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ABSTRACT

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The main objective of this thesis was to study dispersal, colonization success and life-history differences among different waterstrider *Aquarius najas* populations. Life-history studies were carried out in an artificial stream system, and studies on dispersal and colonization success were performed in field. Genetic variation and gene flow within and between different watersheds were studied using RAPD markers. Field studies indicated dispersal differences between populations. Dispersal distances of common garden reared waterstriders were dependent on the size of the habitat patches and the size of dispersal barriers between patches. Individuals that originated from small and isolated patches dispersed less than those originated from long and connected streams. Among laboratory reared waterstriders several winged individuals appeared. The relative frequency of winged individuals was highest in the southern as compared to northern populations. Overwintering survival under laboratory conditions was higher among the wingless individuals. Thus, the survival cost may explain why the proportion of winged individuals was lower in the northern populations. Data from the colonization experiment indicates that genetic variation together with the founder population size is important for the colonization success. Populations founded by large propagule sizes and by individuals of different origins had the highest colonization success. This is a central result for conservation biology as it indicates the value of intraspecific variation for the colonization success. According to the RAPD data, occasional gene flow between streams seems to exist, but mainly to downstream direction within a watershed. Results from life-history studies indicate that waterstriders of different origins have only slightly differing life-histories. The slightness of observed latitudinal differences makes sense, since life-history traits need to be plastic due to temporally varying conditions.

Key words: Dispersal; extinction; fecundity; Gerridae; isolation; small population; water bug; waterstrider.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals. I have personally performed most of the work in papers I-V, and I have performed a significant proportion of the work in analyzing data and writing paper VI.

I Ahlroth, P., Alatalo, R. V., Hyvärinen, E. and Suhonen, J.: Patterns of dispersal and colonization cycle in a waterstrider (*Aquarius najas*). - Manuscript (submitted).

II Ahlroth, P., Alatalo, R. V., Hyvärinen, E. and Suhonen, J. 1999: Geographical variation in wing polymorphism of the waterstrider *Aquarius najas* (Heteroptera, Gerridae). - Journal of Evolutionary Biology 12: 156-160.

III Ahlroth, P., Alatalo, R. V. and Suhonen, J.: Inherited dispersal avoidance in small and isolated habitat fragments - Manuscript.

IV Ahlroth, P., Alatalo, R.V., Holopainen, A., Kumpulainen, T. and Suhonen, J.: Importance of propagule size and genetic variation on the colonization success. - Manuscript.

V Ahlroth, P., Pekkala, S., Ahlroth, M. and Alatalo, R. V.: Genetic variation, genetic identity and dispersal between populations of the waterstrider *Aquarius najas*. - Manuscript.

VI Kumpulainen, T., Ahlroth, P., Alatalo, R. V. and Suhonen, J.: Latitudinal life-history differences between waterstrider (*Aquarius najas*) populations. - Manuscript.

1 INTRODUCTION

1.1 General introduction

Phenotypic variation between individuals may result from dissimilar genotypes or differences in their environments during growth. At the population level, genetic differences may arise due to variation in local selection pressures, mutations or due to genetic drift. Local selection pressures may favour dissimilar features if selection pressures are strong enough and of continuous type. Genetic differences between populations can arise across larger geographical areas (Mayr 1971, Fairbairn 1984, Hanks & Denno 1994, Ayre 1995, Lobón-Cerviá et al. 1996, Starmer et al. 1997) or in a smaller scale, especially if gene flow between populations is limited (Waser & Price 1985, McPheron, et al. 1988; Karban 1989, Singer et al. 1993, Schilthuizen & Lombaerts 1994, Mopper et al. 1995, Herring & Verrell 1996, Mopper 1996, Rohr 1997). However, in a small population the amount of genetic variation may be reduced due to bottlenecks, genetic drift and inbreeding, which may prevent local adaptation (e.g. Mayr 1971, Roff 1992, Stearns 1992, Palacios and Gonzales-Candelas 1997, Bauert et al. 1998). Unpredictability of environment stresses the importance of genetic variation for the persistence of a population (Furnier & Adams 1986). Gene flow between the populations may increase the amount of genetic variation, but at the same time, it may cause break up of local adaptations or prevent local adaptations from arising (see Wilmsen Thornhill 1993, Costa & Ross 1994). If gene flow between populations exists, the genetic structure of a population may be strongly influenced by immigrants. Thus, dispersal plays important role in the evolution of local and geographical adaptations.

In this thesis I look into dispersal and life-history strategies in various populations of *Aquarius najas*. I was mainly interested to examine some central questions with relevance to conservation biology. Human activity has caused the number of *A. najas* populations to decrease during this century and *A. najas* is regarded as an endangered species. Since the species is practically wingless, and limited to occupy lotic habitats, it has a restricted recolonization ability. Limited dispersal ability makes it an excellent tool species to study processes like colonizations and extinctions experimentally. The low natural rate of colonizations and extinctions in this species represents one extreme in the continuum of different types of metapopulation dynamics.

1.2 Dispersal polymorphism (I, II, III)

Dispersal strategies are known to vary widely both between and within species according to the different selection pressures under given environmental conditions (Cohen & Motro 1989, Roff 1990, Rees 1993, Dingle 1994, Holt & McPeek 1996). In general, dispersal is favoured to avoid competition (Hamilton & May 1977, Herzig 1995, Fonseca & Hart 1996), inbreeding (Pusey 1987, Forster Blouin & Blouin 1988, Bollinger et al. 1993, Pusey & Wolf 1996), predators (Cooper 1984, Holyoak & Lawler 1996) and parasites (Brown & Brown 1992, Hart 1997). In contrast, there is a large number of reverse selection pressures explaining the reduced dispersal of many species (Wagner & Liebherr, 1992). Here, I suppose that if the distance between suitable patches increases, the mortality due to dispersal will be increased, and there will be selection pressure against individuals leaving the patch. Thus, in small and isolated patches reduced dispersal may be favoured and in an isolation the size of a patch may determine optimal dispersal range. Instead, typical metapopulation structure favours movements between connected patches (Harrison et al. 1988, Hanski et al. 1995a,b, Olivieri et al. 1995). On isolated, oceanic islands there are several species of flightless birds and insects (Diamond 1981). However, these cases represent examples of interspecific differences in dispersal ability.

If dispersal is extremely costly, smaller costs of reduced dispersal (such as inbreeding depression) may be accepted (see Roff 1977, Rees 1993, Fairbairn 1994). Winglessness of insects is often related to stability and isolation of the habitat (Poisson 1946, Vepsäläinen 1973, 1974, 1978, Denno 1994). Also, increasing latitude and altitude are often associated with the lack of wings (Roff 1990). Under these conditions morphs with reduced hind wings or flying muscles, or even with a total lack of wings may appear.

In wing dimorphic species, dispersal ability and the level of gene flow between populations are often related to the presence of wings. The proportion of winged individuals may strongly fluctuate between populations and in extreme cases, all individuals within a population may have lost their ability to fly. Among semiaquatic bugs alary polymorphism is a common feature, and it is exhibited as discontinuous variation in the wing length within populations. The polymorphism may be determined by genetic differences between morphs (genetic polymorphism) (see Vepsäläinen 1974), environmental conditions under which the morphs develop (environmental polyphenism), or by a combination of these two (Zera et al. 1983) reflecting variable reaction norms.

In waterstriders, both light periodicity and temperature during the larval growth are known to influence wing development (Vepsäläinen 1974). These effects are related to the fact that in bivoltine species the non-diapause generation is typically short-winged and diapause generation long-winged (Møller-Anderssen 1993).

1.3 Colonization cycle in lotic habitats (I)

In stream habitats, adult insects are suggested to disperse mainly upstream to compensate for the downstream drift of eggs and early nymph stages (Mottram 1932, Müller 1954, 1982). The earliest studies concerning compensatory dispersal emphasize its importance for the persistence of the population in a stream. In contrast, later papers (e.g. Fairbairn 1985, Anholt 1995) underline its importance for individual fitness. Compensatory upstream dispersal has been described in lotic species of mayflies (Ephemeroptera) (Madsen et al. 1977, Bagge 1995), stoneflies (Plecoptera) (Madsen et al. 1973, Madsen & Butz 1976), caddisflies (Trichoptera) (Svensson 1974, Bagge 1995) and semiaquatic bugs (Heteroptera, Gerridae) (Fairbairn 1985).

Despite the fact that upstream dispersal is well-documented, causes or alternative hypotheses explaining it have rarely been tested experimentally. In addition, the majority of the previous studies have not been replicated with several populations, and the data are usually not based on observations at the level of individuals.

1.4 Importance of genetic variation (IV, V)

Colonization success may depend on the number of genotypes available for selection. In addition, colonization success may depend upon the size of the founder population and temporal variability in population size (e. g. Ebenhart 1989). The probability of local extinction is suggested to decrease with increasing population size (Shaffer 1981, Shaffer & Samson 1985, Harris et al. 1987, Harrison et al. 1988, Hanski et al. 1995). The risk of extinction in a small population may also rise due to ecological (Schoener & Spiller 1995, Ågren 1996), demographic or genetic reasons (Lande 1988) or due to environmental stochasticity (Armbruster & Lande 1993). Genetic problems tend to accumulate especially along with the decreasing population size (Saccheri et al. 1998). Respectively, colonization success may depend on the size and the quality of the patch or on the degree of predation risk.

Random amplified polymorphic DNA (RAPD) technique (Lynch & Crease 1990, Welsh & McClelland 1990) is an economical method to examine genetic diversity and genetic identity in different populations. This information may be relevant when planning colonization experiments, for example.

1.5 Life history differences between populations (VI)

Differences in the reproductive and growth season occur along large geographical scale and they may affect the evolution of geographical differentiation within species. If individuals are restricted to migrate to more favourable conditions they have to react to unfavourable environmental conditions, for example, by changing behaviour to avoid the environment´s deleterious effects on survival and fecundity (Roff 1980, Ludwig & Rowe 1990, Stearns 1992). However, an individual can react to a short term stress only within the frames of its own genetics, by using physiological responses, i.e. phenotypic plasticity (e.g. Kaitala 1987, Blanckenhorn 1991, Roff 1992, Hill & Gatehouse 1993, Shen & Bach 1997).

1.6 Aim of the thesis

In this thesis I focused into reproduction strategies and dispersal of a waterstrider *Aquarius najas*. Study species is mainly wingless and specialized to live in lotic habitats. The isolation of different stream populations makes it an excellent model organism to study evolution in small populations. I assumed that limited gene flow and dissimilar selection pressures in different parts of the distribution area may have led to evolution of local adaptations.

In the first paper I present the results of a field study in which I investigated the patterns of dispersal in *A. najas*. To test the hypotheses of compensatory upstream dispersal I released individually-marked waterstriders of ten different origins into five rivers devoid of the species and compared dispersal distances and directions between populations and sexes, in autumn and spring.

The second paper (II) focused on geographical variation of wing polymorphism in *A. najas* in Finland, and compared the mortality of different morphs and sexes during the overwintering period under laboratory conditions. Despite the extensive knowledge of ecology of waterstriders, it has not been tested experimentally whether the geographic variation in winglessness, such as that in *A. najas*, is merely phenotypic or whether it is also affected by genetical variation with variable reaction norms. If the absence of wings is clearly genetic in *A. najas*, I should not find any winged individuals even if they were grown under short-day and in warm temperature conditions. On the other hand, any differences in the proportion of winged individuals between populations reared under similar "common garden" conditions, would imply partial genetic control of the variation in the occurrence of the wings.

The third paper (III) examines whether dispersal behaviour of waterstriders is related to the size and the structure of the habitat. My working hypothesis was that in small and isolated patches selection should favour reduced dispersal rates in comparison to large and connected patches. The hypothesis is based on the fact that if the difference between suitable patches is too long, selection should favour those individuals that stay in the patch. The idea assumes that dispersal differences between individuals have a genetic basis.

In the fourth (IV) paper I explored how the size of founder population and the amount of genetic variation influence colonization success in *A. najas*. In the fifth (V) paper I used random amplified polymorphic DNA (RAPD) technique to study genetic diversity, genetic identity and dispersal within and between watersheds.

In the last (VI) study I compared life-histories between ten distant waterstrider populations. In this work individuals of different origins were cultivated under similar laboratory conditions. I measured fecundity and reproduction behaviour of female waterstriders, and compared these variables between the populations of two geographical areas. It could be expected that females from the most northern origins allocate more of their resources in the beginning of their short season than females of more southern origins with longer time available for reproduction.

2 METHODS

2.1 Study species

Among the nine species of waterstriders in Finland *Aquarius najas* is the only species that is specialized to live in stable lotic habitats (Møller Andersen 1990). It occupies small and middle sized, swift streams, which are relatively clean and not excessively acidious (for the species). In central Finland the species lives at the northern range of its distribution area and it occurs more commonly in the southern and south-eastern parts of the country.

A. najas is phenotypically wingless in northern Europe (Finland, Sweden, Norway) (Huldén 1986, Møller Andersen 1993, Ahlroth et al. 1999). Winglessness of *A. najas* increases with increasing latitude (Poisson 1946, Ahlroth et al. 1999). Only four winged individuals (less than 0.01% of the total sample) have been found from a single river in southern Finland (Huldén 1986, own unpublished field observations). Huldén (1979) has reported Polish populations of *A. najas* with up to 1 % winged individuals while in mountainous areas of Spain the winged morph is not rare (Poisson 1946). Since the species cannot disperse over large standing waters, gene flow between populations of *A. najas* is thought to be limited even within watersheds.

Mating and reproduction takes place in spring. Most of the waterstriders are in prolonged mate guarding during the reproduction period. Mate guarding is thought to be costly for the female and inter-sexual conflict can be seen in repeated struggles before and after copulations (for related species see e.g. Fairbairn 1992, Arnqvist 1992, 1997).

