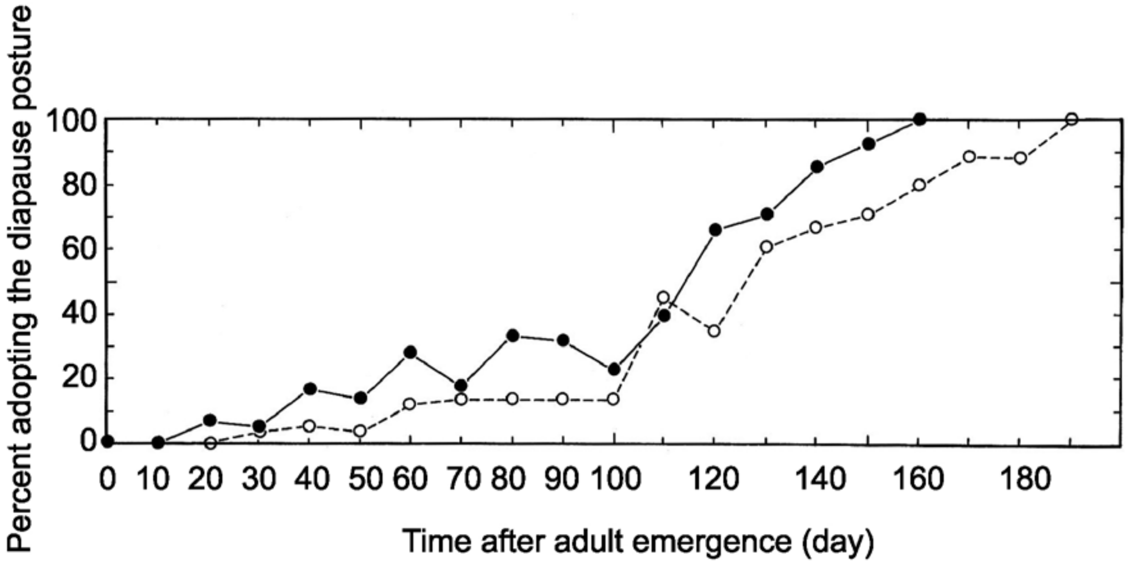

Fig. 9. Effects of photoperiod on adoption of the diapause posture in *Aquarius elongatus*. Open circles and broken lines, 15.5L: 8.5D; solid circles and lines, 12L: 12D.

emerge 1 month later than the other two species. Late and slow growth in May to September seems to be characteristic of the giant species, because larvae of *A. elongatus* are also much larger and more competitive than those of *G. gracilicornis* which share the storage ponds filled with groundwater derived from the surrounding hills and mountains. Adults of *G. latiabdominis* enter reproductive diapause in July, which is coincident with the timing when they leave the water bodies and disperse to the diapause sites on land (Harada, 1991), because *G. latiabdominis* mainly inhabits paddy fields which are only filled with water at the end of March to July in Kochi. Long stays on the water surface even after entering reproductive diapause were shown by *A. elongatus* (Fig. 7) and *G. gracilicornis* (Harada, 2003b) in Kochi. Such long stays are very advantageous for overwintering adults to capture food on the water surface, because they suffer great energy losses due to fundamental metabolism before winter comes in warm temperate zone. On the other hand, *G. latiabdominis* adopts very deep and long-sustained (8 or 9 months from July to the following spring) reproductive and also behavioral diapause systems which were well constructed to maintain high energy-consuming and high-drought-resistant abilities (Harada, 1991, 2003b).

Ecological significance of the photoperiodic responses

The short-day photoperiod caused the molting to the fifth instar or adult stage to occur earlier creating smaller adults of the giant water strider, *A. elongatus* (Tables 1, 2). In contrast to a butterfly, *Limentis archippus* Cramer, a short-day photoperiod promoted slowed larval growth and formation of hibernacula during the third instar, while continuous rapid development to the adult was observed when subjected to a long-day photoperiod (Clark and Platt, 1969). Moreover, starving of final-instar larvae (fifth instar) of a lepidopteran species, *Cnephasia jactatana* Walker, in responce to a long-day photoperiod of 18L: 6D and resulted in decreased duration of the fifth instar and earlier pupal emergence (Ochieng'-Odero, 1991). What is the ecological significance of the earlier molting of *A. elongatus* caused by the short-day photoperiod ?

The short-day photoperiod also promoted earlier adoption of the diapause posture in *A. elongatus* (Fig. 7). Overwintering adults continued to lay eggs from May to August (Fig. 3). Therefore, part of the first offspring generation individuals are produced relatively late in the season in August and September in Kochi. The earlier molting and earlier adoption of the diapause posture caused by the short-day photoperiod are very significant, because they have sufficient time to become adults which can successfully overwinter.

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大水黽的生活史及光週期反應

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摘　　要

本研究的目的，首先以野外取樣及在近似自然環境下飼養試驗的方法釐清水黽的生活史，包括一年幾個世代，其次用室內試驗去檢驗光週期對生長及生殖特性的影響。採集的成蟲呈現二個高峰，4 月至 5 月是過冬的成蟲，而第一代的成蟲則出現在 7 月及 8 月。若蟲生長則經過一段長時間從 5 月至 9 月。休眠狀態發生在越冬的成蟲羽化後 3 個月後，從 10 月 22 日至 12 月 20 日。休眠會在 2004 年 3 月底及 4 月中結束，休眠狀態的開始是與從水面上移至在葉片下的休眠地點同步，而結束則剛好相反。整個若蟲期在 12 小時短日照的光週期環境下是 40 天，這比在 15.5 小時長日照下的 49.5 天顯著較快，原因可能是成蟲體型較小之故。大部分成蟲在短日照下，在羽化後 100～160 天內會開始進入休眠，比在長日照下早了 10 至 20 天。

關鍵詞：生活史、生殖、休眠狀態、光週期、大水黽。