Distribution, phenology and conservation status of three rare water bugs: *Aquarius najas* (De Geer, 1773), *Aphelocheirus aestivalis* (Fabricius, 1794) and *Sigara hellensii* (C.R. Sahlberg, 1819) from lotic waters in Denmark

(Insecta, Hemiptera-Heteroptera: Nepomorpha & Gerromorpha)

Jakob Damgaard

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Distribution, phenology and conservation status is given for three species of water bugs (Hemiptera-Heteroptera: Gerromorpha & Nepomorpha) in Denmark: *Aquarius najas* (De Geer, 1773), *Aphelocheirus aestivalis* (Fabricius, 1794) and *Sigara hellensii* (C.R. Sahlberg, 1819). All three species are mainly confined to the larger water systems in central and southern Jutland, but have quite different distributions outside this region: *Sigara hellensii* is recorded from northwestern Jutland and Funen, but these records are all of considerable age and the continuous existence of the species in these regions needs to be reconfirmed; *Aphelocheirus aestivalis* has probably gone extinct on Funen, but is still present in the river Suså on southern Zealand; *Aquarius najas* has probably gone extinct in northern Jutland and is only found in one stream on Funen and one on Zealand.

Even though the three species may occur within the same water system, they are rarely found on the same locality due to their highly differentiated microhabitats: *Sigara hellensii* is found in slow flowing ditches and streams with a high sedimentation rate; *Aphelocheirus aestivalis* is found in fast flowing streams and rivers with much turbulence and coarse sediments; and *Aquarius najas* is found on sheltered parts of streams and rivers with a moderate flow.

Despite these differences all three species have undergone dramatic declines in distribution and number of populations, due to the massive regulations and polluting of streams and rivers that took place during the twentieth century. Even though the era of massive habitat destruction is now replaced by large scale restorations of streams and rivers, due to their highly reduced dispersal abilities and specific ecological requirements none of the three species are very likely to return to water systems from which they have once gone extinct. Even within water systems still inhabited by one or more of the three species, dispersal and colonization events are probably very limited, and the few remaining populations are still exposed to threats, such as clearing of marginal and submerse vegetation, soil erosion, increased water intake, and accidental spills of toxic or oxygen consuming materials.

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Introduction

Recent surveys have shown that damming, regulation and sediment/soil-erosion is just as critical for the biota of running waters in Denmark as outlets and spills with oxygen-consuming or toxic materials from agriculture, industry, and household (Sand-Jensen & Friberg, 2000). However, while sewage can be segregated and treated and spills can be isolated – or even avoided – both at a reasonable cost and with instant results, physical damages to the shape and flow of streams and rivers are far more expensive to compensate for, and the affected water systems may never return to natural conditions. Still, enormous restoration projects have been initiated in order to improve the conditions for flora, fauna and mankind, and have already led to a general positive trend for birds, fishes and many aquatic insects on the Danish Red List 1997 (Stoltze & Pihl, 1998) when compared to the Red List 1990 (Asbirk & Søgaard, 1991). It can not be generally concluded whether this is due to an actual improvement of the conditions for these organisms or simply to the more precise definitions of the categories employed for the Red List 1997, but in combination with a better monitoring of the species it is almost certain, that the improved conditions will eventually be reflected in the biota.

Water bugs, comprising the aquatic and semiaquatic Heteroptera (Nepomorpha & Gerromorpha), represent a relatively neglected, but very promising group of insects for surveys of environmental quality, since many species are known to depend on specific biotic and abiotic factors, and there is abundant evidence for the succession of species in relation to organic pollution, predation, development of reeds, changes in salinity and emptying and refilling of water bodies, largely summarized by Savage (1989).

However, little attention is given to population dynamics and dispersal abilities of these species, including life span and fertility, distance to nearest communities able to provide potential colonizers and the number and size of such communities, even though such factors are important for the regeneration of freshwater biota (Wiberg-Larsen, 1999); and almost nothing is known about essential historical and evolutionary factors, such as postglacial dispersal, founder effects and local selection and adaptation, even though these factors may be the ultimate reasons for the presence or absence of a given species (Hewitt, 2000).

The Danish fauna of water bugs is well studied, due to a long and relatively continuous tradition for faunal surveys of this group of insects, latest summarized by Damgaard (1997), and 59 species can be considered native to Denmark, most of which do relatively well in the heavily cultivated Danish waterscapes. There are, however, reasons to be concerned with three species inhabiting lotic waters: the water strider (Gerridae) *Aquarius najas* (De Geer, 1773), the ground bug (Aphelocheiridae) *Aphelocheirus aestivalis* (Fabricius, 1794), and the water boatman (Corixidae) *Sigara hellensii* (C. R. Sahlberg, 1819), because they have all shown dramatic declines of distribution during the last century – in Denmark as well as in many other parts of northern Europe (Coulianos & Ossinannilsson, 1976; Jastrey, 1981; Coulianos, 1998; Aukema *et al.*, 2002; Gärdenfors *et al.*, 2002).

