

Responses of life-history traits of brackish- and freshwater populations of the water strider to NaCl *Aquarius paludum* (Hemiptera: Gerridae)

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Abstract. The water strider *Aquarius paludum* inhabits the surfaces of a wide variety of freshwater habitats both temporary and permanent. It can also live on the surface brackish-water around river mouths. Exposure to a brackish rather than freshwater environment may affect a range of adult and offspring life-history traits. In a two-stage experiment *A. paludum* offspring from fresh- (F) and brackish-water (B) populations were obtained and their offspring reared in either a fresh- or brackish-water (0.45% NaCl) environments. The four offspring treatment groups (F-F, F-B, B-F, B-B) varied in terms of the parental and offspring rearing environments. The effect of parental and offspring rearing environment on longevity, fecundity and flight was assessed. Offspring reared in a brackish environment throughout their larval and adult stages had a reduced longevity and egg production. The flight activity of the offspring originated from the brackish-water population was maintained when they were reared in a brackish environment, but inhibited when they were exposed to freshwater. Our results suggest that the life-history strategies depend critically on the degree of salinity in both the current environment and that of their parents.

INTRODUCTION

Environmental change in a habitat is likely to affect the survival of the offspring of insects. Therefore, their ability to escape from unfavorable environments in space and time is particularly important. In insects this is achieved by changes in traits such as reproduction, migration and diapause. The “habitat template” theory of the evolution of life-history strategies in insects suggests that the temporal and spatial characteristics of the habitat mould and select for specific life history traits (Southwood, 1977). However, resources such as food and time are limited. Thus, insects need to allocate resources appropriately in order to prepare for an unpredictable situation in the future. The “trade-off” in the allocation of the resource is well illustrated by the relationship between migratory and reproductive traits, i.e., oogenesis-flight syndrome (Johnson, 1969), in insects such as aphids (Dixon et al., 1993), crickets (Tanaka & Suzuki, 1998), chinch bugs (Fujisaki, 1986), water striders (Harada & Nishimoto, 2007) etc. On the other hand, in many insects, life-history traits are influenced by population variation and parental effects. For example, in the locust *Schistocerca gregaria*, the density of adults affects phase change and several traits in offspring (Bouaichi & Simpson, 2003).

Water striders (Gerridae) occur in various aquatic habitats. Their widespread worldwide distribution, even occupation of oceanic areas (excluding the North and South poles) is associated with this physiological plasticity (Spence & Andersen, 1994; Andersen, 2000). They are able to colonise and adapt to severe environmental condi-

tions by means of reproductive and migratory trade-offs or bet-hedging (Vepsäläinen, 1978; Spence & Andersen, 1994; Harada et al., 2000; Kishi et al., 2002; Harada, 2003a, b). Thus, the evolution of life-history strategies in water striders has provoked a great deal of discussion (Spence, 1989; Fairbairn & Butler, 1990; Murray & Giller, 1990; Kaitala, 1991; Klingenberg & Spence, 1997).

Water striders can use brackish-water habitats inhabited by few aquatic insects, as refuges or temporary reproductive areas (Vepsäläinen, 1978; Kishi et al., 2007). However, occupying a brackish habitat during the larval or adult stage inhibits the reproduction and/or flight activity and shortens the life span of the water strider *Aquarius paludum* (Fabricius) (Kishi et al., 2006, 2007). These studies indicate that the water strider’s plasticity is based on its physiological response to NaCl in the habitat. For larvae of *Gerris thoracicus* (Vepsäläinen, 1978) and *A. paludum* (Kishi et al., 2006) have a large developmental period in brackish-water habitats. If water striders inhabit brackish-water habitats for several generations, natural selection favours those better adapted to brackish-waters conditions. However, although there are many studies on the salinity tolerance of freshwater invertebrates other than insects (Berezina, 2003; Kefford et al., 2004, 2005), there are none on freshwater insects. There are no eco-physiological studies on the adaptation of originally fresh water invertebrates to brackish-water habitats. In this study, the responses to exposure to saline conditions of the life-history traits of *A. paludum* populations colonizing freshwater and brackish-water habitats are compared.

