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Global warming and changes in life history traits from 1995 to 2015 in the water strider *Aquarius paludum* (Fabricius)

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ABSTRACT

This study aims to examine the following three issues concerning the impact of global warming on the populations of the water strider *Aquarius paludum* in the Kochi-Nankoku area (33°30'N) of Kochi prefecture, Japan, based on the data collected from 2012 to 2015. 1. Has the number of generations increased? 2. Has aestivation appeared in summer adults? 3. Have overwintering adults stopped dispersing between the water surface and overwintering land sites which had been located at warm places on lands (for example under the leaves) far away from water habitats? Instead, have they overwintered on the shores of water habitats, because these habitats were warm in winter in recent years? In response to the first question, sampling data showed that the number of generations may have increased from three (1989-2002 strains) and four (2004-2008) to five (2009-2015) per year in Kochi (33°N). In response to question 2, some adults (21.6-30.0%) adopted aestivation in June-August in 2012-2014. However, maximum daily summer temperatures were lower than usual in 2014, and no adults adopted aestivation in 2015. In response to question 3, the ratio of adults with well-developed flight muscles decreased from 45% in 1995 to 24-36% in 2009-2013, 8.6% in 2014 and finally 0% in 2015 in overwintering adults collected from the field during fall. High summer precipitation and lower maximum summer temperatures in the previous year seemed to decrease their tendency to disperse by flight in the following year of 2015. Most overwintering adults appeared to have stopped migration between water bodies and overwintering sites on lands far from the water bodies, and overwinter near the shore instead in 2015. The use of *Aquarius paludum* as a biological indicator (a biological model) may be possible in the future, as this species can respond and change their life history traits quickly in accordance with the global change.

KEYWORDS: adult diapause, aestivation, dispersal, long fore-wing and short hind-wing, semi-aquatic bug, voltinism

INTRODUCTION

Insects other than Heteroptera have shown a wide variety of responses to anthropogenic changes in temperature caused by global warming [1, 2]. There have been generalizations about how insects' population adapts to climate change and how population dynamics and phenology change. The impact of global warming on the lives of insects has been discussed in several studies to date [3-10].

The impact of global warming on insects can possibly be categorized into four as follows. The first is a northern shift in distribution [11]. The second is mismatches between herbivorous insects and their host plants including temporal mismatches in pollination interactions between plants and pollinators [9, 12]. For example, a pronounced mismatch of the current niche spaces has been exhibited by the butterfly, *Boloria titania* and its host plant, *Polygonum bistorta* [7]. Another example is how early eclosion

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of cotton ball worms due to temperature warming has led to the recruitment of more larvae in the first generation and damage to wheat at early growing stages [13]. Recently, Harvey [14] reviewed the potential effects of climate warming, in particular heat waves, on multi trophic interactions involving plants, herbivores, parasitoids and hyper parasitoids. The third category is the impact on the relationship between insect vectors and the pathogens of diseases such as malaria [15, 16] and West Nile fever [17] and modeling for vector-borne infections in general [18], leading to spreading of diseases to new latitudes and altitudes, and sometimes to large cities as the result of the heat island effect. Another example of the meltdown of mutualism between insects and bacteria was shown by Wernegreen [19].

The fourth category is the modification of life history traits to fit into new warming meteorological conditions. For example, the voltine-number may increase due to a prolonged season of reproduction and larval growth [20]. As another example, the ovipositing season for a cicada, *Cryptotympana facialis* has advanced from post-rainy season (beginning of 20th century) to mid-rainy season (late 20th century) as an adaptation to drying of the soil used for oviposition due to global warming [21]. In bees of the genus *Osmia*, the duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures that have changed due to global warming [22]. In an aquatic damselfly, *Ischnura elegans*, a warmer winter (8 °C) resulted in higher winter survival and growth rates compared to the cold winter (4 °C) commonly experienced by former European high-latitude populations [23]. As another unique effect of global warming, warming enhances dropping behavior of an aphid from the host plant [24]. It was suggested that dropping is behavioral thermoregulation to avoid heat stress, as the dropped aphids were still able to control their muscles in the hidden and lower temperature sites near the ground, prior to knockdown by heat.

