

## Small aquatic and ripicolous bugs (Heteroptera: Nepomorpha) as predators and prey: The question of economic importance

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**Abstract.** Some features of the biology and feeding relationships of small waterbugs (Notonectidae, Corixidae, Pleidae, Helotrephidae, Aphelocheiridae) and ripicolous bugs (Gelastocoridae, Ochteridae) are reviewed. Individual families are discussed as predators or as prey of other animals. Special attention is given to characteristics and relationships that affect human beings directly or indirectly. The most important relationships from the economic point of view are: bugs and blood-sucking Diptera, bugs and fish, bugs and some endangered or protected amphibians and water birds. Of less importance is the occasional use of some aquatic bugs as saprobity bioindicators. It seems that the economic importance of these bugs has been underestimated.

### INTRODUCTION

The most comprehensive recent information on the biology and ecology of water bugs, especially of Corixidae and Notonectidae, is given by Jansson (1986), Savage (1989), Williams & Feltmate (1992), and Hutchinson (1993). But these authors do not consider the food relationships from an economic point of view.

Two nepomorphan families comprise ripicolous bugs, the other nine families contain water bugs. Conspicuous giant water bugs (Belostomatidae) (the largest species are 11 cm long), waterscorpions (Nepidae), and creeping water bugs (Naucoridae), are, among others, predators of small aquatic vertebrates. Some belostomatids are used as human food. These families are of some economic importance (Keffer, 2000; Sites, 2000; Venkatesan, 2000). The other nepomorphan families are not thought to be economically important. However, perhaps members of these families are indeed of some economic importance; perhaps we do not know enough about their biology. We do not know how much they affect, by the means of their food niches, those parts of food webs that are of economic interest to humans or of interest in the nature conservation (Papáček, 2000). Small, approximately 0.1–2.0 cm long, predaceous or omnivorous aquatic bugs are often very abundant in various types of water bodies, even in parts of the world like Central Europe, where, for example, giant water bugs do not occur. Under certain conditions at a locality, the importance of these small species can be compared with that of the large predaceous species (Papáček, 2000). The small species of aquatic bugs are probably biologically the most important adult insects in the littoral region of lakes and ponds (Hutchinson, 1993).

The aim of this brief review is to show the role of small nepomorphan bugs\* as animals with possible economic importance, or as animals that deserve attention at least from the point of view of anthropic practice. Another goal of this paper is to present a list of the main literature on this topic.

### SMALL PELAGIC WATER BUGS

The small swimming pelagic water bugs with feeding relationships with neuston, are Notonectidae, Corixidae, Pleidae, and Helotrephidae. They occasionally also attack benthic organisms, and some species feed on a variety of materials on the bottom. Helotrephidae, living also in the sand or roots on the bottom, or under stones (especially species in running waters), have the tightest connection with the benthic way of life among the families mentioned.

#### Notonectidae

**Distribution.** The backswimmers (boat flies, wherry-men; 10 genera, ca. 300 species) occur worldwide in temperate, and tropical regions. Species of the genus *Notonecta* are the most widely distributed (Palearctic, Nearctic, Neotropical, Afrotropical, Oriental Regions). Species of the genera *Enithares*, *Nychia*, and *Anisops* live in the Eastern Hemisphere; *Martarega* and *Buenoa* live in the Western Hemisphere. Species of other genera are distributed in smaller areas (for example – *Paranisops*, *Walambianisops* – Australia; *Enitharoides* – Neotropical; *Aphelonecta* – Oriental).

**Life history.** Basic data on the life cycles of backswimmers were published by Hungerford (1919, 1933) (*Notonecta* spp.), Young (1970, 1978) (Australian *Anisops* spp.), and Gittelman & Severance (1975) (*Buenoa* spp.). The best known model species, from the point of

\* The diagnostic and morphological characteristics of individual families are presented and illustrated, the number of their species estimated, and more detailed data on the distribution presented, e.g., by Mahner (1993) and Schuh & Slater (1995).

view of life cycles and biology, are probably the Old World species *Notonecta glauca* (e.g., Hoppe, 1912; Lehmann, 1923; Weber, 1930; Waitzbauer, 1974; Papáček & Soldán, 1987), and the New World species *Notonecta hoffmanni* (e.g., McPherson, 1965; Fox 1975) and *N. undulata* (Streams, 1982). Detailed reviews of their biology have been published by Savage (1989), Williams & Feltmate (1992), and Hutchinson (1993).

Tropical backswimmers reproduce throughout the year, backswimmers of temperate regions are univoltine or partly bivoltine (Hungerford, 1919; McPherson, 1965; Streams & Newfield, 1972; Vanderlin & Streams, 1977; Young, 1978). Adults live less than one year; they reproduce, they die. Reproductive competence and diapause are regulated by photoperiod (Vanderlin & Streams, 1977). Most notonectid species of temperate regions overwinter in the adult or egg stage (Hungerford, 1919; Hilsenhoff, 1984; Papáček, 1989).

Mating behavior was studied by Clark (1928), Larsén (1938) and Lang & Markl (1981) among others. The female is found visually by the male in Notonectinae. Anisopinae stridulate. Acoustic signals may be important for aggregation of both sexes and mating of *Anisops* and *Buenoa* spp., as in corixids, but no exact data are available (cf. Aiken, 1985; Hutchinson, 1993). Females of some species lay eggs in plant tissues and females of other species on the surface of submerged plants or stones. Fox (1975) measured the reproductive capacity of *Notonecta hoffmanni* under two different food regimes and found that one female can lay  $2.3 \pm 1.2$  or  $0.6 \pm 0.2$  eggs per day, respectively. He showed that fecundity is strictly influenced by the shortage of food. Embryonic development lasts, according to temperature 2–3 weeks. Postembryonic development of the 5 larval stages can last, with close dependence on the amount and composition of food (Gittelman, 1978) and temperature (Hungerford, 1919; McPherson, 1965; Ellis & Borden, 1969), one to two months. The length of individual preimaginal stages can differ by 14–20 days depending on these factors (Waitzbauer, 1976) or on parasitism, for example, by Acarina (Lanciani, 1982; Lanciani & May, 1982). Life cycles of the widely distributed species may be modified by altitude and geographical distribution (cf., e.g., data of Nieser, 1981; Papáček & Soldán, 1987).

**Habitats, spatial distribution, and dispersal potential.** Macropterous backswimmers fly very well, and have, like corixids, an excellent ability to invade most types of waters (e.g., ponds, lakes, rivers, streams, small waters in peatlands, marshes or swamps, and puddles) including artificial water bodies. They are often one of the first successional stages in new waters. Adult macropterous backswimmers can migrate irregularly in response to favourable or unfavourable conditions of food and oxygen concentration in habitats (e.g., Hoppe, 1912; Clark, 1928; Wesenberg-Lund, 1943), or seasonally, before overwintering, after ice break in temperate regions, as well as before drying of habitats in arid or subarid regions (e.g., Hutchinson, 1929). Sympatric, often closely related species, are vertically and horizontally stratified:

they divide the ecological niches from the surface downwards (Gittelman, 1976, 1977; Streams & Shubeck, 1982; Cook & Streams, 1984; Streams, 1986). A similar stratification exists among larvae and adults of the same species. This stratification can change with changes in the amount of energy the females need (Cockrell, 1984a), with changes of temperatures and the concentration of dissolved oxygen (Cockrell, 1984b), or with intra- and inter-specific predation (Sih, 1982; Streams, 1986, 1992a, b; Bailey, 1987).

**Food relationships with possible economic importance.** Backswimmers are very aggressive predators, attacking many pelagic and benthic invertebrates, including their own larvae, invertebrates that fall onto the water surface (larvae and adults of various insects, mites, small crustaceans, annelids, and molluscs), and small vertebrates (fish larvae and amphibian tadpoles) (e.g., Cooper, 1983; Giller, 1986). These polyphagous cannibalistic carnivores detect prey by visual and vibratory signals (Walton, 1943; Schwind, 1980). Notonectids are size-limited predators (Cronin & Travis, 1986), whose food niches change somewhat with developmental stages. The larger the developmental stage, the larger the prey hunted (Fox, 1975). The largest species of *Notonecta* attack prey approximately 2.5–3.5 cm in length (Dahm, 1972; Dubský, 1991). Swimming with the back down correlates with the strategy of respiration. The ventral body surface air bubble, removable when rising to the water surface, helps to keep these bugs with the venter up. Nevertheless, “back down position” is an important phenomenon playing its strategical role in attacking the potential prey, which they recognize and drive towards the water surface. It is evident from the presented facts, that notonectids can under certain conditions influence considerably the structure of freshwater food webs. The following predaceous linkages are most important from an economic point of view: (1) backswimmers and mosquitoes, (2) backswimmers and fishes.