TABLE 1. Effects of four treatments on larval development, survival to adult emergence, adult longevity and reproductive traits of *A. paludum*. F-F, F-B, B-F and B-B denote first the population of origin and the second the laboratory rearing environment. Different letters denote statistically significant differences ($P < 0.05$) (applied Bonferroni correction) between treatment groups.

	Freshwater population				Brackish-water population			
		F-F		F-B		B-F		B-B
Developmental time (days) (n, ME \pm SE)	278	30.1 ^a \pm 0.07	218	30.3 ^{ab} \pm 0.07	258	29.8 ^c \pm 0.06	227	30.4 ^b \pm 0.08
Survival to adult emergence (n, %)	320	86.9 ^a	320	68.1 ^b	320	80.9 ^{ac}	320	70.9 ^{bc}
Percentage of long winged individuals (n, %)	275	96.4	216	99.1	252	96.0	227	97.8
Longevity (days) (n, ME \pm SE)	158	61.9 ^a \pm 2.12	161	49.9 ^b \pm 1.87	160	57.3 ^{ab} \pm 2.02	154	48.1 ^{bc} \pm 2.32
Preoviposition period (days) (n, ME \pm SE)	70	23.5 ^a \pm 0.78	67	21.7 ^{ab} \pm 0.55	70	21.8 ^{ab} \pm 0.59	62	20.7 ^b \pm 0.58
Total number of eggs laid (n, ME \pm SE)	70	344.9 ^a \pm 28.6	67	216.1 ^b \pm 24.6	70	325.8 ^{ab} \pm 33.7	62	287.5 ^{ab} \pm 39.8
Oviposition rate (n, ME \pm SE)	69	4.99 ^a \pm 0.35	67	3.64 ^{ab} \pm 0.32	70	6.23 ^{ac} \pm 0.82	62	4.28 ^a \pm 0.42

MATERIAL AND METHODS

Thirty pairs of adults of *A. paludum* were collected in late July 2003 from a freshwater habitat on the upper Kagami River (0% NaCl concentration at the collection site), and brackish-water habitat, Daizen pond at the mouth of Shimoda river (0.45%), Kochi City (33°N), Kochi Prefecture, Japan. Similarly, thirty pairs were collected in 2004 from a paddy field (0%) and a brackish-water habitat at the mouth of the Niyodo river (0.3%), Kochi City and Ino City (33°N), respectively. Adults from the fresh- and brackish-water populations and the eggs they laid, were maintained on 0% and 0.45% NaCl solutions, respectively, at a 15.5L : 8.5D photoperiod and 20 \pm 2°C. The populations were defined as freshwater or brackish-water populations by their “population origin”.

Newly hatched first instar larvae derived from the eggs that were laid and developed in fresh or brackish-water environments were used in the experiment. Larvae were selected at random. These environments were defined as freshwater and brackish-water environments, respectively. The first instar larvae of each strain were reared to the adult stage on a 0% or 0.45% NaCl solution in the laboratory. Thus, there were four experimental groups: F-F; F-B; B-F; B-B. (F – freshwater; B – brackish-waters; the first letter refers to the habitat from which the original population was collected and the latter to the laboratory rearing environment).