This article addresses the distribution of the three species in Denmark based on a survey of all localities from where one or more of the species have been recorded within the last 25 years, as well as many former and/or potential localities inspected with a negative result during the last decade. Based on the survey and on the available literature concerning ecology, life history and habitat preferences, the biotic, abiotic, and historical factors responsible for the past and present distributions of the three species are reviewed and possible conservation efforts are discussed.

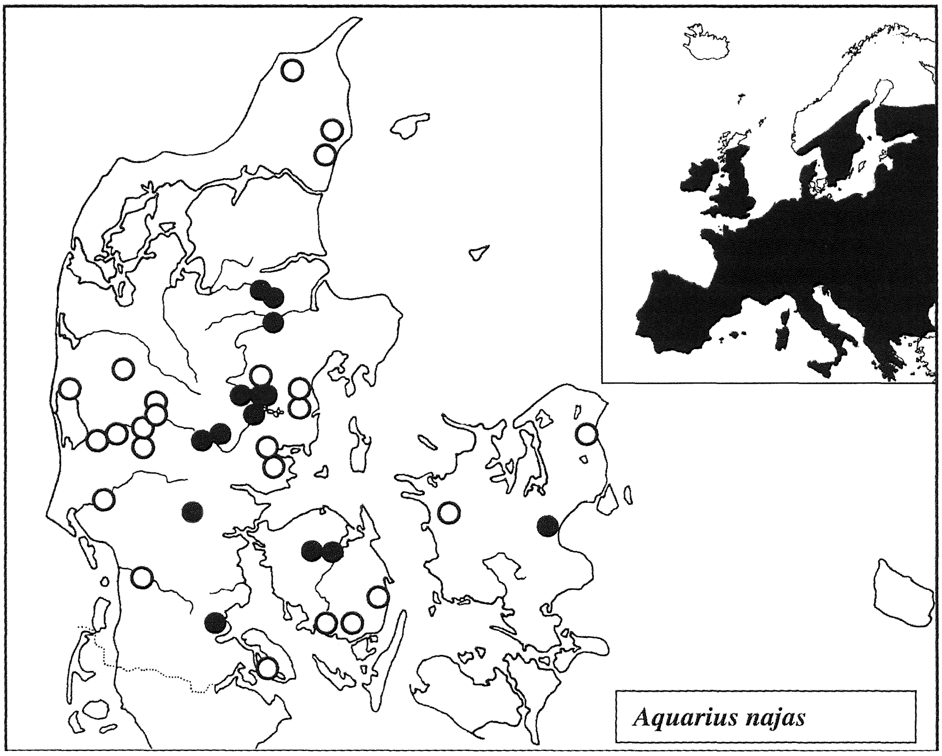

Fig. 1. Distribution map for *Aquarius najas* (De Geer) based on Andersen (1990), Aukema & Rieger (1995) and Damgaard & Andersen (1996). Open dots = old records. Solid dots = records during the recent survey.

Aquarius najas (De Geer, 1773)

Danish references: Schiødte (1869) listed *A. najas* from several localities in Jutland and on Funen. Leth (1943) listed the first records from Zealand. Damgaard & Andersen (1996) compiled a complete list of known Danish records, and Damgaard (1997) reviewed its distribution based on renewed inspection of many localities from where the species had been collected since 1950.

Distribution: *A. najas* is recorded throughout the western Palaearctic Region (Andersen, 1990; Aukema & Rieger, 1995; Damgaard & Andersen, 1996). In Scandinavia it is found in the southern part of Finland (Vepsäläinen, 1973; Lammes & Rinne, 1990), in Sweden as far north as Lapland (Coulianos & Ossiannilsson, 1976) and there are a few, old records from southeastern Norway (Jastrey, 1981; Coulianos, 1998). Historically, *A. najas* has been widely distributed in Denmark (Damgaard & Andersen, 1996), but despite several surveys, only the following water systems are known still to be inhabited by the species: Skjern Å in western Jutland, Gudenå and Skals Å in eastern Jutland, Åkær Å – a tributary to Kolding Å – and Vedbøl Bæk near the outlet from Vedbøl Sø by the village Hoptrup in southern Jutland; Stavis Å on Funen and Køge Å on Zealand. Each of these water systems include from one to several individual populations (Fig. 1).

Habitat: In Denmark *A. najas* is found on shallow parts of small and middle sized swift streams, and may reach high population densities under bridges or overhanging banks and trees or near outlets from lakes and may also occasionally be encountered in the littoral zone of large, oligotrophic lakes (Damgaard & Andersen, 1996). However, it is unknown if the species can reproduce in lentic waters in Scandinavia, as found in Lake Windermere in the English Lake District (Brinkhurst, 1959; 1966). On streams and rivers with a moderate flow, flocks of *A. najas* are found constantly leaping forward in order to compensate for the downstream drift during daytime, but during night they withdraw from open water, perhaps to rest, or as an adaptation to avoid predation by bats (Svensson *et al.*, 2002). Like other water striders, *A. najas* feeds predominantly on dead or drowning insects, and may reach very high densities in parts where drifting food is funneled through limited passages in the stream. Females show food-based territoriality, and nymphs concentrate in lentic lagunae usually downstream from the adults (Vepsäläinen & Nummelin, 1985).