In Finland, the species is univoltine (Huldén 1986), and adult waterstriders overwinter in terrestrial sites such as under rocks or in the moss at the ground layer of the vegetation (Linnavuori 1966, Huldén 1979, Møller Andersen 1993). In spring, waterstriders leave their overwintering sites to forage other insects on the water surface, and to begin reproduction. One week after copulation female lays several egg-clusters on stones and on the leaves of aquatic plants, under the water surface (Huldén 1979). A female may lay up to 200-400 eggs. Eggs of *A. najas* are 1.5 - 2 mm long and about 0.5 mm in diameter. New, recently laid eggs are white in colour, but after about three days from fertilization eggs turn brown and eyes of a larvae become visible; just before hatching the eggs are dark brown, and hatched, empty eggcells are light brown and ragged. Unfertilized and dead eggs stay white, but they soon swell and turn into obscure yellowish colour. Thus, the condition and state of the eggs are easy to observe. Individuals die after the reproduction season and the survived offspring reproduce during the next spring.

2.2 Laboratory (II, III, VI)

I built up an artificial stream system with separated pools (diameter 0.38 m, volume 8 litres) that served as reproduction containers. I covered plastic pools by thin nets that allowed light to go through. All containers were connected to a common stream system, in which the water was circulated with electric pumps. The water was conducted to every pool through a separate duct and was further conducted away from pools through another duct, back to a collector container. Thus, waterstriders were treated with a natural kind of stream habitat with oxygen-rich water.

I fed waterstriders daily with fruit flies (II, III, VI), ants (I, III, VI) and crickets (II). During the whole study period food was provided *ad libidum*. I cleaned reproduction pools daily and the water in the stream system was changed continuously (II, III, VI). I maintained light:dark cycle 12:12 during the first study (I), but during the other laboratory studies (III, VI) I maintained 17:7 light:dark cycle.

2.3 Patterns of dispersal (I)

I carried out field studies during the autumn of 1995 and spring 1996 by releasing marked individuals of *A. najas* from ten different rivers (100 individuals / population) into five experimental rivers in central Finland that lack natural populations of this species. Five of the original populations stemmed from southern Finland and the other five from central Finland. I introduced one population from southern and one population from central Finland in each of the study rivers. This enabled the comparison of populations of two different geographical areas. I marked all the adults individually with coloured paint dots to facilitate the later identification of the individuals in the field. In each experimental river, I released all individuals of both populations at the same site.

I assessed movement of each individual weekly; seven times during the autumn and eight times during the next spring and early summer. I used colored banners to mark every tenth meter along the river bank and I assessed waterstrider movement within one meter. I assigned upstream movements as positive values and downstream movements were assigned negative values.

2.4 Wing polymorphism (II)

I collected paired individuals of *A. najas* from ten streams in Finland. Five of the populations were from southern Finland and another five populations were from central Finland. All the collected *A. najas* individuals were wingless. At the beginning of the experiment one pair of adults was put to each of the 150 plastic containers. I maintained short daylength conditions because my aim was to test if the winglessness of *A. najas* is phenotypically plastic appearing in these more southerly growing conditions. At the same time I could check for any genetic differences causing the variation in the occurrence of winged morphs in offspring raised in similar conditions.

I devided mature individuals into two morphs: winged (macropterous) and "wingless" (apterous, including the few shortwinged individuals). I counted the proportions of morphs per population and compared it to the geographical origin of their parents. Among the laboratory raised offspring, I collected 79 apterous and 61 macropterous individuals and divided them into twelve buckets. Each bucket was filled with moisturized *Sphagnum* moss. I placed all of the winged individuals in a random manner (with respect to the origin of population) to the six buckets and wingless individuals I placed to the other six buckets. On average, there were 11.0 individuals in each bucket. I kept both groups in the buckets for three months at constant temperature of +4 °C. I did not provide food during this period. I did this to simulate the overwintering period to compare survival between the morphs. I assessed overwinter survival in terms of survival in both groups after three months. I used the proportion of survived individuals in each bucket as independent observations in the statistical tests.

2.5 Reduced dispersal in small and isolated patches (III)

In this study I tested whether wingless waterstriders originating from different types of habitats vary in their propensity to disperse and whether these differences were genetically determined.

I studied dispersal propensity in ten waterstrider populations. Some populations were originated from small streams with only few occupied patches, surrounded by unfavourable areas, while other populations originated from long streams with several suitable habitats connected to each other. I released a total of 220 individually marked, laboratory reared waterstriders on a river and observed their dispersal under field conditions, during the autumn.

2.6 Colonization success (IV)

To test how propagule size and the number of origins (genetic variation) influence colonization success, I introduced wingless *A. najas* of various numbers and of different origins into 90 streams devoid of this species. In early

May 1998 I caught waterstriders from three original populations. I manipulated propagule (founder population) size and its genetic diversity by introducing 2, 4, 6, 8 or 16 females from either one or two original populations. The number of waterstriders´ origins simulated the genetic diversity of the population introduced. Before releasing females were mated in the laboratory with males of the same origin. As males were not introduced and the species is univoltine, outbreeding between different populations was avoided during the study period. I repeated each treatment combination in nine streams that were randomized both between and within the treatments. At each stream I released all individuals at the same site. Study streams are located in central Finland in a relatively small area (60 km x 70 km), about 40 km north from the northern range of the natural distribution area of the study species. I counted the number of successful colonizations in two occasions (in late August and early September) and compared the results between the treatments.

2.7 RAPD analyses (V)

I used random amplified polymorphic DNA (RAPD) technique (Welsh & McClelland 1990) to examine genetic diversity and genetic identity in 17 waterstrider populations. I tested sixteen different random primers on a few genomic DNA samples. Three primers giving the largest number of readable bands were chosen for the analyses. I chose study populations from different parts of the distribution area in Finland. Six populations were from southern Finland (central populations) and eleven from the northern limit of the distribution area in central Finland (marginal populations). I defined latitudes of sampling sites and geographical distances between populations according to maps (scale 1:200 000). Latitude values transformed to continuity were used in statistical analyses when testing the importance of geographical distribution for the genetic variation. Additionally, I compared the amount of genetic variation between upstream and downstream populations using five pairs of streams originating from same watersheds. I checked the occurrence of the species upstream from the 17 sampling populations. In total, I checked almost 300 upstream sites. Populations of *A. najas* are usually dense (in autumn about 10 indiv./meter along the riverside) and the presence of the species is easily observed. The number of upstream populations was compared with the amount of genetic variation. I also defined the species habitat range in the stream. The range was defined as the distance between the most distant individuals found. From each of the 17 sampled populations, 30 males were captured for the RAPD analyses.

2.8 Life-history studies (VI)

Studies were carried out during summer 1997 under laboratory conditions. I introduced study individuals to the laboratory, and started measurements of reproductive behaviour after one week acclimatization. Ten randomly formed pairs of waterstriders from each of the ten populations, were released to reproduction containers. I checked all containers for new, fertilized and hatched eggs every third day. The date of each egg-laying, the amount of eggs in clutches, and the number of hatched eggs in previously laid clutches were recorded. I calculated the female life-span from the beginning of the study until death. I also calculated numbers of eggs in each clutch and eggs per female, and also the proportion of eggs hatched. I compared these variables between different populations and between two geographically distant areas. I made comparisons between the properties of egg-clutches of different by comparing the first egg-clutches laid by each female, because most females laid at least one egg-clutch.

3 RESULTS AND DISCUSSION

3.1 Patterns of dispersal (I)

I found significant differences in the dispersal distances and directions among the populations within the releasing rivers, but there were no systematic differences between southern and northern populations. These differences between populations may imply either phenotypic or genetic differences between the populations or a combination of them. Common garden experiments were needed to separate these sources of difference (see III).

The distance and direction of dispersal were not dependent on sex or body length. Dispersal distances were longer in the spring than in the autumn in all the ten populations. During autumn, dispersal was restricted with the mean distance from the place of release being only 2.3 meter upstream from the releasing site. By the end of the spring, 5 individuals (3%) were found inside one meter from the releasing place, about half (52%) of the individuals had dispersed upstream and the other half (45%) downstream, but the distances downstream were longer. In spring, the mean distance was 14.9 meters downstream from the last observation in autumn. Other studies on lotic insects have also shown that during the reproduction period fertile females are especially willing to disperse (Bird & Hynes 1980, Blanckenhorn & Perner 1996). In the case of *A. najas*, both sexes tend to disperse because most of the males are in prolonged mateguarding during the reproduction period (see e.g. Arnqvist 1997). In contrast, dispersal was restricted during the autumn. Despite the long time period, most of the individuals moved only a few meters, mainly upstream. By the end of the spring, total dispersal distances were longer downstream, but no differences in the numbers of animals moving in different directions were found. This result agrees with Fairbairn's (1985) study in *Aquarius remigis* waterstriders, which dispersed equally (in terms of numbers of animals) in both directions. In addition, Ruettiman (1980) has noticed that nymphs of lotic insects are able to compensate for their drift. These results together may imply that some lotic insects are well adapted to lotic environments and that upstream dispersal is not an obligatory strategy for the adult waterstriders.

In eight out of ten populations there was a negative correlation between autumn and spring dispersal distances. In one case, the correlation was not possible to compute due to high overwinter mortality (the average within populations 84± 9 %) and only in one case, the correlation was positive. Thus, the longer an individual dispersed upstream in autumn, the longer it approximately drifted downstream in spring. It is not clear, however, whether individuals adaptively choose the direction and distance of dispersal, or if the result merely reflects differences in the condition of the individuals. As the dispersal distances were longer during the spring, the change in dispersal direction enables the recolonization of the patch from which the dispersal commenced. This supports the proposed strategy of partial allocation of the eggs to the same patch in which a successful parent had developed (Brown & Ehrich 1980, Kuussaari et al. 1996). The successful maturation of the parent provides information that the patch has been suitable at least once.

3.2 Wing polymorphism (II)

In spite of the almost total lack of winged individuals in Finland, many individuals developed to the winged morph in the laboratory conditions. Out of the 396 mature individuals a total of 78 were macropters. This represents almost 20 % of all the mature individuals. Additionally, there were six micropters. The macropter morph was more frequent in females than in males. The highest proportion of macropter morphs (52%) was found in the southernmost population (Pohja) and the lowest (0%) in the northernmost population (Hankasalmi). The proportion of winged individuals was significantly lower in northern populations than in the southern ones, and the proportion of winged individuals decreases against the latitude. In the population of Joroinen (called "Jäppilä" in paper III) the relative number of winged individuals was slightly higher than could be expected according to its geographical location. Interestingly, this is the population where Huldén (1986) found the only two previously known naturally winged individuals in Finland.

During the experimental overwintering period, wingless individuals exhibited greater survivorship than winged individuals. None of the 61 winged individuals survived, but 8 out of the 79 wingless individuals survived over the three month period. All survived individuals were males and seven out of the eight survivors originated from the northernmost population (Hankasalmi).

Results suggest that both phenotypic and genetic components do influence the development of wings. Since the species is mainly wingless in northern populations, differential selection might be the main explanation. Results of higher overwintering survival of wingless morphs indicate that selection pressure against the winged morph is higher in the northern populations. Earlier studies of other gerrid species have reported both supportive (Ekblom 1941) and contradictory evidence (Zera 1984, Vepsäläinen 1974) as compared to our results. Fairbairn (1986, 1988) studied the overwintering survival of *A. remigis* both in the laboratory and field, and she did not find any differences in survival between morphs. On the contrary, winged individuals were found to have higher survival rate than wingless individuals in *Limnoporus canaliculatus* (Zera 1984) and in *Gerris lacustris* (Vepsäläinen 1974). In *G. lacustris*, however, the proportion of winged individuals increases towards the north (Vepsäläinen 1971).

The higher proportion of the macropter morph among females contrasts the view that females might allocate resources to offspring whereas among males mobility would be more important for the reproductive success (Roff 1990). On the other hand Brinkhurst (1959) found no differences in the number of eggs between *Gerris* morphs. In Zera's (1984) experiments, however, wingless females of *L. canaliculatus* laid more eggs than did winged females. Also, there might be differences in egg quality between morphs, but such differences have not been studied so far (see Vepsäläinen 1974). Kaitala and Dingle (1993) compared the mating success between *A. remigis* morphs, and found that wingless males mated more often than winged males. However, in studies of Vepsäläinen (1974) no such differences were found in *G. lacustris*.

3.3 Reduced dispersal in small and isolated patches (III)

The dispersal distances of laboratory reared waterstriders were dependent on the total length of the suitable stream habitat in the watershed from where the parents had been collected. The individuals from the longest stream environments dispersed twice as far as individuals from watersheds with restricted length of suitable streams. Lakes within watersheds represent dispersal barriers to *A. najas* since adults would have difficulties to stay on the water surface without any current. I estimated the minimum total length of the lake barriers needed to contact the stream sections within watershed. Indeed, there appeared a negative effect of barriers on the inherent tendency of waterstriders to disperse, and this effect was equally strong as the previous positive effect of stream length. These results indicate strong genetic control on the dispersal behaviour in waterstriders, and the dispersal is closely linked both to the size of suitable habitat patches and the level of fragmentation between these patches. The result is central for understanding the evolution of dispersal strategies in strongly fragmented environments, and it will have implications for conservation of endangered species living in isolated suitable patches. Most notably, the result indicates that the cost of dispersal may be high in small and isolated patches leading to highly reduced dispersal. Adaptations to local dispersal conditions may operate even between populations within a relatively small geographical scale. At least, this may occur in species with limited dispersal abilities such as the wingless, stream specialized *A. najas*.

Interestingly, it seems that most populations retain a proportion of individuals that attempt to disperse farther, since while median dispersal and the first quartile were highly positively correlated, there was no corresponding correlation for median and the third quartile. Thus, the result corroborates the initial expectation of dispersal polymorphism by Hamilton and May (1977, see also Comins et al. 1980, Frank 1986, Taylor 1988, Cohen & Motro 1989, McPeek & Holt 1992), according to which even under stable conditions, part of the offspring should attempt long-distance dispersal. The polymorphism has significant consequences for the persistence of populations on a larger scale (e.g. Roff 1975, Hamilton & May 1977, Comins et al. 1980, Venable & Brown 1993, Olivieri et al. 1995).

