

Seasonal Development of Aquatic & Semiaquatic True Bugs (Heteroptera)

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Don't panic if your Russian comprehension is not up to scratch! The authors & publishers very kindly allowed us to reproduce the very comprehensive English language Extended Summary of this interesting book.

Reference details of the original are given below.

Eds.

Saulich A.H. & Musolin D.L., 2007

Seasonal Development of Aquatic and Semiaquatic True Bugs (Heteroptera).

Book published by St. Petersburg University Press. 205 pp. (in Russian, with extended 6p English Summary), St. Petersburg. ISBN 978-5-288-04332-1.

www.unipress.ru/2007/sau.html

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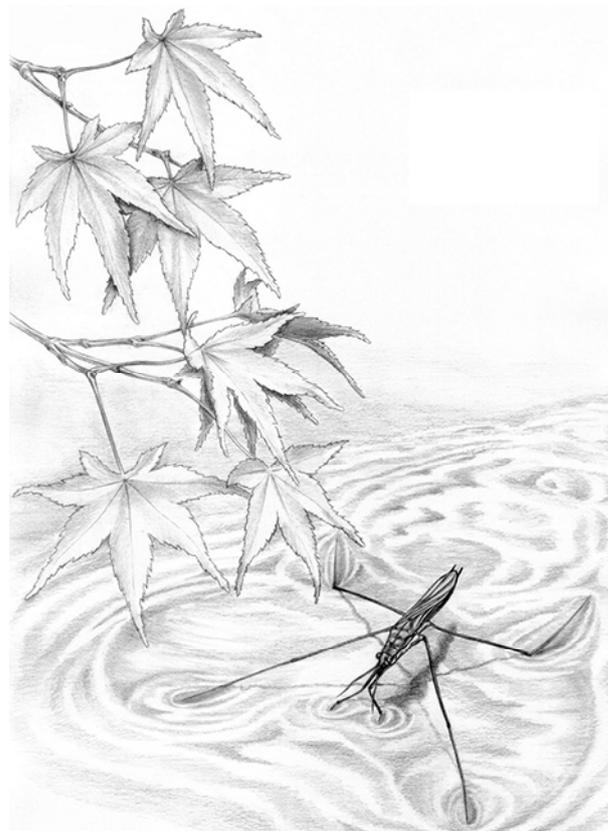
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ILLUSTRATIONS:

- ◆ Drawing of a water skater by Artem Ayvazyan Kyoto 2007, with permission).
- ◆ Drawing by Maria Sibylla Merian (1647–1717) from her *Metamorphosis Insectorum Surinamensium* (Metamorphosis of the Insects of Surinam, 1705). In her book it is called "water scorpion", but must be *Lethocerus maximus*, the largest heteropteran (up to 11 cm).



The book overviews extensive but scattered literature on cycles of seasonal development and seasonal adaptation of aquatic and semiaquatic true bugs (Hemiptera: Heteroptera). It is mostly focused on the Temperate Zone species though whenever possible examples from other geographic zones are also presented and discussed.

Ch. 1. Aquatic & Semiaquatic Heteroptera

Even though Heteroptera with ca. 38,000 described species worldwide [Schuh, Slater, 1995] is a predominantly terrestrial taxon, about 4,500 bug species are ecologically related to different water bodies. They represent five out of eight heteropteran infraorders: Dipsocoromorpha, Ceratocombomorpha, Gerromorpha, Nepomorpha, and Leptopodomorpha. Aquatic and semiaquatic bugs live in a wide range of natural and artificial habitats: humid terrestrial microhabitats (not necessarily close to free water and comprising litter on humid soil), seeping rock faces with algae and moss, marginal aquatic habitats (banks, shores, water edges), plant-covered or open waters in springs, streams, waterfalls, rivers, ponds, lakes (saline, alkaline or fresh), intertidal shore zones and waters of seas and oceans.

Aquatic and semiaquatic Heteroptera faunas are more diverse in the Tropics and Subtropics. Only 631 species from all five infraorders are known from the Palaearctic Region [Aukema, Rieger, 1995], 211 species from Europe [Aukema, 2005] and 166 from Russia [Kerzhner, Jaczewski, 1964; Kanyukova, 2006].

The evolution of morphological and life-history adaptations associated with the long history of the Heteroptera's conquest of semiaquatic and aquatic habitats is summarized and illustrated.

Ch. 2. Life Cycles & Seasonal Development

This briefly describes the life cycle and introduces the principal elements of heteropteran seasonal development typical for terrestrial, aquatic and semiaquatic species. The life cycle of true bugs consists of three stages: egg, nymphal (=larval), and adult. The nymphal stage normally consists of 5 instars, though this number can be 3 or 4 in some taxa. In general, Heteroptera is a thermophilic taxon with a relatively high value for the lower developmental threshold ($T_0 = +12.2 \pm 2.3$ °C) [Kiritani, 1997]. The duration of the complete life cycle greatly depends on temperature and can vary from less than 20 days in some species at high temperature to 2–3 years in others under less favourable conditions.