The notonectids are predators of mosquito and some other blood-sucking Diptera (e.g., Ceratopogonidae) larvae and pupae, which they attack as surface prey. The reports about that fact concern various species (especially of the genera *Notonecta*, *Enithares*, *Martarega*, *Anisops*, and *Buenoa*) and various regions of the World. Gittelman (1974a) characterized *Martarega hondurensis* and *Buenoa antigone* as predators of mosquito larvae in Costa Rica. Fox (1975) stated that *Notonecta hoffmanni* attacks surface prey of an average size of 2.2 (1st instar larvae) to 5.6 mm (adults). That behaviour corresponds with the sizes of various stages of mosquito larvae. In laboratory experiments the same author demonstrated the consumption of 10–15 mosquito larvae per adult of *Notonecta* per day. Giller & McNeil (1981) showed that Old World species, such as *N. glauca*, *N. obliqua*, and *N. maculata*, attack and feed on larvae of *Aedes aegypti*. Cockrell (1984b) noted that *Culex* larvae are prey of *N. glauca*. Murdoch et al. (1984) found that the North American species *N. hoffmanni* and *N. kirbyi* prefer mosquito larvae as their natural diet. Giller (1986) examined the natural diet

of *N. glauca* and *N. viridis* using the electrophoretic methods of gut contents analyses and showed, among others, that the obligatory part of their food is composed by larvae of *Anopheles* sp., *Aedes aegypti*, Culicinae spp., and pupae of Ceratopogonidae. Aly & Mulla (1987) found that the prey of the North American species *N. undulata* are larvae of *Culex quinquefasciatus*. Neri-Barbosa et al. (1997) noted *N. irrorata* as an important predator of mosquito larvae. Wattal et al. (1996) described the predatory potential of *Enithares indica* against mosquito larvae. Other Oriental species of *Enithares* and *Anisops* also attack mosquito larvae (M.P., unpubl. field observations of some species in Vietnam). These results and many other laboratory as well as field experiments and observations (e.g., Laird, 1947; Ellis & Borden, 1970; Hoy & Reed, 1970; Toth & Chew, 1972; Hazelrigg, 1974; Zalom, 1978; McDonald & Buchanan, 1981; Scott & Murdoch, 1983; Miura & Takahashi, 1987, 1988; Streams, 1992a) support the widespread opinion that mosquito density is reduced by notonectids and that the mosquito larvae are the preferable food for some species of notonectids. The strategy of backswimmers' predation could, with some exaggeration, be declared as the "strategy of cleaning of the water surface". This behavioral phenomenon means that notonectids may be used as control agents of mosquitoes on a worldwide basis.

Population density of mosquitoes, however, is reduced not only by direct predation but also by antipredatory behavior of mosquito females. Chesson (1984, 1989) and Blaustein et al. (1995) showed that reduction of mosquito density is influenced by negative selective oviposition at localities inhabited by backswimmers.

Notonectids are predators in the pond culture of various small fishes, as well as of the larvae of various fish species living in still freshwater habitats. This fact was revealed by Torre Bueno (1905) and Clark (1928) in connection with *N. undulata*. Berezina (1955, 1962) estimated that great population of *N. glauca* in ponds with an area of about 0.01 ha can kill from 2,500–3,500 fish larvae per day. A laboratory experiment showed that one adult of *N. glauca* killed on average 2.6 fish larvae per day (Dahm, 1972). Gorai & Chandhuri (1962) recorded that *Anisops bouvieri* is a characteristic predator of fish larvae in India. A similar situation was found by Leong (1962) in the case of *A. breddini*, whose life history was studied in Singapore and Malaysia.

On the other hand, notonectids are the food for several predaceous or insectivorous fishes such as brown trout (*Salmo trutta*) (e.g., Macan, 1977; Sih, 1987), *Lepomis cyanellus* (Cook & Streams, 1984) or *Gambusia affinis* (Washino & Hokama, 1967; Farley & Younce, 1977; Miura et al., 1979, 1984). Some studies indicate that notonectids in some areas prefer to settle in waters with a pH so low that fish cannot live there (Bendell, 1986; Bendell & McNicol, 1987). Bailey (1987) even described the formation of huge aggregations of Australian *Anisops*, with many hundreds of individuals (even of two different species), that are supposed to have an antipredaceous function. This behavioral strategy could be selected for

only by long-lasting predatory pressure by fish. In spite of this fact the backswimmers are of only marginal importance as the food for fish.

Backswimmers attack and feed on small juvenile crayfish (Dye & Jones, 1975; Hirvonen, 1992). Young crayfish are even killed by notonectids or resort to cheliped autotomy to escape predation, but this phenomenon causes a reduction of individual growth in these crustaceans.

Notonectids can have a certain marginal economic importance even as predators or food for some protected, endangered, or vulnerable animals. There are no doubts about predation on amphibian tadpoles of *Rana areolata* (Cronin & Travis, 1986), *Triturus* spp. (Giller, 1986) and *Bombina bombina* (Dubský, 1991). The polarity of food relationships can change during the ontogeny of both participants. Anuran adults feed on notonectid larvae (Morin et al., 1988). Notonectids are also a common part of the natural diet of some aquatic birds, for example, common heron (*Ardea cinerea*) (Exnerová & Boháč, 1991).

### Corixidae

**Distribution.** Water boatmen are the nepomorphan group with the most species (35 genera, ca. 550 species). Corixids are distributed worldwide, but only one genus, *Sigara*, is cosmopolitan, the other 34 genera inhabit smaller areas of distribution (for details see Mahner, 1993).

**Life history.** Various authors have published on the life cycles of corixids (e.g. Hungerford, 1919, 1948; Larsén, 1938; Wróblewski, 1958; Young, 1965; Kaiser, 1966; Pajunen & Jansson, 1969; Pajunen, 1970; Jansson & Scudder, 1974; Scudder, 1976, 1987; Papáček & Bohoněk, 1989; Papáček & Tríska, 1992). The most comprehensive recent outlines or reviews of the biology of corixids are by Scudder (1976), Jansson (1986), Savage (1989), Williams & Feltmate (1992), and Hutchinson (1993).

The number of generations per year varies according to species and climatic conditions. Species in tropical waters reproduce all the year round (e.g. Harrison, 1962; Peters & Spurgeon, 1971). Some species of the warmest regions of temperate areas produce three generations per year (e.g. Wróblewski, 1958). Most corixids of temperate areas are bivoltine, they produce one complete early spring generation and a partial or complete second late summer generation. A few species of temperate regions, for example *Corixa* spp., or species living in the northernmost or southernmost areas or in high mountains, produce only one summer generation. Most corixids of temperate areas overwinter as adults. European Micronectinae overwinter as larval stages 3 or 4. Some species can overwinter in the egg stage – for example *Corixa affinis* in Europe (Poisson, 1935), and *Trichocorixa verticalis interioris* in Saskatchewan (Canada) (Tones, 1975 in Scudder, 1976).

Corixid sexes aggregate by pursuing acoustic signals. Both male and female stridulate, rubbing fields of pegs on the fore femora over flanges on the maxillary plate of the head (Jansson, 1972; Aiken, 1982, 1985). In some species

spontaneous male stridulation concerns the aggregation of the sexes. The reproductive females swim towards the call of a male. Stridulation of corixids has specific audio-spectrographic patterns. These signals play an important role in the ensuring of conspecific mating in sympatric species (see, e.g., Jansson, 1979; Aiken, 1982). The females of European species lay on the average some 5–10 eggs per day for a period of about one month (Jansson, 1986), but the total number of eggs laid by individual female varies from 10 to 1,000 (Young, 1965; Peters & Spurgeon, 1971). Eggs are attached and embedded in cement by a disc or pedicel on the substratum. The incubation period of eggs varies according to temperature (e.g., Scudder, 1966; Martin, 1970). For instance, in several European species of *Corixa* and *Sigara* the length of embryonic development recorded in laboratory is 16–25 days (M.P., unpubl. data). Postembryonic development depends both on the species and climatic conditions. Temperate Micronectinae, overwintering as larvae, have the longest postembryonic development – more than 7–8 months long. On the other hand, for example the larvae of the early spring generation of some temperate bivoltine species, have the shortest development – about 2–3 months long (cf., e.g., Savage, 1989). The maturation process is probably regulated by food, photoperiod, and temperature, although the exact mechanism remains unknown (cf., e.g., Pajunen, 1970; Jansson & Scudder, 1974). Thus even the adult longevity varies, depending on the species and generation.

**Habitats and dispersal potential.** Corixids have a high dispersal potential, which allows them to utilize various available habitats, both continental and insular, still and running, stable and temporary, fresh and saline (Jansson, 1986), including artificial waters (e.g., Williams, 1993) and very small puddles or lithotelms (cf., interesting studies, e.g., by Pajunen, 1979)\*. Most corixids fly very well. Corixids have both flying and non-flying morphs. Flightlessness may be the result either of the shortness of the wings or of a lack of flight muscles. It is most often combined with poor muscle development, which is linked with the development of sexual maturity and with the temperature at the time of attaining the adult stage (Scudder, 1975). The seasonal population dynamics of adult corixids in temperate areas conform to a general pattern in relatively stable communities. Numbers reach a maximum in early summer and in autumn (e.g., Crisp, 1962; Savage, 1979). Nevertheless, seasonal population dynamics is very varied, due mainly to both immigration and emigration in some habitats (e.g., Savage, 1981, 1989). The irregular and seasonal migration of corixids has some common patterns, as in notonectids.

Corixidae seem to be ecologically adaptable to a wide range of environmental conditions. But the results of Bosmans (1982), for example, from Belgium, and Savage (1994a) from the British Isles, document that individual species of Corixidae show distinct preferences for water habitats of a certain water quality. Savage (1994b) and Sládeček & Sládečková (1994) summarize data docu-

menting the relationship of corixids to saprobity (organic pollution) of waters and show that, according to the occurrence of individual species (good indicators), and occasionally according to the proportions in the occurrence of individual species, it is possible to estimate the saprobic index. Presence or absence of some corixid species can help in the general assessment of water-quality levels.

