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THE LIFE CYCLES OF MAYFLIES OF THE EASTERN UKRAINE. SUBFAMILY BAETINAE (EPHEMEROPTERA, BAETIDAE)

A. V. Martynov

Schmalhausen Institute of Zoology, NAS of Ukraine,
vul. B. Khmelnytskogo, 15, Kyiv, 01601 Ukraine
E-mail: martynov_av@ukr.net

The Life Cycles of Mayflies of the Eastern Ukraine. Subfamily Baetinae (Ephemeroptera, Baetidae). Martynov A. V. — The life cycle types of mayflies of the subfamily Baetinae in Eastern Ukraine are determined. The scheme for identification of larval age structure is given. The age structure changes of *Baetis braaschi, B. nexus* and *Alainites muticus* larvae during the year are described in detail. The flight periods of imagoes throughout the studied region are delimited for almost all species of the subfamily. *B. braaschi* is shown to have the bivoltine life cycle, with its populations overwintering as the larval stage (MBws) independently on temperature conditions in the water body. The peculiarities of oviposition are described for this species. The following aspects of life cycles were revealed: nymphs, subimagoes and imagoes of different generations of *B. braaschi* differ considerably in size; the voltinity of *B. vernus* in the region can vary (Us and/or MBss), mainly due to temperature conditions of the water bodies, where its development takes place; geographically isolated populations of *A. muticus* in the Eastern Ukraine reproduce only by thelytoky.

Key words: mayflies, Ephemeroptera, life cycles, bionomy, parthenogenesis, Eastern Ukraine.

Жизненные циклы подёнок Восточной Украины. Подсемейство Baetinae (Ephemeroptera, Baetidae). Мартынов А. В. — Установлены типы жизненных циклов представителей подсемейства Baetinae, которые они демонстрируют в пределах Восточной Украины. Подана схема определения возрастной структуры личинок. Детально описано изменение возрастной структуры личинок *Baetis braaschi, B. nexus* и *Alainites muticus* на протяжении года. Приведены периоды лёта имаго в регионе практически для всех видов подсемейства. Установлено, что независимо от температурного режима водотока *B. braaschi* имеет бивольтинный жизненный цикл с зимовкой на стадии личинки (MBws). Описаны особенности откладки яиц данным видом. Выявлены следующие аспекты жизненных циклов: нимфы, субимаго и имаго разных генераций *B. braaschi* существенно отличаются размерами; вольтинность *B. vernus* в регионе может варьировать (Us и/или MBss) главным образом в зависимости от температурного режима водного объекта, в котором проходит его развитие; географически изолированные популяции *A. muticus* Восточной Украины размножаются исключительно при помощи телитокии.

Ключевые слова: подёнки, Ephemeroptera, жизненные циклы, биономия, партеногенез, Восточная Украина.

Introduction

Despite the short period of detailed research on mayflies, much attention is devoted to their life cycles and several classifications of life cycles are worked out by far (Landa, 1968; Sowa, 1975; Clifford, 1982). Clifford's (1982) classification is the most widely used at present: all known mayfly life cycles are divided into 14 groups, belonging to 5 categories. The life cycle type of one species is shown to vary within its areal. For example, *Centroptilum luteolum* in the range of its areal has two different life cycle types, *Alainites muticus*, whereas *Baetis vernus* has four, and *Cloeon dipterum* has five life cycle types (Clifford, 1982). Considering that the variation of life cycle is typical for most mayfly species, our research aimed to study life cycles of the Eastern Ukraine Baetinae. The obtained data allow determining the most appropriate time for faunistic studies in the region. These data could be used in the bioindicational exploration and to study variation of life cycles through the areal.