Aquarius paludum (Fabricius) is a water strider inhabiting fresh water bodies and included in Gerridae, Heteroptera [25]. This species is distributed over a wide area of the Palearctic zone from England to Japan (western and eastern limits) and from the southern part of Siberia to India (northern and southern limits) [26]. Photoperiodic responses of the Kochi (33°30′N) population of *A. paludum* were examined for wing-form determination and induction of adult diapauses in 1989-1991 [25]. Short-days induced 100% long-winged and 100% diapause adults, whereas long-days induced 60% short-winged and 100% reproductive adults. The critical photoperiod for diapause induction was 13 h light-11 h dark (13L-11D) and for wing-form determination it was 13.75L-10.25D under constant photoperiods [25]. The critical values shifted to longer values of 15L-9D for wing-form and 14L-10D for diapause under gradually shortening photoperiods [25]. Short-days promote high flight propensity and keep flight muscles of insects matured, whereas long-days during the larval stage inhibit flight propensity and enhance flight muscle histolysis before the 40th imaginal day [27]. Moreover, increasing photoperiods even in the range beneath the critical photoperiod lead to less flight activity and promote flight muscle histolysis [27]. The response to changing photoperiods (both decreasing and increasing) disappeared completely and the critical photoperiods for wing-form determination and diapause induction were shortened by more than 30 minutes in 1999-2002 [28].

Sampling studies showed that the number of generations has increased from three (1989-2002 strains) to four or more (2004-2008) per year in Kochi-Nankoku populations (33°30′N) [29]. The extent of photoperiodic response for diapause induction was diminished for the Kochi-Nankoku population [29]. In 2009 and 2010, samplings indicated that the number of generations in the Kochi-Nankoku population appears to reach five [30]. However, it is unclear whether the generation number of five is permanent and also occurred in 2012-2015.

Examinations of ovaries and testes in 2008-2011 seem to indicate that aestivation was being adopted by some adults of both sexes in the Nankoku-Kochi population [29, 30]. It is unknown whether partial aestivation continued in 2012-2015.

At least 60% of overwintering adults collected from the field during fall from 2008 to 2011 no longer had flight muscles, probably as a result of histolysis [29, 30]. However, it is not clear whether the lack of flight between water bodies and overwintering sites on land were temporary or permanent: same was the case in 2012-2015.

In the present study, we aimed to answer the above three questions in relation to whether changes in reproductive and dispersal traits in accordance with global warming continued in 2012-2015 in the Kochi-Nankoku region (33ºN).

MATERIALS AND METHODS

Samplings

Every 2 weeks from January to December in 2012-2015, timed-catch sampling was performed in an agricultural waterway, with a width of about 2 m located in the critical area between Kochi City and its eastern neighbor, Nankoku City (33°31′N, 133°36′E), that is used for supplying water to paddy fields. One hundred sweeps for 40 min. were performed in each timed-catch sampling using a 30 cm diameter round net with a 1 m long stick. Samples were released soon after the number of larvae with each of the five instars, and adults specimens of each sex were counted and wing length in each adult specimen was measured. More than 10 pairs of adults were collected from the Kochi-Nankoku population but more than 30 m far from the sampling site and taken to the laboratory for dissection to examine the reproductive and dispersal organs (ovaries and testes, flight muscles).

Flight muscle rank, melanin deposition rank in alinotum and reproductive diapause

There are three ranks in the extent of flight muscle development (1: completely undeveloped or completely histolysed; 2: partway through development or histolysis; and 3: well developed and functional for flight) according to the criteria described by Inoue and Harada [27], Harada *et al.* [31] and Harada and Nishimoto [32]. It was judged whether adults had entered reproductive diapause based on the maturation of reproductive organs on the 30th day after emergence. If a female had laid no eggs during the first 30 days after emergence and, in addition, had no mature oocytes on the 30th day, she was judged to have entered reproductive diapauses [25]. Estimation of an index of testes volume was performed using the formula, [(diameter of testis x 0.5)^{2}x π x testis length, mm^3] [32]. If a male showed a testes volume index (average of right and left testes) of less than 0.10 mm^3 on the 30th day after adult emergence, he was judged to be in reproductive diapause [29]. Accumulation of the black pigment melanin on alinotum, another cuticle plate underneath the middle-thorax plate, was expressed as five ranks (1 and 2: teneral mainly <10 days after the adult emergence; 3 and 4: more than 10 days after emergence; and 5: overwintered adults that had broken diapause in spring) (Photo 1).