**Food relationships with possible economic importance.** The diet of Corixidae has been studied by various authors. Corixids have a wide spectrum of potential food. Many species are largely phytophagous (Puchkova, 1969); on the other hand, many, for example species of *Arctocorisa*, *Cymatia*, *Cenocorisa*, *Diaprepocoris*, *Glaenocorisa*, or *Stenocorixa*, and some *Corixa* and *Sigara* species, are carnivorous (e.g., Sutton, 1951; Zwart, 1965; Scudder, 1966; Jansson, 1978; Popham et al., 1984). Corixidae constitute one of the important predators, especially in acidified or inland saline waters (Scudder, 1976; Henrikson & Oscarson, 1981). The composition of the diet, respectively the preferred food, can change gradually with ontogeny and maturation, and also with the particular conditions of a habitat (Scudder, 1966; Jansson, 1968, 1973a, b). Corixids can feed on algal cells and filamentous blue-greens, diatoms, the microscopic fauna living on the water bottom, such as protozoans and rotifers, live and dead tubificids, ostracods, cladocerans, copepods, anostracans, mayfly, mosquito, and chironomid larvae, detritus, own eggs and fish eggs, etc. (e.g., Hungerford, 1919, 1948; Walton, 1943; Griffith, 1945; Sutton, 1951; Jaczewski, 1961; Wróblewski, 1963; Scudder, 1969a, b; Sokolovskaya & Zhitneva, 1973; Jansson & Scudder, 1974; Reynolds, 1975; Bakonyi, 1978; Pajunen, 1979). Predation on mosquito larvae and fish eggs, the attacking of fish larvae by corixids, and the predation on corixids by fish and some other vertebrate predators, establish important economic relationships.

Sailer & Lienk (1954) state that corixids are incidental predators on mosquito larvae in Alaska. For example, *Callicorixa audeni* feed on *Aedes* larvae to the exclusion of other food. These water bugs may migrate from pools in which the mosquito population is exhausted. Evident predators of mosquito larvae are *Cymatia*, *Glaenocorisa*, and some *Sigara* spp. that catch the swimming mosquito larvae in the open water (Sokolovskaya & Zhitneva, 1973; Reynolds, 1975; Henrikson & Oscarson, 1985; Nyman et al., 1985; Reynolds & Scudder, 1987a, b). Some corixid species, for example *Sigara lateralis*, *S. falleni*, *S. striata*, and *Cymatia rogenhoferi*, are facultative predators of fish eggs and larvae. Secretory substances of their saliva induce irreversible changes in the blood of fish fry (Sokolovskaya & Zhitneva, 1973). The damage to the eggs of a commercially important fish could once have been caused by *Micronecta omnivora* (see Hutchinson, 1993).

Corixids provide prey for many invertebrates, such as predaceous insects (e.g., Popham, 1941, 1943; Hutchinson, 1993; Stevens & Greven, 1999) and vertebrates in

\* List of the most important Pajunen's papers on the ecology of rock-pool corixids is presented, e.g., by Jansson (1986).

food webs. Predation by fish has been recorded several times (e.g., Frost & Macan, 1948; Fernando, 1956; Scudder, 1976). Some authors (e.g., Applegate & Kieckhefer, 1977) think that fish predation is not very significant, but Macan (1965) showed that predation could have a pronounced effect on the regulation of both the abundance and distribution of Corixidae. The last mentioned author found that a part of the brown trout's food (*Salmo trutta*) is formed by *Callicorixa praeusta* and *Cymatia bonndorfii*, *Hespercorixa castanea*, *H. sahlbergi*, *Sigara scottii*, and *S. distincta* in small moorland ponds in England. Ahmed et al. (1970) found that insectivorous *Gambusia affinis* fed on various corixids. Oscarson (1987) stated that roach (*Rutilus rutilus*) fed on *Glaenocoris propinqua*, *Sigara distincta*, and *S. scotti*. Rask (1983) noted that corixids are an obligatory part of the main food of *Perca fluviatilis* living in small forest lakes.

Henrikson & Oscarson (1978) believe that corixids are a suitable prey for fish and are not adapted to co-existence with fish predators. Predation by fish can reduce the population of corixids (specifically *G. propinqua*). Various corixids have behavioral and color adaptations that save them from predation by fishes. Some Corixidae, as well as some Notonectidae (cf. Bailey, 1987), can form aggregations with many hundreds of individuals of various species. These aggregations have probably an antipredaceous function. Such aggregations, containing both adults and nymphs of different species, were found by field echo-sounding (Lyle & East, 1989; Kubečka et al., 2000). This fact proves the existence of a behavioral pattern of a stable adaptive character selected for over a long period and under the pressure of permanent fish predation.

Salamanders (Griffith, 1945) and anurans (Morin et al., 1988) have also been noted as predators of corixids. Predation by water fowl and waders has been recorded, e.g., by Griffith (1945) and Munro (1945). Swimming corixids can be a prey for some water birds, such as goldeneye duckling (*Bucephala clangula*) (e.g., Eriksson, 1976), shoveller (*Spatula clypeata*) (Hutchinson, 1993) or common heron (*Ardea cinerea*) (Exnerová & Boháč, 1991). Flying corixids may fall prey to bats (Walton, 1943) or birds which catch flying insects (Fernando, 1959).

Hungerford (1948) noted that the number of eggs of some corixids may be so great that they can be gathered and used as human food. Hutchinson (1993), referring to other authors, mentioned that in Mexico the eggs are obtained by allowing the enormous populations of *Kri-zousacorixa* and *Corisella* in Lake Texoco to oviposit on submerged plants, from which the eggs can be scraped; this has been a traditional source of human food known as "ahuautle" or water grain, they are favored on some vigils (e.g., Christmas Eve). The adults and eggs were also eaten by the Aztecs and by humans living in the Nile basin in Egypt. The publications about the corixid eggs as human food were summarized also by Devey (1957). The adults and eggs of some corixids have been dried and

used as food for aquarium fish, caged birds, and other birds bred by humans.

## Pleidae and Helotrephidae

Pleidae and Helotrephidae are closely related families from a morphological, phylogenetic, and biological point of view. They are minute predaceous insects which swim in an inverted position as do notonectids, but they can swim with the dorsum up like corixids. The knowledge of the biology of these bugs is fragmentary, but many aspects of their biology are interesting and unique among all water insects.

### Pleidae

**Distribution.** The family (ca. 40 species) contains three genera, *Plea* (Palearctic), *Neoplea* (Nearctic and Neotropical), and *Paraplea* (tropicopolitan). Most pygmy backswimmers (small backswimmers, lesser water boatmen) live in the tropics.

**Life history.** The morphology and biology, including life cycles of some species, were studied especially by Wefelscheid (1912), Hungerford (1919), Bare (1926), Drake & Chapman (1953), Gittelman (1974b, 1975, 1977, 1978), Takahashi et al. (1979), Kovac (1982), Hilsenhoff (1984), Papáček (1985, 1989), McPherson (1986), Benzie (1989), Kovac & Maschwitz (1989). Two species with the best known biology can be chosen as models, the European *Plea minutissima*, and the American *Neoplea striola*.

Pygmy backswimmers of temperate regions are usually univoltine, although some may also be partly bivoltine (cf. Wefelscheid, 1912; Bare, 1926; McPherson, 1986). They overwinter in the adult stage, in an inactive dormant state. Diapause during overwintering is caused by low temperatures (Gittelman, 1975; Kovac, 1982). Overwintering adults can survive even in a habitat completely frozen to the bottom (Hilsenhoff, 1984). In spring they start to become active again. Females, which are activated by rising temperature during overwintering, are not able to reproduce, as their maturation cannot be completed (Kovac, 1982). They may live two years (Papáček, 1993). Mating and oviposition periods are relatively long, for example from 2 to 2.5 months in *Plea minutissima* (see Papáček, 1985). In Central Europe *P. minutissima* usually starts to breed in May and June; in western Europe *P. minutissima*, and in eastern North America *N. striola*, mate in June and July, later than the sympatric species of other genera of water bugs (Wefelscheid, 1912; Gittelman, 1974b; Papáček, 1985). Eggs are laid in slits in the tissues of submerged aquatic plants. Embryonic development lasts about 3 weeks, and postembryonic development from 40 days to 2 months depending on conditions in the habitat (cf. Papáček, 1985; McPherson, 1986). *P. minutissima* can survive even in a habitat dried up for a short time, finding shelter among the roots of the plants in the bottom mud (facultative aestivation) (Papáček, 1993). It is known that pleids survive very well under other stresses, for instance low temperatures during overwintering or low oxygen concentration. Their stress tolerance and success is supported by their small size, a

relatively ample air bubble, a physical gill mechanism, and partial replenishing of the air bubble with oxygen produced by the peroxydic metathoracic scent gland (cf. Gittelman, 1975; Kovac, 1982; Kovac & Maschwitz, 1989).

**Habitats and dispersal potential.** Pygmy backswimmers live for the most part in both stable and temporary still fresh waters with rich submerged vegetation; their occurrence in running waters is very rare. Nothing is known about the migration of pleids. Most known species are pteridomorphic, with a macropterous morph (long hindwings and claval suture of forewings present), and a micropterous morph (strongly reduced hindwings, claval suture of forewings absent). Macropterous pleids fly relatively well, and can colonize temporary or newly formed water bodies.

**Food relationships with possible economic importance.** Pleidae are cannibalistic predators which attack and feed on small water animals, such as ostracods, cladocerans, and copepods; small larvae of water insects, including own larvae; annelids like *Tubifex* or *Stylaria*; and animals that fall onto the water surface, such as Collembola and small Diptera. Below the water, pleids hunt larger prey than themselves, for example, tubificids and chironomid or mosquito larvae. They find their prey by visual, vibratory and probably also chemical signals. Takahashi et al. (1979) stated that *Neoplea striola* feeds on mosquito larvae and does not attack other mosquito predators, and thus suppresses mosquito populations. Attack on mosquito larvae by pleids was also observed in the field in southeast Asia (M.P., unpubl. field observation). Some laboratory experiments show that in central Europe *Plea minutissima* prefers zooplankton as food, but attacks mosquito larvae as well (Šafář, 1991).

## Helotrephidae

**Distribution.** Most helotrephids (they have no vernacular name) (19 genera, more than 120 species) are distributed, except for two endemic Palearctic species, in the Oriental, Afrotropical, and Madagascan regions. Only a few species of these bugs (Neotrephinae) are known from the Neotropical region, especially from Middle and South America.