Material and methods

The life cycles classification of is used in this paper follows Clifford (1982). To study the age structure changes of 3 species, the larvae were collected in model water bodies (table 1). Fourteen samples of each species were taken with different periodicity from March 2010 to March 2011, but not less than once per month (except

Table 1. Model water bodies and material used for analysis of age structure change of mayfly larvae during the year

Таблица 1. Модельные водотоки и объём материала, использованного для изучения изменений возрастной структуры личинок подёнок на протяжении года

Species	Administrative location of water body	Waterway type, it's characteristic	Coordinates	Number of specimens
Baetis braaschi	Donets'ka oblast, Yasynuvats'kyi district, vicinity of Mineral'ne village, the stream in gullied forest	rhithral stream	48°6'7" N 37°49'44" E	1145
Baetis braaschi	Territory of Donets'k city, Putilyvs'kyi park, the stream flowing out from pond	potamal stream	48°3'53" N 37°47'40" E	745
Baetis nexus	Donets'ka oblast, Yasynuvats'kyi district, vicinity of Mineral'ne village, the stream in the meadow	potamal stream	48°5'52" N 37°49'52" E	744
Alainites muticus	Donets'ka oblast, Yasynuvats'kyi district, vicinity of Debaltseve urban village, Bulavina river	rhithral zone of the river	48°18'55" N 38°26'07" E	622

of winter months in some cases). The coordinates of model water bodies are given according to Google Earth (http://earth.google.com).

Changes of the age structure for mayfly larvae during the year were studied following Jop's (1981) system with some alternations, which are displayed in fig. 1 and described below. The spreadsheet designed by A. Buffangi on the base of Microsoft Office Excel (Tools, 2008) was used to generate histograms, which reflect the larval age structure during the year.

Results and discussion

Age structure definition. To define the age structure of mayfly larvae, K. Jop (1981) system was applied as the basis, except only 10 groups of larval ages are shown for the larvae of Baetidae species (as for Leptophlebiidae): from L0 to L9 (fig. 1), as the larvae ready to become winged with completely developed wings inside the pads, occurred in the L_9–N_{III} age groups of Jop's system. All Baetidae larvae, whose wing pads by developmental degree correspond to L_9–N_{III} in Jop's system were considered to be the variant of L9 in this study. To show the larvae, which are ready to emerge (having completely developed wings inside the pads), and/or winged stages the inclined black arrow was added above the dates of sampling in the histograms of species age structure change (fig. 2, 7).

Life cycles. According to Martynov (2010), the subfamily Baetinae is represented in the Eastern Ukraine by seven species: *Baetis braaschi* Zimmermann, 1980, *B. vernus* Curtis, 1834, *B. fuscatus* (Linnaeus, 1761), *B. buceratus* Eaton, 1870, *B. nexus* Navás, 1918, *Nigrobaetis digitatus* (Bengtsson, 1912), and *Alainites muticus* (Linnaeus, 1758). The life cycles of some of these species remain poorly studied throughout their whole areals, and such data on all these species from the Eastern Ukraine were absent. Furthermore, some of them appear to be situated at the margin of their areal and/or are presented by geographically separated populations in the studied region.

Baetis braaschi Zimmermann, 1980. Life cycle has not been previously studied in details. Our preliminary studies carried out in the mountain regions of the Crimea, revealed the bivoltine life cycle with wintering as the larval stage for the species (MBws) (Sroka et al., 2012). The present paper contains the results of minute research on *B. braaschi* life cycle throughout the Eastern Ukraine. Age structure changes of species during the year were studied on different populations, which inhabit potamal and rhithral zones of streams (table 1). The corresponding water temperature change in model water bodies are presented in fig. 3, 4. As this study shows, such a big difference in temperature conditions of model streams has no influence in species voltinity. *B. braaschi* has the bivoltine life cycle and overwinters as the larval stage (MBws) in both types of waterways (fig. 2).

These populations overwinter in elder, middle and junior larval ages. Larvae do not grow actively during the wintering. As the spring comes, the growth rate increases and