There were eight trials per experimental group. Each trial consisted of 20 larvae selected at random, which were reared in plastic containers (34 cm \times 23.5 cm \times 4.5 cm), from hatching to adult emergence, at a 15.5L : 8.5D photoperiod and 20 \pm 2°C. Adult blowflies, *Lucilia illustris*, were provided as food every day, at a rate of one fly per five first or second instar individuals, one fly per three third or fourth instar individuals, and one fly per two fifth instars. At adult emergence, whether the wings were long or short was recorded. Pairs of long winged individuals each placed in round plastic containers (14 cm in diameter \times 5 cm in height) just after adult emergence and provided with one adult *L. illustris* each day. Wooden sticks floating on the water provided the striders with sites for egg laying and resting. The rearing conditions, a 15.5L: 8.5D photoperiod and 20 \pm 2°C, promote reproduction (Harada, 1992, 1993). Life-history traits such as reproduction, migration and longevity were assessed. The number of eggs laid by each

female was counted every two days until death. The number of eggs laid per female per day was the “oviposition rate”. The flight propensity of all adults was evaluated on the 30th day after emergence. Following the method of Harada et al. (1997), we recorded whether the flight behaviour of each individual was modified by blue light (about 3400 Lx) at a high temperature (32 \pm 2°C).

RESULTS

Developmental time, survival rate

Development was prolonged when the offspring developed in a brackish environment (Tables 1, 2a). In contrast, development was shortened when offspring of the brackish-water population were reared in a freshwater environment (Table 1). The survival of the offspring reared in a brackish environment was lower than that of those reared in a freshwater environment. The percentage survival of offspring originating from the fresh water population and reared in a brackish environment was much lower than that of those originating from a brackish population and reared in a brackish environment (Tables 1, 3a).

Longevity and reproductive traits

Adult longevity was affected not by sex, but by the salinity of the water of the environment in which they developed (Tables 1, 2b). Adult longevity of offspring reared in a brackish environment was significantly shorter than that of offspring reared in a freshwater environment (Table 1). When offspring were exposed to a brackish environment, the length of the pre-oviposition period was shortened. The preoviposition period of the brackish population was also significantly shorter than that of the fresh water population (Tables 1, 2c). Adults that developed in a brackish environment laid few eggs (Tables 1, 2d). The oviposition rate of offspring reared in a freshwater environment was significantly higher than that of those reared in a brackish-water environment (Tables 1, 2e). The brackish-water population tended to have a

TABLE 2. ANOVA of the effect of four treatments on longevity and reproductive traits of *A. paludum* (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

	df	SS	F	P
(a) Developmental time				
Population origin	1	1.096	0.920	0.338
Rearing environment	1	41.675	34.951	<0.001***
Population origin \times rearing environment	1	12.617	10.581	0.001**
(b) Longevity				
Sex	1	541.262	0.783	0.377
Population origin	1	1618.689	2.340	0.127
Rearing environment	1	17734.478	25.641	<0.001***
Population origin \times rearing environment	1	312.943	0.452	0.501
(c) Preoviposition period				
Population origin	1	124.452	4.528	0.034*
Rearing environment	1	140.319	5.106	0.025*
Population origin \times rearing environment	1	7.662	0.279	0.598
(d) Number of eggs laid				
Population origin	1	45995.006	0.673	0.413
Rearing environment	1	468018.227	6.848	0.009**
Population origin \times rearing environment	1	137222.703	2.008	0.158
(e) Oviposition rate				
Population origin	1	59.585	3.161	0.077
Rearing environment	1	182.183	9.665	0.002**
Population origin \times rearing environment	1	6.080	0.323	0.571

higher oviposition rate than the freshwater population (Tables 1, 2e). There were significant positive correlations between longevity and the number of eggs laid in the three experimental groups of F-F, F-B and B-B, but not in group B-F (Fig. 1).

Migratory traits

The percentage of long winged individuals increased when offspring were reared in a brackish compared to a freshwater environment (Tables 1, 3b). However, the percentage of the long winged individuals was unrelated to the origin of the population (Table 3b). Flight propensity was related to sex and to interaction between population origin and rearing environment (Tables 1, 3). The flight propensity of group B-F was significantly lower than that of the other experimental groups F-F, F-B and B-B (χ^2 test: $\chi^2_{\text{cal}} = 38.00$, $df = 3$, $P < 0.001$; Fig. 2). The peak in their flight response was also delayed by exposure to a brackish environment (Kolmogorov-Smirnov's test: $z = 1.789$, $P = 0.003$ for rearing environment; $z = 0.553$, $P = 0.920$ for population origin; Fig. 2).