**Life history.** Helotrephidae are a relatively poorly known family, but there is a growing scientific interest in them. Literature dealing with the Helotrephidae considers mostly their taxonomy, morphology, and distribution. Except for Usinger's (1937) note, the only more or less monothematic study is that by Miyamoto (1952), devoted to the biology of *Helotrephes formosanus*. However, some fragmentary data on the biology occur in some taxonomic papers (e.g., Esaki & China, 1928; Lundblad, 1933; China, 1935, 1940; Papáček et al., 1988, 1989).

Our idea of the life cycles of helotrephids is largely speculative, and is based especially on phenologic data. Miyamoto (1952) found larvae of *Helotrephes formosanus* in Taiwan from January to June. According to his

data, we can not determine precisely if the species is univoltine with a long oviposition period and postembryonic development, or if it is partly bivoltine. Papáček (1993) provided some data on the ontogeny of *Idiotrephes asiaticus* from laboratory cultures.\* Mating and oviposition periods of this species were observed throughout December and January. Females laid eggs on the surface of water plant leaves in clusters containing 2–4 eggs. The shortest time of embryonic and postembryonic development was 14 and 70 days, respectively. The last hatched larvae finished their development in the middle of May.

**Habitats and dispersal potential.** Helotrephids have been found in large and small, stable and temporary, quiet and running waters, in rock pools, water falls, seeping rocks, hot springs, in water tanks, and outdoor ceramic bowls. Various species of helotrephids live in unstable habitats. They can probably cope with stress conditions, an opinion supported by the discovery of *Mixotrephes hoberlandti* in South Iran, so far the only helotrephid found in an arid zone. Circumstances of the find suggest that the species lives there in ephemeral waters, and that it can aestivate as an adult, probably for a considerable part of the year in a nonaquatic environment (Papáček et al., 1989).

**Food niche.** Miyamoto (1952) fed *Helotrephes formosanus* during laboratory rearing with the same small animals he found where he collected the helotrephids: larvae of Chironomidae, Tipulidae, Dryopidae, Ephemeridae, Perlidae, and Gerridae. Reared helotrephids attacked all the prey as well as their own larvae. Papáček (1993) found that *Idiotrephes asiaticus* from Vietnam, reared in the Czech Republic, reproduced successfully when fed on Central European species of cladocerans and copepods, and their own larvae. They attacked and killed redundant prey without eating it. No prey preference was discovered. These bugs, about 1.3–1.4 mm long, even attacked moving prey far bigger than themselves. Based on the observations of this rearing, and the field observations of feeding strategy of *Helotrephes shepardi* in Vietnam (M.P., unpubl. data), the conclusion can be made that helotrephids feed also on mosquito larvae, and can help in mosquito population control together with Corixidae, Notonectidae, and Pleidae.

## SMALL BENTHIC WATER BUGS

### Aphelocheiridae

**Distribution.** All species (1 genus, 60 species) are distributed in the Old World, mostly in the Palearctic area.

**Life history.** The biology of the Palearctic species *Aphelocheirus aestivalis* is the best known, but published data are often controversial (cf. Krajewski, 1966; Kanyukova, 1974; Messner et al., 1980; Sættem, 1986; Papáček, 1989). The species is probably semivoltine or univoltine with “cohort splitting populations” and a two- to three-year long postembryonic period. The life cycles of individual populations, living in various regions of

\* In November 1989 live adults of *I. asiaticus* were transported from Vietnam to the Czech Republic and kept under simple laboratory conditions at room temperatures oscillating from 18 to 25°C. The laboratory rearing was discontinued in July 1990.

their distribution, are modified or even differentiated. Females lay eggs from spring to autumn on the surface of various objects on the bottom, on the cuticle of crustaceans, and shells of Bivalvia. Late summer and autumnal eggs overwinter. Larvae of instars 1–3 appear from spring to autumn, larvae of instars 4 and 5, and adults all the year long (cf. Krajewski, 1966). Adults live at least two years, some females have two ovipositional periods, and males have continual multiwaved spermatogenesis (Papáček & Soldán, 1996).

**Habitats and dispersal potential.** Aphelocheirids occur especially in lakes, streams, and rivers. They have a relatively wide ecological valence, but these bugs, having plastron respiration, prefer aerated water. They live on a gravel-sand bottom, under the stones, in the river rapids and calms, on lake bottoms, among roots of plants, or buried in the bottom. Most specimens or populations of some species (e.g., *A. aestivalis*) are micropterous and flightless. Some species in the tropics and subtropics are macropterous (see Polhemus & Polhemus, 1988) and fly very well (M.P. field observation). Individual populations in rivers and streams migrate seasonally (Messner et al., 1983).

**Food niche.** Aphelocheirids feed on various benthic insect larvae including larvae of simuliids, and small crustaceans and bivalves.

## RIPICOLOUS BUGS

### Gelastocoridae

**Distribution.** Most toad bugs (3 genera, ca. 100 species) are pantropical and pansubtropical.

**Life history.** The major works on the biology of gelastocorids are by Hungerford (1922) and Todd (1955). The life cycle of the Old World species *Gelastocoris oculatus* was studied by Hungerford (1922). This species is univoltine, with overwintering adults. Females lay up to 200 eggs (1–14 per day) on the surface of various objects. Postembryonic development lasts 60–100 days.

**Habitats.** Toad bugs are saltatory riparian or amphibian predacious insects. They live in various habitats such as under water, under stones, on muddy or sandy banks, or rock faces while some species are found in soil remote from water, particularly in rain forests.

**Food niche.** Toad bugs very actively attack their prey, usually small insects living in the same habitats.

### Ochteridae

**Distribution.** Velvety shore bugs (3 genera, ca. 50 species) are distributed world-wide in the tropics and the subtropics and in the warm parts of temperate regions.

**Life history.** The major data on the biology of velvety shore bugs were published by Takahashi (1923), Jaczewski (1934), Schell (1943), Bobb (1951), and Poisson (1957). The biology of *Ochterus marginatus* is probably the best known. This species is univoltine, and adults and instars 4 or 5 overwinter. Only adults compose the early spring population. Females have a relatively long ovipositional period; they lay 2–3 eggs per day in groups of

25–30 eggs on the surface of sandy grains, plants, or roots of plants. Larvae develop for 2 months.

**Habitats.** Ochterids are terricolous or littoral bugs which live along the shores of ponds or streams, they occur especially in sandy stretches near the water, but they also run on aquatic plants and hunt their prey even under water.

**Food niche.** Poisson (1957) states that these predators hunt small larvae of Diptera and small crustaceans, such as *Gammarus* spp.

## DISCUSSION AND CONCLUSIONS

Although Notonectidae and Corixidae, also Pleidae and Helotrephidae, differ from each other in their life strategies, they have a similar spatial distribution in individual habitats. All have a somewhat similar function in food webs. Their behaviour in nature and the consequences arising for their economic importance for humans are summed up. Notonectidae and Corixidae are surely economically the most important of these families. All notonectids are definitely aggressive, size-limited predators, which kill small animals beyond their food needs.

The feeding strategy and niches of corixids are more complicated. Although food relationships of economic importance have been documented only in some dozen corixid species, it is probable that more species of the family have similar function in food webs.

The economic importance of Pleidae and Helotrephidae is not mentioned in the literature. Yet it is probable that under certain conditions pleids and helotrephids can be useful in controlling mosquito larvae.

The economic importance of these “pelagic families” of water bugs can be characterized from these points of view:

(a) Positive economic importance. (1) Notonectids, corixids, pleids, and helotrephids function as biological mosquito control agents. (2) Corixidae especially are food for insectivorous fish, amphibians, birds, and bats. (3) Humans use the eggs, nymphs, and adults of corixids as food for poultry, dried feed for aquarium fish; and rarely the eggs are used as a food for humans themselves. (4) It seems that corixids can be good indicators of water quality.

(b) Damage. (5) Both Notonectidae and some Corixidae attack fish eggs and fry, and under certain conditions the enormous overpopulation (due to migration or successful reproduction) can cause serious damage to fish culture. (6) Notonectids attack and feed on small larvae of amphibian species, some of which are listed as endangered or protected.

The economic importance of small benthic or ripicolous bugs varies. Benthic Aphelocheiridae, on the one hand, could suppress populations of some blood-sucking dipterans (larvae of Simuliidae); on the other hand, they also suppress populations of predators (larvae of Trichoptera), which also feed on simuliids. Ripicolous Gelastocoridae and Ochteridae also participate in suppressing populations of these blood-sucking dipterans with (a) swimming larvae breathing air on the water surface, (b) larvae living



in small water bodies in holes in the sand or in rock pools, and (c) saprophagous larvae living on the banks.

The economic effect of these heteropterans (especially of notonectids and corixids) for human activity and health has yet not been calculated, either as a worldwide average, or under extreme conditions. They can be very damaging in ponds where fish fry are bred. Several papers follow and estimate the damage to fish culture (for example – the number of killed fish larvae/per bug/per day or per square area-unit) (e.g., Berezina, 1955, 1962; Dahm, 1972; Sokolovskaya & Zhitneva, 1973). The financial effects are not presented either. The studies fail to deal with the energy demands of the bugs' production (with the exception of some papers – e.g., Toth & Chew, 1972 and Waitzbauer, 1976), or the energy needs of food relationships that do have an economic effect. We also do not know the percentage of the biomass of mosquito larvae that water bugs can destroy under various conditions. Missing, therefore, are reliable quantitative data for the financial expression of the damage or for the economic benefit. Getting better knowledge of the biology of water bugs, and acquiring the quantitative characteristics of some food relations, are interesting and important tasks for future research.