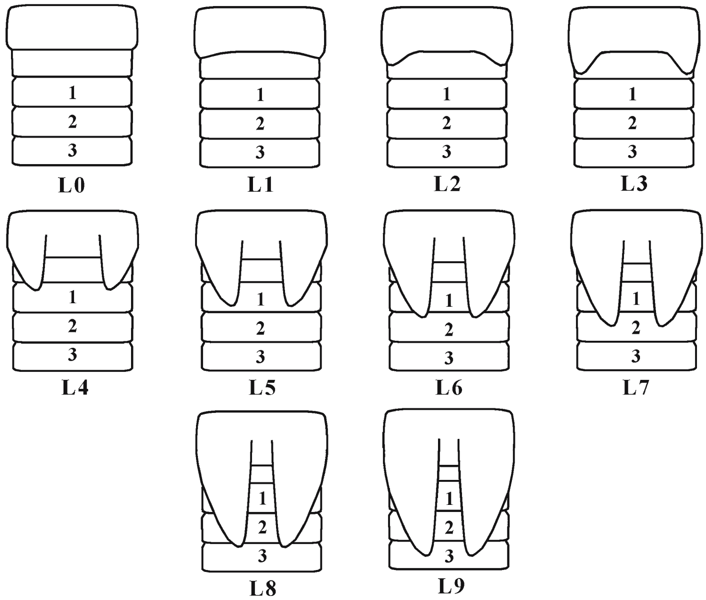

Fig. 1. The developmental degree of wing pads of larvae in different age groups: 1–3 — abdominal segments; L0–L9 — age groups.

Рис. 1. Степень развития зачатков крыльев у личинок поденок различных возрастных групп: 1–3 — сегменты брюшка; L0–L9 — возрастные группы.

overwintered larvae of elder ages soon complete their germination. The larvae of first generation, been developing in the potamal zone, become winged from March to the end of May. The larvae, whose germination took place in the rhithral zone, become winged until the mid-June (fig. 2). The reason for such a long period, when the winged stages and first generation larvae ready for emergence could be registered, is the wintering in all larval ages from L0 to L8. The peak of winged stages emergence is in the end of April — beginning of May. Emergence of the second generation subimago can insignificantly overlap with the end of the first generation or begins just after it, due to the long period, when

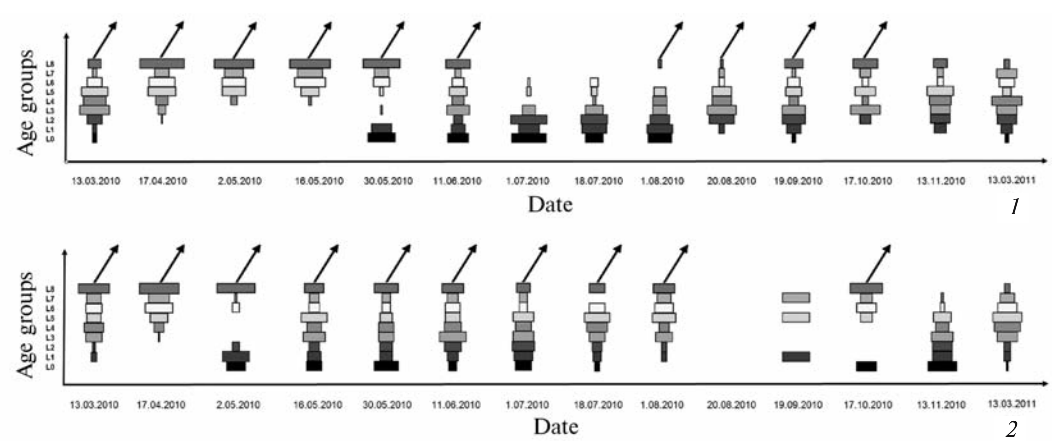

Fig. 2. The age structure change of *Baetis braaschi* during the year: *1* — rhithral stream (vicinity of Mineral'ne village, 2010–2011); *2* — potamal stream (territory of Donets'k city, Putilyvs'kyi park, 2010–2011).

Рис. 2. Изменение возрастной структуры *Baetis braaschi* на протяжении года: *1* — ритральный ручей (окр. с. Минеральное, 2010–2011 гг.); *2* — потамальный ручей (г. Донецк, Путиловский парк, 2010–2011 гг.).