Increasing habitat destruction by humans poses many animal populations to novel situations with highly fragmented and isolated population patches. If there is no sufficient time for selection to reduce dispersal rates, the extinction in small patches may take place just due to the individuals dispersing to the hostile surroundings before dispersal reduction evolves.

3.4 Colonization success (IV)

Both the propagule size and the number of origins were found to influence colonization success. In the autumn the proportion of survived populations was higher in the cases when parental individuals originated from two different populations. This result is valuable for conservation programmes as it indicates that intraspecific genetic variation is important for colonization success. The result indicates that the probability of a propagule to manage in a new environment depends upon the amount of genetic variation available for selection. The amount of genetic variation may be essential for the long term survival of the population, although negative effects related to artificially increased amount of genetic variation may also arise. Outbreeding depression may take place due to break up of co-adapted gene complexes, but in this study I eliminated this effect during the study period by releasing only mated females. Moreover, the proportion of successful colonizations was the highest with largest propagules. This result is in accordance with the more common concept that smaller populations are in a higher risk of extinction (Shaffer & Samson 1985, Harrison et al. 1988, McCauley 1991, Hanski et al. 1995), and according to my result, this concept can also be applied to founder populations.

Much attention has been paid on the genetic consequences of the founder population size and its influence on the genetic structure of populations (founder effect) (Haig et al. 1993), but less attention has been focused on ecological reasons and their influence on the risk of local extinction in small founder populations. My result shows that both propagule size, as well as genetic diversity of propagule, are important for the colonization success. This information is needed when planning restoration projects and especially introductions of endangered species.

3.5 RAPD analyses (V)

The amount of genetic variation within populations was dependent upon the number of upstream populations. In addition, in four out of five cases populations situated closer to the headwaters showed less genetic variation than populations in the lower courses of the watersheds. However, this trend with the small sample size was not statistically significant. There are at least three three alternative explanations suggesting that there is less genetic variation in headwater populations.

Colonization may have originated from the lower courses of a watershed. In that case, small fragments of the populations would have dispersed upstream and the amount of genetic variation decreases towards more peripheral headwater populations. According to this explanation, once an allele disappears during the colonization of the upper streams, it should not emerge again in populations further upstream. However, primary data does not support this view, since upstream populations were lacking some alleles, and at the same time, downstream populations may have lacked other alleles.

Alternatively, streams in both upper and lower courses of the watershed have been colonized "independently", but smaller streams in headwaters can only maintain smaller populations. Thus, the probability that genetic drift will fix an allele in a population is higher in smaller headwater populations. However, I tested the dependence between the range of the living area of the populations and the amount of genetic variation and found no correlation.

Third explanation is that occasional gene flow between streams does exist, but mainly in the downstream direction along a watershed. This idea explicitly predicts the correlation between the amount of genetic variation in a sampling site and the number of colonized streams upstream along the watershed. It is possible that rare downstream drift is maintained by weakened individuals or detached eggs, for example. However, in a previous field study (I), I found that compensatory upstream dispersal is not particularly common in this species, indicating that downstream drift of earlier lifestages is likely to be uncommon.

Populations in Varkaus and Jäppilä are geographically close to each other, while the distance along the watershed is long. However, genetic identity between the populations is over 0.99. The only winged individuals in Finland are found in the Jäppilä population (see Ahlroth et al. 1999). Thus, it is possible that the high genetic identity between these populations could be due to dispersal of winged individuals. Unfortunately, the data based on one observation only does not allow for more sophisticated statistical analyses or generalizations.

Varvio-Aho and Pamilo (1980) found that genetic variation is dependent upon the dispersal ability of the species. Winged waterstrider species were more polymorphic than those mainly or totally wingless (Varvio-Aho 1980). *A. najas* is primarily wingless in the northern Europe, but when rearing waterstriders under short daylength and warm conditions (II), both winged and wingless individuals hatched (Ahlroth et al. 1999). Proportion of winged individuals among reared individuals varied between populations and the only "totally wingless" population was that from Hankasalmi. According to genetic identities in this study Hankasalmi is the most differentiated population. Thus, it seems likely that even occasional presence of winged individuals prevents differentiation.

Using allozyme analysis, Varvio-Aho (1980) did not find any genetic variation within or between different *A. najas* populations. In contrast to Varvio-Aho's results, we found genetic variation both within and between populations (range of H_e 0.077-0.198). The difference may be explained by the fact that allozymes and random DNA segments have dissimilar evolutionary dynamics with respect to mutation and selection (Ayres & Ryan 1997). Other studies commonly suggest significantly higher levels of genotypic diversity with RAPD analysis than determined utilizing allozyme analysis (Waycott 1998). Moreover, out of 16 different primers tested, three chosen for the analysis were not only most readable and repeatable but also provided more variation than rejected primers. As the used primers are not chosen randomly, expected heterozygosity levels may seem exceptionally high for a species living mainly in isolated populations. Furthermore, if the estimation of the levels of heterozygosity are based on RAPD data, the levels of genetic variation should not be compared between different studies (see Rieseberg 1996, for example).

The results of this study indicate the importance of connections along the watersheds for the gene flow in *A. najas*. Rare dispersal or drift between populations seems to occur, if populations are situated along the same watershed. The result is parallel to those of Preziosi and Fairbairn (1992), and those of Zera (1981). According to their allozyme analyses of *A. remigis*, gene flow between the populations of *A. remigis* is highly restricted.

Gene flow along watersheds seems to be downstream biased leading to increase genetic variation within the downstream populations. However, some populations are likely to be isolated. There may be active dispersal by winged individuals, but the role of winged individuals for the gene flow remains obscure and requires further studies.

From the conservational point of view, even if (smaller) populations situated in headwaters maintain less genetic variation per population, they may be more critical for the conservation of genetic variation in larger scale (see IV) than the populations in lower courses of the watershed. My data suggests that populations situated in headwaters are more isolated than populations in downstreams and if dispersal is downstream biased, populations in headwaters may be more differentiated.

3.6 Life-history studies (VI)

Female life-span and the length of the egg-laying period did not differ between different populations. These results suggest that the egg-laying capacity of females does not significantly differ between the studied populations, eventhough the populations are situated at two geographically distant areas.

As expected, females that survived longest, produced more hatched juveniles, on average. The more eggs a female produced, the lower was the proportion of hatched offspring. The proportion of eggs hatched was lowest among long-living females. This is because the mean proportion of eggs hatched was higher in the first, than in the last laid egg-clutch. Also, the first egg-clutch was, on average, larger than the last one. Thus, these results do not indicate a trade-off between the number and the quality of offspring. Instead, a positive relation between the size of the first clutch and the number of eggs laid after the first clutch indicates a silverspoon effect (Cockburn 1991).

Although the mean size of the first clutch showed no variation between the populations, the number of hatched eggs in the first clutch, was on average higher in northern than in southern *A. najas* populations. In northern populations, it may be advantageous to allocate more resources in the first egg clutches because the suitable season for reproduction and growth is shorter towards the north. In southern populations, also eggs laid later during the season may have enough time to develop before the autumn. Since only the mature waterstriders are able to overwinter, northern females should produce as many eggs as possible at the beginning of the reproductive period. In southern populations, the need to allocate into the first egg-clutch is relatively less important. Waterstriders in their most northern Finnish populations are living at the northern range of the distribution area of the species. Thus, changes in reproductive allocation to cope with the short reproductive season are likely to be favoured. In general, however, inherent geographical differences in life-history traits were slight which may indicate the need for phenotypic plasticity in temporally varying conditions (e.g. Blanckenhorn 1994, Blanckenhorn & Fairbairn 1995) or lack of selection processes strong enough for differentiation.

4 CONCLUSIONS

The results of this thesis indicate that variation in dispersal and reproduction strategies may evolve due to variation in local environmental conditions (II, III) or in a larger geographical scale (VI). Differences in abiotic conditions, such as patch size, day length, temperature or the length of season, may favour evolution of dissimilar behaviours and resource allocation strategies.

Seasonal dispersal differences in adult waterstriders (I) provide a new source for understanding the colonization cycle of lotic species. Results also emphasize that individuals from different origins disperse in different ways. The results are not in contrast to previous studies on colonization cycles, but help to explain why adults of some lotic species do not need disperse mainly upstream. Results from dispersal studies (I, III) are supported by the results from RAPD analyses (V), which indicated limited gene flow between populations, mainly taking place within watersheds. Moreover, RAPD data indicate that gene flow along watersheds is likely to be downstream biased.

Probably the clearest evidence for genetic differences between studied populations was the difference in wing morphism between the populations (II). Apart from phenotypic plasticity, there seems to be some genetic control over the occurrence of wings (II), and the latitudinal trend coincides with the direction in natural populations over a larger European scale. As the overwinter survival in our laboratory conditions was highest among the wingless individuals, the survival cost may explain why the proportion of winged individuals was lower in the northern populations with more extreme overwintering conditions than in the southern ones.

A notable result is that there is inherited dispersal avoidance in small and isolated habitat patches (III). This result and the results from colonization study (IV) are relevant to the conservation of endangered animals, especially in man-made, fragmented habitats. The results stress the fact that when introducing founder populations of endangered species, the history of a population is important. The ever increasing habitat destruction by humans poses animal populations to novel situations. If there is no time for selection to reduce dispersal rates, the risk of extinction may increase due to dispersal to the hostile areas. Furthermore, results from the colonization study (IV) are novel in the sense that they suggest the importance of intraspecific genetic variation on the colonization success. The study also indicated that the propagule size is essential on the successful colonization. This result coincides with current views on the dependence between population size and the risk of extinction.

Results from the life-history study (VI) indicate that slightly different life-histories have evolved between geographically distant populations of *Aquarius najas*. In the north, females allocate more resources to reproduction in early spring than females in the south south. However, short egg-laying periods may be favoured in both northern and southern populations in some years due to the strongly varying climatic conditions of northern Europe. This environmental variation may be responsible for phenotypic plasticity in egg-laying behaviour, and thereby in restricting inherent differences between latitudinally differing populations. In general, females of all populations invest most of their resources to reproduction during the beginning of the season. The more resources invested by a female early on, the more offspring she will also later produce. The slightness of observed latitudinal differences makes sense for life-history traits that need to be plastic due to varying conditions.

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YHTEENVETO

Populaatioiden väliset erot virtavesimittareiden (*Aquarius najas*) elinkierrossa ja leviämiskyvyssä.

Väitöskirjatyössäni tutkin, maantieteellisten erojen ja paikallisten sopeumien kehittymistä eristyneissä populaatioissa. Erityinen painoarvo töissäni oli yksilöiden leviämiskyvyllä. Vertailin myös eri populaatioista peräisin olevien yksilöiden perimää molekyylibiologisia menetelmiä apuna käyttäen. Lisäksi selvitin perustajapopulaation koon ja geneettisen monimuotoisuuden merkitystä kolonisaatiomenestykseen. Käytin tutkimuksessani mallilajina virtavesimittaria (*Aquarius najas*). Laji on siivetön ja erikoistunut elämään virtaavissa vesissä. Oletin tutkimuksia aloittaessani, että eri joissa elävät vesimittaripopulaatiot ovat verraten eristyneitä. Erityneisyys ja erot paikallisissa valintapaineissa saattavat pitkällä aikavälillä johtaa paikallisten sopeumien syntyyn. Sopeumien syntyä eristyneissä populaatioissa kuitenkin rajoittaa populaation perimäaineksen yksipuolistuminen sukusiitoksen ja sattuman seurauksena. Lisäksi yksilöiden ilmiasun joustavuus lisää niiden kykyä selvitytyä vaihtelevissa oloissa. Tämän seurauksena valinnan merkitys paikallisen populaation perimäaineksen muovaajana vähenee.

Laboratorio-olosuhteissa joissa kaikkien tutkittavien vesimittareiden kasvuolot oli vakioitu, kehittyi sekä siivellisiä että siivettömiä yksilöitä, vaikka Suomen ilmasto-oloissa virtavesimittarit ovat luonnossa lähes poikkeuksetta siivettömiä. Siivellisten yksilöiden osuus kasvatetuista vesimittareista väheni sitä mukaa mitä pohjoisempaa kasvatettujen yksilöiden emot olivat peräisin. Kaikkein pohjoisimman populaation jälkeläisistä kaikki olivat siivettömiä. Talvehtimiskokeissa kaikki siivelliset yksilöt kuolivat, mikä saattaa selittää siivettömyyden pohjoisissa populaatioissa.

Vertailin laboratoriossa kasvatettujen vesimittareiden liikuvuutta luonnossa ja havaitsin, että vesimittarit, joiden emoyksilöt olivat peräisin pienistä ja eristyneistä esiintymistä, liikkuivat vähemmän kuin ne, joiden alkuperä oli suurista ja toisiinsa läheisessä yhteydessä olevista esiintymistä. Tutkimus tukee ajatusta, jonka mukaan valinta suosii vähäisempää liikkuvuutta pienissä ja eristyneissä elinympäristöissä.

Molekyylibiologisilla menetelmillä saadut tulokset tukivat aiempaa käsitystä geenivirtojen vähyydestä eri jokien välillä. Tulosten mukaan näytteenottojoesta havaittu geneettisen monimuotoisuuden määrä riipuu yläpuolisten populaatioiden määrästä samalla vesireitillä. Lisäksi tulokset antoivat viitteitä siitä, että jokireiteillä latvavesien populaatiot ovat perimältään yksipuolisempia kuin vesireittien alempien osien populaatiot. Virran mukana kulkeutuu mahdolliseti irronneita munia tai heikentyneitä yksilöitä vesireittiä myöten alavirtaan.

Kolonisaatiotutkimusten mukaan sekä perimäaineksen monimuotoisuudella että perus-tajapopulaation koolla on huomattava merkitys kolonisaation onnistumisen toden-näköisyyteen. Perimäaineksen monipuolisuus lisää todennäköisyyttä, että ainakin jollain yksilöllä on ominaisuuksia, jotka ovat eduksi uudessa elinympäristössä.

