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With author's compliments

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Ekologia i biogeografia jętek *(Ephemeroptera)* wód płynących w polskiej części Karpat.
2. Cykle życiowe

Ecology and biogeography of mayflies *(Ephemeroptera)* of running waters in the Polish part of the Carpathians.
2. Life cycles

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Abstract — The growth and life cycles of 21 species of mayflies in selected streams of the Beskid Mountains and in the River Raba are presented. Life cycles of 54 other species were distinguished according to the material from the whole investigation territory. 54 univoltine, 21 bivoltine, and 4 semivoltine species were found. In extreme developmental conditions some of the bivoltine species produce only a single generation in a year. Classification of Carpathian mayflies is given as to their life cycles, 9 groups of species being distinguished. The dependence between the nature of growth of species and the size and altitudinal situation of the running waters inhabited by them is discussed.

1. Introduction

For a fairly long period of time, information on the phenology of particular species of European mayflies, including also their life cycles, could be found, above all, in systematic and faunistic elaborations. Moreover these more frequently concerned the emergence of adult forms than the rate and character of growth of nymphs. Rising interest in mayfly life cycles has been noted only in the last 20 years; among the reasons for this, at least two, also of practical value, should be mentioned in the first place: a very great participation of *Ephemeroptera* in the secondary production of running waters and the significance of the species of this order as biological indicators of purity of inland waters. In the latter case very significant is the possibility of foreseeing — by means of studies of life cycles — when the complete absence or poor numbers of a given species or species communities, at determined growth stages and in determined environmental conditions, result from the character of

the development of species and when it is connected with a deterioration in these conditions.

From the existing studies on the life cycles of mayflies the publications by Moon (1939), Macan, (1957, 1970), Macan and Maudsley (1968), Hynes (1961), Gledhill (1959), Langford (1971), and Elliott (1967, 1972) concern species from Great Britain; Larsen's (1968) is from the territory of Norway, those by Thomas and Sowa (1970), and Thibault (1971, 1971a, 1971b) from Southern France, Plescot (1958, 1961, 1961a) and Bretschko (1965, 1966) from Austria, Landa (1968, 1969) from various regions of Czechoslovakia, and Ulfstrand (1968) from Northern Sweden. Altogether, the life cycles of over 70 European species have been analysed so far - this constituting about one third of the mayflies distinguished here. Apart from rare or poorly known species there are still a great number of European species, especially from large rivers, whose life cycles have not yet been studied. Further comparative investigations on already elaborated life cycles are also necessary in view of the developmental flexibility, known in many species, in various geographical regions and various environmental conditions in a given region. In the territoiy of the Polish part of the Carpathian Mts the life cycles of mayflies have not hitherto been investigated. A synthetic paper by Landa (1968), valuable for comparison, though not containing detailed unequivocal data, concerns in part the territory of the Carpathian Mts. The development of some lowland species was recently elaborated by Jażdżewska (1971).

The life cycles of 21 species of mayflies were studied in various sections of the water system Olszowy-Koninka-Porębianka-Raba (region III). For one species the material from station 1 in the Wielka Puszcza stream in the Beskid Mały (region I) was used. A detailed description of investigations of the environment and distribution of mayfly species in it is found in the first part of the present paper (Sowa 1975) where also a description of the general method of investigations can be found. In order to draw histograms of the growth of nymphs of particular species from the catchment area of the River Raba, use was made of the material from quantitative samples collected in 1969/1970. This material was completed with nymphs from semiquantitative samples from the same stations and investigation dates. Fixed nymphs were classified in millimeter size intervals, measuring their length from the anterior margin of the head to the posterior margin of the tenth abdominal tergite. For measurements all nymphs from the sample were taken, eliminating only specimens damaged or distorted by fixation. In this way the following size classes of nymphs were distinguished: class 1. — nymphs to 1 mm long; class 2. — nymphs from 1.1 to 2 mm long; class 3. — nymphs from 2.1 to 3 mm, long etc. Very young nymphs, to about 0.5 mm length, among them also newly hatched ones, were not caught to a great extent in consequence of the applied net mesh density (3 mesh per 1 mm length of the net), thus, not all could be taken into account in the histograms. The range of the period of emergence of a given species was established by means of catching winged forms and by recording the presence and numbers in the samples of nymphs ready to emerge, i. e. with dark wing pads. In determining the character of growth of nymphs and of the type of life cycle for other species, the author took as a basis

observations made in the whole investigation territory (Sowa 1975), recording the presence and numbers of particular nymphal stages distinguished mainly (Mikulski 1936, Plescot 1958, Bretschko 1965) on the basis of the degree of development of wing pads.

2. Species discussion

2.1. Family: *Heptageniidae*

2.1.1. *Rhithrogena hybrida* Etn.

The growth of nymphs of this species at station 3 in the Olszowy stream is presented in fig. 1 B. In spite of a small number of nymphs, a fairly uniform growth of the species at successive dates was visible also in winter. The emergence period at this station is short and lasts from the end of April till the end of May. By the end of July nymphs of classes 2. and 3. appear. It may be supposed that the species has here no quiescent period in embryonal development. In larger rivers of the Tatra Highlands, e. g. in the Białka Tatrzańska below Jurgów or in the Czarny Dunajec below Kojsówka (region IV), where *R. hybrida* occurs in great numbers, the growth of the nymphs proceeds in a similar way, whereas in the streams of the Tatras at an altitude of 1000 to 1100 m, i. e. near the border of the upper range of the species, its emergence is retarded by about 1.5 months, adults still being caught there at the beginning of August.

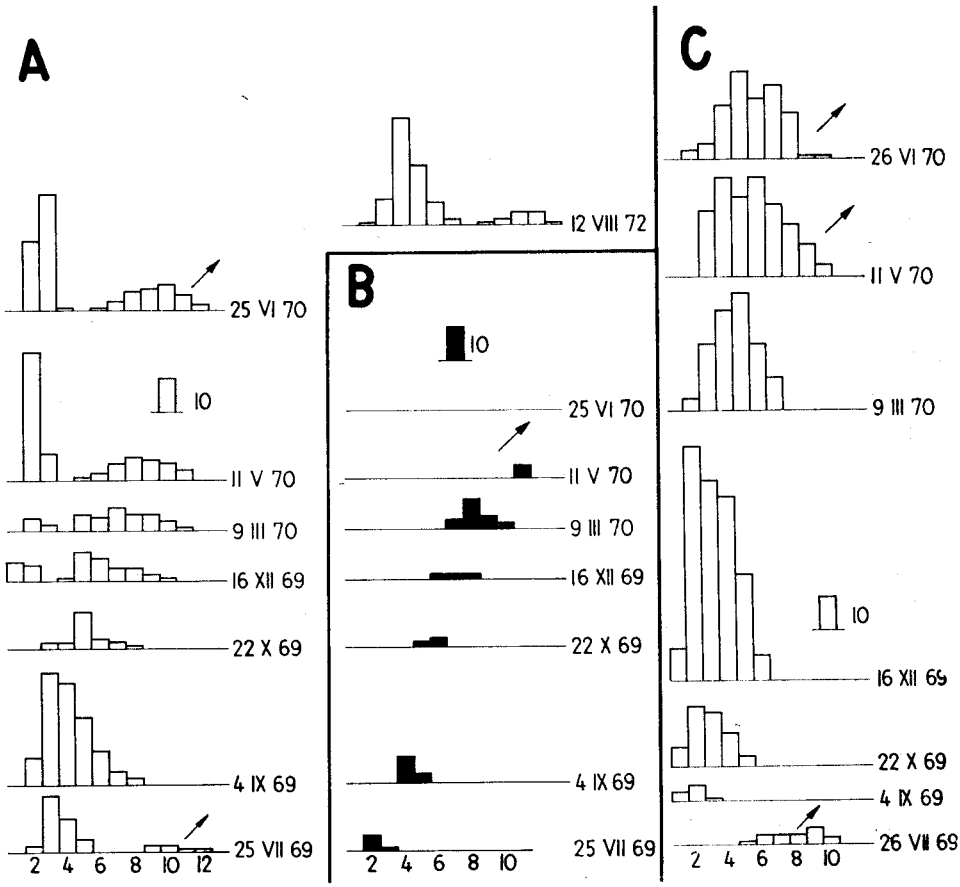
2.1.2. *Rhithrogena ferruginea* Navás.