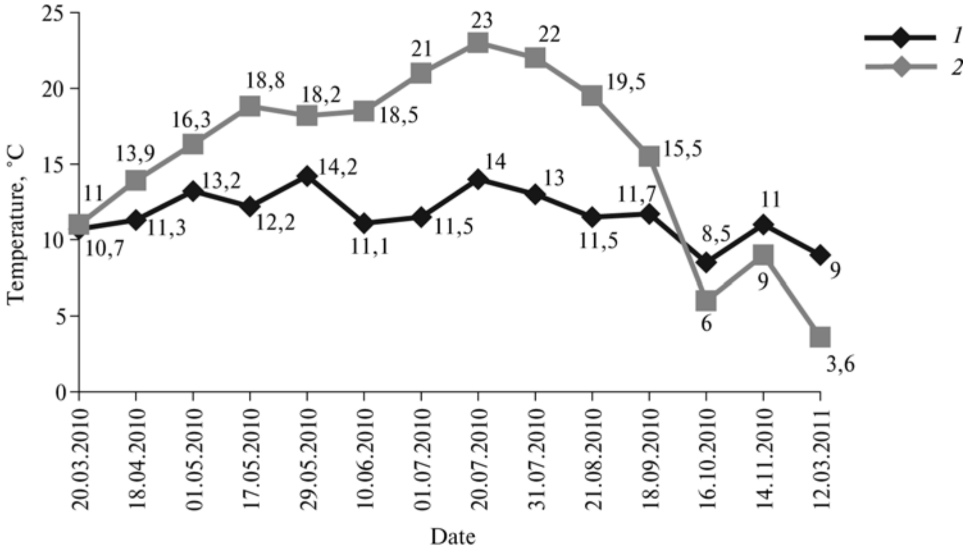

Fig. 3. The water temperature changes in model water bodies during the year: 1 — the rhithral stream (vicinity of Mineral'ne village, 2010–2011); 2 — the potamal stream (vicinity of Mineral'ne village, 2010–2011).

Рис. 3. Изменение температуры воды в модельных водных объектах на протяжении года: 1 — ритральный ручей (окр. с. Минеральное, 2010–2011 гг.); 2 — потамальный ручей (окр. с. Минеральное, 2010–2011 гг.).

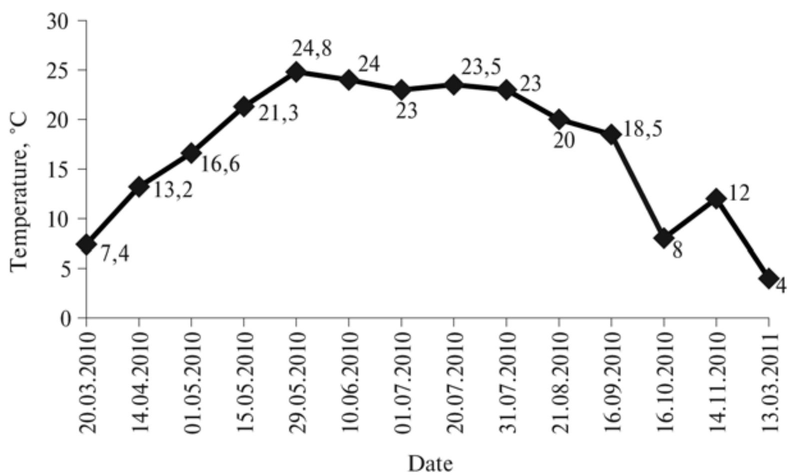

Fig. 4. The water temperature change in potamal stream during a year (Donetsk City, Putilyvs'kyi park, 2010–2011).

Рис. 4. Изменение температуры воды в потамальном ручье на протяжении года (г. Донецк, Путиловский парк) (2010–2011 гг.).

the first generation gets winged, the short period of egg stage existence and the rapid development of the second generation larvae (owing to water temperature increase)

The winged stages of the second generation emerge until the end of October. The most intensive emergence of winged stages of both generations is observed in the middle of day (12.00–14.00), the male swarming — from 12.00 to 17.00. The swarms are usually seen not far from water surface or strait along the bank, and consist of no more than 15 males. Small swarms (5–10 males) can be close to each other and remain separated. The undisturbed males do not fly up higher than 3–3.5 m in the swarm, and all the swarm stays at a height of 1.5–2.5 m. The number of swarming males is considerably less closer to twilight.

For oviposition, *B. braaschi* female crawls (under the water) to the bottom side of stones and other objects with strait surface (foam plastic blocks, flooded boards, etc.). Then, female takes a position facing the upstream to increase the streamlining and oviposits 3000–3500 eggs. The eggs are aggregated in set, which resembles an elongated oval or obtruncated pear (fig. 5). In general, the egg set is single-layered, double-layered only in some parts. The female dies after the oviposition. The hatching of the first generation larvae to overwinter, begins in September and lasts until the end of the autumn (fig. 2).