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## REFERENCES

- AHMED W., WASHINO R.K. & GIEKE P.A. 1970: Further biological and chemical studies on *Gambusia affinis* (Baird and Girard) in California. *Proc. Calif. Mosq. Control Assoc.* **38**: 95–97.
- AIKEN R.B. 1982: Sound production and mating in waterboatman *Palmarcorixa nana* (Heteroptera: Corixidae). *Anim. Behav.* **50**: 54–61.
- AIKEN R.B. 1985: Sound production by aquatic insects. *Biol. Rev.* **60**: 163–211.
- ALY CH. & MULLA M.S. 1987: Effect of two microbial insecticides on aquatic predators of mosquitoes. *Z. Angew. Entomol.* **103**: 113–118.
- APPLEGATE R.L. & KIECKHEFER R.W. 1977: Ecology of Corixidae (water boatmen) in Lake Poinsett, South Dakota. *Am. Middl. Nat.* **97**: 198–208.
- BAILEY P.C. 1987: Abundance and age-specific spatial and temporal distribution in two waterbug species, *Anisops danaei* (Notonectidae) and *Ranatra dispar* (Nepidae) in three farm dams in South Australia. *Oikos* **49**: 83–90.
- BAKONYI G. 1978: Contribution to the knowledge of the feeding habitats of some water boatmen: *Sigara* spp. (Heteroptera: Corixidae). *Folia Entomol. Hung.* **31**: 19–24.
- BARE C.O. 1926: Life histories of some Kansas "backswimmers". *Ann. Entomol. Soc. Am.* **19**: 93–101.
- BENDELL B.E. 1986: The effects of fish and pH on the distribution and abundance of backswimmers (Hemiptera: Notonectidae). *Can. J. Zool.* **64**: 2696–2699.
- BENDELL B.E. & MCNICOL D.K. 1987: Fish predation, lake acidity and the composition of aquatic insect assemblages. *Hydrobiologia* **150**: 193–202.
- BENZIE J.A.H. 1989: The immature stages of *Plea frontalis* (Fieber, 1844) (Hemiptera: Pleidae), with a redescription of the adult. *Hydrobiologia* **179**: 157–171.
- BEREZINA N.A. 1955: On the feeding of some waterbugs – competitors and pest of fish fry. *Trudy Mosk. Technol. Inst. Rybn. Promyshl.* **7**: 142–148 (in Russian).
- BEREZINA N.A. 1962: Control of predatory aquatic insects. *Rybovod. Rybolov.* **5**: 25–26 (in Russian).
- BLAUSTEIN L., KOTLER B.P. & WARD D. 1995: Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. *Ecol. Entomol.* **20**: 311–318.
- BOBB M.L. 1951: Life history of *Ochterus banksi* Barb. (Hemiptera: Ochteridae). *Bull. Brooklyn Entomol. Soc.* **46**(4): 92–100.
- BOSMANS R. 1982: Distribution and ecology of Belgian Corixidae (Hemiptera). *Acad. Analecta* **44**: 23–60.
- CHESSON J. 1984: Effect of notonectids (Hemiptera: Notonectidae) on mosquitoes (Diptera: Culicidae): Predation or selective oviposition? *Envir. Entomol.* **13**: 531–538.
- CHESSON J. 1989: The effect of alternative prey on the functional response of *Notonecta hoffmani*. *Ecology* **70**: 1227–1235.
- CHINA W.E. 1935: New and little-known Helotrephidae (Hemiptera-Helotrephidae). *Ann. Mag. Nat. Hist. (Ser. 10)* **15**: 593–614.
- CHINA W.E. 1940: New South American Helotrephidae (Hemiptera-Heteroptera). *Ann. Nat. Mag. Hist. (Ser. 11)* **5**: 106–126.
- CLARK L.B. 1928: Seasonal distribution and life history of *Notonecta undulata* in the Winnipeg Region, Canada. *Ecology* **9**: 383–403.
- COCKRELL B.J. 1984a: Effect of water depth on choice of spatially separated prey by *Notonecta glauca* L. *Oecologia (Berlin)* **62**: 256–261.
- COCKRELL B.J. 1984b: Effect of temperature and oxygenation on predator-prey overlap and prey choice of *Notonecta glauca*. *J. Anim. Ecol.* **53**: 519–532.
- COOK V.L. & STREAMS F.A. 1984: Fish predation on *Notonecta* (Hemiptera) relationship between prey risk and habitat utilization. *Oecologia* **64**: 177–183.
- COOPER S.D. 1983: Selective predation on cladocerans by common pond insects. *Can. J. Zool.* **61**: 879–886.
- CRISP D.T. 1962: Estimates of the annual production of *Corixa germari* (Fieb.) in an upland reservoir. *Arch. Hydrobiol.* **58**: 261–280.
- CRONIN J.T. & TRAVIS J. 1986: Size-limited predation on larval *Rana areolata* (Anura: Ranidae) by two species of backswimmer (Insecta: Hemiptera: Notonectidae). *Herpetologica* **42**: 171–174.
- DAHME E. 1972: Zur Biologie von *Notonecta glauca* (Insecta, Hemiptera) unter besonderer Berücksichtigung der fischereilichen Schädwirkung. *Int. Rev. Ges. Hydrobiol.* **57**: 429–461.
- DUBSKÝ L. 1991: *Predation on the Amphibian Larvae (Amphibia, Anura) by Bugs of the Genus Notonecta (Heteroptera)*. MSc thesis. Univ. South Bohemia, Ped. Fac., České Budějovice, 72 pp. (in Czech).
- DEVEY E.S. 1957: Limnologic studies in Middle America. *Trans. Conn. Acad. Arts Sci.* **39**: 217–238.
- DRAKE C.J. & CHAPMAN H.C. 1953: Preliminary report on the Pleidae (Hemiptera) of the Americas. *Proc. Biol. Soc. Wash.* **66**: 53–60.