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Original papers

I

Patterns of dispersal and colonization cycle in a waterstrider (*Aquarius najas*)

by

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Manuscript (submitted)

Patterns of dispersal and colonization cycle in a waterstrider (*Aquarius najas*)

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Summary. Local selection pressures largely determine dispersal strategies. In lotic environments, adult insects are suggested to disperse mainly upstream to compensate for the downstream drift occurring during earlier lifestages. Compensatory upstream dispersal applies to lotic, aquatic species and has also been suggested to apply to some semiaquatic bugs living on the stream surface. We studied dispersal in the lotic waterstrider *Aquarius najas*. Marked individuals of *A. najas* from ten different origins were introduced into five streams which lacked natural populations of this species. All individuals were released in autumn and the movements of each individual was observed to the end of the next spring. The limited movements observed during autumn were upstream biased. In spring, the total absolute distances of dispersal were longer downstream, but we found no differences in the numbers of animals moving in different directions. Populations of different origins varied in their dispersal directions and distances. An individual's direction of dispersal in autumn was negatively associated with its direction of dispersal in spring, and the longer a waterstrider moved upstream in autumn, the longer it approximately moved downstream in spring. Our results indicate that compensatory upstream dispersal is not particularly important in this species. Instead, the seasonal change in the direction of dispersal may serve as a mechanism that enables the recolonization of the natal patch.

Dispersal strategies are known to vary widely both between and within species according to the different selection pressures under given environmental conditions (Cohen and Motro 1989, Roff 1990, Rees 1993, Holt and McPeek 1996). For example, dispersal is favored to avoid competition (Hamilton and May 1977, Herzig 1995, Fonseca and Hart 1996), inbreeding (Pusey 1987, Forster Blouin and Blouin 1988, Bollinger et al. 1993, Pusey and Wolf 1996), predators (Cooper 1984, Holyoak and Lawler 1996) and parasites (Hart 1997). However, it may be advantageous to allocate some descendants to the same patch where parent successfully matured if a given patch has proven suitable at least once (see Brown and Ehrich 1980, Kuussaari et al. 1996, Peck et al. 1998).

In lotic conditions, compensatory upstream dispersal (Mottram 1932, Müller 1954, 1982) is suggested to maintain the colonization cycle. Adult insects, especially females with eggs, are suggested to disperse mainly upstream to compensate the downstream drift of eggs and early nymph stages. Alternative explanation is that downstream drift may arise as a predator avoidance behaviour. The earliest studies concerning compensatory dispersal emphasize its importance for the persistence of the population in a stream. In contrast, later papers (see Fairbairn 1985, Anholt 1995, for example) underline the importance for individual fitness.

Compensatory upstream dispersal has been described in lotic species of mayflies (Ephemeroptera) (Madsen et al. 1977, Bagge 1995), stoneflies (Plecoptera) (Madsen et al. 1973, Madsen and Butz 1976), caddisflies (Trichoptera) (Svensson 1974, Bagge 1995) and semiaquatic bugs (Heteroptera, Gerridae) (Fairbairn 1985). Thus, phylogeny alone does not explain the phenomena; rather, the similarities in conditions in which they have evolved are important. Despite the fact that upstream dispersal is well-documented, causes or alternative hypotheses explaining it have rarely been tested experimentally. In addition, the majority of the previous studies lack replication with several populations and data are usually not based on observations at the level of individuals.

We investigated the patterns of dispersal in a mainly wingless waterstrider species, *Aquarius najas*. This species is a stream specialist that lives in middle sized streams in north-central Europe. In Finland, the species is univoltine and adults overwinter and reproduce in spring (Huldén 1986). Winglessness of *A. najas* increases with increasing latitude (Poisson 1946, Ahlroth et al. in press). In northern Europe *A. najas* is considered to be monomorphic apterous (Huldén 1986, Møller-Anderssen 1993) and the gene flow between populations of *A. najas* is thought to be limited. Therefore, local adaptive differences in the dispersal behavior of local populations is possible (cf. Blanckenhorn 1991). To test the hypotheses of compensatory upstream dispersal, we released individually-marked waterstriders of ten different origins into five streams devoid of the species and compared dispersal distances and directions between populations and sexes, in autumn and spring.

METHODS

Study populations and study sites. Studies were carried out by releasing marked individuals of *A. najas* from ten different rivers of origin (100 individuals / population) into five experimental streams in central Finland that lack natural populations of this species. Five of the original populations stemmed from southern Finland and the other five from central Finland (Table 1). In each of the study streams we introduced one population from southern and one population from central Finland. This enables the comparison of populations of two different geographical areas. Both the streams and the populations were replicated to improve the generalization of the result. As populations in central Finland live at the northern limit of the distribution range of the species, these populations are henceforth called "northern" populations in contrast to the "southern" ones. All *A.*

najas individuals caught were wingless. Adults were collected at the end of August 1995, soon after maturation in natural conditions, and were released approximately five days later. All adults were marked individually with coloured paint dots to allow their later identification in the field. We also measured the body length of each individual (from the front of head to the end of abdomen) to the nearest 0.01mm by digital calipers. Between periods of capture and release, individuals were kept in plastic containers with moist *Sphagnum* moss. In each experimental stream all individuals of both populations were released at the same site.

Dispersal. Movement of each individual was assessed weekly; seven times during the autumn (September 1st - November 20th) and eight times during the next spring and early summer (May 2nd - June 28th). Upstream dispersal was assigned positive values and downstream dispersal or drift was assigned negative values. Colored banners were used to mark every tenth meter along the stream bank and waterstrider movement was assessed within one meter. The movements during the autumn were calculated using data beginning from the releasing site and ending with the last observation in autumn. The spring dispersal was calculated using data from the last observation in the autumn to the last observation in the spring.

Statistical analyses. We used the methods of meta-analysis (Hedges and Olkin 1985) for combined tests over the ten populations, since heteroscedasticity prevented the use of MANOVA. When comparing the distances of autumn and spring dispersal, we first computed Pearson's correlation coefficients for the log-transformed distances of autumn and spring dispersal for each population. The combined test was calculated for these correlations after Fisher's z-transformation and each population was weighted with the sample size. The differences in dispersal were described by the unbiased effect size estimator d (difference in standard deviation units), and again, populations were weighted with sample size using a random effects model (Hedges and Olkin 1985).

RESULTS

The importance of size, sex and origin. The distance and direction of dispersal were not dependent on sex (autumn: range of d -0.54 - +0.30, combined probability $Z = 0.51$, $P = 0.61$, spring; range of d -0.23 - +1.26, $Z = 1.68$, $P = 0.09$) or body length (males in autumn: range of $r = -0.25$ - +0.31, (weighted mean) $r = 0.03$, $P = 0.57$; females in autumn: range of $r = -0.30$ - +0.15, (weighted mean) $r = -0.03$, $P = 0.57$; males in spring: range of $r = -0.86$ - +0.36, (weighted mean) $r = -0.004$, $P = 0.97$; females in spring: range of $r = -0.32$ - +0.66, (weighted mean) $r = 0.16$, $P = 0.32$).

However, significant differences were found in the dispersal distances and directions among the populations within the releasing streams (Table 2), but there were no systematic differences between southern and northern populations.

Seasonal differences in dispersal. Dispersal distances were longer in the spring than in the autumn in all ten populations (range of d = -4.14 - -0.04, $Z = -4.53$, $P < 0.001$). During autumn, movements were restricted with the mean distance from the place of release being only 2.3 meter upstream from the releasing site. By the end of the spring, 5 individuals (3%) were found inside one meter from the releasing place, about half (52%) of the individuals had dispersed upstream and the other half (45%) had either dispersed or drifted downstream. The distances downstream were longer. In spring, the mean distance was 14.9 meters downstream from the last observation in autumn.

In eight out of ten populations there was a negative correlation between autumn and spring dispersal. In one case, the correlation was not possible to compute due to high overwinter mortality (the average within populations 84± 9 %) and only in one case, the correlation was positive (range of r = -0.90 - +0.35, (weighted mean) $r = -0.36$, $P < 0.001$). Thus, the longer an individual moved upstream in autumn, the longer it drifted downstream in spring (Fig. 1).

DISCUSSION

Differences between the populations. In most of the cases, populations of different origins tested within the same experimental stream differed in their average dispersal distances or directions but not in a systematic way (southern vs. northern populations, for example). These differences between populations may imply either environmental or genetic differences between the populations or a combination of them. Common garden experiments are needed to separate these alternatives. Blanckenhorn (1991) has previously demonstrated life-cycle differences between isolated populations of *Aquarius remigis* a close relative of *A. najas*. In his studies, waterstriders of two different types of origins differed in size and developmental time when reared at similar conditions. His results imply that isolated populations of waterstriders may be locally adapted, even over short distances. However, we have not succeeded in connecting dispersal differences between the populations with any factors (southern vs. northern populations). Thus, it is possible that chance (genetic drift, for example) can account for differences between the populations, if any genetic basis for the observed behaviour differences exist (see Dingle 1994).

Colonization cycle. Movements of individuals were restricted during the autumn. Despite the long time period, most of the individuals moved only a few meters, mainly upstream. Thus, restricted movements during the autumn indicate rather lack of dispersal for most of the individuals than any compensatory behaviour. Previous studies on lotic insects have shown that during the reproduction period fertile females are especially willing to disperse (Bird and Hynes 1980, Blanckenhorn and Perner 1996). In a long term study in a small stream, however, males outnumbered females in dispersal activity of dominatind caddisfly species (Svensson 1974). Also in the case of *A. najas*, most of the dispersal occurred in spring. However, in this species both sexes tend to move alike because most of the males are in prolonged mateguarding during the reproduction period (see Arnqvist 1997, for example). By the end of the spring, total distances of the movements were longer downstream but no differences in the numbers of animals moving in different directions were found. Downstream movements can occur either due to active dispersal or due to passive drift. In both cases moving downstream require less energy than moving upstream. The condition of an individual may weaken during the season. In such a case it is not only dispersal that we observe but also passive drift of weakened individuals may explain observed movements (see Dingle 1996, for example). Our results coincide with Fairbairn's (1985, 1986) results in sibling species *Aquarius remigis*. In her studies (Fairbairn 1986) movements of over 100 meters were rare. She also found waterstriders to disperse equally (in numbers of animals) in both directions (see also Svensson 1974). Ruettiman (1980) has noticed that nymphs of some lotic insects are equally able to compensate for their drift. These results together may imply that some lotic insects species are well adapted to lotic environments and that upstream dispersal alone is not an obligatory strategy for the adult waterstriders.

In this study, an individual's direction of dispersal or movements in autumn was negatively associated with the direction of movements in the spring, and the further a waterstrider moved upstream in the autumn, the further it approximately moved downstream in the spring. It is not clear, however, whether individuals adaptively choose the direction and distance of dispersal, or if the result merely reflects differences in the condition of the individuals. As dispersal distances were longer during the spring, the change in dispersal direction enables the re-colonization of the patch from which the dispersal commenced. This supports the proposed strategy of partial allocation of the eggs to the same patch in which a successful parent had developed (Brown and Ehrich 1980, Kuussaari et al. 1996, Svensson 1998). The successful maturation of the parent provides information that the patch has been suitable at least once.

In conclusion, our finding on seasonal dispersal differences in adult waterstriders provides a source for understanding the colonization cycle of lotic species. We also emphasize that individuals from different origins disperse unequally. Our results are not in contrast to previous studies on colonization cycle, but may help to explain why adults of some lotic species do not disperse mainly upstream.

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TABLE 1 The experimental rivers (Bold) and the origins of the populations (N = Northern populations, S = Southern populations) with numbers of males and females released.

Areas	N/S	Longit.	Latit.	Males	Females
Tiilimaa (1)		**62°14′N**	**25°15′E**		
Tammela	S	60°46′N	23°59′E	37	63
Muurame	N	62°22′N	26°32′E	50	50
Kintaus (2)		**62°17′N**	**25°19′E**		
Pohja	S	60°04′N	23°28′E	63	37
Leivonmäki	N	61°59′N	25°59′E	50	50
Mustajoki (3)		**62°16′N**	**25°31′E**		
Espoo	S	60°19′N	24°37′E	56	44
Hankasalmi	N	62°22′N	26°32′E	50	50
Kalmujoki (4)		**62°22′N**	**25°39′E**		
Hyvinkää	S	60°35′N	25°02′E	52	48
Joroinen	N	62°16′N	27°33′E	50	50
Tikkakoski (5)		**62°24′N**	**25°39′E**		
Virolahti	S	60°37′N	27°38′E	49	51
Varkaus	N	62°16′N	27°53′E	50	50

TABLE 2 Autumn and spring dispersal in meters in five experimental rivers (numbers according to Table 1). Differences between each pair in a river were tested by Mann-Whitney U-test. In every comparison an individual is used as an observation unit. Positive values denote upstream, negative values downstream dispersal.