Phenology: *A. najas* is recorded from early April to late October (Damgaard & Andersen, 1996), but may be present on the water even in wintertime if the weather is mild (Damgaard, unpublished).

In spring the abdomen of the egg-bearing female becomes swollen due to the ripening eggs. Males search actively for mates, and initiate mating by simply lunging at females without prior courtship. A male that is successful in achieving physical contact with a conspecific female will grasp her thorax with his forelegs, rapidly extend his genital segments, and attempt to insert his phallic organ into the genital opening of the female. Both the large size difference between the smaller male and bigger female, the strongly flattened ventral surface of the male body and the incrassate and arched male fore femora are adaptations associated with the strong mate guarding behavior in this species (Andersen, 1994). Even after copula the smaller male stays mounted on the female for days or even weeks, and the female appear almost incapable of dislodging the male, despite vigorous struggling (Sattler, 1957). About one week after copulation the female, sometimes with the male still attached, goes deep underwater and lays several egg-clusters on stones and on the leaves of aquatic plants (Huldén, 1979), and she may – at least in the laboratory – produce as much as 400 eggs. It is assumed, that all reproducing individuals will die rather shortly after reproduction (Ahlroth *et al.*, 1999). In May or June the eggs will hatch, and after five nymphal instars the new generation appears in late summer or early autumn. Since small numbers of first instar nymphs may appear relatively late in the season, Murray & Giller (1990) suggested that some populations in southern Ireland of this mainly univoltine species may have a partial second generation. Adults of the new generation hibernate on land under rocks, in moss at the ground layer of the vegetation, or in crevices of trees, buildings and boats close to the water (Damgaard & Andersen, 1996; Damgaard, unpublished), and overwintering mortality is high, ranging between 58-96% (Huldén, 1979; Ahlroth *et al.*, 1999).

Dispersal abilities: In northern Europe, *A. najas* is usually apterous, the macropterous morph being extremely rare (Huldén, 1979; Damgaard & Andersen, 1996). In southern Europe the winged morph is apparently not rare (Poisson, 1957), but quantitative studies of its frequency are still missing. It is known though, that some of the macropterous specimens have undeveloped indirect flight muscles and are actually unable to fly (Brinkhurst, 1966).

Ahlroth *et al.* (1999) induced the macropterous morph in Finnish populations by rearing eggs under short day length and high temperature, thereby simulating more southern latitudes. They found that the northernmost population gave rise to no macropterous individuals, while there was a significant increase in the frequency of this morph towards the south, reaching 52% in the southernmost population, but also that none of the macropterous individuals survived the winter.

Ahlroth *et al.* (2003) found indications for a strong genetic control on the dispersal behavior, and that the dispersal was closely linked both to the size of suitable habitat patches, and the level of fragmentation between these patches, but also that there was