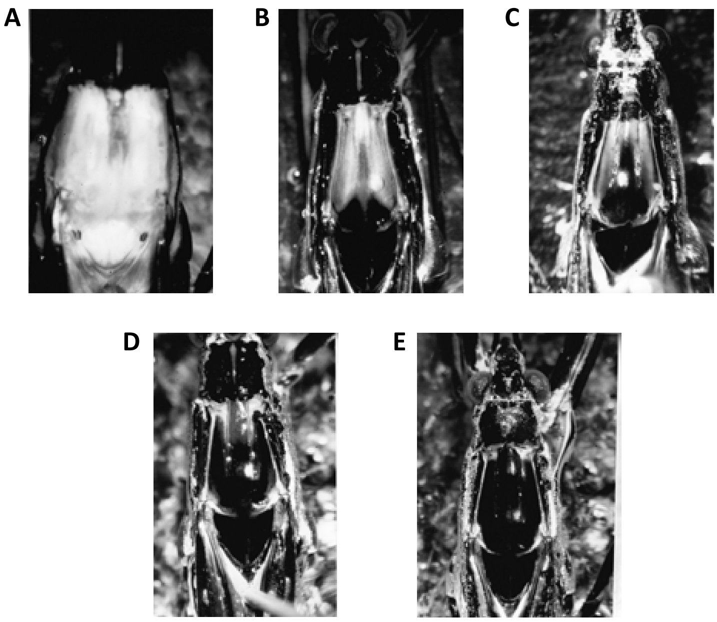

Photo 1. Melanin deposition index of alinotum plate in the meso-thorax of adult individuals of *Aquarius paludum.* 1 and 2: teneral within 10 days after adult emergence; 3 and 4: after 10 days; 5: individuals after overwintering under reproductive diapause.

Statistical analysis

SPSS (12.0 J for windows) software was used for statistical analysis. Mann-Whitney U-tests were used for the analysis of daily maximum temperatures and daily precipitation in summer between 2013 and 2014. The ratios of fifth instars in the two continuous samplings were compared using χ^2 test when new adult emergences seem to occur (Table 1). Adults with no mature oocytes (Table 2) in the samples were compared between August and surrounding seasons using χ^2 tests. The ratios of short- (or long-) wings and flight muscle ranks were also compared among seasons using χ^2 tests.

RESULTS

Number of generations per year

In 2012, the number of generations decreased to four (Figure 1A), likely due to the rapid decrease

Table 1. Results of χ^2-test for two samplings when the ratio of number of 5th instar larvae was decreased; that is the timing of new generation recruitment in 2012-2015.

2012					
	1st generation	**2nd generation**	**3rd generation**	**4th generation**	**5th generation**
	(May-June)	(June)	(September)	(Oct-Nov)	-
χ^2-value	8.076	5.324	1.684	4.311	-
df	1	1	1	1	-
P-value	0.04*	0.021*	0.194	0.038*	-
2013					
	1st generation	**2nd generation**	**3rd generation**	**4th generation**	**5th generation**
	(May-June)	(July)	(September)	(October)	(November)
χ^2-value	52.782	19.223	8.511	39.235	0.522
df	1	1	1	1	1
P-value	<0.001***	<0.001***	0.004**	<0.001***	0.470
2014					
	1st generation	**2nd generation**	**3rd generation**	**4th generation**	**5th generation**
	(June)	(July)	(August)	(September)	(October)
χ^2-value	61.602	1.939	9.923	2.77	37.86
df	1	1	1	1	1
P-value	<0.001***	0.164	0.002**	0.096	<0.001***
2015					
	1st generation	**2nd generation**	**3rd generation**	**4th generation**	**5th generation**
	(May-June)	(July)	(August)	(October)	(November)
χ^2-value	48.038	1.322	9.589	38.867	38.867
df	1	1	1	1	1
P-value	<0.001***	0.250	0.002**	<0.001***	<0.001***

*: 0.05>P>0.01, **: 0.01>P>0.001, ***: 0.001>P

Table 2. Results of χ^2-test between the seasons when adults in aestivation were included in the seasons before and after the "aestivation" season in 2013-2015 (No data in 2012).

2013			**2014**			**2015**		
(Jul. vs Jun plus Sep.)			**(Aug. vs Jul. plus Sep.)**			**(Aug. vs Jul. plus Sep.)**		
χ^2-value	*df*	*P-value*	*χ^2-value*	*df*	*P-value*	*χ^2-value*	*df*	*P-value*
7.979	1	0.005**	11.316	1	0.001**	3.068	1	0.080