Autumn dispersal

	Southern populations			Northern populations			*U*-test	
River	mean	SD	*n*	mean	SD	*n*	z	*P*
1	-4.1	6.6	75	-1.3	7.5	87	-2.47	0.014
2	2.1	3.6	90	1.9	4.2	91	-0.78	0.436
3	0.8	1.6	88	6.1	13.2	75	-6.09	<0.001
4	-3.6	5.9	79	-1.3	1.4	84	-4.40	<0.001
5	17.2	16.4	68	10.3	24.9	58	-1.58	0.115

Spring dispersal

	Southern populations			Northern populations			*U*-test	
River	mean	SD	*n*	mean	SD	*n*	*u*	*P*
1	4.5	7.4	22	4.0	8.7	13	133.0	0.732
2	18.4	19.3	12	6.5	0.7	2	7.5	0.410
3	-0.6	18.9	7	-58.8	16.4	4	0.0	0.008
4	-18.5	12.2	4	57.2	53.4	17	2.0	0.004
5	-47.5	40.2	12	-112.5	47.3	19	37.5	0.002

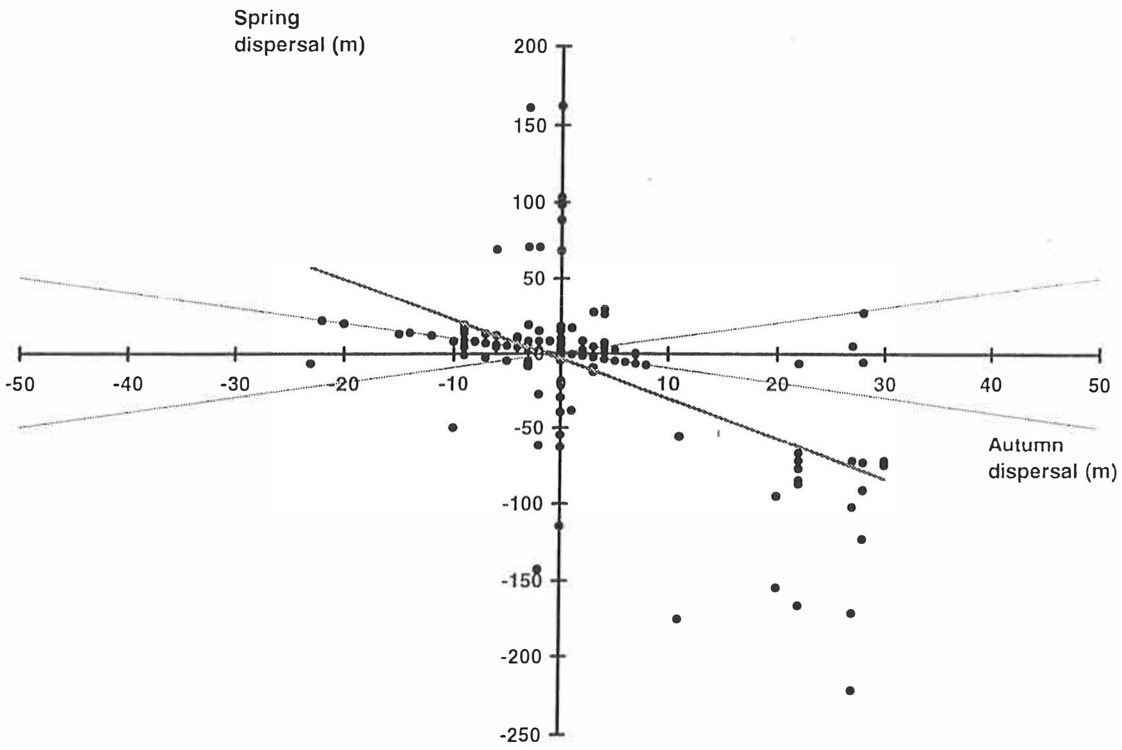

FIGURE 1 Relationship between autumn (from releasing place to last observation in autumn) and spring dispersal (from the last observation in autumn; x-axis to last observation in spring; y-axis) and a fit line (dark gray). Positive values denote upstream, negative values downstream dispersal. 1:1 lines (round dot) come across at the releasing site (origo). The data include those (165) individuals observed at least once both in autumn and in spring. In autumn, dispersal was restricted but biased upstream. In spring, dispersal distances were longer and downstream biased. There was a negative association between autumn and spring dispersal indicating seasonal differences in dispersal.

II

Geographical variation in wing polymorphism of the waterstrider *Aquarius najas* (Heteroptera, Gerridae)

by

Petri Ahlroth, Rauno V. Alatalo, Esko Hyvärinen and Jukka Suhonen

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III

Inherited dispersal avoidance in small and isolated habitat fragments

by

Petri Ahlroth, Rauno V. Alatalo and Jukka Suhonen

Manuscript

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IV

Importance of propagule size and genetic variation on the colonization success

by

Petri Ahlroth, Rauno V. Alatalo, Anne Holopainen, Tomi Kumpulainen and Jukka Suhonen

Manuscript

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V

Genetic variation, genetic identity and dispersal between populations of the waterstrider *Aquarius najas*

by

Petri Ahlroth, Satu Pekkala, Mervi Ahlroth and Rauno V. Alatalo

Manuscript

Genetic variation, genetic identity and dispersal between populations of the waterstrider *Aquarius najas*

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Summary. The waterstrider *Aquarius najas* is primarily wingless in northern Europe and limited to live in lotic habitats. Previous field studies in this species indicate that dispersal is restricted even within streams. Thus, we suggest that the populations in different streams should be rather isolated. We used random amplified polymorphic DNA (RAPD) technique to study the genetic diversity and identity both within and between watersheds, in 17 waterstrider populations from southern and central Finland. From each population, 30 males were used for the analysis. Out of 16 primers tested, three giving the most repeatable and readable band patterns were chosen for the analysis. A total of 43 band patterns were construed. Amount of genetic variation in sampled populations increased with the increasing number of upstream populations. Neither the range of living area nor the geographical location of the sampling site explained differences in the amount of genetic variation between populations. The results suggest that occasional gene flow between streams does exist, but mainly in the downstream direction along the watershed. However, some alleles that are present (or in extreme cases fixed) in upstream populations were lacking in the downstream populations indicating restricted downstream drift or dispersal. On a larger geographical scale, no clear dependence between genetic identity and distance between populations emerged. This might be a consequence of initially panmictic populations with winged forms during the ancient warmer period. Later, after cooling of the climate winglessness has prevailed and long-distance dispersal is now absent.

In small and peripheral populations, genetic variation is generally reduced due to genetic drift and inbreeding (e.g.Varvio-Aho and Pamilo 1980, Palacios and Gonzales-Candelas 1997, Bauert et al. 1998, Lammi et al. 1999). The probability that a given allele will be fixed by genetic drift depends mainly upon the initial frequency of the allele and the size of the population. Fixation rate may also be strongly influenced by immigrants if gene flow between populations occurs (e.g. Varvio-Aho and Pamilo 1980). In lotic environments, passive downstream drift or dispersal from several upper streams towards lower courses of the watershed, may maintain variation differences between the populations.

Previous studies on some lotic organisms indicate restricted gene flow between different stream populations (Preziosi and Fairbairn 1992, Liao and

Hsiao 1998). Studies on the dispersal of lotic waterstriders *Aquarius najas* and *A. remigis* (Fairbairn 1985, Ahlroth et al. unpubl. data) have shown that dispersal may be limited even within a single river. In the case of *A. najas*, there are two factors limiting dispersal. The species is a stream specialist and dispersal over large lakes is probably rare. Another limitation for dispersal is the lack of winged individuals in northern Europe (Poisson 1946, Møller-Anderssen 1993, Ahlroth et al. 1999). Winged individuals occur frequently in southern and central Europe, but in Finland only four winged individuals have been found in a single stream: two by Hulden (1986) and two by us. Thus, we suggest that most of the *A.najas* populations are isolated from each other. Previously, Preziosi's and Fairbairn's (1992) analyses of allozymes in sibling species *A. remigis* revealed that gene flow between *A. remigis* populations is highly restricted. Zera's (1981) studies in the same species reinforced the same conclusion.

In lotic habitats, adult insects tend to disperse upstream to compensate for the downstream drift of earlier life stages (Motram 1932, Müller 1954, Madsen et al. 1973, Svensson 1974, Madsen and Butz 1976, Madsen et al. 1977, Müller 1982, Fairbairn 1985, Bagge 1995). According to our recent field studies, the movements of *A. najas* are slightly upstream biased during autumn, but not in spring (Ahlroth et al. unpubl. data). Thus, we suggest that in this species downstream drift of earlier life-stages is not particularly common. Regardless of the previous dispersal data, observations of the movements of adult waterstriders does not allow us to dismiss the possibility of downstream drift or rare dispersal over the lakes (see Fairbairn 1986). Genetic analyses allow us to make more comprehensive conclusions on the gene flow within and between different watersheds.

We used random amplified polymorphic DNA (RAPD) technique (Lynch and Crease 1990, Welsh and McClelland 1990) to examine genetic diversity and genetic identity in 17 *A. najas* populations. We constructed a dendrogram showing the relationships of the populations using Nei's genetic identity index. Also, using genetic identities, we performed a Mantel's test to describe the importance of geographical distance for the genetic identity of populations. Our aim was to answer the following questions: 1) does gene flow occur through lakes, and if so, 2) does it occur in both directions along the watersheds and 3) does geographical distance explain genetic identity. In addition, we compared the number of fixed alleles and expected heterozygosity with the size of the living area and between the geographical locations of the sampling populations. With this data we discuss the role of active and passive dispersal in this species and the importance of wings for the gene flow.

MATERIALS AND METHODS

Study populations. Study populations were chosen from different parts of the distribution area in Finland. Six populations were in southern Finland (central populations) and eleven in the northern limit of the distribution area in central Finland (marginal populations). Latitudes of sampling sites and geographical distances between populations were defined according to maps (scale 1:200 000). Transformed latitude values were used in statistical analyses when we tested the importance of geographical distribution for the genetic variation. Additionally, we compared the amount of genetic variation between upstream and downstream populations using five pairs of streams originating within watersheds. The occurrence of the species was checked upstream from the 17 sampling populations. In total, almost 300 upstream sites were checked. Populations of *A. najas* are usually dense (in autumn about 10 indiv. / meter along the riverside) and the occurrence of the species is easily observed. The number of upstream populations was compared with the amount of genetic variation. We also defined the species habitat range in the stream. The range was defined as the distance between the most distant individuals. Data on habitat range is based on our observations during three years. From each of the 17 sampled populations 30 male individuals were captured for the RAPD analyses.

Extraction of genomic DNA. Male waterstriders were chosen for RAPD analysis, since mated females might have exhibited mixed RAPD patterns due to the presence of sperm in their reproductive tract (Hooper and Siva-Jothy 1996). The waterstriders were surface sterilized by soaking them in 1% sodium hypochlorite for 20 min with occational vortexing. The dead individuals were rejected. The insects were then killed by quick freezing in liquid nitrogen, and stored in -70°C.

Frozen insects were quickly diced using sterile scalpels and the dices were homogenized by shaking for 5 min at 1600 rpm in Mikro-Dismembrator U (B. Braun Biotech International) with 0.4 g of glass beads (∅ 0.10 mm) and 400 ml of digestion buffer (100 mM NaCl, 10 mM Tris-Cl pH 8, 25 mM EDTA pH 8 and 0.5% SDS). Then, 0.5 mg/ml of Proteinase K (Sigma) was added and the homogenates were incubated at +50°C for 2 h. After digestion, the homogenates were extracted once with phenol-chloroform and once with chloroform-isoamyl alcohol, and the DNA was precipitated with isopropanol. The DNA pellet was dissolved in TE buffer and concentration measured. To ensure the quality of the DNAs, 500 ng of each sample was run in 0.8% agarose gel. Fragmented DNAs were discarded, and only high-molecular weight DNA preparates were used in RAPD.

RAPD analysis. Sixteen different random primers were tested on a few genomic DNA samples. Three primers giving the largest number of readable bands (Fig 1.) were chosen; primer RAPD2 (RAPD analysis kit, Pharmacia) and primers OPA2 and OPA8 (Operon Technologies). These primers also gave differing band patterns on individuals from different populations. The sequences of the random primers were: 5′-GTT TCG CTC C-3′ (RAPD2), 5′-TGC CGA CTG-3′ (OPA2) and 5′-GTG ACG TAG G-3′ (OPA8).

Amplification was performed in Hybaid Touch Down thermal cycler using thin-walled 0.2 ml tube strips. The reaction mixture (total volume 25 ml) consisted of 25 ng of template DNA, 20 pmol of primer, 0.4 mM of dNTPs and 1.5 units of Taq DNA polymerase (Life Technologies) in PCR buffer consisting of 500 mM Tris-HCl (pH 9.2), 160 mM $(NH_4)_2SO_4$, 22.5 mM $MgCl_2$, 20% DMSO and 1% Tween-20. Molecular biology grade ultrapure water (5 prime → 3 prime Inc®, Boulder, USA) was used for the reaction and for working dilutions of the primers and dNTPs. The reactions were overlaid with paraffin oil and the following cycle, after an initial denaturation of 5 min at +95°C, was repeated 45 times: denaturation at +95°C for 1 min, annealing at +30°C for 1 min, extension at +72°C for 2 min. Two negative controls for the primer were included in each PCR. To ensure the consistency of the results, amplification of one sample from the previous PCR was repeated in every PCR experiment. The PCR products were run on 1.5% agarose gel and photographed. To avoid misinterpretation of the results, band sizes were manually measured. Some samples from different populations were also run on gel side by side to see if apparently similar bands actually are of the same size.

Statistical analyses. We used POPGENE -program, version 1.21 to calculate Nei's unbiased measures of genetic identity (see Nei 1972, 1978 for details). The estimation assumes that band patterns simulate dominant Mendelian genetic traits (Stott et al. 1997). We constructed a dendrogram based on the genetic identities using UPGMA (modified from NEIGHBOR procedure of PHYLIP, version 3.5) and calculated Mantel's test based on genetic identity and geographical distances between the origins of populations.

Fixation rate and expected heterozygosity. An allele which did not show variation within a population was interpreted as fixed. Those alleles that did not show any variation in any population were excluded from the statistical analyses. Alternatively to the fixation we have used band patterns to estimate the expected heterozygosity levels. The estimation assumes that the observed band patterns (43) represent dominant markers of alleles that follow the Hardy-Weinberg equilibrium.

The number of fixed alleles and expected heterozygosity were compared with the latitude of the sampling site and also with the range of the living area in each stream. To test the reliability of the results, we have also made comparisons between the fixation and expected heterozygosity.