The distribution of nymph sizes of this species at station 5 in the Porębianka is shown in fig. 1 C. *R. ferruginea* predominates quantitatively over other species of *Rhithrogena* Etn. Apart from it *R. germanica* and *R. semicolorata* also live there. Nymphs of the first three size classes of these species are not yet distinguishable, so that histogram may include in this range also nymphs of the other species and, in autumn, mainly nymphs of *R. semicolorata*. *R. ferruginea* emerges at this station from the beginning of May till the middle of August. Nymphs of class 1. to 3., originating from eggs laid in the spring appear in September. The number of these nymphs increases in October and December, when the largest ones are 6 mm long. During the winter the growth, though retarded, continues. It may be concluded from the comparison of the data from March and from the beginning of May 1970 that all, or almost all eggs laid in the previous year go through their embryonal development

before the winter. In larger Tatra streams the emergence of *R. ferruginea* is extended till the middle of September. The species has a single generation in a year. Its life cycle has not been investigated as yet.

2.1.3. *Rhithrogena loyolaea* Navás.

The growth of this species at station 2 in the Olszowy is presented in fig. 1 A. Its emergence begins from the middle of June and lasts till the middle of August. At particular dates, except September and October 1969, heterogeneity of the



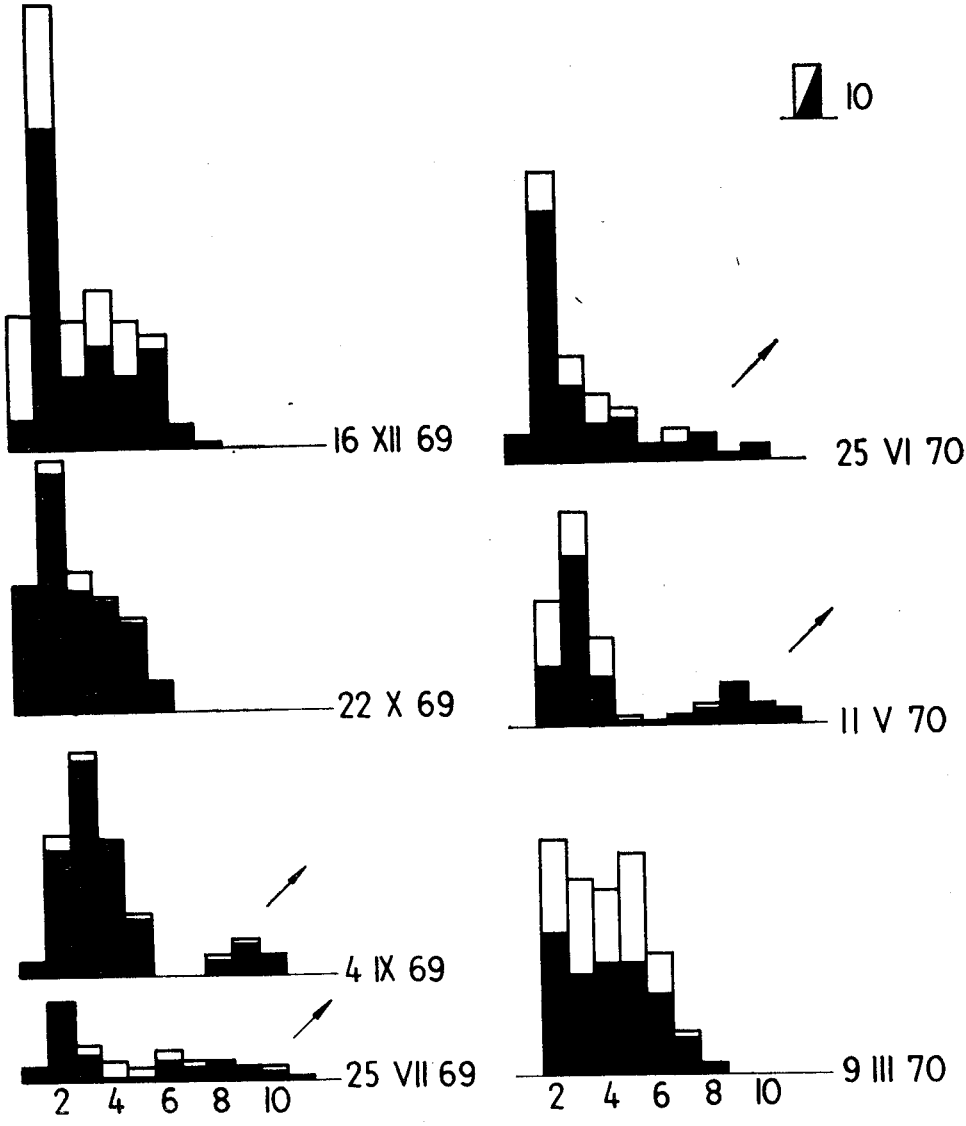
Ryc. 1. Rozkład klas wielkości larw *Rhithrogena loyolaea* (A), *R. hybrida* (B) i *R. ferruginea* (C) w dorzeczu Raby w roku 1969/1970. A — stanowisko 2; B — stanowisko 3; C — stanowisko 5. Strzałka oznacza wylot subimagines, izolowane słupki określają liczbę larw. U góry, nad przedziałem B podano dane dla larw *R. loyolaea* z potoku Suchy na stanowisku 10 (reg. II), z sierpnia 1972

Fig. 1. Size class distribution of nymphs of *Rhithrogena loyolaea* (A), *R. hybrida* (B) and *R. ferruginea* (C) in the catchment area of the Raba in 1969/1970. A — station 2; B — station 3; C — station 5. Arrow denotes emergence of subimagines, isolated columns — the number of nymphs. At the top over section B data are given for nymphs of *R. loyolaea* from the Suchy stream at station 10 (region II), from August 1972

population was noticeable. Young nymphs of classes 1. and 2. appear by the end of autumn and probably originate from spring oviposition. The appearance of a great number of young nymphs in May 1970, apart from nymphs of markedly greater dimensions, can be explained by the fact that majority of eggs laid in the previous year do not undergo full embryonal development before the onset of winter and have a period of quiescence lasting several months, probably of diapause character. Nymphs hatch as late as spring. If we study the further development of this group of nymphs by means of interpolation of the data from 1969, we can see that they grow slowly during the summer and still more slowly during the autumn and winter, attaining emergence ability only late in the spring of the following year. Supplementary material from the Suchy stream in the massif of the Babia Góra (station 10, region II) from August 1972 confirmed the existence of two populations of *R. loyolaea* nymphs also in that month. It seems, thus, that in the streams of the Beskid Mts, this species completes its life cycle within two years, only a small part of the population being able to complete it in the course of one year. In the existing literature detailed data on the growth of the nymphs and on the life cycle of the species are lacking. Landa (1968, 1969) included *R. loyolaea* (under the name *R. tatrica* Zel.) in the group of species with a univoltile cycle having an embryonal diapause of many months duration. According to that author, the nymphs, after a fast growth, achieve emergence ability during two or three summer months. This, however, is in disagreement with the data presented here nor is it confirmed at other stations in the Polish part of the Carpathian Mts where this species appears, and where nymphs of *R. loyolaea* in various size classes can be found throughout the year.

2.1.4. *Rhithrogena iridina iridina* Kol.

The histogram of growth of nymphs of this subspecies (fig. 2), presented on the basis of the material from stations 2 and 3 in the Olszowy stream, is hard to interpret, in spite of the fact that even nymphs of class 1. can be fairly easily distinguished from the nymphs of *R. loyolaea* found in the same habitat, by the colourless nerval ganglions on the ventral side of the body, and from *R. hybrida* nymphs by the presence of a dark spot on the femur. The emergence period is extended in time and lasts at both stations from the beginning of May till the beginning of October. By the end of July 1969 two peaks are marked in the distribution of the nymph sizes. One is formed by nymphs of classes 1. to 3. which could have originated from the earliest oviposition in this year, and the other is formed by nymphs of various sizes which, especially in classes 6. to 11. originate from oviposition of the previous year. At the beginning of September nymphs belonging to the latter part of the population are already scarce, their emergence already coming to an end. The population of nymphs from the current year grows fairly fast during the summer, slower in autumn and winter, and is gradually enriched by nymphs hatched during the summer. The presence of a great number of nymphs of classes 2. to 3. in the material



Ryc. 2. Rozkład klas wielkości larw *Rhithrogena iridina iridina* na stanowisku 2 (słupki białe) i 3 (słupki czarne) w potoku Olszowym (reg. III) w roku 1969/1970. Strzałka oznacza wylot subimagines; izolowany słupek określa liczbę larw

Fig. 2. Size class distribution of nymphs of *Rhithrogena iridina iridina* at station 2 (white columns) and 3 (black columns) in the Olszowy stream (region III) in 1969/1970. Arrow denotes emergence of subimagines, isolated column — the number of nymphs