**: 0.01>P>0.001

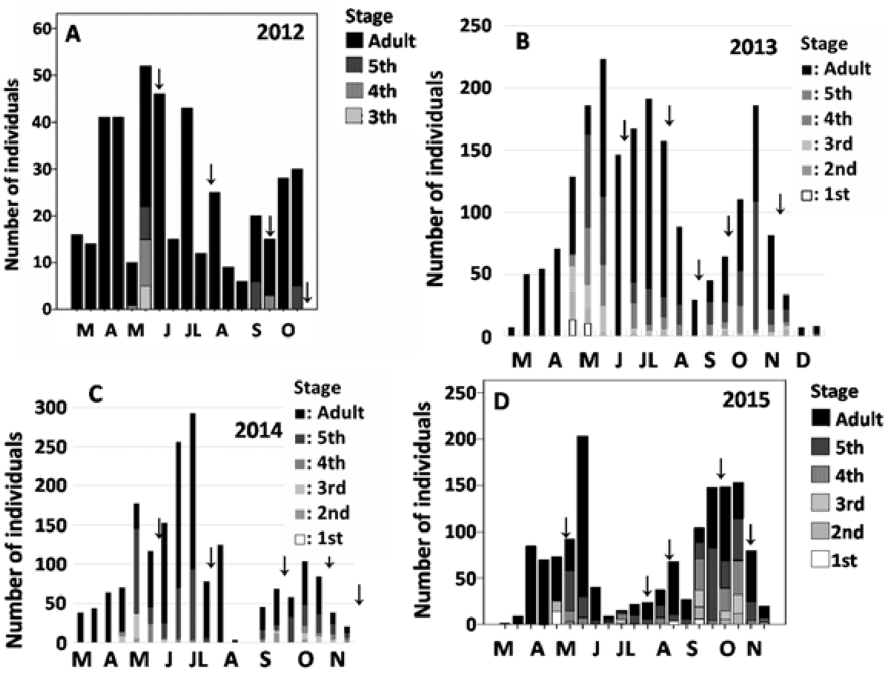

Figure 1. Seasonal variation in the number of larvae in each of the five stages and adults collected during 2012-2015 in the timed-catch samplings. Arrows show the points when the number of fifth instar larvae decreased, indicating the recruitment of new generation adults.

in temperature during fall that year. The number returned to five in 2013-2015 (Figure 1B-D). The recruitment of a new generation was judged by the decreased ratio of fifth instars collected and significant differences in χ^2 analysis for most generations (Table 1).

Adult aestivation and flight muscle conditions

In 2012, 30-40% of females collected in May-June had no mature oocytes (Figure 1A). These females with immature ovaries were 'teneral' specimens with melanin-deposition of rank 1 or 2 that appear within 10 days after adult emergence (Figure 2B). No immature females were collected in July, although no data was obtained in August 2012 (Figure 2A). In 2013 and 2014, 50% and 33% of females, respectively, collected during the period from late July to early August 2013 (Figure 3A) and August 2014 (Figure 3B) had no oocytes. No females lacking mature oöcytes were collected during the summer of 2015 (Figure 3C). Females appeared to have entered aestivation only occasionally or temporarily in the summer season in 2012-2015 in the Kochi-Nankoku population. Sixty percent in 1995, 49.0% in 2009 [30], 12.5% in 2012, 34.4% in 2013, 8.3% in 2014 and 0% in 2015 had well-developed flight muscles of rank 3 in October and November before overwintering [shown by arrow(s): Figure 4]. The ratio was decreasing gradually in accordance with year (Pearson's correlation analysis, $r = -0.838$, $n = 8$, $p = 0.037$).

Meteorological data

In 2015, no aestivation in adults and no adults with well-developed flight muscles of rank 3 were observed throughout the season. These two phenomena are quite different from those of the previous three years from 2012 to 2014. Daily maximum temperatures in summer may be related to aestivation in the next summer season (an occasional high temperature in one summer and adopting aestivation in the next year), and precipitation and temperature in one summer (lower precipitation linked to higher temperature and vice versa in summer) may be linked to flight activity in the next summer (high precipitation and low flight propensity). We examined maximum summer temperature and precipitation in the years prior to 2014 and to 2015 (Figures 5 and 6) when we examined the aestivation rate and flight muscles in summer.