- DYE L. & JONES P. 1975: The influence of density and invertebrate predation on the survival of young-of-the-year *Orconectes virilis*. *Freshwat. Crayfish* **2**: 529–538.
- ELLIS R.A. & BORDEN J.H. 1969: Effects of temperature and other environmental factors on *Notonecta undulata* Say. *Pan-Pac. Entomol.* **45**: 20–25.
- ELLIS R.A. & BORDEN J.H. 1970: Predation by *Notonecta undulata* (Heteroptera: Notonectidae) on larvae of the yellow fever mosquito. *Ann. Entomol. Soc. Am.* **63**: 963–973.
- ERIKSSON M.O.G. 1976: Food and feeding habits of downy goldeneye *Bucephala clangula* (L.) ducklings. *Ornis Scand.* **7**: 159–169.
- ESAKI T. & CHINA W.E. 1928: A monograph of the Helotrephidae, subfamily Helotrephinae (Hem., Heteroptera). *Eos* **4**: 129–172.
- EXNEROVÁ A. & BOHÁČ D. 1991: Diet of grey heron, *Ardea cinerea*, in breeding season. *Sylvia* **28**: 77–88 (in Czech, English abstr.).
- FARLEY D.G. & YOUNCE L.C. 1977: Effects of *Gambusia affinis* (Baird and Girard) on selected nontarget organisms in Fresno County rice fields. *Proc. Calif. Mosq. Vector Control Assoc.* **45**: 87–94.
- FERNANDO C.H. 1956: On the food of four common freshwater fish of Ceylon. *Ceylon J. Sci.* **7**: 201–217.
- FERNANDO C.H. 1959: The colonization of small freshwater habitats by aquatic insects. 2. Hemiptera (The water-bugs). *Ceylon J. Sci. Biol. Sci.* **2**: 5–32.
- FOX L.R. 1975: Some demographic consequences of food shortage for the predator, *Notonecta hoffmanni*. *Ecology* **56**: 868–880.
- FROST W.E. & MACAN T.T. 1948: Corixidae (Hemiptera) as food of fish. *J. Anim. Ecol.* **17**: 174–179.
- GILLER P.S. 1986: The natural diet of the Notonectidae: field trials using electrophoresis. *Ecol. Entomol.* **11**: 163–172.
- GILLER P.S. & McNEIL S. 1981: Predation strategies, resource partitioning and habitat selection in *Notonecta* (Hemiptera/Heteroptera). *J. Anim. Ecol.* **50**: 789–808.
- GITTELMAN S.H. 1974a: *Martarega hondurensis* and *Buenoa anti-gone* as predators of mosquito larvae in Costa Rica (Hemiptera: Notonectidae). *Pan-Pac. Entomol.* **50**: 84–85.
- GITTELMAN S.H. 1974b: The habitat preference and immature stages of *Neoplea striola* (Hemiptera, Pleidae). *J. Kans. Entomol. Soc.* **47**: 491–503.
- GITTELMAN S.H. 1975: Physical gill efficiency and winter dormancy in the pigmy backswimmer, *Neoplea striola* (Hemiptera, Pleidae). *Ann. Entomol. Soc. Am.* **68**: 1011–1017.
- GITTELMAN S.H. 1976: Swimming ability of Notonectidae (Hemiptera). *Psyche* **83**: 319–323.
- GITTELMAN S.H. 1977: Leg segment proportions, predatory strategy and growth in backswimmers (Hemiptera: Pleidae, Notonectidae). *J. Kans. Entomol. Soc.* **50**: 161–171.
- GITTELMAN S.H. 1978: Optimum diet and body size in backswimmers (Heteroptera: Notonectidae, Pleidae). *Ann. Entomol. Soc. Am.* **71**: 737–747.
- GITTELMAN S.H. & SEVERANCE P. 1975: The habitat preference and immature stages of *Buenoa confusa* and *B. margaritacea* (Hemiptera: Notonectidae). *J. Kans. Entomol. Soc.* **48**: 507–518.
- GORAI A.K. & CHAUDHURI D.N. 1962: Food and feeding habits of *Anisops bouvieri* Kirk. (Heteroptera: Notonectidae). *J. Asiat. Soc.* **4**(3–4): 135–139.
- GRIFFITH M.E. 1945: The environment, life history, and structure of the water boatman, *Rhamphocorixa acuminata* (Uhler) (Hemiptera, Corixidae). *Univ. Kans. Sci. Bull.* **30**: 241–365.
- HARISON A.D. 1962: Hydrobiological studies on an alkaline and acid still waters in the western Cape Province. *Trans. R. Soc. S. Afr.* **36**: 213–244.
- HAZELRIGG J.E. 1974: *Notonecta unifasciata* as predators of mosquito larvae in simulated field habitats. *Proc. Calif. Mosq. Control Assoc.* **42**: 60–65.
- HENRIKSON L. & OSCARSON H. 1978: Fish predation limiting abundance and distribution of *Glaenocoris p. propinqua*. *Oikos* **31**: 102–105.
- HENRIKSON L. & OSCARSON H. 1981: Corixids (Hemiptera-Heteroptera), the new top predators in acidified lakes. *Verh. Int. Verein. Theor. Angew. Limnol.* **21**: 1616–1620.
- HENRIKSON L. & OSCARSON H. 1985: Waterbugs (Corixidae, Hemiptera-Heteroptera) in acidified lakes: Habitat selection and adaptations. *Ecol. Bull.* **37**: 232–238.
- HILSENHOFF W.L. 1984: Aquatic Hemiptera of Wisconsin. *Great Lakes Entomol.* **17**: 29–50.
- HIRVONEN H. 1992: Effects of backswimmer (*Notonecta*) predation on crayfish (*Pacifastacus*) young: autotomy and behavioural responses. *Ann. Zool. Fenn.* **29**: 261–271.
- HOPPE J. 1912: Die Atmung von *Notonecta glauca* (Hemiptera, Heteroptera). *Zool. Jb. (Allg. Zool. Physiol.)* **31**: 189–244.
- HOY J.B. & REED D.E. 1970: Biological control of *Culex tarsalis* in a California rice field. *Mosq. News* **30**: 222–230.
- HUNGERFORD H.B. 1919: The biology of aquatic and semi-aquatic Hemiptera. *Univ. Kans. Sci. Bull.* **11**: 1–341.
- HUNGERFORD H.B. 1922: The life history of the toad bug. *Univ. Kans. Sci. Bull.* **24**: 145–171.
- HUNGERFORD H.B. 1933: The genus *Notonecta* of the world. *Univ. Kans. Sci. Bull.* **21**: 5–195.
- HUNGERFORD H.B. 1948: The Corixidae of the western hemisphere (Hemiptera). *Univ. Kans. Sci. Bull.* **32**: 1–827.
- HUTCHINSON G.E. 1929: A revision of the Notonectidae and Corixidae of South Africa. *Ann. S. Afr. Mus.* **25**: 359–474.
- HUTCHINSON G.E. 1993: *A Treatise on Limnology IV. The Zoobenthos*. J. Wiley & Sons, New York, Chichester, Brisbane, Toronto, Singapore, 944 pp.
- JACZEWSKI T. 1934: Notes on some Palearctic aquatic and semi-aquatic Heteroptera, chiefly from South Eastern Europe. *Ann. Zool. Mus. Polon. Hist. Nat.* **10**(14): 267–288.
- JACZEWSKI T. 1961: Notes on the biology of Corixidae (Heteroptera). *Polsk. Pismo Entomol.* **31**: 295–300.
- JANSSON A. 1968: Diel periodicity of the stridulating activity of *Callicorixa producta* Reuter (Heteroptera, Corixidae). *Ann. Zool. Fenn.* **5**: 265–269.
- JANSSON A. 1972: Mechanism of sound production and morphology of the stridulatory apparatus in the genus *Cenocorixa* (Hemiptera, Corixidae). *Ann. Zool. Fenn.* **9**: 120–129.
- JANSSON A. 1973a: Stridulation and its significance in the genus *Cenocorixa* (Hemiptera, Corixidae). *Behaviour* **46**: 1–36.
- JANSSON A. 1973b: Diel periodicity of stridulating activity in the genus *Cenocorixa* (Hemiptera, Corixidae). *Ann. Zool. Fenn.* **10**: 378–383.
- JANSSON A. 1978: Viability of progeny in experimental crosses between geographically isolated populations of *Arctocorixa carinata* (C. Sahlberg) (Heteroptera, Corixidae). *Ann. Zool. Fenn.* **15**: 77–83.
- JANSSON A. 1979: Reproductive isolation and experimental hybridization between *Arctocorixa carinata* and *A. germari* (Heteroptera, Corixidae). *Ann. Zool. Fenn.* **16**: 89–104.
- JANSSON A. 1986: The Corixidae (Heteroptera) of Europe and some adjacent regions. *Acta Entomol. Fenn.* **47**: 1–94.
- JANSSON A. & SCUDDER G.G.E. 1974: The life cycle and sexual development of *Cenocorixa* species (Hemiptera, Corixidae) in

- the Pacific Northwest of North America. *Freshwat. Biol.* **4**: 73–92.
- KAISER E.W. 1966: Micronecta species in Denmark (Hemiptera, Corixidae). *Flora og Fauna* **72**: 139–147 (in Danish, English abstr.).
- KANYUKOVA E.V. 1974: True bugs of the family Aphelocheiridae (Heteroptera) in the fauna of USSR. *Zool. Zh.* **53**: 1726–1731 (in Russian, English abstr.).
- KEFFER S.L. 2000: Economic importance of water scorpions (Nepidae). In Schaefer C.W. & Panizzi A. (eds): *Heteroptera of Economic Importance*. CRC Press, Boca Raton, FL (in press).
- KOVAC D. 1982: Zur Überwinterung der Wasserwanze *Plea minutissima* Leach (Heteroptera: Pleidae): Diapause mit Hilfe der Plastronatmung. *Nachr. Entomol. Ver. Apollo NF* **3**(3): 59–76.
- KOVAC D. & MASCHWITZ U. 1989: Secretion-grooming in the water bug *Plea minutissima*: a chemical defence against microorganisms interfering with the hydrofuge properties of the respiratory region. *Ecol. Entomol.* **14**: 403–411.
- KRAJEWSKI S. 1966: Biology and development of *Aphelocheirus aestivalis* (Fabr.) in the Grabí river. *Zesz. Nauk. Univ. Łódź (Ser. II)* **21**: 63–73 (in Polish).
- KUBEČKA J., FROUZOVÁ J., ČECH M., PETERKA J., KETELAARS H., WAGENWOORT A.J. & PAPÁČEK M. 2000: Hydroacoustic assessment of pelagic stages of freshwater insect. *Aquat. Living Resources* (in press).
- LAIRD M. 1947: Some natural enemies of mosquitoes in the vicinity of Palmalmal, New Britain. *Trans. R. Soc. N. Z.* **76**: 453–476.
- LANCIANI C.A. 1982: Parasite-mediated reductions in the survival and reproduction of backswimmer *Buenoa scimitra* (Hemiptera: Notonectidae). *Parasitology* **85**: 593–603.
- LANCIANI C.A. & MAY P.G. 1982: Parasite-mediated reductions in the growth of nymphal backswimmers. *Parasitology* **85**: 1–7.
- LANG H.H. & MARKL H. 1981: Sex discrimination in the back swimmer *Notonecta glauca* upon contact with conspecific (Heteroptera: Notonectidae). *Entomol. Gener.* **7**: 175–191.
- LARSÉN O. 1938: Untersuchungen über den Geschlechtsapparat der aquatilen Wanzen. *Opusc. Entomol. (Suppl. I)*: 1–388.
- LEHMANN H. 1923: Biologische Beobachtungen an *Notonecta glauca*. *Zool. Jb. Syst.* **46**: 121–159.
- LEONG C.Y. 1962: The life-history of *Anisops breddini* Kirk. (Hemiptera, Notonectidae). *Ann. Mag. Nat. Hist. (Ser. 5)* **13**: 377–383.
- LUNDBLAD O. 1933: Zur Kenntnis der aquatilen und semiaquatilen Hemipteren von Sumatra, Java und Bali. *Arch. Hydrobiol. (Suppl. Bd. 12, Trop. Binnengewässer)* **4**: 1–195, 263–498.
- LYLE A.A. & EAST K. 1989: Echo location of corixids in deep water in an acid loch. *Arch. Hydrobiol.* **115**: 161–170.
- MACAN T.T. 1965: Predation as a factor in the ecology of water bugs. *J. Anim. Ecol.* **34**: 691–698.
- MACAN T.T. 1977: The fauna in the vegetation of a moorland fishpond as revealed by different methods of collecting. *Hydrobiology* **55**: 3–15.
- MAHNER M. 1993: Systema cryptoceratorum phylogenicum (Insecta, Heteroptera). *Zoologica* **143**: 1–302.
- MARTIN N.A. 1970: The distribution and ecology of the Corixidae (Hemiptera-Heteroptera) in Leicestershire. *Trans. Leicester Lit. Phil. Soc.* **64**: 101–121.
- MCDONALD G. & BUCHANAN G.A. 1981: The mosquito and predatory insect fauna inhabiting fresh-water ponds, with particular reference to *Culex annulirostris* Skuse (Diptera: Culicidae). *Aust. J. Ecol.* **6**: 21–27.
- MCPHERSON J.E. 1965: Notes on the life history of *Notonecta hoffmanni* (Hemiptera: Notonectidae). *Pan-Pac. Entomol.* **41**: 86–89.
- MCPHERSON J.E. 1986: Life history of *Neoplea striola* (Hemiptera: Pleidae). *Great Lakes Entomol.* **19**: 217–220.
- MESSNER B., GROTH I., GÖLLNER-SCHIEDING U. & HANSCHKE R. 1980: Erster Nachweis der Grundwanze *Aphelocheirus aestivalis* (F.) in Mecklenburg, zugleich ein Beitrag zur Biologie und Verbreitung. *Entomol. Ber.* **1980**: 13–20.
- MESSNER B., GROTH I. & TASCHENBERGER D. 1983: Zum jahreszeitlichen Wanderverhalten der Grundwanze *Aphelocheirus aestivalis*. *Zool. Jb. Syst.* **110**: 323–331.
- MIURA T. & TAKAHASHI R.M. 1987: Augmentation of *Notonecta unifasciata* eggs for suppressing *Culex tarsalis* larval population densities in rice fields. *Proc. Pap. Calif. Mosq. Vector Control Assoc.* **55**: 45–49.
- MIURA T. & TAKAHASHI R.M. 1988: The relationship between the absolute population density and sweep net samples of notonectids in California rice fields. *Proc. Pap. Calif. Mosq. Vector Control Assoc.* **56**: 164–169.
- MIURA T., TAKAHASHI R.M. & STEWART R.J. 1979: Habitat and food selection by the mosquitofish *Gambusia affinis*. *Proc. Calif. Mosq. Vector Control Assoc.* **47**: 46–50.
- MIURA T., TAKAHASHI R.M. & WILDER W.H. 1984: Impact of the mosquitofish (*Gambusia affinis*) on a rice field ecosystem when used as a mosquito control agent. *Mosq. News* **44**: 510–516.
- MIYAMOTO S. 1952: Biology of *Helotrephes formosanus* Esaki et Miyamoto, with descriptions of larval stages. *Sieboldia* **1**(1): 1–10.
- MORIN P.J., LAWLER P.S. & JOHNSON E. 1988: Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* **69**: 1401–1409.
- MUNRO J.A. 1945: The birds of the Cariboo Parklands, British Columbia. *Can. J. Res.* **23**: 17–103.
- MURDOCH W.W., SCOTT M. & EBSWORTH P. 1984: Effects of the general predator *Notonecta* (Hemiptera) upon a freshwater community. *J. Anim. Ecol.* **47**: 581–592.
- NERI-BARBOSA J.F., QUIROZ-MARTINEZ H., RODRIGUEZ-TOVAR M.L., TEJADA L.O. & BADI M.H. 1997: Use of Bactimosá briquets (B.t.i. formulation) combined with the backswimmer *Notonecta irrorata* (Hemiptera: Notonectidae) for control of mosquito larvae. *J. Am. Mosq. Control Assoc.* **13**: 87–89.
- NIESER N. 1981: Notes on life cycles of semiaquatic and aquatic Heteroptera in Northern Tirol (Austria) (Insecta: Heteroptera). *Ber. Nat.-Med. Ver. Innsbruck* **68**: 111–124.
- NYMAN H.G., OSCARSON H.G. & STENSON J.A.E. 1985: Impact of invertebrate predators on the zooplankton composition in acid forest lakes. *Ecol. Bull.* **37**: 239–243.
- OSCARSON H.G. 1987: Habitats segregation in a water boatman (Corixidae) assemblage – the role of predation. *Oikos* **49**: 133–140.
- PAJUNEN V.I. 1970: Adaptation of *Arctocoris carinata* (Sahlb.) and *Callicorixa producta* (Reut.) populations to a rock pool environment. *Proc. Adv. Study Inst. Dynamics Popul. (Oosterbeek)* **1970**: 148–158.
- PAJUNEN V.I. 1979: Competition between rock pool corixids. *Ann. Zool. Fenn.* **16**: 138–143.
- PAJUNEN V.I. & JANSSON A. 1969: Dispersal of the rock pool corixids *Arctocoris carinata* (Sahlb.) and *Callicorixa producta* (Reut.) (Heteroptera, Corixidae). *Ann. Zool. Fenn.* **6**: 391–427.