RESULTS

Genetic variation in populations. According to analyzed 43 band patterns (Fig 1), the range of expected heterozygosity in different populations varied between 0.077 and 0.198. Respectively, the number of fixed alleles varied between 9 and 23. Using fixation or expected heterozygosity in statistical analyses led to parallel results. Fixation is inversely correlated with expected heterozygosity ($r_s = -0.787$, $n = 17$, $p < 0.001$). In both cases, the number of upper colonized streams (ln-transformed) explains the amount of genetic variation in the sampling population. Instead, the range of the living area in the stream or the latitude of origin are not related to genetic variation. (Table 1, Fig. 2-3).

We compared the amount of genetic variation in pairs of populations within a watershed. Five pairs from different watersheds were included. In four cases out of five, populations situated closer to the headwaters showed less genetic variation than populations in the lower course of the watershed. However, this trend with a small sample size is not statistically significant (Paired t-test, for fixation: $t = -1.81$ $df = 4$, $p = 0.145$; for heterozygosity: $t = 1.64$, $df = 4$, $p = 0.176$).

Genetic identity within and between watersheds. Geographical distances and connections along the water route are in accordance with the dendrogram in small geographical scales (Mantel's test, $z = -1.80$, one-tailed $p = 0.032$) (Fig. 4), but in larger scale, the structure of dendrogram is more randomly ordered. Thus, both the structure of the dendrogram and the result from the Mantel's test indicate isolation for most of the populations. In short distances (<35 km) genetic identity is related to geographical distances, but in long distances (> 100 km) genetic identity remains in equal level (Fig 5). Genetic identities and geograpgical distances between the sampling sites are summarized in table 2. Table 3 summarizes the numbers and sizes (lengths) of the lakes that isolate populations situated within the same watersheds. The distances between populations are defined as the minimun distances between the estuaries of the streams, while in table 2 distances were measured between the sampling sites.

DISCUSSION

According to our results, the amount of genetic variation in a sampling population is dependent upon the number of upstream populations. In addition, in four out of five cases populations situated closer to the headwaters showed less genetic variation than populations in the lower courses of the watersheds. However, this trend with the small sample size was not statistically significant. We present three alternative explanations suggesting that there is less genetic variation upstream populations. These explanations are not mutually exclusive.

Colonization may have originated from the lower courses of a watershed. In that case, small fragments of the populations would have dispersed upstream and the amount of genetic variation decreases towards more peripheral headwater populations. According to this explanation, once an allele disappears during the colonization of the upper streams, it should not emerge again in populations further upstream. However, our primary data does not support this view, since upstream populations were lacking some alleles and at the same time downstream populations may have lacked other alleles.

Alternatively, streams in both upper and lower courses of the watershed have been colonized "independently", but smaller streams in headwaters can only maintain smaller populations. Thus, the probability that genetic drift will fix an allele in a population is higher in smaller head water populations. However, we tested the dependence between the range of the living area of the populations and the amount of genetic variation and found no correlation. Thus, this explanation alone is not likely to explain the observed phenomena.

Third explanation is that occasional gene flow between streams does exist, but mainly in the downstream direction along a watershed. This idea explicitly predicts the correlation between the amount of genetic variation in a sampling site and the number of colonized streams upstream along the watershed. In addition, this explanation is consistent with the structure of the dendrogram, as well as with the result of the Mantel's test. If only occasional downstream drift or dispersal occurs, we may expect genetic identity between neighbouring populations. Results in this study are also parallel to the previous results of Preziosi and Fairbairn (1992) and Zera (1981). According to their allozyme analyses in a sibling species (*A. remigis*), gene flow between the populations turned out to be highly restricted. In sum, the third explanation provides the most likely explanation for the observed patterns.

Populations in Varkaus and Jäppilä are geographically close to each other, while the distance along the watershed is long. However, in the dendrogram Varkaus is placed near Jäppilä, and the genetic identity between the populations is over 0.99. The only winged individuals in Finland are found in the Jäppilä population (see Ahlroth et al. 1999). Thus, it is possible that the high genetic identity between these populations could be due dispersal of winged individuals. Unfortunately, the data based on one observation only does not allow for more sophisticated statistical analyses or generalizations.

Varvio-Aho and Pamilo (1980) found that genetic variation is dependent upon the dispersal ability of the species. Winged waterstrider species were more polymorphic than mainly or totally wingless waterstriders (Varvio-Aho 1980). *A. najas* is primarily wingless in the northern Europe, but when rearing waterstriders under short daylength and warm conditions both winged and wingless individuals hatched (Ahlroth et al. 1999). Proportion of winged individuals among reared individuals varied between populations and the only "totally wingless" population was from Hankasalmi. According to genetic identities in this study, Hankasalmi is the most differentiated population.

Using allozyme analysis, Varvio-Aho (1980) did not find any genetic variation within or between different *A. najas* populations. In contrast to Varvio-Aho's results, we found genetic variation both within and between populations (range of H_e 0.077-0.198). The difference between Varvio-Aho's and our results can be explained by the fact that allozymes and random DNA segments have dissimilar evolutionary dynamics with respect to mutation and selection (Ayres and Ryan 1997). Studies commonly suggest significantly higher levels of genotypic diversity with RAPD analysis than determined utilizing allozyme analysis (Waycott 1998, 1995). Moreover, out of 16 different primers tested, three chosen for the analysis were not only most readable and repeatable, but also provided more variation than rejected primers. As the used primers were not chosen randomly, estimated heterozygosity levels may seem exceptionally high for a species living mainly in isolated populations. Furthermore, if the estimation of the levels of heterozygosity are based on RAPD data, the levels of heterozygosity should not be compared between different studies (see Rieseberg 1996, for example), if studies are carried out using different primers or under otherwise different conditions (which is usually the case). Weak comparability between different studies is not the only problem when using RAPDs. The method is exceptionally sensitive to contaminations, which is not always taken into account. In fact, there is enormous number of RAPD based studies lacking negative controls. However, when carried out with care, RAPDs provide an economical way of obtaining useful data.

In this study, we succeeded to clarify the importance of connections along the watersheds for the gene flow of *A. najas* using RAPD analyses. Rare dispersal or drift between populations seems to occur, if populations are situated along the same watershed. Gene flow along watersheds seems to be downstream biased thus increasing the amount of genetic variation in downsteram populations. On a larger geographical scale, no clear dependence between genetic identity and distance between populations emerged. This might be a consequence of initially panmictic populations with winged forms during the ancient warmer period. Later, after cooling of the climate winglessness has prevailed and long-distance dispersal is now absent. There may occur active dispersal by winged individuals, but with present data the role of winged individuals for the gene flow is unclear.

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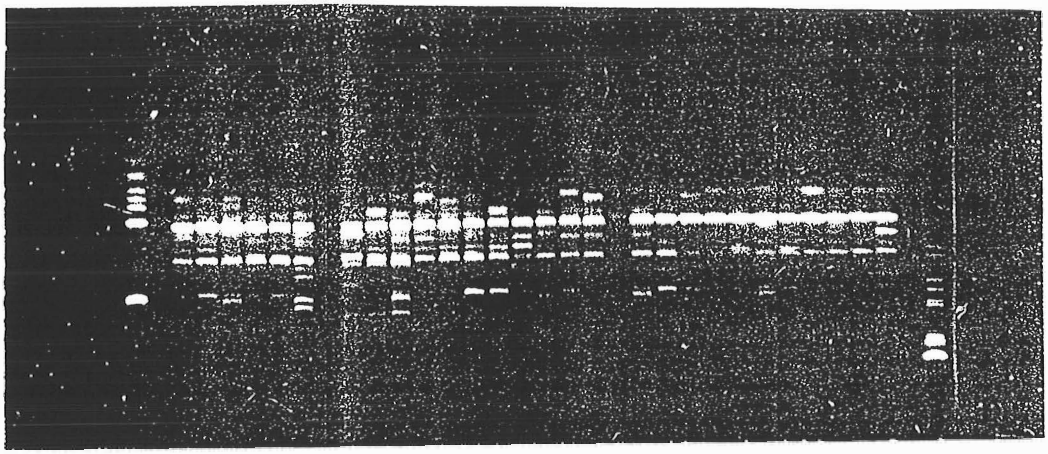


FIGURE 1 An example of a gel elcetrophoresis picture. At the first and the last lanes there are molecular weight markers and negative controls next to them. Construed samples (30 indiv. / population) are between negative controls. In each gel there are lanes for samples from three populations. The repeatability of the results was controlled in extra runs that contained 6 individuals from each population.

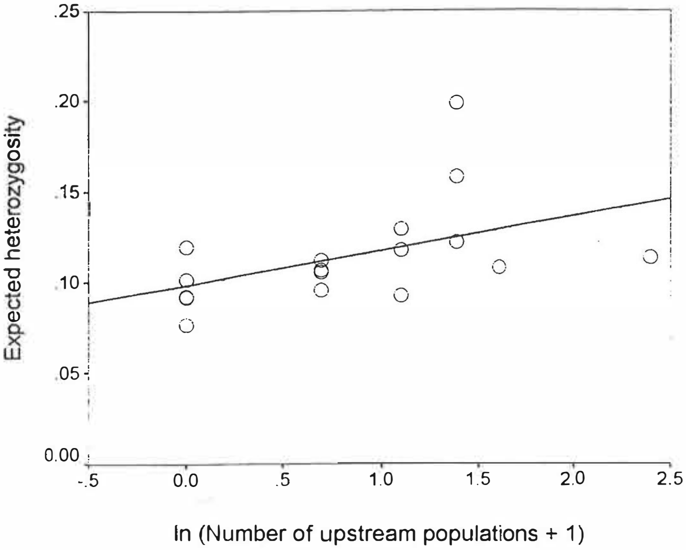


FIGURE 2 Expected heterozygosity and the number of upper populations from the sampling site. The result suggests that the higher is the number of upstream populations, the more genetic variation there will be in the sampling population (see table 1 for statistical analyses).

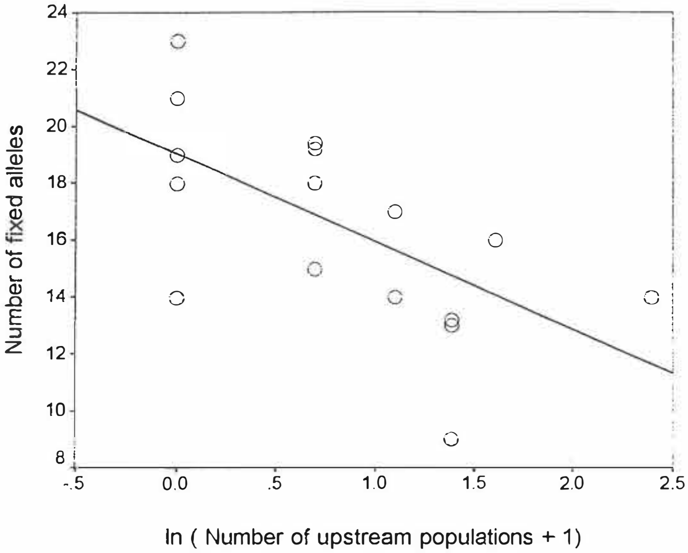
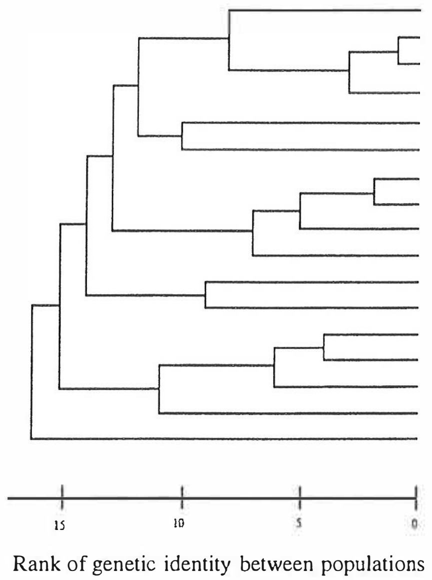


FIGURE 3 Fixation and the number of populations upstream from the sampling site. The number of fixed alleles in a population is inversely correlated with the number of colonized rivers upstream from the sampling site (see table 1 for statistical analyses).



Population	Symbol of watershed	Geographical area (South / North)
Hyvinkää		S
Jäppilä	▲	N
Varkaus		N
Syvänsi	▲	N
Espoo		S
Pohja 1	■	S
Leivonmäki	◆	N
Rutajoki	◆	N
Niemisjärvi	▼	N
Janhola	▼	N
Pohja 2	■	S
Saukkola	●	N
Neulajoki	●	N
Siuntio		S
Virolahti		S
Tammela		S
Hankasalmi		N

FIGURE 4 Dendrogram based on Nei's unbiased measures of genetic identity (Mantel's test, Z = -1.8045, one-tailed p = 0.032). The scale is for the ranked values of the genetic identities between the populations. Populations in Jäppilä, Varkaus and Syvänsi are geographically situated near to each other and Jäppilä and Syvänsi populations are situated along the same watershed (▲). Around Jäppilä region there are at least 15 known *A. najas* populations within the area of 20 x 20 km. Similarly, populations around Leivonmäki (named Leivonmäki and Rutajoki in the dendrogram) are situated along the same watershed (◆). They are also geographically close to populations in Niemisjärvi and Janhola (▼). There is only one relatively small lake between two populations populations in Pohja (■) (named Pohja 1 and Pohja 2 in the dendrogram). Three lakes isolate populations in Saukkola and Neulajoki. These populations are also situated along the same watershed (●), but the genetic identity between these populations is lower than among populations in Jäppilä and Leivonmäki regions.