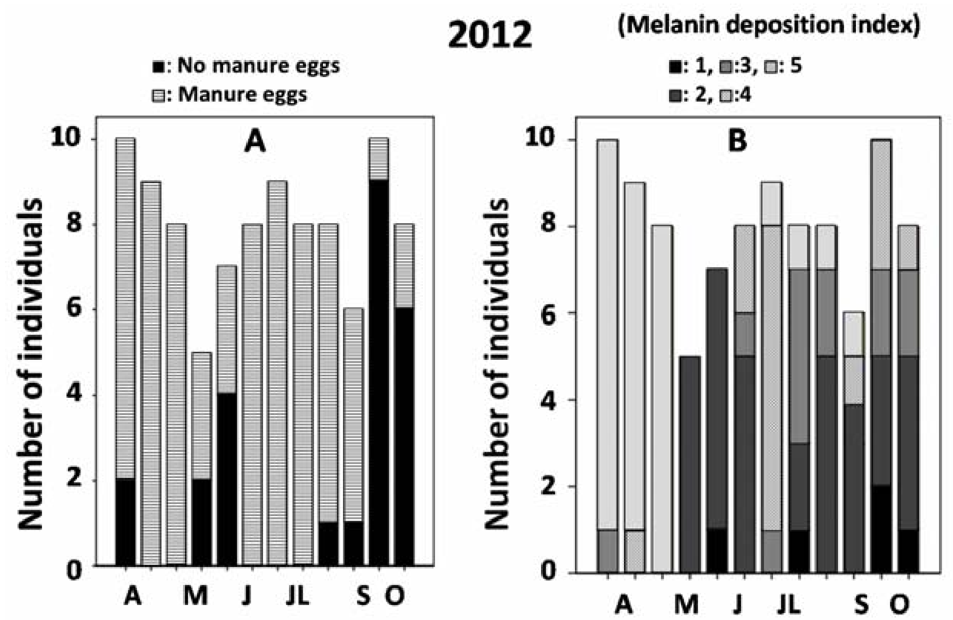

Figure 2. Seasonal variation in 2012 in the number of adults with mature oöcytes and adults without oocytes (A) and seasonal variation in the number of adults with each of the ranks showing the extent of melatonin (black pigment) deposition on allinotum (a cuticle plate underneath the cuticle skin in the meso-thoracic segment) (B) showing days after adult emergence: 1 and 2 mainly show teneral indicating a young stage within 10 days after adult emergence; 3 and 4: mainly after 10 days; 5: mainly overwintered adults in spring.

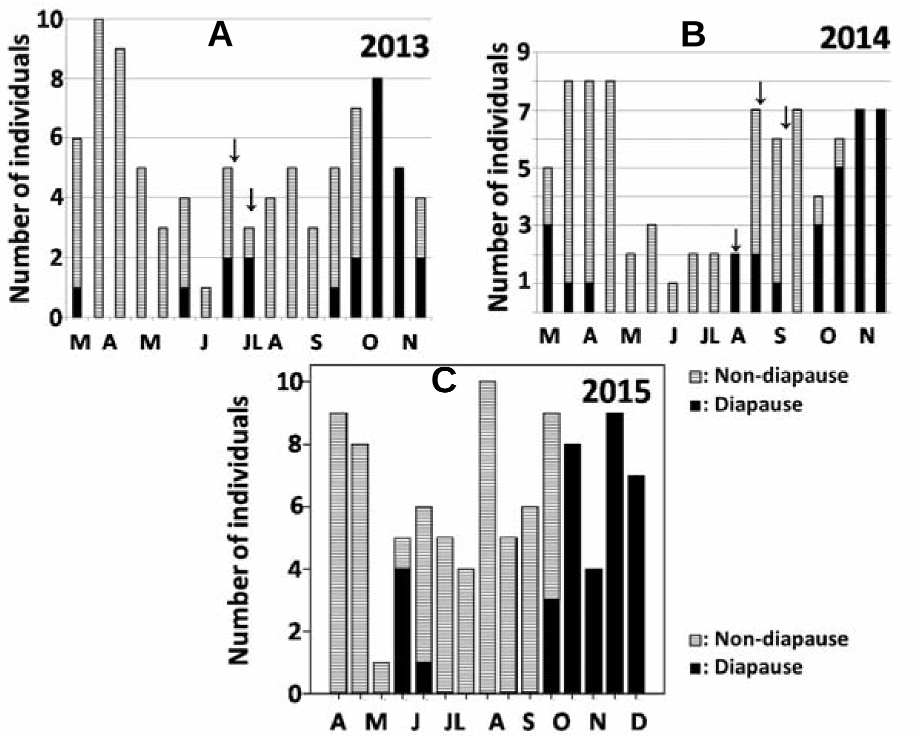

Figure 3. Seasonal variation in the number of adults with mature oöcytes and without oöcytes in 2013-2015: A: 2013, B: 2014, C: 2015.