There is no considerable difference in duration of larval germination period and winged stages flight between *B. braaschi* populations developed in rhithral and potamal zones (fig. 2). The populations of species germinating in crenal zone (rheocrene) have not been examined in this study. However, we can suggest, that thes species also have the bivoltine life cycle — MBws (overwintering as the larval stage) under these conditions.

The last generation larvae, as well as subimagoes and imagoes of different generations, considerably vary in size. Thus, the overwintered larvae of first generation are 2–2.5 times bigger than the second generation larvae (fig. 5) (Sroka et al., 2012). Such difference in size of various generations is stipulated by temperature conditions, under which the larval growth took place, and is recorded for most species with bivoltine life cycles and larvae to overwinter (Cianciara, 1979; Humpesch, 1979; Hwang et al., 2005, etc.). The size difference between both nymphs and winged stages of *B. braaschi* generations developed in rhithral and potamal zones is absent.

Nigrobaetis digitatus (Bengtsson, 1912). The life cycle is poorly known. In Europe it has monovoltine life cycle, with its populations overwinting as the larval stage (Uw) (Jop, 1981; Söderström, 1991; Bauernfiend, Soldán, 2012). It is difficult to determine the life cycle type of *N. digitatus* in the Eastern Ukraine due to the lack of data and restricted field period (spring). However, a lot of larvae ready for emergence and imagoes have been registered in the first decade of May. This fact can be an evidence of wintering as the larval stage. There is no data on *N. digitatus* voltinity throughout the Eastern Ukraine. At present we can only suppose that this species has monovoltine life cycle and overwinters as the larval stage (Uw) in the studied region, as well as in other European counties.

Baetis vernus Curtis, 1834. Due to obtained data, the bivoltine life cycle of this species, with its populations overwinting as the stage of egg (MBss) throughout the Eastern Ukraine, can be confirmed. A similar life cycle *B. vernus* most often reveals in the majority of European countries (Landa, 1968, 1969; Elliott et al., 1988; Soldán, Zahrádková, 2000; Bauernfiend, Soldán, 2012), but in Germany this species can have two or three generations during the year (MB–MP) (Haybach, 1998). Similarly, *B. vernus* is shown to have the monovoltine life cycle with wintering as the stage of egg or larva (Us, Uw) in Europe (Bauernfiend, Soldán, 2012).

The hatching from overwintered eggs begins at the first days of April, and the winged stages emergence gets started to the middle of May in the studied region. Emergence of the second generation larvae is registered from the middle of July. There are no clear bounds between the imagoes flight of first and second generations. Generally, the flight of *B. vernus* imagoes was observed from the middle of May until the first decade of November inclusive. As Bohle (1969) showed in the laboratory studies that duration of *B. vernus* egg diapause varies from 1 to 5 months and depends on the water temperature. The latter circumstance can influence not only on the terms of generation development, but on the species voltinity. Thus, this species has the monovoltine life cycle (Soldán, Zahrádková, 2000) in some cold-water bodies in the mountain regions of Czech Republic. In our opinion, *B. vernus* can also have monovoltine life cycle, wintering as an egg (Us) in crenal zone of the Eastern Ukrainian waterways, where the water temperature is stably low during all the year. In addition, the quantitative sampling in rhithral zone of Bulavina River during the year shows that second generation larvae of this species are much less nume-

Fig. 5. The egg sets of *Baetis braaschi* and *Alainites muticus*, female nymphs of *Baetis braaschi* of the first and second generations: *1* — general egg set shape of *B. braaschi*; *2* — group of egg sets of *B. braaschi* on the bottom side of a stone; *3* — aggregation of *Alainites muticus* egg sets on the bottom surface of flooded log; *4* — first generation nymph of *B. braaschi*; *5* — second generation nymph of *B. braaschi*. Scale bar 10 mm.