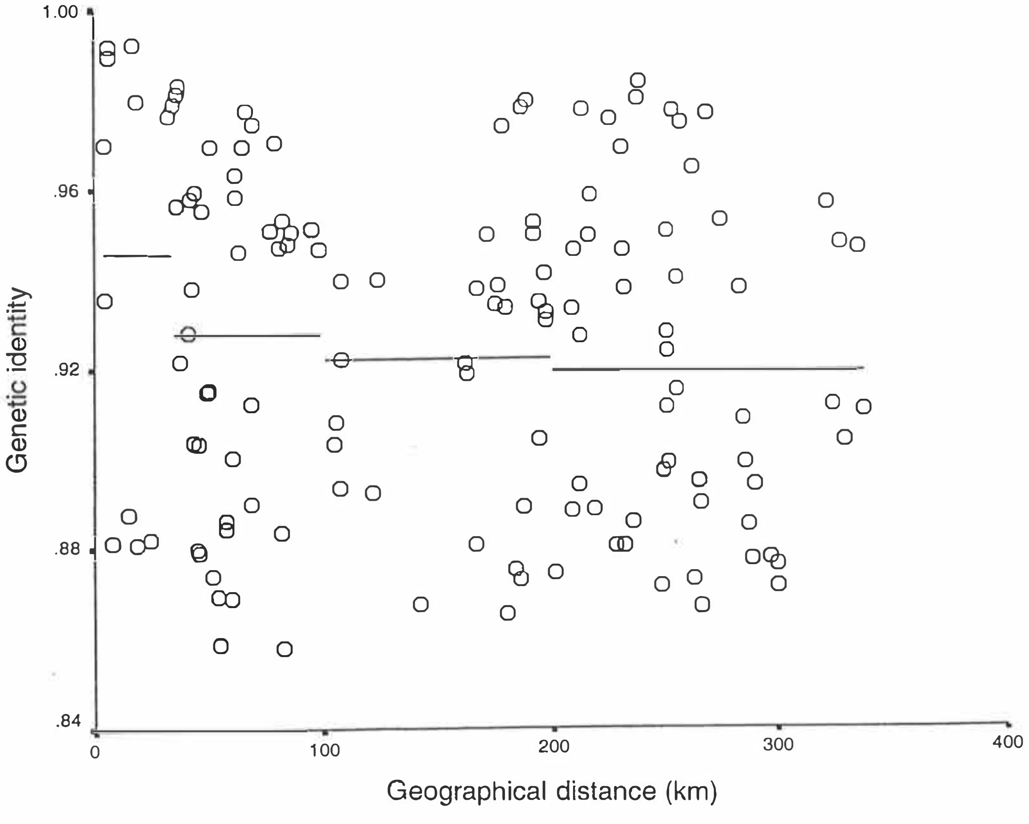


FIGURE 5 Geographical distances and genetic identities between the populations. The result suggests that gene flow is rare even between close populations. The lines indicate mean identities for the following geographical distance gategories: 0-35 km, 36-100 km, 101-200 km, > 200 km.

TABLE 1 Factors explaining genetic variation, analyzed with multiregression analysis

A) Dependent variable: **Expected heterozygosity**

Model:	R^2	df	F	p
Regression	0.677	3	3.67	0.041

	B	SE	t	p
constant	0.869	0.388	2.24	0.043
upper populations	0.022	0.009	2.41	0.031
living area	-0.004	0.003	-1.26	ns
latitude	-0.012	0.006	-1.96	ns

B) Dependent variable: **Number of fixed alleles**

Model:	R^2	df	F	p
Regression	0.498	3	4.29	0.026

	B	SE	t	p
constant	-39.6	45.5	-0.87	0.401
upper populations	-3.24	1.05	-3.09	0.009
living area	0.36	0.36	0.99	ns
latitude	0.94	0.75	1.26	ns

TABLE 2 Genetic identities and geographical distances between populations

	Hyvinkää	Espoo	Jäppilä	Varkaus	Pohja 1	Neulajoki	Leivonm.	Rutajoki	Tammela	Virolahti	Janhola	Niemisj.	Siuntio	Pohja 2	Hankas.	Syvänsi	Saukkola
Hyvinkää		36.4	226.4	238.4	64	186.4	162.4	163.2	58.4	141.8	196.8	197.6	60	104.8	212	232	180
Espoo	0.9564		263.2	275.2	70.2	219.2	197.6	194.4	61	167	232	232.8	24.2	69.6	248	269.6	212.8
Jäppilä	0.9752	0.9644		16.6	323.2	106.8	81.6	85.6	252	179.2	66.8	62.4	288.8	325.6	54	5.8	108
Varkaus	0.9797	0.9525	0.9922		336.8	121.6	96	99.2	265.6	184	80	77.6	297.6	339.2	69.6	18	124
Pohja 1	0.946	0.9743	0.9563	0.9465		263.2	251.2	251.2	82.2	232.8	284	285.6	46.4	1.8	300	328.8	256
Neulajoki	0.8728	0.8886	0.8936	0.8925	0.8727		47.8	42	187.2	213.6	43	44.6	239.2	266.4	55	106	7.6
Leivonmäki	0.9208	0.9303	0.9474	0.9516	0.911	0.9552		6	176.8	167.2	34.4	36.2	216.8	254.4	50	83.2	43.4
Rutajoki	0.9188	0.9344	0.9479	0.9469	0.9277	0.9579	0.9917		176	172	32.4	37.2	217.6	249.6	50.2	86.8	37.4
Tammela	0.8843	0.9004	0.8988	0.8947	0.8837	0.9778	0.9381	0.9341		192.8	208.8	209.6	63	82.8	224.8	256	180
Virolahti	0.8675	0.8805	0.8738	0.8751	0.8801	0.9771	0.9376	0.9497	0.9497		194.4	192.8	189.6	236	201.6	188	208.8
Janhola	0.941	0.946	0.9773	0.9702	0.9375	0.938	0.9788	0.9764	0.9329	0.904		4.4	251.2	286.4	18	66	41.8
Niemisjärvi	0.9322	0.9374	0.9581	0.9512	0.9087	0.9595	0.9812	0.9823	0.9461	0.952	0.9697		251.2	287.2	14.4	61.6	46
Siuntio	0.8689	0.8823	0.8772	0.8776	0.8793	0.9824	0.9491	0.9581	0.9632	0.9794	0.9235	0.9503		45.6	266.4	290.4	228.8
Pohja 2	0.9034	0.9124	0.9114	0.9104	0.9356	0.8667	0.8769	0.8967	0.8579	0.8855	0.8986	0.8847	0.88		300	330.4	258.4
Hankasalmi	0.8938	0.8714	0.8693	0.89	0.8714	0.8589	0.915	0.9152	0.8389	0.8741	0.8811	0.8879	0.8897	0.876		52.2	57.8
Syvänsi	0.9688	0.9765	0.9893	0.9798	0.9477	0.9082	0.9535	0.9508	0.9148	0.8891	0.9652	0.9694	0.894	0.9036	0.8738		107.6
Saukkola	0.9335	0.9271	0.9395	0.9397	0.9386	0.8815	0.9036	0.9218	0.8652	0.8882	0.9281	0.9031	0.8804	0.9745	0.8863	0.9221	

TABLE 3 Lakes isolating populations within watersheds. The size of each lake is measured as the minimum distance between the estuaries of the streams.

Pairs of streams within watershed		N of lakes between streams	Sizes of lakes (km)	genetic identity
Syvänsi	Jäppilä	1	2.0	0.99
Leivonmäki	Rutajoki	2	4.9, 1.0	0.99
Janhola	Niemisjärvi	1	0.6	0.97
Pohja 1	Pohja 2	1	1.6	0.94
Saukkola	Neulajoki	3	2.5, 0.6. 0.8	0.88

VI

Latitudinal life-history differences between waterstrider (*Aquarius najas*) populations

by

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and Jukka Suhonen

Manuscript

Latitudinal life-history differences between waterstrider (*Aquarius najas*) populations

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Summary. Geographical variation in life-history strategies may evolve due to differences in continuous selection pressures. Differences in abiotic conditions, such as day length, temperature or the length of season, may favor dissimilar behaviour and allocation of resources. We studied whether life-history tactics differ between ten populations of waterstrider *Aquarius najas*, in an artificial stream system, with similar conditions for all individuals. We measured fecundity, life-span and behavioural variables, describing the allocation of females' resources and compared the variables between geographically distant populations. In general, we found a negative relation between the number and the quality of offspring. However, this relation appears because the quality of eggs decreases during the season. If a female has a short life-span, she only produces egg-clutches of high quality. Females with a long life-span also produce eggs of inferior quality, during their later reproductive period. In this study however, females with large first clutches also laid more eggs later, thereby indicating silver spoon effect. In addition to the offspring quality, the mean size of the egg-clutch decreased during the season. Thus, the female´s reproductive effort was found to decrease during the season, as more was invested in the first than in the last offspring. Females of northern origin allocated more of their resources to their first clutch, compared with females of more southern origin. However, the length of the egg-laying period did not differ between the populations. Our results indicate that waterstriders of different origins have slightly differing life-histories. Differences in allocation to reproduction are related to latitudinal differences between origins. Thus, our results may be a sign of local adaptation of populations to long-term climatic patterns. The slightness of observed latitudinal differences makes sense for life-history traits that need to be plastic due to varying climatic conditions.

Natural selection often poses different pressures on a single trait when the environment of the organism changes. Environmental conditions are often suboptimal for a single organism (Kaitala 1987, Roff 1992, Stearns 1992). Therefore, an organism has to respond to unfavorable environmental conditions for example by changing it´s behaviour, to avoid the environment´s deleterious effects on survival and fecundity (Roff 1980, Ludwig & Rowe 1990, Stearns 1992). However, an individual can react to a short term stress only within the frame of its own genotype by using physiological responses, i.e. the phenotypic plasticity (Kaitala 1987, Roff 1992, Hill & Gatehouse 1993, Shen & Bach 1997).

Intraspecific life-history differences may exist among different geographical areas, as for example along latitudinal clines (Mayr 1971, Fairbairn 1984, Hanks & Denno 1994, Ayre 1995, Lobón-Cerviá et al. 1996, Starmer et al. 1997, Ahlroth et al. 1999). This is mainly because environmental conditions such as the length of the reproductive and growth season vary along the latitudinal scale (Stearns 1992), and because individuals may be restricted to migrate to more favorable conditions (Fairbairn & Desranleau 1987, Cobb & Whitham 1993). Similar life-history differences can also exist on a smaller geographic scale, among close populations, especially if the gene flow between these populations is otherwise limited, for example due to a steep altitudinal cline (Waser & Price 1985, McPheron et al. 1988, Karban 1989, Singer et al. 1993, Costa & Ross 1994, Schilthuizen & Lombaerts 1994, Mopper et al. 1995, Herring & Verrell 1996, Mopper 1996, Rohr 1997).

We compared life-histories between ten distant waterstrider *Aquarius najas* (Degeer) populations under similar laboratory conditions. We measured fecundity and reproductive behaviour of female waterstriders, and compared these variables between the populations of two geographical areas, separated by latitude. We also tested whether the females invested more in their first than in their last offspring. Five out of ten of our study populations originated in the northern range of the distribution area of the species and length of the reproductive season may set a limit for the distribution.

METHODS

Study species. *Aquarius najas* is a stream specialist occupying only stable lotic habitats (Møller Andersen 1990). In central Finland the species lives at the northern range of its distribution area and it occurs in the southern and south-eastern parts of the country. *A. najas* is univoltine and phenotypically wingless in northern Europe (Ahlroth et al. 1999). Adult waterstriders overwinter in terrestrial sites such as under rocks or in the moss at the ground layer of the vegetation (Linnavuori 1966, Huldén 1979, Møller Andersen 1993). In spring, waterstriders leave their overwintering sites to forage other insects on the water surface, and to begin reproduction. A week after copulation, the female lays egg-clusters on stones and on the leaves of aquatic plants (Huldén 1979). Individuals die soon after the reproduction season and the surviving offspring reproduce during the next spring.

Parental individuals were collected from ten separate origins (Table 1.), five of which were located in central Finland and the other five in the coastal area of southern Finland. Waterstriders were captured with an insect net during spring 1997, immediately after they had returned to lotic habitats from their overwintering sites. To prevent mating before the laboratory studies, females and males were kept in separate containers. Study individuals were introduced to the laboratory, and reproductive behaviour was studied after one week of acclimatization time.

Laboratory. Studies were carried out during summer 1997 under laboratory conditions. An artificial stream system was built up with separated pools (diameter 0.38 m, volume 8 litres) functioning as reproduction containers. Plastic pools were covered by thin nets allowing light to penetrate. All containers were connected to a common stream system in which the water was circulated with electric pumps. The water was conducted to every pool through a separate duct and was further conducted away from pools through another separate duct back to a collector container. Thus, waterstriders were inhabiting a natural kind of stream habitat with oxygen-rich water. In every pool there were two standard sized bricks (7 x 7 x 12 cm) on which waterstriders could rest and lay their eggs.

Waterstriders were fed daily with fruit flies (*Drosophila spp.* about 10 flies per individual) and ants (*Formica* spp. about three ants per individual). During the whole study period food was provided *ad libidum.* Reproduction pools were cleaned daily and the water in the stream system was changed continuously. In the laboratory a 17:7 light:dark cycle was maintained, and water and air temperatures were held at 19 °C (+/- 1°C) during the whole study period.

Before the studies, one male and one female, both from the same population, were transferred to each reproduction pool. Ten pairs of waterstriders from each of the ten populations were formed. Containers were checked for new, fertilized and hatched eggs every third day. Eggs of *A. najas* are 1,5 - 2 mm long and about 0,5 mm in diameter. New, recently laid eggs are bright white in color, but after about three days following fertilization, eggs turn brown and the larval eyes become noticeable; just before hatching the eggs are dark brown, and hatched, empty eggcells are light brown and ragged. Unfertilized and dead eggs stay white, but they soon swell and turn into obscure white-yellow. Thus, the condition and state of the eggs were easy to observe.

The date of egg-laying, the number of eggs in the clutches, the number of hatched eggs in previously laid clutches and the female life-span were recorded. The number of eggs in each clutch and eggs per female, as well as the proportion of eggs hatched were calculated. These variables were compared between different populations and between the two geographically distant areas. Comparisons between the properties of egg-clutches of different females were made by comparing the first egg-clutches laid by each female, because most females laid at least one egg-clutch.