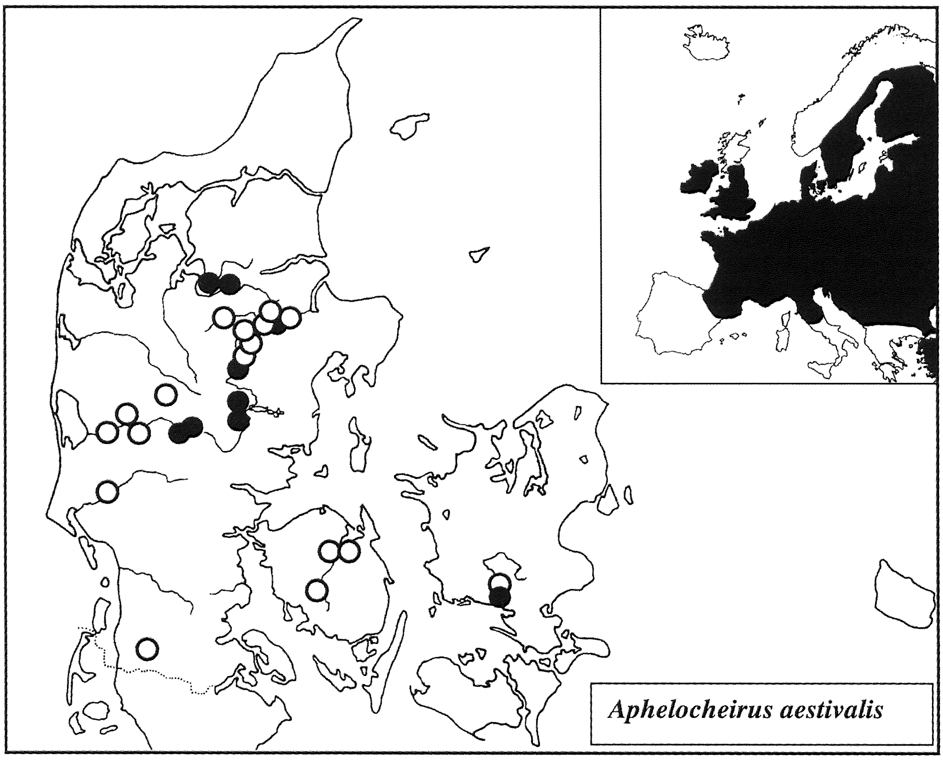

Fig. 2. Distribution map for *Aphelocheirus aestivalis* (Fabricius) based on Aukema & Rieger (1995). Open dots = old records. Solid dots = records during the recent survey.

some downstream gene flow, and that the chance for a successful colonization was positively correlated with the propagule-size and the number of source populations.

Aphelocheirus aestivalis (Fabricius, 1794)

Danish references: *A. aestivalis* was first recorded from deep waters in the river Gudenå close to the town Randers in eastern Jutland (Jensen-Haarup, 1907). Soon after, it was recorded from a tributary to the Gudenå, but this time from shallow and fast running waters (Ussing, 1908). With this larger and more variable material, it became increasingly uncertain whether the Danish material should be assigned to one or more species but, in his taxonomic revision, Reuter (1912) found that all central and northern European material should be assigned to *A. aestivalis*. Meanwhile, more records were reported from the Gudenå water system (Ussing, 1918; 1926), as well as from other larger water systems, including Linding Å (Kryger, 1916), Skjern Å (Jensen, 1943) and Arnå (Leth, 1946) in Jutland, Lindved Å on Funen (Balsløv, 1931) and Suså in southern Zeeland (Kaiser, 1939).

Distribution: *A. aestivalis* is found widespread throughout Europe and Siberia (Aukema & Rieger, 1995). From Norway, Sweden and Finland it is known only from the southern provinces (Jastrey, 1981; Coulianos, 1998; Coulianos & Ossiannilsson, 1976; Lammes & Rinne, 1990). In Denmark today only Skjern Å, Gudenå and Skals Å in Jutland and Suså in southern Zealand are known to be inhabited by *A. aestivalis* (Fig. 2).

Habitat: *A. aestivalis* was first recorded from 4-5 meters depth in the river Gudenå on a substratum of gravel, rocks, and sediments from the *Littorina* period consisting of blue clay and sub fossil shells of mollusks and balanids (Jensen-Haarup, 1907). The site was free of vegetation, but had a fauna rich in mollusks and insects, especially web spinning larvae of Trichoptera. Later studies documented *A. aestivalis* from a much broader range of habitats, and thorough descriptions of the new localities were published (Ussing, 1908; Kryger, 1916; Balsløv, 1931; Kaiser, 1939; Jensen, 1943). One of these new records from shallow waters was from a part of the stream Arnå in southern Jutland that was surveyed in 1949 and again in 1970-1971 (Glenstrup, 1974). The site was 15 m long, 5.5 m broad, had a middle depth of 40 cm; an annual amplitude from 25 to 70 cm; a water current of up to 180 cm/sec; and coarse sediments consisting of rocks covered with mosses, green algae and diatoms, with sparse patches of gravel and sand. Ussing (1918; 1926) found that *A. aestivalis* became increasingly rare in the river Gudenå the closer to the outlet in the brackish Randers Fjord he collected, and even though he never recorded the species from Randers Fjord, he did find it near the harbor in Randers, where the water occasionally was slightly brackish.

A. aestivalis is one of few species of aquatic bugs that usually does not come to the water surface to breathe. Because observations could not identify the typical hydrofuge hairs commonly found in aquatic insects, it was initially believed that *A. aestivalis* was totally dependent on dermal respiration. Later it was shown that only nymphs have a closed traché system, and absorb oxygen from the water via the body surface, while the adult has an open traché system, and uses a thin layer of air (a plastron) around its body (reviewed in Wichard *et al.*, 2001).

A. aestivalis is a predator that uses the long rostrum to paralyze and suck out its prey, which probably consists of immature stages of aquatic insects. Earlier reports of it using the long rostrum to feed on mussels (Wesenberg-Lund, 1943) need verification. Ussing (1918) found *A. aestivalis* hiding between rocks and shells during daytime, only to come out at night, and concluded that it was primarily nocturnal.