Species of aquatic and semiaquatic heteropterans demonstrate all known patterns of voltinism. Many species and populations are univoltine (producing one generation per year), bivoltine (two complete generations per year or one complete generation and one partial, i.e. only in a part of the population) and these patterns of voltinism are typical for the Temperate Zone. Some species or populations are tri- or multivoltine having three or more generations annually, usually in the Tropics and/or Subtropics. In the regions

where environmental conditions are constantly stable and favourable, some heteropteran species may breed all year round, thus having a homodynamic type of seasonal development. On the contrary, under severe environmental conditions (mostly, seasonally cold), life cycles of some species may last more than a year and then seasonal development is semivoltine.

Among particular seasonal adaptations special attention is paid to diapause (a profound state of dormancy, which can be facultative or obligatory and occurs in winter or summer), migrations and polyphenism (or seasonal polymorphism).

The following chapters, Ch. 3... Ch. 7, treat individually all infraorders and families of aquatic and semiaquatic true bugs.

Ch. 3. Dipsocoromorpha

This is the smallest infraorder of semiaquatic bugs and consists of 2 families and about 30 species from all geographic zones. They live in humid habitats along shores of diverse water bodies. Seasonal development is poorly studied, but probably species typically overwinter as adults. Brachypterous and macropterous wing forms (=morphs) are known.

Ch. 4. Ceratocombomorpha

A small infraorder of semiaquatic bugs that consists of 3 families and about 170 species from the Tropics and the Temperate Zone. Species inhabit humid leaf litter, decaying wood, mosses, swamps, bogs, and shores of different water bodies. Seasonal development is poorly studied. Some species are known to overwinter as adults, others as eggs. Brachypterous and macropterous adults are known and some species have coleopterous wings.

Ch. 5. Gerromorpha – Semiaquatic Bugs

A large infraorder of semiaquatic heteropterans that consists of 8 families and about 1,940 species. They are distributed worldwide. Gerromorphs are known from almost the whole range of aquatic and semiaquatic habitats, i.e. from humid forest leaf litter to the open oceans. Most species of Gerromorpha can move easily over water surface film. Water striders (Gerridae) and riffle bugs (Veliidae) spend most of their time on the water and *Halobates* spp. (Gerridae) are the only insects inhabiting the oceans.

Many gerromorphs are multivoltine and different species produce up to 3, 4, or 5 generations annually even in the Temperate Zone; some other species are univoltine. Most representatives of Gerridae, Macroveliidae, Hydrometridae, Veliidae, and some species in other families overwinter as adults on land, sometimes far from water bodies, in forest leaf litter, close to roots of plants, or under stones. All known species of Mesoveliidae and some species of Gerridae overwinter as eggs laid under water and facultative diapause is induced in adults of the maternal generation in at least some of these species. The water cricket *Velia caprai* (Veliidae) seems to have a very plastic overwintering strategy in Europe: late instar nymphs and both non-reproductive and egg-bearing females may be found during the winter. Some *Velia* spp. and *Microvelia* spp. may be active on water during warmer days in the winter.

Wing polymorphism is known and well pronounced in many gerromorph species, and at least in some cases it is seasonal and environmentally controlled (by day-length, population density, availability of food, etc.). In some species, e.g., in Macroveliidae and Hermatobatidae, only apters are so far known, or brachypters are dominant. There is seasonal body colour polyphenism in some water striders and the

diapause generation is darker than the directly breeding one. The cuticle structure may also differ between the non-diapause and diapause generations (e.g., in Gerridae). After overwintering and migration, females of some water striders are able to hystolize wing muscles and then redirect resources to reproduction. A few species are known to have summer diapause (aestivation).

Ch. 6. Nepomorpha – Aquatic & Water Bugs

This is the largest infraorder of semiaquatic and truly aquatic bugs, it consists of 11 families and about 2,050



species. Nepomorphs are distributed worldwide, but are most diverse in the Tropics. Different families and species live in different habitats ranging from shores of small ponds and banks of streams to deep inland water bodies. Many species are very skillful swimmers and some can live deep under water (up to 10 m). Some giant water bugs (Belostomatidae) are strong fliers and have lunar cycles of flight activity.

Most of the nepomorph species studied produce one generation annually, though some others are multivoltine or even have homodynamic development in the Tropics. Some species of Aphelocheiridae have very slow development and need 2–3 years to complete the life cycle.