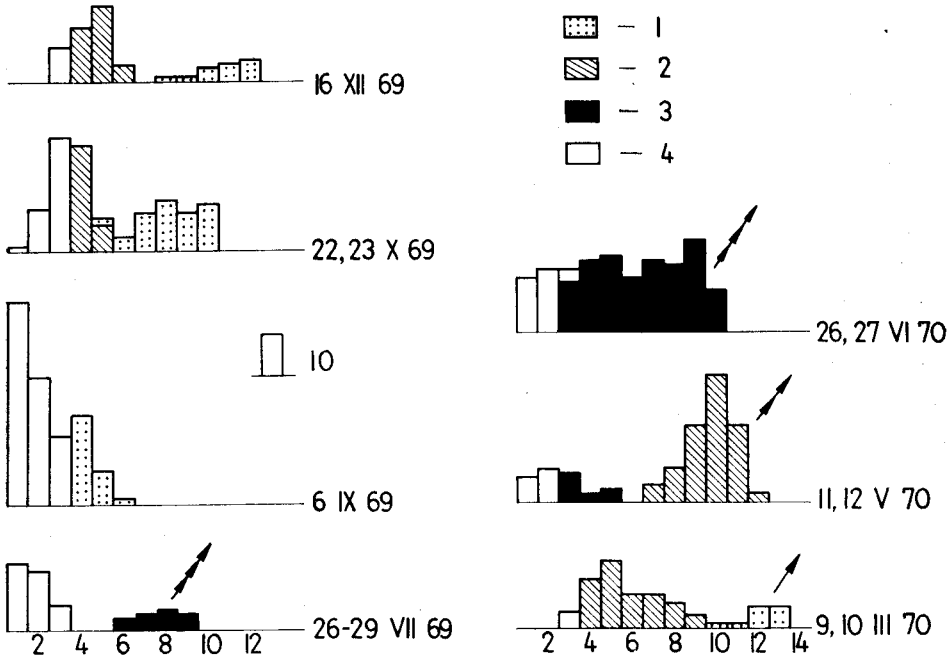
from May 1970 is quite interesting. Because of the too short period separating these nymphs from the time of appearance of the first imagines it is evident that they cannot originate from oviposition of the current year. They must therefore originate from eggs laid in the previous year, most probably in autumn, from which they

hatch as late as spring after a quiescent period in the embryonal development in winter. This supposition is confirmed by the absence in the samples of nymphs of class 1. caught later. These nymphs grow quickly at the beginning of summer and join, with respect to size, the population of winter nymphs, attaining emergence ability later in the summer or at the beginning of autumn. The species has a single generation during a year of heterogeneous development.

The life cycle of *R. iridina iridina* has not been investigated as yet. The subspecies *R. i. picteti* Sowa, widespread in the Alps and Pirenees has, according to Thibault (1971 b), in the Lissuraga stream in the Low Pirenees, a still longer period of emergence — from February till November, this undoubtedly being connected with the higher water temperature in winter, which there does not fall below 5°C. The developmental period of eggs of *R. i. picteti* lasts there one month both in spring and in autumnand Thibault admits the existence, in those climatic conditions, of a single generation during a year.

2.1.5. *Rhitáthrogena germa nica* Etn., *R. semicolorata* (Curt.) and *R. diaphana* Navás.

The growth of nymphs of these three species is presented together on the basis of the material from stations 8—10 in the Raba (fig. 3). Nymphs of *R. diaphana* of classes 1. and 2. are not distinguishable from those of the other two species. Nymphs of class 3. and larger ones of this species can be accurately determined owing to the absence of the fold on the upper surface of the first gill lamellae which is visible in the nymphs of the two other species. In this section of the Raba a distinct succession of emergence of three species during the year was observed: from the beginning of March till the middle od April *R. germanica* emerges, from the end of April till the middle of June *R. semicolorata*, and from the beginning of June till the end of August *R. diaphana*. At the end of July 1969, apart from nymphs of *R. diaphana*, nymphs of classes 1. to 3. are found in the river, these most probably belonging to *R. germanica*. Towards the end of summer nymphs of the latter species reach a length to 4 to 6 mm and towards the end of autumn some of them are almost of maximum size. They also grow, though very slowly, during the winter and by its end the majority are capable of emerging. In a similar way, though with a certain retardation, the population of *R. semicolorata* grows. A great majority of the nymphs of classes 1. and 2. caught at the beginning of September 1969 belonged to this species as well as probably all the nymphs of classes 1. to 3. collected at the end of October, when the largest nymphs were already 5 mm long. The population grows, though very slowly, also in autumn and winter. The annual distribution of size classes of the *R. diaphana* nymphs suggests that this species, contrary, to the preceding two species, overwinters as eggs; at the end of autumn 1969 and in March 1970 the absence of nymphs of classes 1. and 2. was noticed in the samples and nymphs of class 3. belonged to *R. semicolorata*. This would confirm Landa's (1968) observations, according to which this species (*R. aurantiaca* sensu Landa) has a long period of egg-diapause in winter. All three species have in that part of the Raba and in other



Ryc. 3. Rozkład klas wielkości larw *Rhithrogena germanica* (1), *R. semicolorata* (2), *R. diaphana* (3) oraz larw młodocianych co najmniej jednego z tych gatunków (4) w Rabie, na stanowiskach 6—8 łącznie, w roku 1969/1970. Podwójna strzałka oznacza wylot *R. semicolorata*, strzałka potrójna wylot *R. diaphana*. Wysokość izolowanego słupka określa liczbę okazów dla każdego z trzech gatunków

Fig. 3. Size class distribution of nymphs of *Rhithrogena germanica* (1), *R. semicolorata* (2), *R. diaphana* (3), and young nymphs of at least of one of these species (4) in the Raba, at stations 6 to 8 jointly, in 1969/1970. Double arrow denotes emergence of *R. semicolorata*, triple arrow — emergence of *R. diaphana*. The height of the isolated column denotes the number of specimens of the three species

Carpathian rivers a single generation in a year. Retardation of emergence near to the upper range limit is very small in the case of *R. germanica* (= *R. georgii* Landa, 1968 nom. nud.) and *R. semicolorata* and fairly great about one month — in the case of *R. diaphana*. In England and Denmark the emergence of *E. germanica* is retarded in comparison with the Raba and is prolonged until June (Macan 1970). On the other hand, in England, *R. semicolorata* has according to Macan (1957, 1970) an only slightly longer period of emergence, though in those climatic conditions some of the eggs have the development period prolonged till the end of autumn.

2.1.6. Other species of *Rhithrogena* Etn.

The life cycle of *R. gorganica* Klap. in the Wołosatka stream in the Bieszczady (region V) is similar to that of *R. hybrida* in the Olszowy stream in the Gorce Mts. *R. hercynia* Landa, which occurs concomitantly with *R. hybrida* in certain sections of large streams and rivers of the Tatra Highlands, emerges at common stations

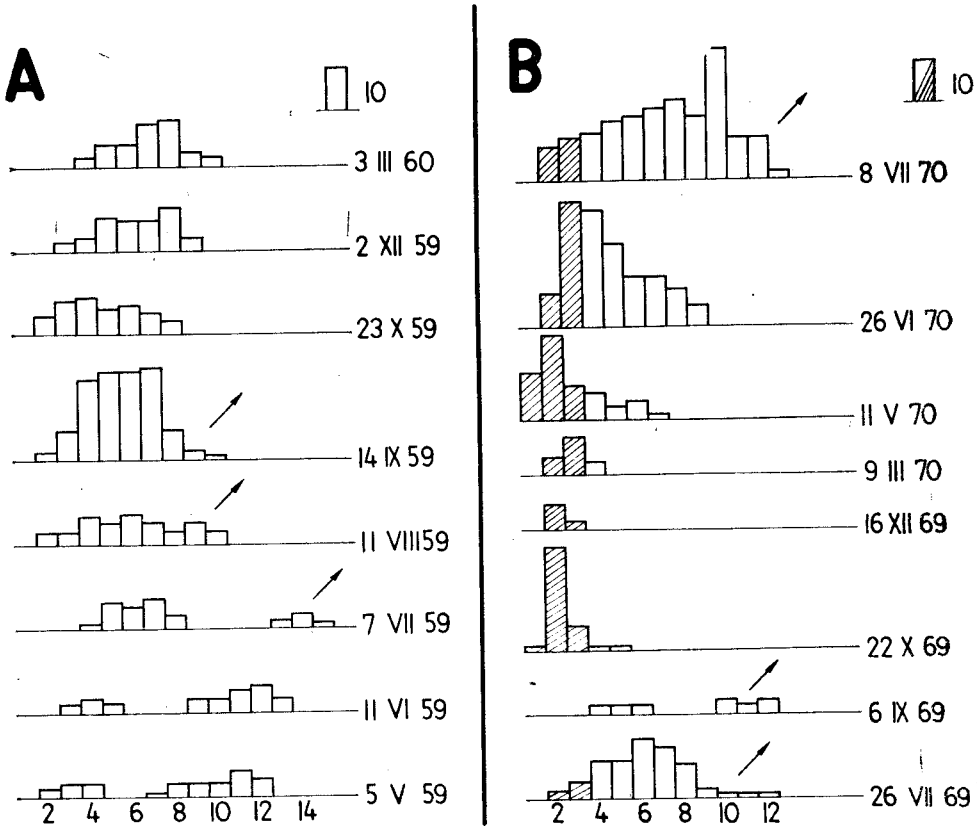
a little earlier — from the middle of April till the middle of June — this being the result of a faster growth of *R. hercynia* nymphs during the winter and early spring. In autumn nymphs of the two species are of similar size. The emergence of *R. hercynia* in the Czechoslovak rivers begins, according to Landa (1969, 1970), already in March. All the species discussed in the present paper have in the Polish part of the Carpathian Mts a single generation in a year.