Phenology: Ussing (1918; 1926) found eggs deposited on the external surface of subfossil shells of mollusks on deep waters in the river Gudenå in July and August. In captivity the eggs hatched from late September to early October, and the newly hatched nymphs measured 2 mm. During his continuous searches from 1907-1916, he only found eggs in mid summer, and the smallest nymphs, measuring 3 mm, were sampled in July 1909. He found no general synchronizing between the time of the year and the length of the nymphs, and concluded that nymphal growth was relatively slow, and that the life cycle of *A. aestivalis* probably was not completed within a year. Based on examination of museum material Damgaard (1997) hypothesized, that *Aphelocheirus* probably is univoltine, and that nymphs can be found from March to November with a tendency for larger nymphs to occur later in the year. However, samples from two localities: Mattrup Å (a tributary to the Gudenå) near the outlet from the lake Stigsholm Sø (May 19.1997, J. Damgaard leg.) and Skals Å north of the village Vammen (May 23.1997, J. Damgaard leg.) had the composition of adults and nymphs shown in Table 1, and indicate that all nymphal stages can be found throughout the year, even in smaller and shallower parts

Table 1. Numbers of nymphs and adults of *Aphelocheirus aestivalis* (Fabricius) sampled at two Danish stream localities in May 1997. More information in the text.

	Nymphal instars					Adults	
Locality	I	II	III	IV	V	♂	♀
Mattrup Å	1	3	2	6	4	4	4
Skals Å	–	–	1	2	2	1	3

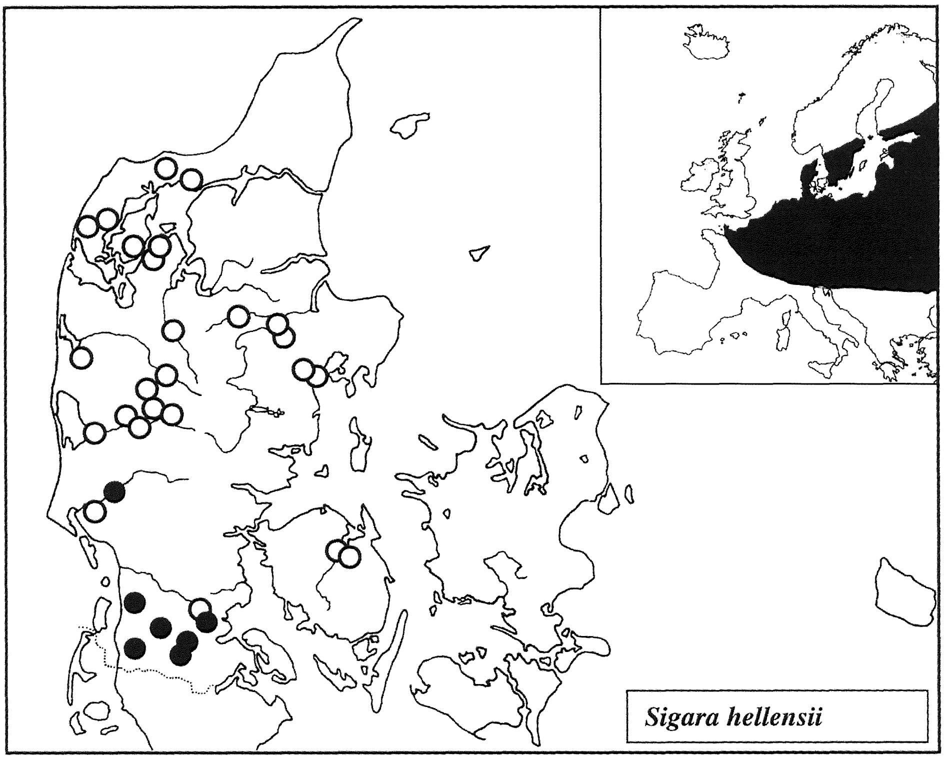

Fig. 3. Distribution map for *Sigara hellensii* (C.R. Sahlberg) based on Jansson (1986), Aukema & Rieger (1995) and Gärdenfors *et al.* (2002). Open dots = old records. Solid dots = records during the recent survey.

of the Gudenå Drainage system. This does, however, not rule out the possibility that egg-laying is restricted to the summer period.

Dispersal abilities: In Denmark as generally in northern Europe *A. aestivalis* is apparently monomorphic micropterous, but macropterous specimens are known from central Europe (Aukema *et al.*, 2002; Hoffmann, 2004) and have even been recorded from light traps in southern Europe (Larsén, 1927). Little is known about the underlying genetic and environmental factors determining wing development in *A. aestivalis*, but nymphal development in stagnant waters seems to increase the number of the macropterous morph (Aukema *et al.*, 2002). However, due to its specific habitat requirements and scarcity of the macropterous morph it must be concluded that the dispersal ability of *A. aestivalis* in Denmark is extremely limited.

Sigara hellensii (C.R. Sahlberg, 1819)

Danish references: Schiødte (1869) initially listed *S. hellensii* from small ponds in Jægersborg Dyrehave on Zealand, just north of Copenhagen. Unfortunately no remaining material of this record is known, but Leth (1943), Kaiser (1966) and Damgaard (1997) all agree, that the record must have been due to misidentification or mislabeling of species, whereas the record was still cited by Jansson (1986: 60, Fig. 37). The first reliable Danish record of *S. hellensii* is based on material collected in the river Lilleå in eastern Jutland in 1912-13 (Jacobsen, 1914). Later authors have reported the species from other water systems in Jutland and on Funen (Hoffmeyer, 1920; Leth, 1943; Kaiser, 1966; Damgaard, 1997).