Рис. 5. Кладки *Baetis braaschi* и *Alainites muticus*, нимфы самок *Baetis braaschi* первого и второго поколений: *1* — общий вид кладки *B. braaschi*; *2* — группа кладок *B. braaschi* на нижней поверхности камня; *3* — скопление кладок *Alainites muticus* на нижней поверхности погруженного в воду бревна; *4* — нимфа первого поколения *B. braaschi*; *5* — нимфа второго поколения *B. braaschi*. Масштабная линейка 10 мм.

rous, than of the first one. Increasing of water temperature can cause of quantity reduction of second generation larvae, which is rather noxious for the species. Thus, H. V. Bohle's laboratory research revealed, that 15.6 °C temperature causes the death of 75 % of diapausing eggs, and under 20 °C about 85 % of them die. As the fig. 6 shows, the temperature over 15 °C has been registered in Bulavina river from middle of May until the end of July. This is exactly the time, when the development of eggs (which originate the second generation of *B. vernus*) takes place in the river.

In addition, it is possible that the majority of eggs, laid by first generation females, falls into a long diapause until the spring, and the small part of eggs gives rise for the second generation larvae without any delay. If this assumption is true, some populations of *B. vernus* and/or their parts have the monovoltine life cycles and overwinter as the egg stage (Us) in the Eastern Ukraine.

Baetis fuscatus (Linnaeus, 1761). This species has a bivoltine life cycle, its populations overwinter as the egg stage (MBss) throughout the Eastern Ukraine, as in the vast part of Europe (Landa, 1968, 1969; Sowa, 1975; Elliott et al., 1988; Soldán, Zahrádková, 2000; Bauernfiend, Soldán, 2012). The represented phenological data are based on studies carried throughout Donetsk and Priazovskaya elevated areas. The larvae ready for emergence and winged stages of the first generation were registered from the middle of May until the end of June, and those of the second generation from the middle of August until the first decade of October inclusively.

This species overwinters as a larva (MBws) (Clifford, 1982; Haybach, 1998) in some European water bodies. Similarly, *B. fuscatus* has up to three generations in the year (MB-

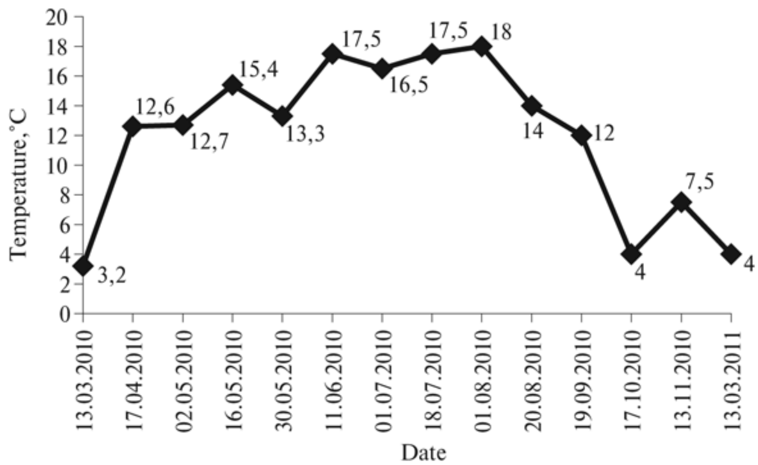

Fig. 6. The water temperature change in model section of Bulavina river during the year (vicinity of Debaltseve) (2010–2011).

Рис. 6. Изменение температуры воды в модельном участке реки Булавина на протяжении года (окр. Дебальцево) (2010–2011).

MP) in Germany and in the big rivers of Czech Republic (Haybach, 1998; Soldán, Zahrádková, 2000). The water temperature is a determinative factor in both cases. It is quite possible that the species has three generations per year and/or overwinters as the larval stage in such big rivers of the Eastern Ukraine as Siverskyi Donets, Oskol, Aydar and others.

Baetis buceratus Eaton, 1870 has two generations per year, its wintering takes place on the stage of larva (MBws) throughout the main part of Europe, as in the Ukrainian Carpathians. Thus, it can reveal three generations per year (MP) in some European countries under favorable conditions (Godunko, 2001; Landa, 1968, 1969; Elliott et al., 1988; Haybach, 1998; Soldán, Zahrádková, 2000; Bauernfiend, Soldán, 2012). *B. buceratus* has the bivoltine life cycle, with its population wintering as the larval stage (MBws) in the studied region. The larvae ready for emergence and winged stages of the first generation were recorded from the end of April until the middle of July, of the second generation — during whole September. The first generation first instar larvae (overwintered) were observed at the second decade of October.