2.1.7. *Ecdyonurus dispar* (Curt.)

The life cycle of this species was investigated in the Raba at stations 6 and 7 together (fig. 4 B). *E. dispar* emerges here from the end of June till the end of September. In 1969 the main emergence took place in August and September. Nymphs of size classes 2. and 3. are not distinguishable from the nymphs of *E. aurantiacus* (Burm.) and *E. insignis* Etn. cohabiting at these stations. Hence the corresponding columns of the histogram may include also a certain number of nymphs of these two species. Nymphs of class 1. are practically not distinguishable from the corresponding nymphs of other species of *Ecdyonurus* Etn. For similar reasons the histogram is hard to interpret. In July in these two years the nymphal population was distinctly differentiated as to size. This can be explained by an extended emergence period. The very small number of young nymphs of *Ecdyonurus* spp. during late autumn supports the hypothesis that only a few of the eggs laid in summer undergo full embryonal development before the onset of winter, while the majority of them attains it only in spring after a long quiescent period in winter. The species seemed to have at both stations a single generation in a year. Macan and Maudsley (1968) found in Lake Windermere in England two generations of *E. dispar*, nymphs being present there throughout the year except in June when the second generation begins. In other lakes, however, as found by these authors, *E. dispar* nymphs do not occur in winter, this indicating the existence of only a single generation in them.

2.1.8. *Ecdyonurus subalpinus* Klap.

The life cycle of *E. subalpinus* was studied on the material collected at station 1 in the Wielka Puszcza stream (region I) where it was fairly numerous (fig. 4 A). Emergence in 1959 took place there from the end of June till the end of September. The population of the species was distinctly heterogeneous during the spring and beginning of summer: apart from very large specimens, which in spite of their size, 11 to 13 mm, were still in the stage on half grown nymphs, nymphs of classes 2. to 5. were also caught. The first group on nymphs emerge from the water towards the end of June and during July, the second attaining emergence ability only in August and September, having in comparison with the first group a much smaller maximum size. At the beginning of August nymphs of classes 2. to 4. again appear, most probably originating from eggs laid late in spring. These nymphs grow relatively fast in summer and early autumn, slowly in late autumn and in winter, the population



Ryc. 4. Rozkład klas wielkości larw *Ecdyonurus subalpinus* (A) na stanowisku 1 i w potoku Wielka Puszcza (reg. I) w roku 1959/1960 oraz *E. dispar* (B) na stanowiskach 6 i 7 łącznie w Rabie w roku 1969/1970. Zakreskowane słupki na histogramie B mogą zawierać pewną ilość pomiarów larw innych gatunków *Ecdyonurus* Etn. Strzałka oznacza wylot subimagines; izolowane słupki określają liczbę larw

Fig. 4. Size class distribution of nymphs of *Ecdyonurus subalpinus* (A) at station 1 in the Wielka Puszcza stream (region I) in 1959/1960 and *E. dispar* (B) at stations 6 and 7, jointly in the Raba in 1969/1970. Hatched columns in the histogram B may contain a certain number of measurements of nymphs of other species of *Ecdyonurus* Etn. Arrow denotes emergence of subimagines, isolated columns — the number of nymphs

being successively enriched with nymphs from later ovipositions. The presence of nymphs of class 2. in spring, and their absence at the end and at the beginning of winter, suggests that some of the eggs laid in the previous year undergo in their development a longer quiescence period and nymphs hatch from the eggs as late as spring. The rate of growth of these nymphs is high, they are ready for emergence at smaller size, and they emerge from the water still in the same year. Landa (1968) considers that in biotopes on the territory of Czechoslovakia, similar to the examined one, *E. subalpinus* has two generations in a year. This, however, seems improbable in the Wielka Puszcza stream and in other investigated streams of the Polish part of the Carpathian Mts (Sowa 1975).

Tabela I. Okres występowania w ciągu roku postaci skrzydlatych (——) oraz nimf (- - -), począwszy od nimf młodocianych, 75 gatunków jętek w wodach płynących w polskiej części Karpat i na terenach przylegających. Dla gatunków o znacznych zasięgach wzdłużnych dane odnoszą się do miejsc, w których osiągają one większą liczebność. W kolumnie określającej typ cyklu życiowego podano także jego rozpoznane odmiany. Dane dla gatunków z rodzaju Cloeon odnoszą się do stawów w okolicy Krakowa.

Table I. Period of occurrence in the course of a year of winged forms (——) and nymphs (- - -) beginning from young nymphs, of 75 species of mayflies in running waters in the Polish part of the Carpathian Mts and on the neighbouring territories. For species of considerable longitudinal ranges data refer to places in which they attain a greater abundance. In the column determining the type of the life cycle, its identified varieties were also given. Data on species of the genus Cloeon refer to ponds on the vicinity of Cracow

Gatunek / Species — Miesiąc / Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Typ cyklu / Type of cycle
Potamanthus luteus	- - -	- - -	- - -	- - -	- - -	———	———	———	———	———	- - -	- - -	B3
Ephemera danica	- - -	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	- - -	A1
Ephemera lineata	- - -	- - -	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	A1
Ephemera vulgata	- - -	- - -	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	A1
Ephoron virgo				- - -	- - -	- - -	- - -	———	- - -				B1
Rhithrogena germanica	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	- - -	- - -	- - -	B2
Rhithrogena hercynia	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	- - -	- - -	B2
Rhithrogena hybrida	- - -	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	- - -	B2
Rhithrogena loyolaea	- - -	- - -	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	A2
Rhithrogena gorganica	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	- - -	- - -	B2
Rhithrogena semicolorata	- - -	- - -	- - -	- - -	———	- - -	- - -	- - -	- - -	- - -	- - -	- - -	B2
Rhithrogena iridina iridina	- - -	- - -	- - -	- - -	———	———	———	———	———	- - -	- - -	- - -	B4
Rhithrogena ferruginea	- - -	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	- - -	B2
Rhithrogena diaphana				- - -	- - -	———	———	———	- - -				B1
Epeorus sylvicola	- - -	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	- - -	B3
Ecdyonurus subalpinus	- - -	- - -	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	B4
Ecdyonurus carpathicus	- - -	- - -	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	B3
Ecdyonurus macani	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	- - -	- - -	B2
Ecdyonurus torrentis	- - -	- - -	- - -	- - -	———	———	- - -	- - -	- - -	- - -	- - -	- - -	B2
Ecdyonurus venosus	- - -	- - -	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	B3
Ecdyonurus starmachi	- - -	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	- - -	B3
Ecdyonurus submontanus					- - -	- - -	———	———	———				B1
Ecdyonurus insignis			- - -	- - -	- - -	———	———	- - -					B1
Ecdyonurus dispar	- - -	- - -	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	B4
Ecdyonurus aurantiacus			- - -	- - -	———	———	———	———	- - -				B1
Ecdyonurus affinis	- - -	- - -	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	B2
Ecdyonurus lateralis	- - -	- - -	- - -	———	———	———	———	- - -	- - -	- - -	- - -	- - -	B3
Ecdyonurus quadrilineatus	- - -	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	- - -	B2
Heptagenia coerulans	- - -	- - -	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	B2
Heptagenia flava	- - -	- - -	- - -	- - -	———	———	———	———	———	- - -	- - -	- - -	B3
Heptagenia longicauda	- - -	- - -	- - -	- - -	———	———	———	———	———	- - -	- - -	- - -	B3
Heptagenia sulphurea	- - -	- - -	- - -	- - -	———	———	———	———	———	- - -	- - -	- - -	B3
Habroleptoides modesta	- - -	- - -	- - -	———	———	———	- - -	- - -	- - -	- - -	- - -	- - -	B2