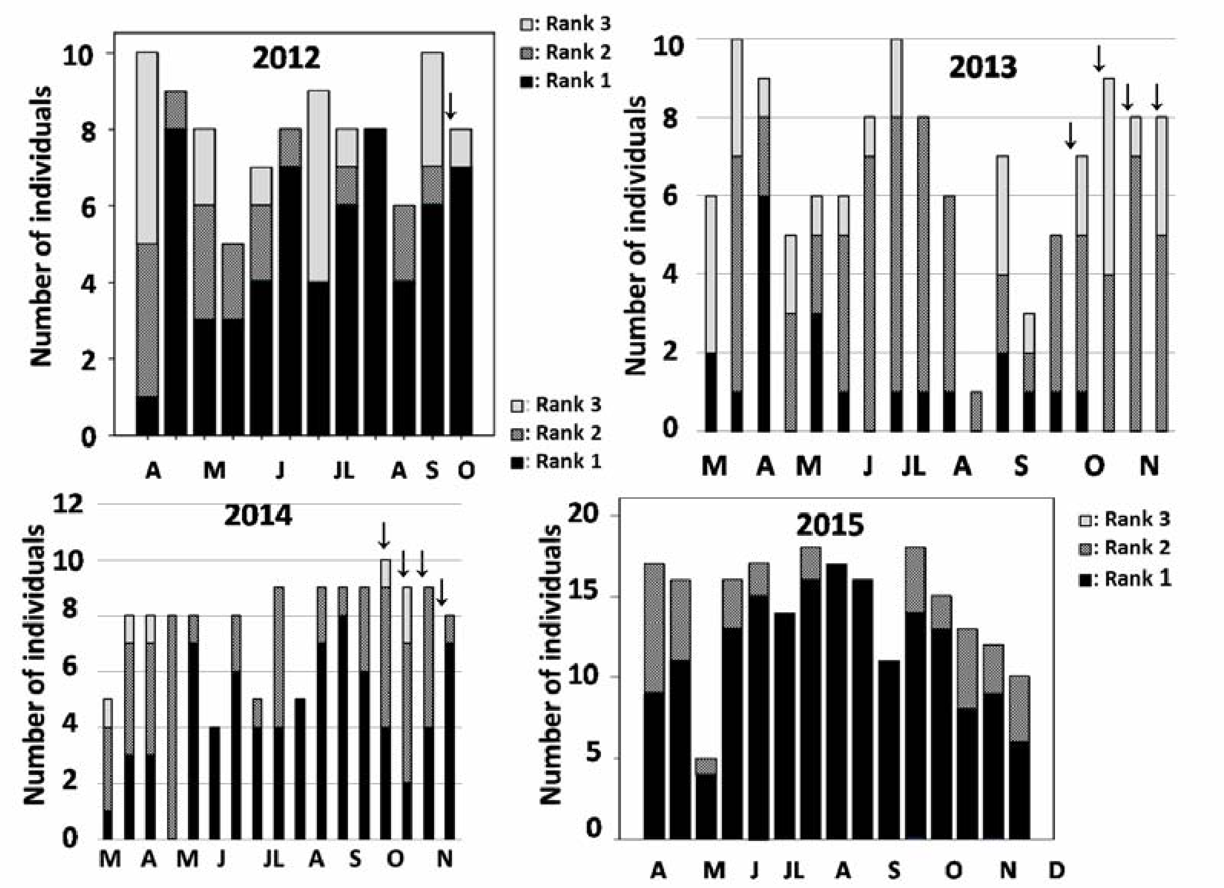

Figure 4. Seasonal variation in the number of adults with indirect longitudinal flight muscles of three stages of ranks 1-3 in the mid thorax [32] (the reference number is given as part of the information provided in the legend rather than as source for the figure).

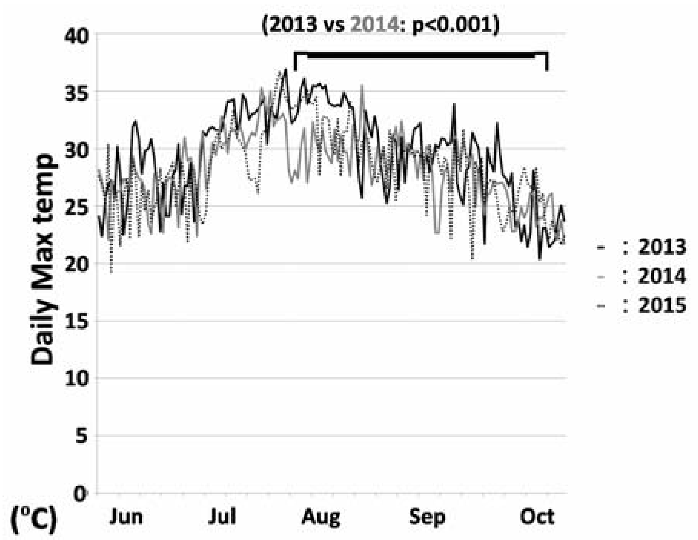

Figure 5. Seasonal variation in daily maximum temperature during 2013-2015 [37] (the reference number is given as part of the information provided in the legend rather than as source for the figure).