Baetis nexus Navás, 1918. The life cycle has not been studied in detail due to species rarity through the main part of Europe. Casual data were recounted in the paper on the species population from the vicinity of Lion (France) (Camousseight, Fontaine, 1990); the bivoltine life cycle (population overwinter in the larval stage (MBws)) was recorded for *B. nexus* . It is considered to be one of the most commonly occurring rheobionts (Martynov, 2012) in the Eastern Ukraine, where lies current eastern boundary of it distribution. In the Eastern Ukraine, *B. nexus* has the life cycle similar to that in France — MBws. Study of the age structure changes of *B. nexus* larvae in the potamal stream (fig. 7) shows that it overwinters as the larvae of first and middle age (the water temperature change in model water body is shown in fig. 3). The active growth of larvae was not observed during the winter. When spring comes, the growth rate is restored, and the active flight of winged stages of the first generation is registered until the middle of May. Mass hatching of the first generation larvae, characterised by rather rapid growth, begins from the second half of May. There is no clear border between the imago flight period of the first and second generations. The general flight period lasts from the middle of May until the middle of September. The first generation larvae, which are going to overwinter, emerge from October to November.

Alainites muticus (Linnaeus, 1758). Generally, the species has the bivoltine life cycle, with its populations overwintering as the larval stage (MBws) in Europe (Landa, 1968,

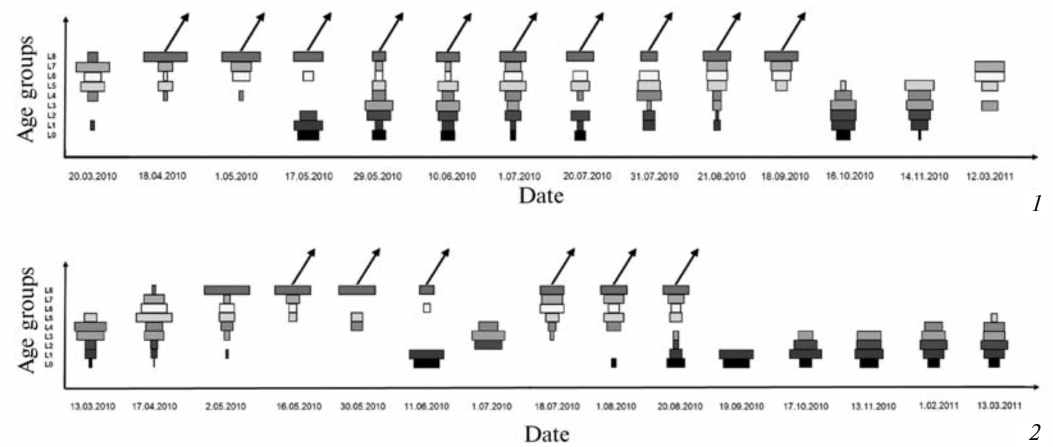

Fig. 7. The age structure change of *Baetis nexus* и *Alainites muticus* during the year: *1 — Baetis nexus*, the potamal stream (vicinity of Mineral'ne village, 2010–2011); *2 — Alainites muticus*, the rhithral zone of Bulavina river (vicinity of Debaltseve urban village, 2010–2011).

Рис. 7. Изменение возрастной структуры *Baetis nexus* и *Alainites muticus* на протяжении года: *1 — Baetis nexus*, потамальный ручей (окрестности с. Минеральное, 2010–2011 гг.); *2 — Alainites muticus*, ритральная зона реки Булавина (окр. пгт Дебальцево, 2010–2011 гг.).

1969; Sowa, 1975; Soldán, Zahrádková, 2000; Bauernfiend, Soldán, 2012), but it has one generation per year (Uw) in Scandinavia, high-mountain regions of Czech Republic and in Alps, and tree in Atlantic Pyrenees (MP) (Ulfstrand, 1968; Thibault, 1971; Soldán, Zahrádková, 2000).