Tab. I c.d.
Tab. I contd

Gatunek / Species — Miesiąc / Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Typ cyklu / Type of cycle
Habrophlebia lauta	-	-	-	-	-	—	—	—	—	—	-	-	B3
Paraleptophlebia submarginata	-	-	-	—	—	-	-	—	-	-	-	-	B2
Paraleptophlebia cincta	-	-	-	-	-	—	—	-	-	-	-	-	B2
Leptophlebia vespertina	-	-	-	-	—	—	-	-	-	-	-	-	B2
Choroterpes picteti					-	-	—	—	—				B1
Ameletus inopinatus	-	-	-	-	—	—	—	—	-	-	-	-	B5
Siphlonurus lacustris			-	-	-	—	—	—	-				B1
Baetis alpinus	-	-	-	—	—	—	—	—	—	-	-	-	C2 (B2)
Baetis melanonyx				-	-	—	—	—	—	-			B1
Baetis lutheri	-	-	-	-	—	—	—	—	—	-	-	-	C2 (B2)
Baetis vardarensis	-	-	-	—	—	—	—	—	—	-	-	-	C2
Baetis sinaicus				-	-	—	—	—	-				B1
Baetis rhodani	-	-	—	—	—	—	—	—	—	—	-	-	C2 (B2)
Baetis beskidensis				-	—	—	—	—	-				C1
Baetis fuscatus				-	—	—	—	—	—	—			C1
Baetis scambus				-	-	—	—	—	—				C1 (B1)
Baetis buceratus	-	-	-	-	—	—	—	—	—	-	-	-	C2 ?
Baetis niger	-	-	-	-	—	—	—	—	—	-	-	-	C2 (B2)
Baetis gracilis				-	-	—	—	—	-				C1
Baetis muticus	-	-	-	—	—	—	—	—	—	-	-	-	C2
Pseudocloeon inexpectatum	?	?	?	?	-	-	—	—	—	?	?	?	C1-?
Centroptilum luteolum	-	-	-	-	—	—	—	—	—	—	-	-	C2
Centroptilum pulchrum				-	-	—	—	—	—	—			C1
Centroptilum pennulatum				-	-	—	—	—	—	—			C1
Procloeon bifidum			-	-	—	—	—	—	—	—			C1
Procloeon ornatum			-	-	—	—	—	—	—	—			C1
Cloeon simile	-	-	-	-	-	—	—	—	—	—	-	-	C2
Cloeon cognatum	-	-	-	-	—	—	—	—	—	—	-	-	C3
Cloeon dipterum	-	-	-	-	—	—	—	—	—	—	-	-	C3
Cloeon inscriptum	-	-	-	-	—	—	—	—	—	—	-	-	C3
Oligoneuriella mikulskii				-	-	-	—	—	-				B1
Oligoneuriella pallida				-	-	—	—	-					B1
Oligoneuriella rhenana				-	-	—	—	—	-				B1
Ephemerella ignita				-	-	—	—	—	—	—			C1 (B1)
Ephemerella mesoleuca				-	-	—	—	-					B1
Ephemerella krieghoffi	-	-	-	-	—	—	-	-	-	—	-	-	B2
Ephemerella notata	-	-	-	-	—	—	-	-	-	-	-	-	B2
Ephemerella major	-	-	-	-	-	—	—	—	-	-	-	-	B3
Caenis rivulorum	-	-	-	-	-	—	—	-	-	-	-	-	B2
Caenis beskidensis				-	-	-	—	—	—				B1
Caenis pseudorivulorum				-	-	-	—	—	—	—			C1
Caenis macrura	-	-	-	-	-	—	—	—	-	-	-	-	C2 ?

2.1.9. Other *Heptageniidae*

All the other species of the family *Heptageniidae* produce in the Polish part of the Carpathian Mts a single generation in a year. As to their life cycle they can be divided into three groups. The most numerous one consists of species whose nymphs of various size classes, are found in suitable biotopes throughout the year. To this group belong: *Ecdyonurus lateralis* (Curt.), E. *venosus* (Fabr.), *E. starmachi* Sowa, *E. carpathicus* Sowa, *Epeorus sylvicola* (E. Pict.), *Heptagenia sulphurea* (Mull.), *H. flava* (Rost.), and *H. longicauda* (Steph.). The emergence of these species is extended in time and lasts from spring till autumn (Table I), the growth of nymphs being very slight or arrested during winter. It would appear that the extended emergence period is the result of an asynchronic growth of nymphs hatched from eggs with a differentiated rate of embryonal development. The phenomenon of wintering of some of the eggs laid late in summer or in autumn is probably fairly common in this group of species.

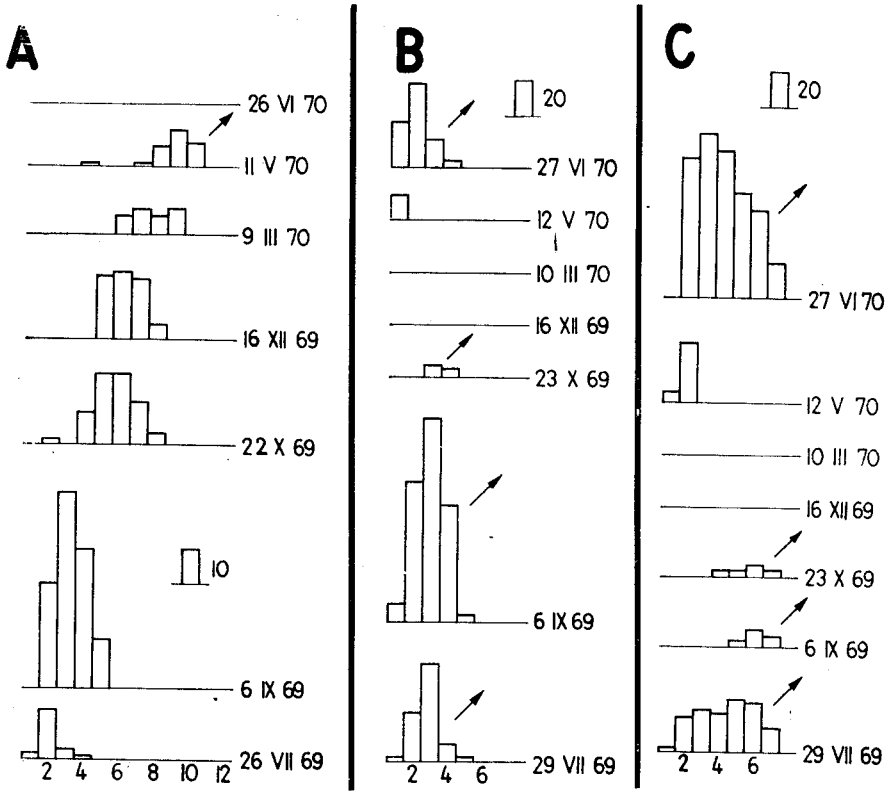
The second group is formed by: *Ecdyonurus macani* Thom. and Sowa, *E. torrentis* Kimm., *E. quadrilineatus* (Landa), *Heptagenia coerulans* (Rost.), and *H. fuscogrisea* (Retz.). These species too, overwinter in nymphal stage, their emergence, however, being more concentrated in time, restricted to spring and summer or early autumn, and at a certain period of summer or early autumn no determinable nymphal stages of these species are present in samples from the appropriate biotopes. The eggs, judging by the relatively short period of time separating the beginning of appearance of imagines from the appearance of nymphs of the next generation, undergo their embryonal development without a quiescent period or, as seems to be the case with *H. fuscogrisea*, have a superficial eastivation of oligopause type. In spite of a longer emergence period, *Ecdyonurus affinis* Etn. should also be included in this group.

The third group consists of: *Ecdyonurus submontanus* Landa, *E. aurantiacus* (Burm.), *E. insignis* (Etn.), and, taking into consideration investigations by Landa (1968, 1969), also *Arthroplea congener* Bngtss. Nymphs of these species are not found late in autumn nor in winter, which confirms Landa's (op. cit.) data on their overwintering as eggs. In spring the most intensive growth is demonstrated by *A. congener*, a less intensive one by nymphs of *E. aurantiacus* and *E. insignis*, while young nymphs of *E. submontanus* appear in the streams of the Polish Carpathian Mts as lateasin summer. It is possible that *Ecdyonurus fascioculatus* Sowa belongs to this group.

2.2. Family *Leptophlebiidae*

2.2.1. *Habroleptoides modesta* Hag.

The growth of nymphs is presented according to the material from station 6 in the Raba (fig. 5 A). *H. modesta* emerges there from the end of April till the beginning of June — similarly as at the majority of their stations of occurrence in



Ryc. 5. Rozkład klas wielkości larw *Habroleptoides modesta* (A), *Caenis pseudorivulorum* (B) i *Ephemerella ignita* (C) w Rabie w roku 1969/1970. A — stanowisko 6; B i C — stanowisko 9 i 10 łącznie. Strzałka oznacza wylot subimagines, izolowane słupki określają liczbę larw

Fig. 5. Size class distribution of nymphs of *Habroleptoides modesta* (A), *Caenis pseudorivulorum* (B) and *Ephemerella ignita* (C) in the Raba in 1969/1970. A — station 6; B and C — station 9 and 10 jointly. Arrow denotes emergence of subimagines, isolated columns — the number of nymphs

the Polish part of the Carpathian Mts. At the end on July 1969 already nymphs of class 2. were caught. The population reaches its greatest numbers at the end of summer when some of the nymphs are 4 to 5 mm in size. The population also grows fairly uniformly in autumn and in winter, reaching maximum size early in spring. The species has a single generation in a year and the rate of growth of the nymphs is rather weakly regulated by water temperature. A similar life cycle is given for *H. modesta* by Landa (1968, 1969) in the territory of Czechoslovakia; with respect to the character of nymph growth, he classified it as a typical „winter species".