Distribution: *Sigara hellensii* is recorded from southern Scandinavia to Schwitzerland and eastward to Ukraine (Jansson, 1986; Aukema & Rieger, 1995). Recent surveys in Sweden (Gärdenfors *et al.*, 2002) and the Netherlands (Aukema *et al.*, 2002) have shown that *S. hellensii* is becoming increasingly rare, and this is also the case in Denmark where recently it has only been recorded in Linding Å in western Jutland and in the Brede Å and Vidå water systems in southern Jutland (Fig. 3).

Habitat: Hoffmeyer (1920) reported numerous specimens of *S. hellensii* from Gudenå near Laurbjerg, where the current was slow enough to allow sedimentation of detritus on the bottom, and found that in most cases *S. hellensii* was by far the most abundant species of water boatman. The species is also reported from a 20 cm deep ditch running through a bog near the lake Possø at Svankær in northwestern Jutland, and with slow current and a substratum rich in organic material (E.B. Boisen-Bennike, data on label, coll. Zool. Mus. Copenhagen). In Sweden *S. hellensii* is known from small, slow flowing ditches in peat bogs (Lundblad, 1936), and Gärdenfors *et al.* (2002) reported that it is often found in ditches and small streams near farmland, but never in mountain streams or other fast flowing waters. In the Netherlands Nieser (1969) reported adults and nymphs from a 30 m long stretch of a 15 cm. deep and very slowly streaming rivulet without aquatic vegetation, with a thick layer of soft, brown mud.

Only little is known about the biology of *S. hellensii.* Taxonomically it is the sole member of the subgenus *Microsigara* Poisson, 1957 (Jansson, 1986), and its restriction to lotic habitats is highly unusual for water boatmen, and seems to be unique among European species. The association of *S. hellensii* with slow flowing waters and a high sedimentation rate may be related to its foraging behavior and food preferences, but this is in demand of further investigations.

Phenology: Very little is known about the phenology of *S. hellensii.* The nymph was described by Nieser (1969), and the species is probably univoltine in northern Europe (Gärdenfors *et al.*, 2002).

In corixids the mating is often accompanied by intense stridulating, and eggs are normally deposited on solid objects such as rocks, twigs and submerse vegetation (Savage, 1989). Studies of the mating behavior and egg-laying substrate for *S. hellensii* are highly warranted.

Dispersal abilities: Nothing seems known about the dispersal abilities of *S. hellensii.* Many corixids are readily fliers, that can be attracted to all kinds of reflecting surfaces and they are often found in light traps. Collectors of moths and butterflies have brought a substantial amount of water bugs to our museums, but so far no material of *S. hellensii.* Due to their impressive dispersal abilities, corixids are sometimes found in areas or habitats that are not characteristic for these species, but the complete absence of *S. hellensii* in ponds and lakes, as well as its highly restricted distribution in Denmark, altogether indicates that the species is not a readily flyer.

Discussion

Postglacial colonization of Denmark by the limnic fauna

Danish streams and rivers were formed by melting water from the glaciers that covered Scandinavia during the last ice age, and even though a considerable number of invertebrate populations in glacial- and interglacial periods managed to survive altering climates in springs and wells with a constant temperature (Nielsen, 1975), most were confined to different refugia in more southern latitudes (Hewitt, 2000). When the climate became inhabitable, many of these organisms expanded northwards and eventually reached the postglacial Danish waterscapes. 11.000-13.000 years ago the water level of the North Sea was low and rivers in western Jutland, fed by the retreating ice cap, were tributaries to the Elbe River system, which at that time advanced in a northwesterly direction (Nielsen, 1975). The water level of the North Sea gradually increased, and from approximately 7.500 years ago these rivers became disconnected from the Elbe River, and probably isolated populations of fishes, such as the alpine bullhead (*Cottus poecilopus poecilopus* Haeckel, 1837), grayling (*Thymallus thymallus* Linnaeus, 1758) and common dace (*Leuciscus leuciscus* Linnaeus, 1758) became isolated in western Jutland (Larsen, 1980). The whitefish (*Coregonus lavaretus* Linnaeus, 1758) was more tolerant to brackish water, and managed to disperse further to the Gudenå River system in eastern Jutland system via this rivers outlet, which for a long time (1000 years or more) was situated in the Limfjord Area (Nielsen, 1975), as has been shown in studies of mitochondrial DNA and microsatellite markers (Hansen *et al.*, 1999). Due to the economical and recreational values and the growing interests in conservation and sustainable management of local populations, such studies of freshwater fishes may eventually lead to generalizations about the phylogeographic structure of freshwater biota. However, since fishes both have strong dispersal abilities, are capable of crossing large stretches of otherwise inhospitable habitats; and are prone to stocking and human mediated transfer, they may be less suited as representatives of the freshwater fauna as a whole, whereas populations of the three species of water bugs considered here may offer excellent opportunities for studies of the postglacial dispersal routes in European water systems. The author (Damgaard, in press) has studied the phylogeography of *Aquarius najas* and found that populations from central and northern Europe only differed very little in their mitochondrial DNA, while populations from the Mediterranea differed by several orders of magnitude. Based on a phylogenetic reconstruction he concluded that the lineage that colonized northern Europe after the termination of the glacial periods most likely came from a refugium in northern Italy and/or the Balkan Region.