DISCUSSION

Effect of population origin and rearing environment on larval fitness

The brackish environment had a detrimental effect on the larval development and survival of the freshwater population (Table 1), probably due to physiological stress. This finding accords with that of previous studies (Vepsäläinen, 1978; Kishi et al., 2006). Exposure to

brackish-water may result in an increase in the osmotic pressure of the haemolymph of larvae.

Effects of population origin and rearing environment on longevity, reproduction and migratory status

The longevity of freshwater adults decreased in the brackish-water environment. The longer lifespan of females reared in a freshwater environment resulted in a higher fecundity than in the brackish-water environment (Fig. 1), although few reports have correlated fecundity

TABLE 3. Wald χ^2 -test following logistic regression analysis of the effect of four treatments on the survival to adult and the flight propensity of *A. paludum* (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Factors	df	Wald χ^2	P
(a) Survival to adult emergence			
Population origin	1	1.461	0.227
Rearing environment	1	31.283	<0.001***
Population origin \times rearing environment	1	5.714	0.017*
(b) Percentage of long winged individuals			
Population origin	1	0.522	0.470
Rearing environment	1	4.478	0.035*
Population origin \times rearing environment	1	0.199	0.656
(c) Flight			
Sex	1	16.568	<0.001***
Population origin	1	28.944	<0.001***
Rearing environment	1	12.096	0.001***
Population origin \times rearing environment	1	19.646	<0.001***