2.2.2. Other *Leptophlebiidae*

All species of this family have in the Polish part of the Carpathian Mts a single generation in a year. A similar life cycle to that of *H. modesta* is found in *Paraleptophlebia submarginata* (Steph.) and *Leptophlebia vespertina* (L.). The main growth

of nymphs of these species takes place in autumn and for a long time during the summer they are not present in the samples. This indicates either a prolonged embryonal development or results from the fact that neonate or young nymphs may stay in deeper parts of the bottom than those examined. The possibility that these species undergo a quiescent period during the summer (aestivation of oligopause character) would be confirmed also by the data of other authors (Landa 1968, 1969, Macan 1970). Young nymphs of *Paraleptophlebia cincta* (Brauer) appear already at the beginning of September and are also present during the winter. Nymphs of *Habrophlebia lauta* (McLachl.) are present in the samples practically all the year round, their growth being arrested in winter. At lower situated stations emergence begins at the end of spring but in higher situated ones only in summer. It is not excluded that some of the eggs of this species overwinter there. *Choroterpes picteti* Etn. seems to undergo an egg diapause of several months in winter. Nymphs are absent in the samples from late autumn till the beginning of May. The main growth takes place in summer and is fairly asynchronous. Emergence starts at the end of July and lasts till the beginning of October. According to Landa (1968), in Czechoslovakia a similar development is undergone by *Habrophlebia fusca* (Curt.), whose nymphs in the Polish part of the Carpathian Mts, are encountered from early May till September.

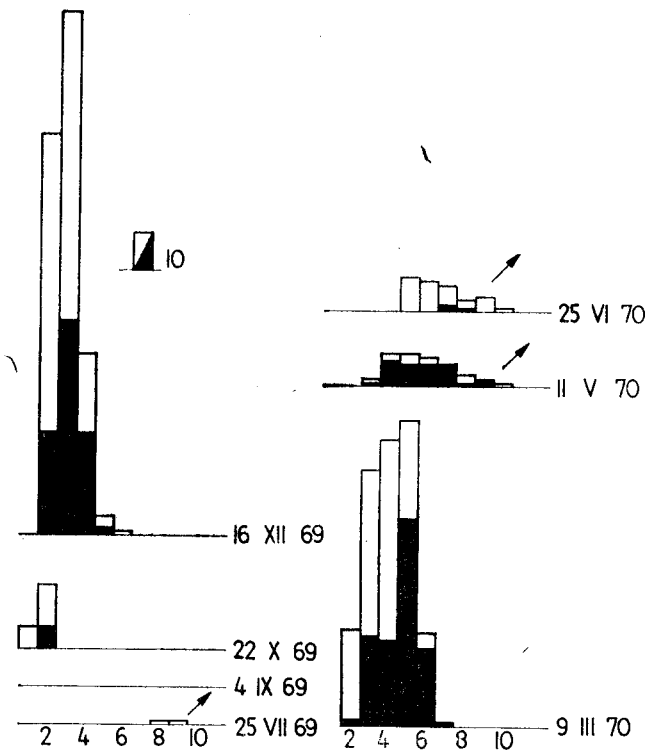
2.3. Family *Siphlonuridae*

2.3.1. *Ameletus inopinatus* Etn.

The life cycle of *A. inopinatus* was studied on the material from stations 2 and 3 in the Olszowy stream (fig. 6). Emergence takes place there from the middle of April till the beginning of August. At station 3 it is concluded before the middle of July. The appearance of a great number of nymphs of classes 1. and 2. at the end of autumn 1969, and their complete absence in samples from September and July of that year as well as from June of the following year, indicates a considerable extension of embryogenesis, to 4 or 5 months or, which is however less probable, a periodical quiescence of young nymphs in deeper parts of the bottom than those investigated. The species produces here — similarly as in the whole investigated territory — a single generation in a year. According to Ulfstrand (1968), the life cycle of *A. inopinatus* in the rivers of Lapland has a similar process. Emergence is intensified there in July; in November nymphs are still absent in the samples and their main growth takes place at the end of winter and in spring. Gledhill (1959) supposes, on the example of one stream in the Lake Dictrict in England, that from some of the eggs laid in autumn the nymphs hatch as late as in spring of the next year, causing a similar „split" in the population as was observed (2.1.8) for *E. subalpinus*. Such a type of development was not confirmed for *A. inopinatus* in the Olszowy stream.

2.3.2. Species of *Siphlonurus* Etn.

Siphlonurus lacustris Etn. was found in the investigation territory in nymphal stage from early spring till late summer. During the spring the growth of nymphs is fast but asynchronous. Nymphs ready to emerge were recorded in the Wołosatka stream (region V, station 5) already at the end of May, and apart from them young and half grown nymphs were also found there. In the Polish part of them Carpathian Mts the species has one generation a year. In a mountain stream in Wales Hynes (1961) recorded the presence of young nymphs of this species also in winter. Some of the eggs must have passed there a quiescent period of some months, since the enrichment of the population by young nymphs went on till April inclusive. According to Macan (1970), *S. lacustris* can overwinter either in the form of young nymphs or as eggs. Bretschko (1966) and Landa (1968, 1969) admit the possibility of existence of two generations in a year for this species though it was not observed in the Polish part of the Carpathian Mts. In consequence of scarce material, the life



Ryc. 6. Rozkład klas wielkości larw *Ameletus inopinatus* na stanowisku 2 (słupki białe) i 3 (słupki czarne) w potoku Olszowym (reg. III) w roku 1969/1970. Strzałka oznacza wylot subimagines. izolowany słupek określa liczbę larw

Fig. 6. Size class distribution of nymphs of *Ameletus inopinatus* at station 2 (white columns) and 3 (black columns) in the Olszowy stream (region III) in 1969/1970. Arrow denotes emergence of subimagines, isolated column — the number of nymphs

cycles of *S. armatus* Etn. and *S. aestivalis* Etn. were not studied. Their nymphs were also caught in winter. According to Landa (1968, 1969), these two species have in Czechoslovakia a single generation in a year.

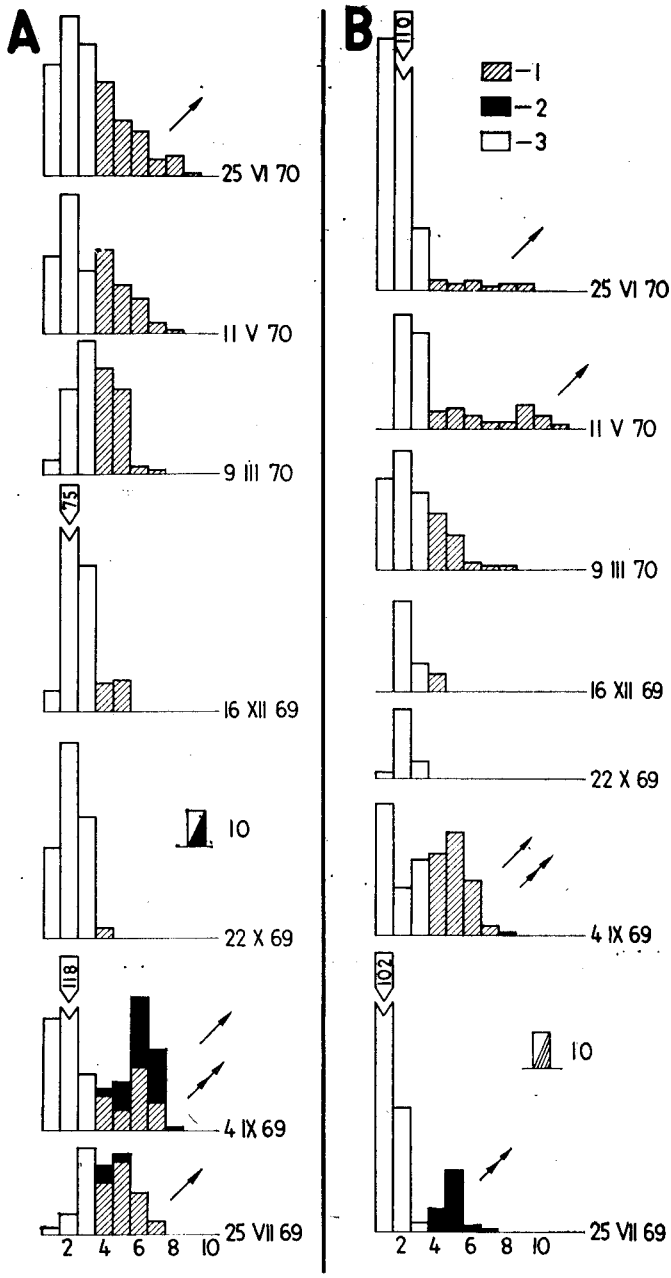
2.4. Family *Baetidae*

2.4.1. *Baetis alpinus* (Pict.) and *B. melanonyx* (Pict.)