- PAPÁČEK M. 1985: Der Lebenszyklus und die Entwicklung des Zwergrückenschwimmer (*Plea leachi*, McGregor et Kirkaldy, 1899) (Heteroptera, Pleidae) im Becken von České Budějovice. *Sbor. Jihočes. Muz. v Čes. Budějovicích (Přír. vědy)* **25**: 73–85 (in Czech, German abstr.).
- PAPÁČEK M. 1989: Life cycles of univoltine water bugs (Heteroptera, Nepomorpha) in Czechoslovakia. *Práce Slov. Entomol. Spol. SAV (Bratislava)* **8**: 45–52 (in Czech, English abstr.).
- PAPÁČEK M. 1993: *On the Morphology and Bionomy of Water Bugs of the Superfamilies Pleoidea and Notonectoidea (Heteroptera: Nepomorpha)*. Assoc. Prof. thesis, Univ. South Bohemia, České Budějovice, 232 pp. (in Czech).
- PAPÁČEK M. 2000: Small aquatic bugs (Nepomorpha) with slight or underestimated economic importance. pp. 591–600. In Schaefer C.W. & Panizzi A. (eds): *Heteroptera of Economic Importance*. CRC Press, Boca Raton, London, New York, Washington D.C., 828 pp.
- PAPÁČEK M. & BOHONĚK K. 1989: The life cycle and ovarian development of *Corixa punctata* (Heteroptera, Corixidae) in South Bohemia. *Acta Entomol. Bohemoslov.* **86**: 96–110.
- PAPÁČEK M. & SOLDÁN T. 1987: Development of the female internal reproductive system of *Notonecta glauca* (Heteroptera, Notonectidae) and the life cycle in South Bohemia. *Acta Entomol. Bohemoslov.* **84**: 161–180.
- PAPÁČEK M. & SOLDÁN T. 1996: Structure and development of the internal reproductive system of *Aphelocheirus aestivalis* (F.) (Heteroptera: Aphelocheiridae). *Proceedings of the XXth International Congress of Entomology, Firenze, Italy, August 25–31, 1996*. Firenze, p. 122.
- PAPÁČEK M. & TRÍSKA K. 1992: Lebenszyklus und Entwicklung der Ruderwanze *Cymatia coleoptrata* (Heteroptera, Corixidae) in Südböhmen (Mitteleuropa). *Zool. Jb. Syst.* **119**: 425–435.
- PAPÁČEK M., ŠTYS P. & TONNER M. 1988: A new subfamily of Helotrephidae (Heteroptera, Nepomorpha) from Southeast Asia. *Acta Entomol. Bohemoslov.* **85**: 120–152.
- PAPÁČEK M., ŠTYS P. & TONNER M. 1989: A new genus and species of Helotrephidae from Afghanistan and Iran (Heteroptera: Nepomorpha). *Věst. Čs. Společ. Zool.* **53**: 107–122.
- PETERS W. & SPURGEON J. 1971: Biology of the water-boatmen *Krizousacorixa femorata* (Heteroptera: Corixidae). *Am. Middl. Nat.* **86**: 197–207.
- POISSON R. 1935: Les Hémiptères aquatiques, Sandaliorrhyncha Börn, de la faune française. *Arch. Zool. Exp. Gén.* **77**: 455–563.
- POISSON R. 1957: Hétéroptères aquatiques. *Faune de France* **61**. Fédération Française des Sociétés Sciences Naturelles, Paris, 263 pp.
- POLHEMUS J.T. & POLHEMUS D.A. 1988: The Aphelocheirinae of tropical Asia (Heteroptera: Naucoridae). *Raffles Bull. Zool.* **36**: 167–300.
- POPHAM E.J. 1941: The variation in the colour of certain species of *Arctocoris* (Hemiptera, Corixidae) and its significance. *Proc. Zool. Soc. Lond.* **111**: 135–172.
- POPHAM E.J. 1943: Ecological studies of the commoner species of British Corixidae. *J. Anim. Ecol.* **12**: 124–136.
- POPHAM E.J., BRYANT M.T. & SAVAGE A.A. 1984: The role of front legs of British corixid bugs in feeding and mating. *J. Nat. Hist.* **18**: 445–464.
- PUCHKOVA L.V. 1969: On the trophic relationships of waterboatmen and influence of *Sigara striata* on the water plants (Corixidae). *Zool. Zh.* **48**: 1581–1583 (in Russian, English abstr.).
- RASK M. 1983: Differences in growth of perch (*Perca fluviatilis*) in two small forest lakes. *Hydrobiologia* **101**: 139–144.
- REYNOLDS J.D. 1975: Feeding in corixids (Heteroptera) of small alkaline lakes in central B.C. *Verh. Int. Verein. Limnol.* **19**: 3073–3078.
- REYNOLDS J.D. & SCUDDER G.G.E. 1987a: Experimental evidence of the fundamental feeding niche in *Cenocorixa* (Hemiptera: Corixidae). *Can. J. Zool.* **65**: 967–973.
- REYNOLDS J.D. & SCUDDER G.G.E. 1987b: Serological evidence of realised feeding niche in *Cenocorixa* species (Hemiptera: Corixidae) in sympatry and allopatry. *Can. J. Zool.* **65**: 974–980.
- SAETTEM L.M. 1986: The life history of *Aphelocheirus aestivalis* Fabricius (Hemiptera) in Norway. *Arch. Hydrobiol.* **106**: 245–250.
- ŠAFÁŘ P. 1991: *pH as Abiotic Factor of Water Environment*. MSc thesis, Univ. South Bohemia, Ped. Fac., České Budějovice, 69 pp. (in Czech).
- SAILER R.I. & LIENK S.E. 1954: Insect predators of mosquito larvae and pupae in Alaska. *Mosq. News* **14**: 14–16.
- SAVAGE A.A. 1979: The Corixidae of an inland saline lake from 1970 to 1975. *Arch. Hydrobiol.* **86**: 355–370.
- SAVAGE A.A. 1981: The Gammaridae and Corixidae of an inland saline lake from 1975 to 1978. *Hydrobiologia* **76**: 33–44.
- SAVAGE A.A. 1989: Adults of the British aquatic Hemiptera Heteroptera. A key with ecological notes. *Sci. Publ. Freshwat. Biol. Assoc.* **50**: 1–173.
- SAVAGE A.A. 1994a: The distribution of Corixidae in relation to the water quality of British lakes: a monitoring model. *Freshwat. Forum* **4**: 32–61.
- SAVAGE A.A. 1994b: Corixidae and water quality. *Freshwat. Forum* **4**: 214–216.
- SCHUH T.R. & SLATER J.A. (eds) 1995: *True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History*. Cornell University Press, Ithaca, 336 pp.
- SCHILL D.V. 1943: The Ochteridae (Hemiptera) of the Western Hemisphere. *J. Kans. Entomol. Soc.* **16**: 29–47.
- SCHWIND R. 1980: Geometrical optics of the *Notonecta* eye: adaptations to optical environment and way of life cycle. *J. Comp. Physiol.* **140**: 59–68.
- SCOTT M.A. & MURDOCH W.W. 1983: Selective predation by the backswimmer, *Notonecta*. *Limnol. Oceanogr.* **28**: 362–366.
- SCUDDER G.G.E. 1966: The immature stages of *Cenocorixa bifida* (Hung.) and *C. expleta* (Uhler) (Hemiptera: Corixidae). *J. Entomol. Soc. Brit. Col.* **63**: 33–40.
- SCUDDER G.G.E. 1969a: The distribution of two species of *Cenocorixa* in inland saline lakes of British Columbia. *J. Entomol. Soc. Brit. Col.* **66**: 32–41.
- SCUDDER G.G.E. 1969b: The fauna of saline lakes on the Fraser Plateau in British Columbia. *Verh. Int. Verein. Limnol.* **17**: 430–439.
- SCUDDER G.G.E. 1975: Field studies on the flight muscle polymorphism in *Cenocorixa* (Hemiptera: Corixidae). *Verh. Int. Verein. Theor. Angew. Limnol.* **19**: 3064–3072.
- SCUDDER G.G.E. 1976: Water boatmen of saline waters (Hemiptera: Corixidae). In Cheng L. (ed.): *Marine Insects*. North-Holland Publ., Amsterdam, Oxford, American Elsevier Publ., New York, pp. 263–289.
- SCUDDER G.G.E. 1987: Aquatic and semiaquatic Hemiptera of peatlands and marshes in Canada. *Mem. Entomol. Soc. Can.* **140**: 65–98.
- SHIH A. 1982: Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* **63**: 786–798.