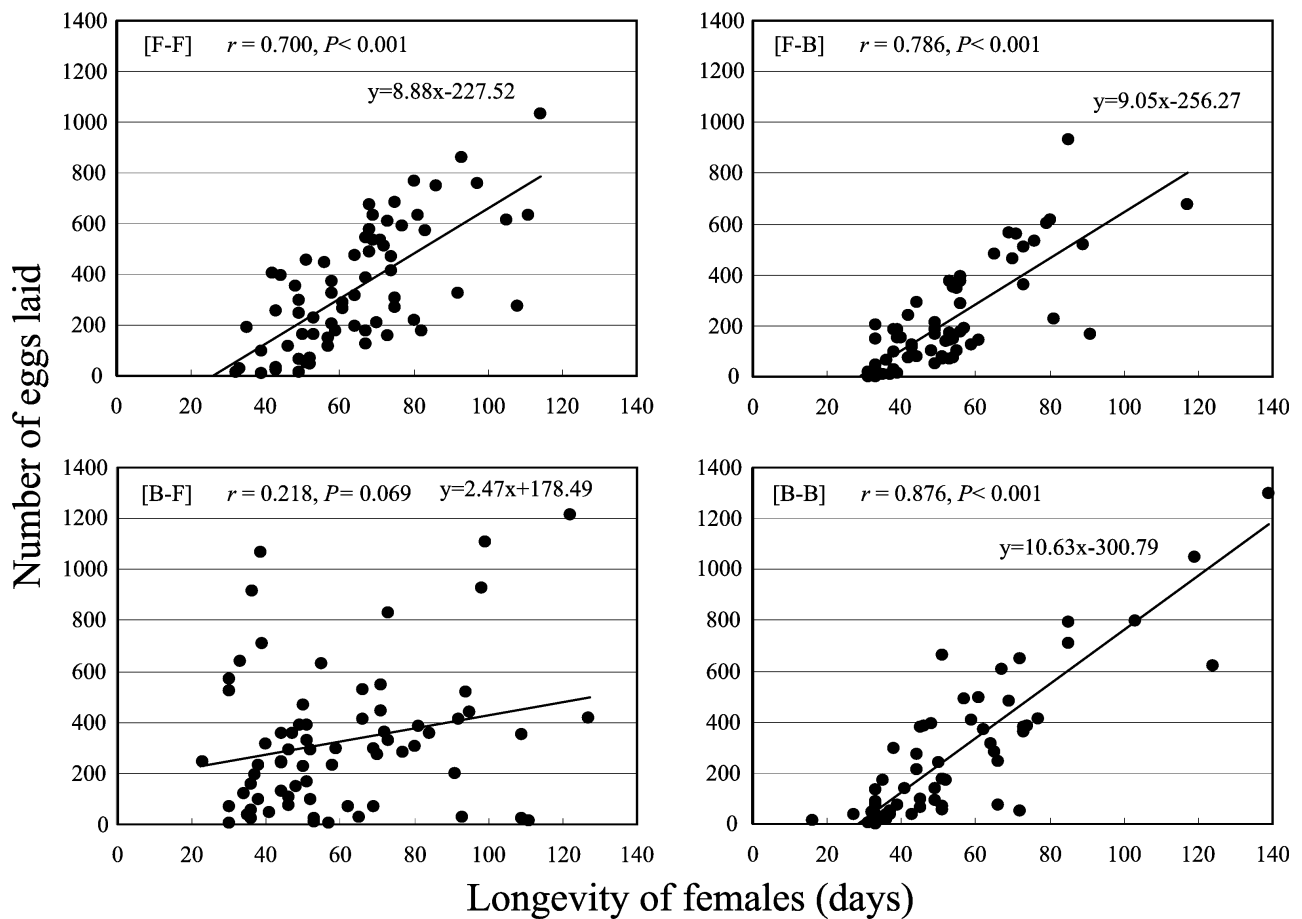


Fig. 1. Effect of four treatments on the relationships between longevity and number of eggs laid by *A. paludum*. The four graphs show the results for (F-F), the offspring of a freshwater population reared in a freshwater environment; (F-B) those of a freshwater population reared in a brackish-water environment; (B-F) those of a brackish-water population reared in a freshwater environment; and (B-B) those of a brackish-water population reared in a brackish-water environment, respectively.

with longevity in other water striders (Spence & Andersen, 1994). On the other hand, the offspring of the brackish-water population compensated somewhat for the shorter longevity by a higher oviposition rate, which may have implications if mortality is higher in the field than in the laboratory. The brackish-water population exposed to freshwater did not allocate resources to dispersal but to increased reproductive activity (short preoviposition period and high fecundity), which may be an example of the “oogenesis-flight syndrome” (Johnson, 1969). This response may serve as another compensation for the lower fitness in the previous generation in the brackish-water environment.

Thus, the parameters of reproductive performance (earlier onset of reproduction and higher fecundity) in the brackish environment were enhanced by the brackish population as compensation for the previous lower fitness in a brackish-water environment. Other studies record that the lower fitness of aquatic organisms living in brackish habitats is due to physiological stress associated with salinity adversely affecting larval development, body size, survival, reproduction, etc. (caddis fly: Haage, 1968; mayfly: Chadwick & Feminella, 2001; toad: Robert et al., 1998; Gomez-Mestre & Tejedo, 2003). Thus, the adapta-

tion to salinity may occur in the parents and during embryonic development. The brackish-water population may develop a flexible system that controls the osmotic pressure of haemolymph. The fecundity of brackish-water populations of the anuran, *Bufo calamita*, does not increase when reared in freshwater, as its tolerance of high salinity is genetically determined (Gomez-Mestre & Tejedo, 2003). On the other hand, the peak in flight activity of brackish population offspring was delayed when they were reared in a brackish-water environment, most likely because flight muscle development was inhibited by the salinity induced physiological stress.