The development of these two morphologically closely allied species is presented together according to the material from stations 2 and 3 in the Olszowy stream (fig. 7). This was a necessity because a correct determination of young nymphs, to class 3. inclusive, was impossible. From other nymphs of the species of *Baetis* Leach the two species can be distinguished fairly easily, even in class 1. by the colour and characteristic glossy surface of the body. *B. alpinus* emerges at station 3 from the end of April till the beginning of October, whereas at station 2 the beginning of emergence is delayed by about 2 to 3 weeks. *B. melanonyx* emerges at a lower situated station from the middle of July till the beginning of September and at a higher situated one from the end of August till the middle of October. In the emergence of *B. alpinus* at station 3 a distinct pause takes place in the middle of summer, no nymphs ready to emerge being present in the stream. It may be supposed that *B. alpinus* has here two generations in a year. At a higher situated station, on the other hand, emergence goes on without a summer pause the possible second generation being hard to detect; it may be here only partial. *B. melanonyx* has at these two stations a single generation in a year. Emergence of this species takes place at station 3 during the break between the emergence of the two generations of *B. alpinus*, whereas at station 2 it proceeds concomitantly with the emergence of this species, though in comparison with it it starts later. The appearance of older nymphs of *B. melanonyx* at station 3 as late as in summer and at station 2 towards the autumn permits the supposition that this species overwinters as eggs. The life cycle of *B. melanonyx* has not been examined as yet. Müller-Liebenau (1969) supposed that in Central Europe it may have a single generation in a year. According to Landa (1968, 1969), the life cycle of *B. alpinus* is variable in dependence on the altitude; at lower altitudes the species has two generations, in higher mountain streams, on the other hand, only a single on in a year.

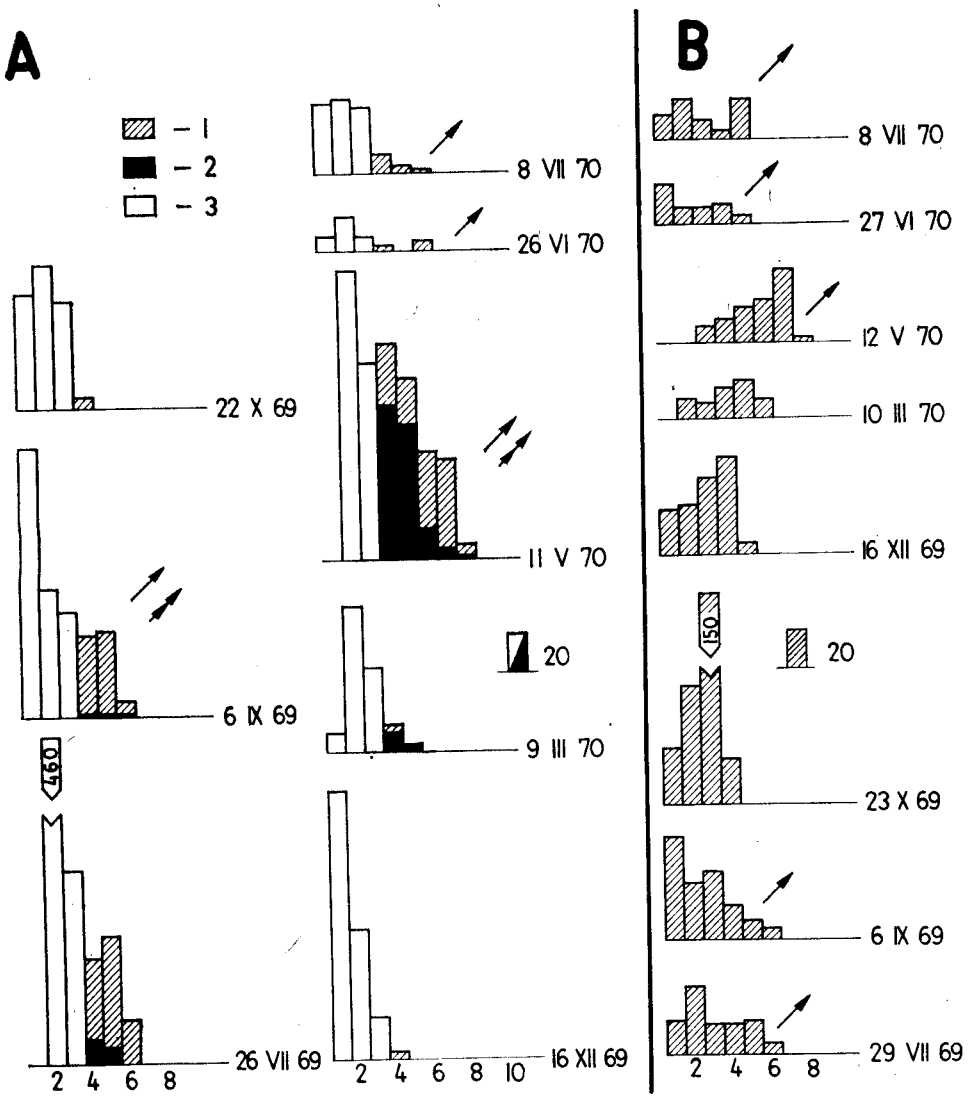
2.4.2. *Baetis lutheri* Müll.-Lieb. and *B. vardarensis* Ikon.

The growth of these morphologically closely allied species was studied at stations 6 and 7 and *B. vardarensis* additionally at stations 9 and 10 in the Raba (fig. 8). Young nymphs of the two species are not distinguishable from each other up to class 3. inclusive. From nymphs of other *Baetis* species are distinguished relatively



Ryc. 7. Rozkład klas wielkości larw *Baetis alpinus* (1) i *B. melanonyx* (2) na stanowisku 2 (A) i 3 (B) w potoku Olszowym (reg. III) w roku 1969/1970. Larwy młodociane (3) należą do jednego lub obu gatunków. Podwójna strzałka oznacza wylot *B. melanonyx*, izolowane słupki liczbę okazów obu gatunków

Fig. 7. Size class distribution of nymphs of *Baetis alpinus* (1) and *B. melanonyx* (2) at station 2 (A) and 3 (B) in the Olszowy stream (region III) in 1969/1970. Young nymphs (3) belong to one or to the two species. Double arrow denotes emergence of *B. melanonyx*, isolated columns — the number of specimens of the two species



Ryc. 8. Rozkład klas wielkości larw *Baetis vardarensis* (1) i *B. lutheri* (2) na stanowiskach 6 i 7 łącznie (A) oraz na stanowisku 10 (B) w Rabie w roku 1969/1970. Larwy młodociane (3) w przedziale A należą do jednego lub dwu gatunków. Podwójna strzałka oznacza wylot *B. lutheri*, izolowane słupki liczbę okazów obu gatunków

Fig. 8. Size class distribution of nymphs of *Baetis vardarensis* (1) and *B. lutheri* (2) at stations 6 and 7 jointly (A) and at station 10 (B) in the Raba in 1969/1970. Young nymphs (3) in part A belong to one or the two species. Double arrow denotes emergence of *B. lutheri*, isolated columns — the number of specimens of the two species

easily even in class 1. on account of the uniform colour of the abdominal tergites and the dull appearance of the dorsal part of the body surface. At stations 9 and 10 all the young nymphs were classified as *B. vardarensis*, since *B. lutheri* occurs there sporadically. *B. vardarensis* emerges at these stations from the end of April till the

end of September. Nymphs of class 1. occur in samples from June till December which, considering the length of the emergence period as well, permits the supposition that the species has in this section of the river two generations in a year. The first generation, with markedly larger maximum sizes (7—8 mm), emerges from April till the middle of July. The growth of nymphs of the second generation probably begins already 3 to 4 weeks after oviposition. Their growth-rate is high and the first ones are ready to emerge towards the end of July. It would seem from the distribution of the presence of nymphs, that the hatching of eggs of the winter generation is in autumn prolonged, though for the most part it takes place before winter. At stations 6 and 7 the life cycle of *B. vardarensis* is similar but the start of emergence of the first generation is there retarded by about 2 weeks and that of the second generation extends till the end of October, the two generations thus partly overlapping.