Adaptations to different but stable habitats

Even though the three species in focus are restricted to lotic waters, their microhabitats are highly differentiated, and they are rarely – if ever – found on the same localities. *Aphelocheirus aestivalis* and *Sigara hellensii* seem to prefer mutually exclusive habitats, since dense populations of *Aphelocheirus aestivalis* aggregate near outlets from lakes, and on stretches of rivers and streams with turbulent water and coarse sediments, while dense populations of *Sigara hellensii* are associated with slow flowing parts rich in organic detritus. *Aquarius najas* is probably less directly depending on the physical and chemical conditions of the water system, but dense populations of this species near lake outlets and in forested areas are probably directly depending on hatching of adults of the aquatic insects they prey upon, and the immature stages of these are certainly depending on the quality of the water. Only in the stream Linding Å in Nørholm Forest in western Jutland all three species have been found at the same site (Leth, 1943), still they probably were collected in different microhabitats.

The large "flotillas" of *Aquarius najas* on certain localities have attracted entomologists and limnologists for many decades, showing that very high population densities can be found on the same site during extensive periods of time, probably for centuries or more. On such "classical" localities, *A. najas* is likely to be a dominant faunal element, at least for the water surface habitat, which results in a high degree of intraspecific competition for food and reproduction. Vepsäläinen & Nummelin (1985) described the female food based territoriality of *A. najas,* and this, along with the different habitats of adults and nymphs, may be due to a high degree of cannibalism and/or competition. The mate guarding in *A. najas* is known as the longest in any water strider species (Arnqvist, 1995) and has probably evolved in response to reproductive competition. However, the most evident adaptation to life in stable and predictable habitats is the reduced dispersal ability, both in terms of loss of flight ability and the strong genetic control of dispersal behavior (Ahlroth *et al.*, 2003). Andersen (1993) considered the development of the macropterous morph to be predominantly under genetic control. Anyway the increasing frequency of this morph with decreasing latitudes (Poisson, 1957) and the rearing of a high percentage of macropterous specimens from apterous populations in Finland by Ahlroth *et al.* (1999) clearly demonstrate, that most *A. najas* populations are at least potentially wing dimorphic and that wing development is influenced by both genetic and environmental factors. It is reasonable to assume, that the more unstable and unpredictable conditions in streams and rivers in southern Europe, especially with regard to seasonal drought, will favor the development of the macropterous morph of *A. najas*, while the situation is reversed in northern latitudes, where habitats are more predictable. Predictable habitats may favor selection for investment of resources in reproduction instead of flight ability, the so called "oogenesis-flight syndrome" of Johnson (1969); reviewed for water striders by Andersen (1982) and Spence & Andersen (1994). However, there are local divergences in both northern and southern latitudes, and the situation may be further complicated by the higher overwintering mortality in the macropterous morph found by Ahlroth *et al.* (1999), all of which may be related to refugial origins, local adaptations and founder effects (Hewitt, 2000).

Aphelocheirus aestivalis and *Sigara hellensii* are much less studied, but since they also show reduced dispersal ability and may be dominant faunal elements in certain habitats, studies of the adaptive strategies for these species are highly warranted.

Conservation of the three species

Both *Aquarius najas*, *Aphelocheirus aestivalis* and *Sigara hellensii* have their distribution in Denmark largely confined to the larger water systems in central and southern Jutland, and are very scarce outside of this area. It is documented here as well as in earlier publications (Damgaard & Andersen, 1996; Damgaard, 1997) that all three species had a much wider distribution a century ago, and that many populations have disappeared since then, primarily due to human impacts. How widely distributed they were in Denmark prior to human impacts will never be known, since no large-scale surveys of water bugs had been carried our before K. O. Leth began his surveys around 1930 (Leth, 1943; 1945; 1946). It is well known that massive regulation projects accelerated the destruction of the fauna in many rivers and streams during the first half of the twentieth century, but human impacts began long time before that, first by the clearing of woods that covered most of Denmark and later with the establishment of water mills and the increasing pollution and spills from household and industry.

As mentioned above, the stream Linding Å at Nørholm Forest in western Jutland is the only site where all three species have been found (Leth, 1943). According to Jensen (1978) the upper parts of Linding Å were later regulated, causing a massive transport of sediments downwards, and the water quality was furthermore affected by dredging and polluting with sewage from nearby villages. *A. aestivalis* has not been recorded from the site since 1916 (Kryger, 1916) and no records of *A. najas* are known since 1966 (Damgaard & Andersen, 1996). During the recent survey only *Sigara hellensii* was still present at the site.