- SIH A. 1987: Predators and prey lifestyles: an evolutionary and ecological overview. In Kerfoot W.C. & Sih A. (eds): *Predation: Direct and Indirect Impacts on Aquatic Communities*. Univ. Press of New England, Hanover, New Hampshire, USA, pp. 203–224.
- SITES R.W. 2000: Economic importance of creeping water bugs (Naucoridae). In Schaefer C.W. & Panizzi A. (eds): *Heteroptera of Economic Importance*. CRC Press, Boca Raton, FL (in press).
- SLÁDEČEK V. & SLÁDEČKOVÁ A. 1994: Corixidae as indicators of organic pollution. *Freshwat. Forum* **4**: 211–213.
- SOKOLOVSKAYA N.P. & ZHITNEVA L.D. 1973: A contribution to the biology of Corixidae (Heteroptera), pests of fish culture in the Rostov district. *Zool. Zh.* **52**: 1330–1335 (in Russian, English abstr.).
- STEVENS M. & GREVEN H. 1999: Food and feeding behaviour of deutonymphs and adults of the water mite *Hydrachna skoricowi* (Acari: Hydrachnellae), with notes on the structure of their mouthparts. In Bruin J., van der Gest L.P.S. & Sabelis M.W. (eds): *Ecology and Evolution of the Acari*. Kluwer Academic Publishers, Netherlands, pp. 381–387.
- STREAMS F.A. 1982: Diel foraging and reproductive periodicity in *Notonecta undulata* Say (Heteroptera). *Aquat. Insects* **4**: 111–119.
- STREAMS F.A. 1986: Foraging behavior in a notonectid assemblage. *Am. Middl. Nat.* **117**: 353–361.
- STREAMS F.A. 1992a: Age-dependent foraging depths of two species of *Notonecta* (Heteroptera: Notonectidae) breeding together in a small pond. *Aquat. Insects* **14**: 183–191.
- STREAMS F.A. 1992b: Intrageneric predation by *Notonecta* (Hemiptera: Notonectidae) in the laboratory and in nature. *Ann. Entomol. Soc. Am.* **85**: 265–273.
- STREAMS F.A. & NEWFIELD S. 1972: Spatial and temporal overlap among breeding populations of New England *Notonecta*. *Univ. Conn. Occas. Pap. (Biol. Sci.)* **2**: 139–157.
- STREAMS F.A. & SHUBECK T.P. 1982: Spatial structure and intra-specific interactions in *Notonecta* populations. *Envir. Entomol.* **11**: 652–659.
- SUTTON M.F. 1951: On the food, feeding mechanism and alimentary canal of Corixidae (Hemiptera, Heteroptera). *Proc. Zool. Soc. Lond.* **121**: 465–499.
- TAKAHASHI R.M. 1923: Observations on the Ochteridae. *Bull. Brooklyn Entomol. Soc.* **18**: 67–68.
- TAKAHASHI R.M., STEWART R.J., SCHEFER C.H. & SJOGREN R.D. 1979: An assessment of *Plea striola* (Hemiptera: Pleidae) as a mosquito control agent in California. *Mosq. News* **39**: 514–519.
- TODD E.L. 1955: A taxonomic revision of the family Gelastocoridae (Hemiptera). *Univ. Kans. Sci. Bull.* **37**: 277–475.
- TORRE BUENO J.R. DE LA 1905: The genus *Notonecta* in America north of Mexico. *J. N.Y. Entomol. Soc.* **13**: 143–167.
- TOTH R.S. & CHEW R.M. 1972: Development and energetics of *Notonecta undulata* during predation on *Culex tarsalis*. *Ann. Entomol. Soc. Am.* **65**: 1270–1279.
- USINGER R.L. 1937: Notes on the biology of *Hydrotrepes balnearius* (Helotrephidae, Hemiptera-Heteroptera). *Entomol. Month. Mag. (Ser. 3)* **23**: 179–180.
- VANDERLIN R.L. & STREAMS F.A. 1977: Photoperiodic control of reproductive diapause in *Notonecta undulata*. *Envir. Entomol.* **6**: 258–262.
- VENKATESAN P. 2000: Economic importance of giant water bugs (Belostomatidae). In Schaefer C.W. & Panizzi A. (eds): *Heteroptera of Economic Importance*. CRC Press, Boca Raton, FL (in press).
- WAITZBAUER W. 1974: Die Larvalentwicklung einiger aquatischer Wanzenarten (Ins., Heteroptera, Hemiptera) *Naucoris*, *Notonecta*, *Ranatra*. *Sitzungsber. Öster. Akad. Wiss. Math. Naturw. Kl. Abt.* **182**: 77–102.
- WAITZBAUER W. 1976: Energieumsatz aquatischer Hemipteren *Naucoris cimicoides* L., *Notonecta glauca* L., *Ranatra linearis* L. *Oecologia (Berlin)* **22**: 179–209.
- WALTON G.A. 1943: The water bugs (Rhynchota-Hemiptera) of North Somerset. *Trans. Soc. Br. Entomol.* **8**: 231–290.
- WASHINO R.K. & HOKAMA Y. 1967: Preliminary report on the feeding pattern of two species of fish in a rice habitat. *Proc. Calif. Mosq. Vector Control Assoc.* **35**: 84–87.
- WATTAL S., ADAK T., DHIMAN R.C. & SHARMA V.P. 1996: The biology and predatory potential of notonectid bug, *Enithares indica* (Fabr.) against mosquito larvae. *SEast Asian J. Trop. Med. Public Health* **27**: 633–636.
- WEBER H. 1930: *Biologie der Hemipteren*. Julius Springer, Berlin, 543 pp.
- WEFELSCHIED H. 1912: Über die Biologie und Anatomie von *Plea minutissima* Leach. *Zool. Jb. Syst.* **32**: 389–474.
- WESENBERG-LUND C. 1943: *Biologie der Süßwasserinsekten*. Julius Springer, Berlin, 664 pp.
- WILLIAMS D.D. & FELTMATE B.W. 1992: *Aquatic Insects*. CAB International, Wallingford, Redwood Press, Melksham, UK, 358 pp.
- WILLIAMS G.M. 1993: The colonisation of mining subsidence ponds by water boatmen (Hemiptera: Heteroptera). *Entomologist's Gaz.* **44**: 67–78.
- WRÓBLEWSKI A. 1958: The Polish species of the genus *Micronecta* Kirk. (Heteroptera, Corixidae). *Ann. Zool. Warsz.* **17**: 247–381.
- WRÓBLEWSKI A. 1963: Notes on Micronectinae from USSR (Heteroptera, Corixidae). *Bull. Acad. Pol. Sci.* **10**: 319–324.
- YOUNG E.C. 1965: Teneral development in British Corixidae. *Proc. R. Entomol. Soc. (A)* **40**: 159–168.
- YOUNG E.C. 1970: Seasonal changes in populations of Corixidae and Notonectidae (Hemiptera, Heteroptera) in New Zealand. *Trans. R. Soc. N. Z.* **12**: 113–133.
- YOUNG E.C. 1978: Seasonal cycles of ovarian development in Corixidae and Notonectidae, aquatic Hemiptera-Heteroptera. *N. Z. Entomol.* **6**: 361–362.
- ZALOM F.G. 1978: Backswimmer prey selection with observations on cannibalism (Hemiptera: Notonectidae). *SWest Nat.* **23**: 617–622.
- ZWART K.W.R. 1965: On the influence of some food substances on survival of Corixidae (Heteroptera). *Proceedings of the XIIIth International Congress of Entomology*, London, pp. 411–412.

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