The daily maximum temperature in summer of 2013 was significantly higher than that in 2014 (Mann-Whitney U-test: $p < 0.001$; figure 5). On the other hand, the daily precipitation in summer of 2013 was significantly less than that in 2014 (Mann-Whitney U-test: $z = -4.106$, $p < 0.001$; figure 6). The high precipitation and low temperature in summer of 2014 could be linked to the lack of aestivation (Figure 3C) and of flights muscles of rank 3 throughout the year in 2015 (Figure 4D).

Mosaic-typed morphology

Adults with a mosaic-typed wing morphology with long, black fore-wings and short hind-wings which have been found for the first time in 2009-2011 (Harada *et al*., 2013) were also collected in 2012-2015 from the Kochi-Nankoku overwintering population, with a particularly large number of males (Figures 7, 8). These adults with a mosaic-typed wing morphology could not fly. The long, black fore-wings may have functioned to absorb sunlight in the daytime in winter.

DISCUSSION

Number of generations

In 1988-1995, there were three generations in Kochi-Nankoku populations [33, 25, 34, 28]. Both three and four generations were observed in the populations in 2004 [28]. In 2007-2009, four generations per year were dominant [29].This number increased to five in 2011 [30]. In 2007, the voltine number may have increased to four or more, as the recruitment of new generation adults occurred four times or more. The recruitment of new generations was judged to occur when the number of 5th instar larvae sampled decreased and instead the number of adults sampled increased. The change in the number of 5th instars and adults collected meant the season of new adult emergence [29]. The number of generations in Kochi could be estimated to be five in 2010 and 2011 [30]. Fifth instars grew in November and December and 40% of females were reproductive even in November in 2009-2011 [30]. However, there were only four generations in 2012, likely due to extremely low temperatures in November and December that year, resulting from a low temperature jet air flow coming down into the Japan islands (Kochi Meteorological Station, 2012) [35, 36]. The number of generations stabilized to five in 2012-2015 as noted in this study. This number may be the saturation point for this species in recent years.

Adult aestivation

A high proportion of males had smaller testes and a high proportion of females had no mature oocytes in September 2008 [29]. Such smaller testes were

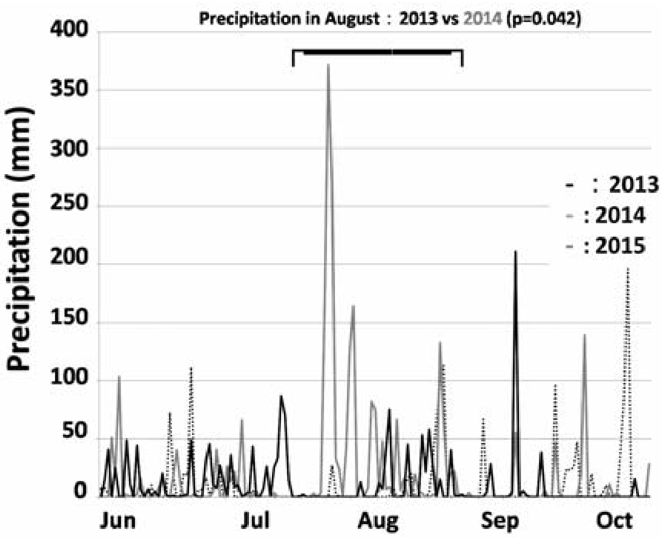

Figure 6. Seasonal variation in daily precipitation during 2013-2015 [37] (the reference number is given as part of the information provided in the legend rather than as source for the figure).

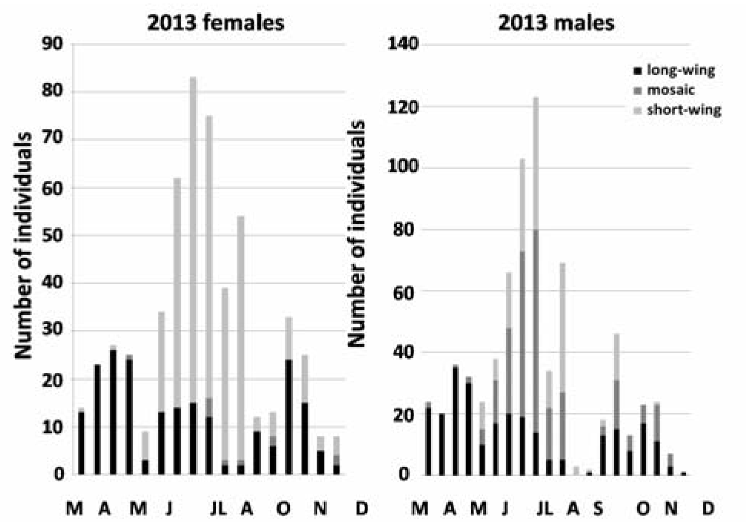

Figure 7. Seasonal variation in the number of adults having one of the three types of wing morphology: long-winged, mosaic (long fore wings and short hind wings) and short-winged.