Ecological significance of population origin and rearing environment

Rearing in a brackish-water environment decreased longevity and fecundity in *A. paludum*, irrespective of the population origin. The brackish habitat appears to be unsuitable for freshwater animals (Kelts, 1979; Venkatesan, 1981; Chadwick & Feminella, 2001; Silverbush et al., 2005). However, *A. paludum* populations occur in brackish habitats where the NaCl concentration is relatively low, such as the mouths of rivers and wilderness lakes (Kishi et al., 2007, unpubl. data). Although exposure to an abrupt increase in NaCl concentration at adult

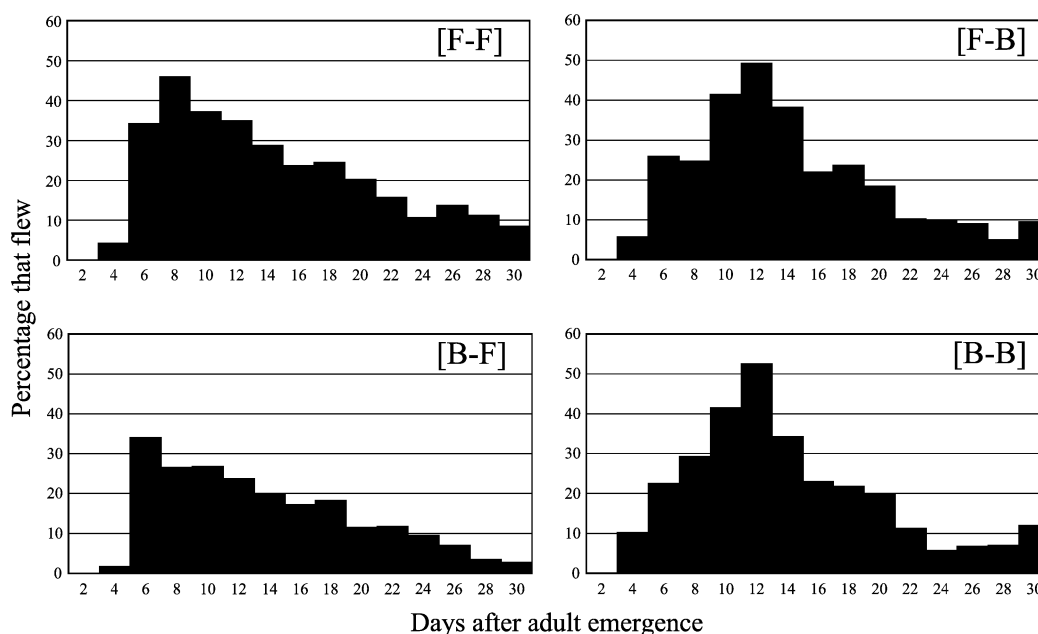


Fig. 2. Effects of four treatments on the incidence of flight in *A. paludum*. The four graphs show the results for the F-F, F-B, B-F and B-B respectively. The first capital letters denote population of origin and the second the laboratory rearing environment.

emergence promotes flight in *A. paludum* (Kishi et al., 2006, 2007), long term exposure to a constant NaCl concentration did not. Instead, the strategy in brackish environments seems to be to “breed here and now” (Southwood, 1977). In this study, the flight propensity of group B-F was significantly lower than that of experimental groups F-F, F-B and B-B. The brackish population also adopted the “breed-here-and-now” strategy in freshwater to compensate for the lower fitness of the previous generation in the brackish-water environment.

By living in low NaCl brackish-water habitats the water striders may avoid the negative effects of salinity, such as shorter longevity and lower larval survival. Moreover, in brackish-water habitats with a relatively low NaCl concentration of less than 0.9%, water striders might find rich insect food resource of mayflies, caddis flies, stoneflies, etc. (Williams & Williams, 1998; Chadwick & Feminella, 2001; Kefford et al., 2004, 2005). In addition, the number of predators may be relatively low in brackish-water habitats. For example, with the exception of a few species, such as *B. calamita* (Beebee, 1985; Gomez-Mestre & Tejedo, 2003), most amphibians avoid inhabiting and breeding in saline and brackish environments, because of their poor osmo-regulatory ability (Balinsky, 1981; Boutilier et al., 1992). Thus, *A. paludum* may benefit from the security of brackish-water environments, despite costs associated with the physiological stress of salinity.

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