Statistical analyses. To achieve normality, the numbers of "eggs laid after the first clutch" and "female lifespan", were square root transformed before statistical analysis (ANCOVA) was performed. The proportions of hatched eggs in the first and second clutch, and the total proportion of eggs hatched were analyzed using non-parametric ANOVA models for ranked values (Zar 1996). Test value H was calculated as SS_{SOURCE} / MS_{TOTAL}, and it asymptotically follows the chi-square distribution with df_{SOURCE}.

RESULTS

Life-history parameters are summarized in table 2. The female life-span did not differ between the populations (ANOVA, $F_{9,93} = 0.79$, $P = 0.63$), and neither did the length of the egg-laying period (ANOVA, $F_{9,93} = 1.29$, $P = 0.26$). As expected, females that survived longest, produced, more hatched juveniles in all ten populations (ANCOVA, Female life-span $F_{1,93} = 25.1$, $P < 0.001$; population $F_{9,93} = 0.83$, $P = 0.59$). The more eggs a female produced the lower was the proportion of hatched eggs (non-parametric ANCOVA for ranked values of the proportion of hatched eggs, eggs $H = 7.64$, $df = 1$, $P = 0.008$,populations $H = 7.64$, $df = 9$, $P = 0.64$).

The proportion of eggs hatched was lowest among long-living females (non-parametric ANOVA for ranked quantities of hatched eggs $H = 20.5$, $df = 1$, $P < 0.001$, populations $H = 8.45$, $df = 9$, $P = 0.53$; Fig. 1). This is because in all studied populations, the mean proportion of eggs hatched was higher in the first than in the last laid egg-clutch (repeated measures ANOVA for ranked values of the proportion of hatched eggs $F_{1,77} = 23.38$, $P < 0.001$, population $F_{9,77} = 0.87$, $P = 0.56$). Also, the first egg-clutch was, on average, bigger than the last one in all populations (repeated measures ANOVA, clutch size $F_{1,77} = 555.98$, $P < 0.001$, populations $F_{9,77} = 1.75$, $P = 0.091$; Fig. 2).

The females whose first clutches were the largest, also laid the most eggs later during the reproductive period (ANCOVA, eggs $F_{1,93} = 6.82$, $P = 0.011$, populations $F_{9,93} = 1.49$, $P = 0.17$; Fig. 3). This phenomenon appeared in all ten populations. Although the mean size of the first clutch showed no variation between the populations (ANOVA, $F_{9,93} = 1.17$, $P = 0.33$), the amount of hatched eggs in the first clutch, was significantly higher in northern than in southern *A. najas* populations (Table 3, Fig. 4). However, there is no relation between female life-span and the mean size of the first clutch, in any population (ANCOVA, size of the first clutch as a covariate $F_{1,93} = 1.32$, $P = 0.25$, populations $F_{9,93} = 0.77$, $P = 0.65$). There were also no differences in the total amounts of eggs produced per female, between populations (ANOVA, $F_{9,93} = 1.14$, $P = 0.22$). When we tested the relationship between the female life-span and the mean size of the first clutch, both between all populations and between populations of southern and northern origins, we found no relation or geographical differences between these variables (Table 4).

DISCUSSION

Our results indicate geographical differences in female´s egg-laying behaviour and resource allocation during the reproductive period, between *Aquarius najas* populations. In previous waterstriders studies, both parallel and contradictory results to ours have been found. For example, Fairbairn (1984) found microgeographic variation in a long-winged waterstrider *Limnoporus notabilis* (Drake and Hottes), although this species is an excellent disperser. On the other hand, Blanckenhorn (1994) found high degrees of phenotypic plasticity in adjacent populations of the largely wingless waterstrider *Aquarius remigis* (Say). In another study with same species, Blanckenhorn (1991) observed remarkable genetic differentiation in body size, development rate and reproduction of adjacent populations. As Blanckenhorn & Fairbairn (1995) also studied the life-history adaptation of *A. remigis* along a long latitudinal gradient, they found differences in size and also in the reproductive efforts between the females from different latitudes. Their results revealed both phenotypic plasticity and local adaptations to long-term climatic patterns. Strong morphological differentation has also been found among latitudinally distant populations of *A. remigis* (Brennan & Fairbairn 1995) and *A. najas* (Ahlroth et al. 1999).

Female life-span and the length of the egg-laying period did not vary geographically, under laboratory conditions. The total amount of eggs per female also did not vary between populations. These results suggest that the egg-laying capacity of females does not significantly differ between the studied populations, even though the populations are situated at two geographically distant areas.

According to our results, females of northern origin allocate more resources in the first clutch than females of the southern origin. This may be advantageous because the growth and reproductive seasons shorten towards the north. In southern populations, also eggs laid later during the season have enough time to develop before the autumn and to reach the overwintering condition. Thus, in southern populations, the need to allocate in the first egg-clutch is less obvious. Waterstriders in most northern Finnish populations are living at the northern range of the distribution area of the species. Thus, changes in reproductive allocation used to cope with the short reproductive season are favoured. As only the mature waterstriders are able to overwinter, northern females should produce as many eggs as possible at the beginning of the reproductive period. However, in *Aquarius remigis* (a close relative to *A. najas*) female ovarioles can produce only a certain quantity of eggs (48) at a time (Galbraith & Fernando 1977). Thus, females are possibly unable to produce all of their eggs during a short period.

In this study, life-span corresponded, on average, with more produced offspring. In addition, a larger first egg-clutch size corresponded with a larger number of eggs laid after the first clutch. However, a large clutch size was linked with lower proportion of hatched eggs. This negative relation occurred because in the first laid egg-clutches the proportion of hatched juveniles is higher than in the last laid clutches. Thus, these results do not indicate a trade-off between the number and the quality of offspring. In previous studies Preziosi et al. (1996) however, found a trade-off between the size and the number of eggs of the North-American *A. remigis*. In our studies instead, a positive relation between the size of the first clutch and the number of eggs laid after the first clutch indicates silverspoon effect (Cockburn 1991). Also, the mean size of the first egg-clutch was bigger than the mean size of the last egg-clutch. As in many animals, female waterstriders seem to invest more in their first than last offspring (e.g. Roff 1992, Stearns 1992). At least two hypotheses may explain this: 1) Allocating more resources in spring may be favored due to short season (e.g. Huldén 1979, Kaitala 1987). 2) The weakening condition of females later in season may affect the quality of her offspring (Stearns 1992).

The relationship between the mean size of the first clutch and the amount of eggs produced after the first clutch, may indicate that the egg-laying potential of female *A. najas* is not strongly reduced by her investment in the first clutch. Thus, some females are more fertile than others. Fertile females lay the largest egg-clutches in early spring, but they also produce the most numerous offspring later in the reproductive season.

In conclusion, our main results suggest that only slightly different life-history traits have evolved between geographically distant populations of *A. najas*. Differences between populations are related to geographical differences. In north, females allocate more resources in early spring. However, short egg-laying periods may be favored in both northern and southern populations in some years due to the strongly varying climatic conditions of northern Europe. This enviromental variation may be responsible for phenotypic plasticity in egg-laying and thereby restrict detectable differences between latitudinally differing populations. In general, females of all populations invest most of their resources during the beginning of the season. The more resources invested by a female early on, the more offspring she will later produce.

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TABLE 1 The waterstriders for our laboratory studies were collected from five southern and five northern populations in Finland. N is the number of pairs of waterstriders from each population.

Population	Location	N
Southern populations		
A. Pohja I	(60°03´N, 23°29´E)	8
B. Pohja II	(60°04´N, 23°28´E)	10
C. Hyvinkää	(60°35´N, 25°02´E)	10
D. Virolahti	(60°37´N, 27°38´E)	10
E. Tammela	(60°46´N, 23°59´E)	8
Northern populations		
F. Leivonmäki	(61°59´N, 25°59´E)	9
G. Muurame	(62°11´N, 25°29´E)	10
H. Joroinen	(62°16´N, 27°33´E)	10
I. Varkaus	(62°16´N, 27°53´E)	9
J. Hankasalmi	(62°22´N, 26°32´E)	10

TABLE 2 The pooled data from reproductive and life-span measurements.

	Southern populations			Northern populations		
Measured variable	Mean	SD	n	Mean	SD	n
Female life-span (days)	34.2	16.1	46	38.7	22.4	48
Egg-laying period (days)	19.2	15.6	46	23.4	18.2	48
No. of eggs	119.7	94.7	46	136.1	92.4	48
No. of hatched	92.6	78.2	46	104.3	66.9	48
Prop. of hatched	0.78	0.29	46	0.80	0.20	48
No. of eggs after first clutch	103.4	93.8	46	119.8	88.9	48
No. of eggs in last clutch	12.7	8.0	39	9.9	6.4	39
Prop. hatched in first clutch	0.84	0.29	46	0.92	0.20	48
Prop. hatched in last clutch	0.63	0.43	39	0.60	0.45	39
No. of eggs in first clutch	16.3	8.4	46	16.4	7.0	48
No. of hatched in first clutch	14.5	9.0	46	15.6	7.2	48

TABLE 3 The amount of hatched eggs in the first clutch of each female, analyzed with nested ANOVA

	df	Mean squares	F	sig.
Corrected model	10	559.6	86.3	< 0.001
Female origin (South / North)	1	27.5	4.2	0.043
Female population	8	85.6	13.2	< 0.001
Size of the first clutch (eggs)	1	4883.8	752.7	< 0.001
Error	83	6.5		
Total	94			
Corrected total	93			

TABLE 4 Female lifespan (days from the beginning of the experiment), analyzed with nested ANOVA

	df	Mean squares	F	sig.
Corrected model	10	334.9	0.86	0.576
Female origin (South / North)	1	482.8	1.2	0.269
Female population	8	288.4	0.74	0.657
Size of the first clutch (eggs)	1	558.4	1.4	0.235
Error	83	390.6		
Total	94			
Corrected total	93			

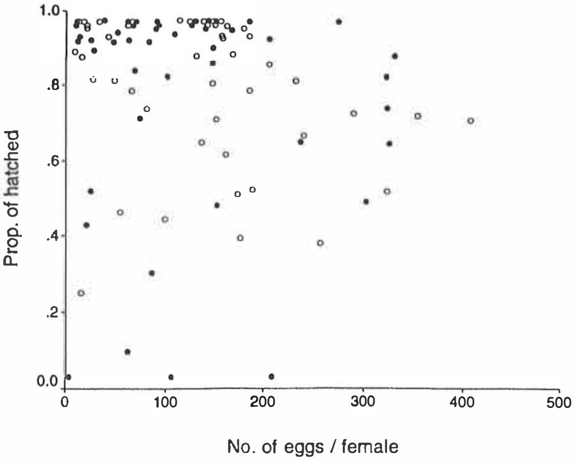

FIGURE 1 Relationship between number of eggs laid per female and proportion of hatched eggs per female, in southern (solid circles, $n = 46$) and northern populations (open circles, $n = 48$). Proportions of hatched eggs were ranked before computing ANOVAs.

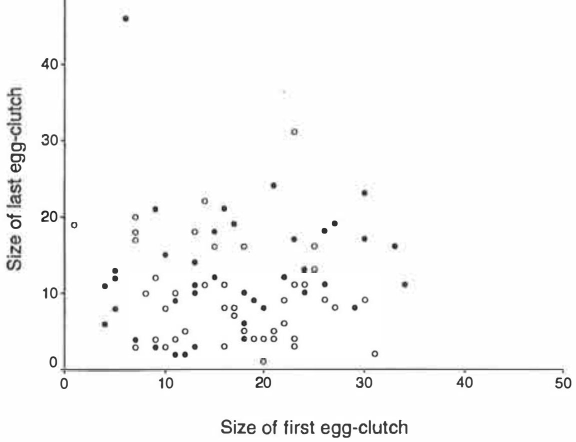

FIGURE 2 Size of the first clutch in relation to the size of the last clutch, in southern (solid circles, $n = 39$) and northern populations (open circles, $n = 39$).

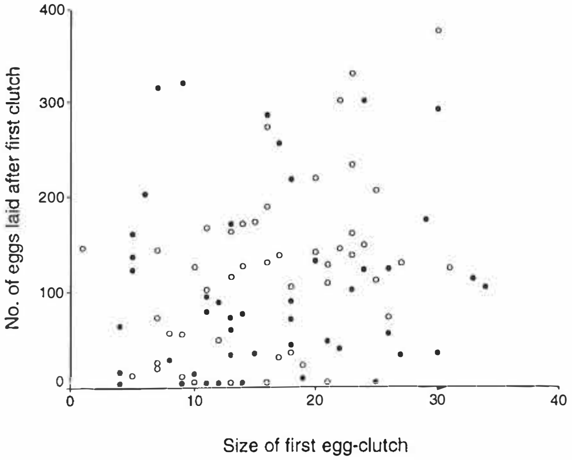

FIGURE 3 Relationship between size of the first clutch and the number of eggs laid after the first clutch, in southern (solid circles, *n* = 46) and northern populations (open circles, *n* = 48).

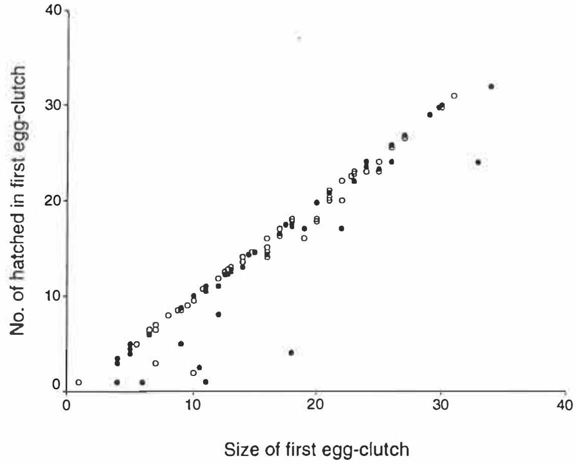

FIGURE 4 Relationship between females from southern (solid circles) and northern (open circles) populations of *A. najas*. Although the mean size of the first clutch did not differ between northern and southern populations, the amount of hatched eggs in northern populations was higher than in the southern ones. For statistical tests, see Table 3.