Probably all species of Belostomatidae and Pleidae and many species of Corixidae, Notonectidae, and Nepidae overwinter as adults under water on the bottom or in mud or detritus. At least two Pleidae species that overwinter as adults on the bottom of ponds are known to switch from physical gill to plastron respiration for overwintering. Adults of different species use very different microhabitats for overwintering: forest leaf litter (a number of belostomatids), soil in forests (some naucorids) and air bubbles in ice (*Cymatia americana*; Corixidae). Some species of Nepidae fly from ponds to streams to overwinter.

A number of nepomorph species are known to overwinter as nymphs in litter or moss on the soil (some ochterids), in

swift streams (some naucorids), on the bottom of water bodies (some corixids). Some species of Corixidae and Notonectidae overwinter as eggs under water. Species of Aphelocheiridae can probably overwinter on the bottom of streams at any developmental stage.

Reproductive diapause has been proved to be under photoperiodic control at least in some nepomorph species. Adults of a number of species can live longer than a year and it has been shown that the timing of reproduction and dormancy is controlled by day-length and temperature in *Kirkaldyia* (= *Lethocerus deyrollei*) (Belostomatidae). Adults of some Corixidae and Naucoridae species can have two copulation seasons – in the autumn and spring, being sexually mature both before and after overwintering. Oviposition in several species can also start before overwintering, then stop for the winter and resume in the spring.

Lethocerus americanus (Belostomatidae) has a seasonal period ('drift') from the autumn to spring, when adults swim in rivers (sometimes under ice) as a means of dispersal. A number of notonectids swim under ice in the winter and active adults of *Glaenocoris propinqua cavifrons* (= *G. quadrata*; Corixidae) were collected from water in a pond covered with 45 cm of ice in Alaska when air temperature was -38°C [Sailer, 1952].

Some adults of Belostomatidae and Corixidae have flight muscle polymorphism, a phenomenon in which wings are fully developed but muscles are underdeveloped in young adults and their further growth is dependent on environmental conditions. Muscles can grow if conditions in the water body deteriorate and migration is necessary. Flight muscles can degenerate after migration and then the resources can be re-directed to reproduction. Body colour polymorphism is known in Corixidae and wing polymorphism is well represented in many families. A few nepomorph species are known to have summer diapause (aestivation).

Ch. 7. Leptopodomorpha

This infraorder of semiaquatic bugs consists of 4 families and more than 300 species. The infraorder is distributed worldwide, but the biggest family (Saldidae) is more diverse in the Temperate Zone than in the Tropics. Species mostly inhabit shores of various water bodies and the inter-tidal zone of seas, though some species dwell in terrestrial habitats, sometimes far from open water.

Seasonal development of Leptopodomorpha is poorly studied. Many species of Saldidae and, perhaps, Aepophilidae and Leptopodidae overwinter as adults. Some genera of Saldidae typically overwinter as eggs, though some other species in this family can overwinter as nymphs. In general, some species of Saldidae seem to have rather unstable seasonal cycles and overwintering strategy may differ both between and within populations, a feature very unusual for Heteroptera. Saldids produce 1–3 generations in the Temperate Zone. Micropterous *Aepophilus bonnairei* (Aepophilidae) spends most of its life under the water, probably overwinters as adults and produces one generation annually. Wing polymorphism is common in Saldidae, though it is probably not seasonal.

Conclusions

Seasonal development of aquatic and semiaquatic Heteroptera is strongly influenced by their relationship with water habitats and seasonality of this environment. In the

Temperate Zone, these insects typically overwinter as adults and annually produce 1 or 2 generations (sometimes the 2nd generation is only partial). Many other species, however, overwinter as eggs or nymphs, produce more generations or have semivoltine cycles. Subtropical and tropical species or populations often breed all the year round and thus have homodynamic pattern of seasonal development. Aquatic and semiaquatic heteropterans utilize a very wide range of aquatic, terrestrial and sometimes subterrestrial microhabitats for overwintering.

The physiological mechanism controlling facultative winter diapause has been studied only in a few species of Gerridae, Veliidae, Belostomatidae, and Notonectidae, but perhaps at least its induction is generally under the photoperiodic control.

Sexual maturation before overwintering, winter activity, and instability of seasonal cycles are features unusual for terrestrial heteropterans but are known in some aquatic and/or semiaquatic bug species.

Wing polymorphism is typical for many aquatic and semiaquatic Heteroptera species. It can be under environmental control, at least in some species, and sometimes is associated with polymorphism of both flight muscles and coloration.

Seasonal timing of growth, reproduction and dormancy, migrations, polymorphism and seasonal polyphenism as well as other seasonal adaptations create great diversity of seasonal cycles making each species of heteropterans ecologically unique. These seasonal adaptations allow true bugs' populations to survive under environmental conditions with pronounced alternation of favorable and unfavorable seasons.

Seasonal development of many aquatic and semiaquatic taxa of Heteroptera remains poorly studied. Further detailed research of phenology and seasonal eco-physiology is needed for better understanding of ecology and evolution of these unusual insects in their unusual environment.

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