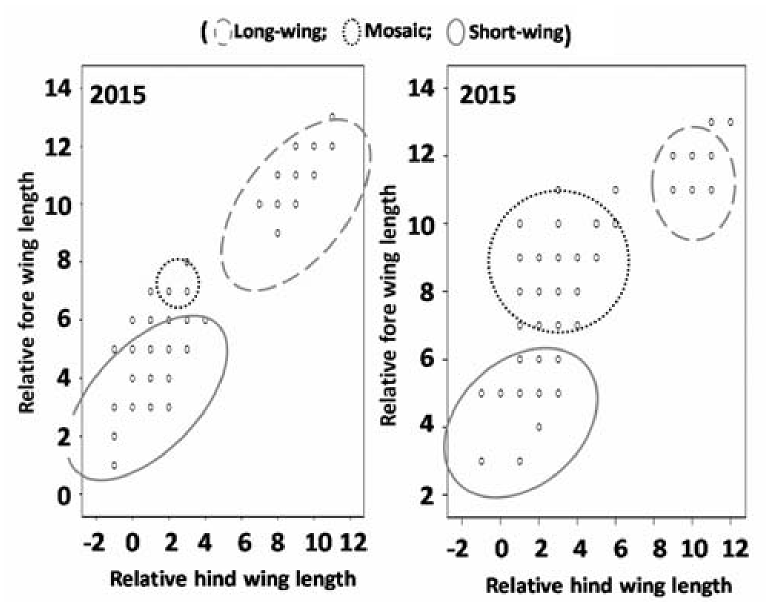

Figure 8. Distribution of fore wing length and hind wing length of long-winged, mosaic and short-winged adults throughout 2015.

also observed in the last half of September in 2009-2011 [30]. In 2012, there were no females that appeared to enter aestivation in summer. There were also no females in aestivation in 2015. However, 33% and 50% of females entered aestivation in July or August in 2013 and 2014, respectively. This may suggest that aestivation in Kochi-Nankoku population females occurred only partially and temporarily in 2013-2014. However, evidence based on adequate laboratory rearing experiments will remain in the near future for the induction and termination of aestivation.

Overwintering near the shore

Some of overwintering and overwintered adults had no mature flight muscles in 2007 [29]. In 2009-2011, only 19.5% of overwintering and diapause adults from October to December had well-developed flight muscles with rank 3 [30]. However, 60% of overwintering adults possessed them in 1995 [29]. In 2012-2014, only 8.5 to 34.4% of overwintering females had well-matured flight muscles of rank 3 in October. There were no females with mature flight muscles in 2015. This could suggest that many adults in reproductive diapause in fall could no longer disperse between the water bodies and overwintering sites on lands far from water bodies, instead may overwinter on lands near to water bodies. If warming in winter continues in the future, the risk of overwintering near the shore may decrease and overwintering in the shore can become dominant.

Meteorological explanation of the lack of females in aestivation and without well-developed flight muscles in 2015

The maximum temperature was very high in the summer of 2013 compared to that of 2014. The selection pressure for aestivation could have been higher in 2013 compared with 2014, resulting in a relatively high number of individuals adopting aestivation in the next year (2014). In contrast, the number of adults with well-developed flight muscles could drop to zero in 2015 after a year of no or little selection for aestivation because of a lower maximum summer temperature and higher precipitation in 2014.

The summer of 2013 was marked by high maximum temperatures in daytime and lower precipitation than 2014. Natural selection for high dispersal ability could have occurred in the summer of 2013. Therefore higher ratio of adults showed well-developed flight muscles, meaning higher dispersal ability in the next year of 2014. This would mean that the shortage of water bodies in 2013 could result in the natural selection of adults with high dispersal potential during summer, and this might lead to higher proportion of summer population with high dispersal ability in the next year generation. On the other hand, the maximum temperature in the summer was low and summer precipitation was high in 2014. The selection pressure for dispersal in the summer of 2014 was lower and this lower pressure would result in the lack of adults with rank 3 flight muscles in the following year, 2015.

CONCLUSION

This study showed that the three characteristics observed till 2011 as the effects of global warming also continued in 2012-2015, and also demonstrated that the aestivation ratio in one summer could be effected by the precipitation and the accompanying maximum summer temperatures (high summer temperature and aestivation selected in one summer, and low summer temperature and no aestivation selected in another summer) in the water strider *Aquarius paludum*.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest with regard to this study.

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