The sad fate of the Linding Å biota is characteristic for what has happened to the majority of populations of these three species in Denmark. *Aphelocheirus aestivalis* probably went extinct on Funen when a large stretch of Odense Å was regulated in 1958-1960 causing a massive sediment transport, that destroyed the habitats downstream (Riis *et al.* 1999), whereas Lindved Å was affected by heavy spills of manure and liquid silage in November 1955 (Wiberg-Larsen, pers. comm.). Also the regulations of the stream Arnå in southern Jutland seem to have caused a local extinction of *Aphelocheirus aestivalis* (Glenstrup, 1974).

In order for the three species to survive as elements in the Danish freshwater biota, it is important to protect the few remaining populations from the physical and chemical threats, that continue to work against them, such as: local spills of toxic or oxygen consuming material, especially pesticides, manure, sewage etc.; intake of water for household and industry; algal blooms in lakes with outlet to watersheds. And above all: The too efficient maintenance of water flow by removal of sediments and vegetation. Especially *Sigara hellensii* seems to be vulnerable towards these threats, since it often inhabits very small streams and rivers in farmland, with few other scientifically or recreationally interesting species, leaving a high risk of getting in contact with harmful pesticides that accumulates in the detritus (Friberg *et al.*, 2003). Furthermore, while *Aquarius najas* and *Aphelocheirus aestivalis* are mostly found in very large and well established populations, all new records of *Sigara hellensii* are based on singletons or very few individuals, indicating low populations sizes and therefore a high risk of inbreeding depression and increased vulnerability towards attacks by parasites and diseases.

Even though the improved conditions in several streams and rivers during the last few decades have generally reversed the negative trend in many freshwater organisms, the highly reduced dispersal abilities, even within water sheds, altogether makes it very unlikely, that the three species of water bugs can re-colonize water systems from where they have once gone extinct.

If the intention is to secure the fauna of the Danish freshwater systems – particularly the three species in question – and thus regain biota in streams and rivers that resemble what was around before the accelerating destructions of habitats began, it may eventually be taken into consideration to reintroduce such species. In order to do so, it must be recommended to release a large number of specimens, as this will improve the chance of a successful colonization (Ahlroth, 2003). It is a question still to be solved, whether it should be recommended to take a large number of individuals from a single large population, or a smaller number from several individual populations. In favor of the first method is that local adaptations are maintained, source populations are not depleted for too much genetic variation; and parasites and diseases are less likely to be transmitted. In favor of the last is that inbreeding depression may be avoided, and source populations from different kinds of habitats may stand a better chance to colonize a new habitat. Whatever might be decided, it is very important that a thorough survey is carried out before any such releases, and that the source population is well known. Each individual population represents its own evolutionary entity, and mixing of populations may not only disrupt the remaining phylogeographic patterning, but could also weaken the chance of survival of both the founder and the source population. Yet, with strong regard for such problems, it could eventually be taken into consideration to support the return of a threatened species with low dispersal ability into a recovered water system.

Dansk sammendrag

Udbredelse, livscyklus og bevaringsmæssig status gennemgås for tre danske vandtæger (Hemiptera-Heteroptera, Gerromorpha & Nepomorpha): åskøjteløberen (*Aquarius najas*), dybvandstægen (*Aphelocheirus aestivalis*) og bækbugsvømmeren (*Sigara hellensii*). Alle tre arter er langt overvejende fundet i rindende vande og har tilsyneladende en enkelt generation årligt, desuden har de alle en meget dårlig spredningsevne, såvel indenfor som imellem vandløb. Hovedudbredelsen i Danmark er for alle tre arter i vandsystemer i Midt- og Sønderjylland, mens fund udenfor dette område er meget sparsomme og

spredte. Arternes forskellige habitatskrav gør dog, at de kun sjældent findes sammen. *Sigara hellensii* lever i langsomtflydende vand i grøfter, bække og åer med høj sedimentationsrate og et tykt lag organisk materiale på bunden; *Aphelocheirus aestivalis* lever i hurtigtstrømmende vandløb med megen turbulens og et bundlag bestående af sten og grus; endelig lever *Aquarius najas* på overfladen af moderat strømmende bække og åer, gerne hvor disse løber igennem skovområder samt nær afløb fra søer. Trods forskelle i levested og udbredelse har alle tre arter gennemgået en dramatisk tilbagegang i løbet af det 20. århundrede, og de findes nu hovedsagelig i stærkt isolerede bestande, som stadig er udsat for trusler i form af hårdhændet vedligeholdelse, jorderosion, øget vandindvinding samt udledninger af giftige eller iltforbrugende stoffer. Totaludryddelse i mange vandsystemer kombineret med arternes ringe spredningsevne kan derfor gøre det relevant at overveje genudsætning i vandløb, hvor betingelserne igen er blevet forbedret.

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