Alainites muticus reveals the bivoltine life cycle, with its populations overwintering as the larval stage (MBws) in the Eastern Ukraine. The age structure changes of its larvae during the year has been studied on the most numerous *A. muticus* population, which inhabits the rhithral zone of Bulavina River (fig. 7). The species overwinters as larvae of junior and middle ages. One can find the junior age larvae (L0–L1) in March and April due to hatching of small part of population in spring or due to very slow developmental and growth rates of larvae in winter months (fig. 7). The winged stages of the first generation are registered from the middle of May until the middle of June.

The females oviposit on the bottom surface of stones and on the sunken logs. Meanwhile, the density of egg sets can be very high and sets can be arranged one over another (fig. 5) in the areas with a few stones on the bottom (with the shortage of places suitable for oviposition). The second generation larvae begin to emerge in first days of June. They develop very quickly, probably, due to the high water temperature in this period (fig. 6). The flight of winged stages of the second generation lasts from the second half of July until the end of August. The hatching period of the first generation larvae is rather long: it begins in August and lasts during all the autumn months.

It should be pointed out, that all known *A. muticus* populations in the Eastern Ukraine reproduce by thelytoky (a form of parthenogenesis, with the unfertilized ovi develop into females). Degrange (1960) has reported this species to propagate from time to time by facultative parthenogenesis. In Funk's opinion, most of (maybe even all) bisexual species of mayflies are able to reproduce by facultative parthenogenesis (Funk et al., 2010).

Though, virginal reproduction in bisexual species is generally registered occasionally, being alternated with reproduction with fertilization (Harker, 1997; Funk et al., 2010). At present, the obligate parthenogenesis is declared only for a few mayfly species from North America, South America and Africa (Froehlich, 1969; Gibbs, 1977; Bergman, Hilsenhoff, 1978; Gillies, Knowles, 1990, etc.). Five-year long studies on *A. muticus* population in the rhithral zone of Bulavina River revealed that all its generations were reproducing only by parthenogenesis.

In our opinion, *A. muticus* population in Bulavina River, as other populations of this species in the Eastern Ukraine, has completely switched to obligate parthenogenetic reproduction.

Other populations of *A. muticus* in the Eastern Ukraine have not been subjected to long-term investigation yet, but periodical sampling have not revealed males in the larval, subimaginal and imaginal stages of the species.

By far, the mechanisms causing such a switch remain unknown. The studies in collaboration with I. A. Kozeretska and S. V. Serga (Taras Shevchenko National University of Kyiv) to investigate the infectiousness of *A. muticus* populations from Bulavina River by *Wolbachia* sp. and *Spiroplasma* sp. causing parthenogenesis and male killing (Werren et al., 2008) gave negative results.

In addition, populations of species through the studied region are geographically isolated from the main part of their areals. It is possible that in this case the display of geographical parthenogenesis is observed, which is typical for insular and isolated from the main parts of areal populations (Victorov, 2006).

There is one more fact confirming this: we revealed the parthenogenetical population of *Nigrobaetis niger* (Linnaeus, 1761) in the mountain region of the Crimea, which is geographically isolated from the main areal. It is also possible that parthenogenesis is caused by specific conditions observed during larval development (temperature in the first place), which, in some authors' opinions, mostly influence on appearance of parthenogenesis in mayflies (Humpesch, 1980, 1981).

Conclusions

1. The life cycle types of mayflies in the subfamily Baetinae are determined. Most species in the region of studies have bivoltine life cycles (MBws or MBss) and only some of them have other cycles (Us or Uw). We failed to determine the life cycle types for several species due to their rarity in the studied region.

2. *B. braaschi* was shown to have the bivoltine life cycle, with its populations overwintering as a larval stage (MBws) regardless of temperature conditions in water body. Females of this species oviposit under the water and their eggs appear to be aggregated into sets. Nymphs, subimagoes and imagoes of different generations of this species considerably differ in size.

3. The voltinity of *B. vernus* in the region can vary (Us and/or MBss), mainly due to temperature conditions of the water body, where its development takes place.

4. Geographically isolated populations of *A. muticus* in the Eastern Ukraine reproduce only by thelytoky.

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