Also at stations 6 and 7 *B. lutheri* has two generations in a year. Nymphs of the first generation of larger sizes emerge from the water from the beginning of May. Their emergence seems more concentrated in time in relation to *B. vardarensis*; at the end of 1970 no mature nymphs were found at either station. Data from 1969 permit the supposition that the second generation, of smaller maximum size, emerges only in August and September. In the summer period there is thus a distinct gap between the emergence of the two generations. *B. lutheri* is a fairly cold stenothermic species, its growth at stations 9 and 10 perhaps being limited by the high summer temperatures recorded there, so that the species can produce only a single generation in a year — i. e. a winter generation. The life cycle of *B. vardarensis* has not been investigated so far. Landa (1968, 1969) supposes that in Czechoslovakia, *B. lutheri* has as a rule a single generation in a year, though he admits the possibility, in favourable environmental conditions, of a second, summer generation.

2.4.3. *Baetis fuscatus* (L.)

The life cycle of this species is presented on the basis of the materials from stations 9 and 10 in the River Raba (fig. 9 A and B). *B. fuscatus* emerges there from the end of May till the middle of October. During late autumn and in winter no nymphs occur in the samples. This is confirmed by the reports of Macan (1970), Landa (1968, 1969), and Langford (1971) on the several months stay of this species in the water in the form of eggs, from which the nymphs hatch as late as spring. In the lower section of the Raba the growth of the nymphs is in this period very rapid. Taking into consideration the permanent presence of young nymphs at successive dates in summer 1969 and the general distribution of the nymph sizes, it may be supposed that at least two generations exist in this section of the Raba. Most probably the second generation already begins its emergence in the first half of August and is markedly more abundant than the first generation, the maximum sizes of the nymphs being similar.

2.4.4. *Baetis muticus* (L.)

The histogram of growth is based on the material from stations 6 and 7 in the Raba (fig. 9 C). Imagines are encountered there from the middle of May till the end of September with the exception of high summer. The existence of two generations of *B. muticus* in this section of the Raba can be assumed, on the one hand, from there being a distinct pause in the emergence of subimagines, and on the other from the great numbers of nymphs in size classes 2. and 3. found in July. The summer generation, which begins its emergence in August, is less abundant, the nymphs being of smaller maximum size. Two generations were also distinguished in this species by Macan (1957) in a stony stream in England. Development of a some of the eggs of the winter generation is in those climatic conditions prolonged till the winter months and nymphs of the summer generation are characterized by rapid and regular growth.

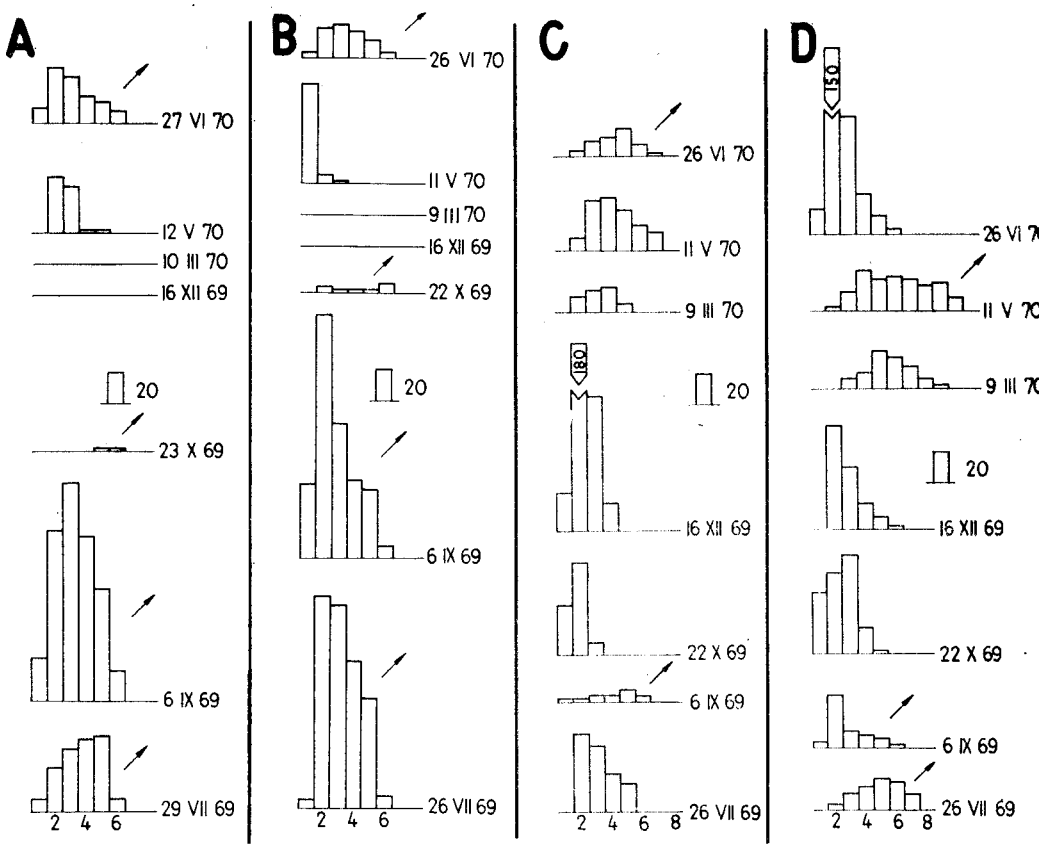
2.4.5. *Baetis rhodani* (Pict.)

The life cycle of this species was studied at the same stations as that of *B. muticus* (fig. 9 D). The range of emergence of *B. rhodani* is here very large — from the end of March till the end of September. The species has two generations in a year. The nymphs of the first generation grow in autumn, the growth rate being only slightly reduced in winter in consequence of which the maximum size of nymphs of this generation is much greater (8—10 mm) than that of nymphs of the second generation (6—7 mm). The emergence of the first generation comes to an end in June. At that time young nymphs of the second generation already appear, their emergence starting in the second half of July. Nymphs of the second generation do not seem to find in summer suitable growth conditions at these stations in the Raba. The number of mature nymphs is not great. In the lower course of the Raba no nymphs of this species were found from June to September, though they occur there from late autumn till the middle of spring. It may be that in this section of the Raba *B. rhodani* has only one, winter generation in a year.

2.4.6. Other species of *Baetis* Leach.

Baetis sinaicus (Bog.) has in the investigated territory a single generation in a year, no nymphs being present in the rivers in late autumn or winter. They appear only as late as in May. Their growth is rapid and they begin their emergence in June, this lasting until August. At higher situated stations, e. g. in the Białka Tatrzańska (region IV) emergence may extend even till September.

Baetis beskidensis Sowa., *B. gracilis* Bog. and Tab. and *B. scambus* Etn. have in the Polish part of the Carpathian Mts two generations in a year. Their nymphs are not found in the samples from late autumn till early spring, which suggests



Ryc. 9. Rozkład klas wielkości larw *Baetis fuscatus* (A i B), *B. muticus* (C) i *B. rhodani* (D) na stanowiskach 9 i 10 łącznie (A) oraz na stanowiskach 6 i 7 łącznie (B—D) w Rabie w roku 1969/1970. Strzałka oznacza wylot subimagines, izolowane słupki określają liczbę larw

Fig. 9. Size class distribution of nymphs of *Baetis fuscatus* (A and B), *B. muticus* (C), and *B. rhodani* (D) at stations 9 and 10 jointly (A) and at stations 6 and 7 jointly (B—D) in the Raba in 1969/1970. Arrow denotes emergence of subimagines, isolated columns — the number of nymphs

the existence of a long quiescent period in the embryonal development of their first, winter generation. Young nymphs appear at the stations in the first half of spring, and after a rapid growth they are ready to emerge already in May (*B. beskidensis*) or at the beginning or in the middle of June (*B. gracilis* and *B. scambus*). Nymphs of the second generation also grow rapidly, their emergence taking place during the summer and coming to an end in early autumn. To this group of species also *B. vernus* (Curt.) most probably belongs, or at least its populations from the lower situated stations. In the Suchy stream and in the Massif of the Babia Góra (region II, stations 9, 10 and 28) this species seems to have only a single generation, wintering, at least partly, in the form of young or medium sized nymphs which start their emergence at the end of spring. Also *B. niger* (L.) shows flexibility in its life cycle

in dependence on the altitudinal distribution. In the lower course of the Raba (station 9) it behaves in a similar way as *B. rhodani* (2. 4. 5), whereas in the meadow stream at Zawoja-Widły (station 24 region III) it produces, after a fast and synchronous growth of nymphs, a second generation which emerges already in August. On account of the scarce material and taxonomical difficulties, it was not possible to determine the life cycle of *B. digitatus* Bgtss., *B. buceratus* (Etn.), *B. tricolor* Tshern., or *B. calceratus* Kefferm. Young nymphs of *B. buceratus* were also encountered in winter and of the two last species also in spring.

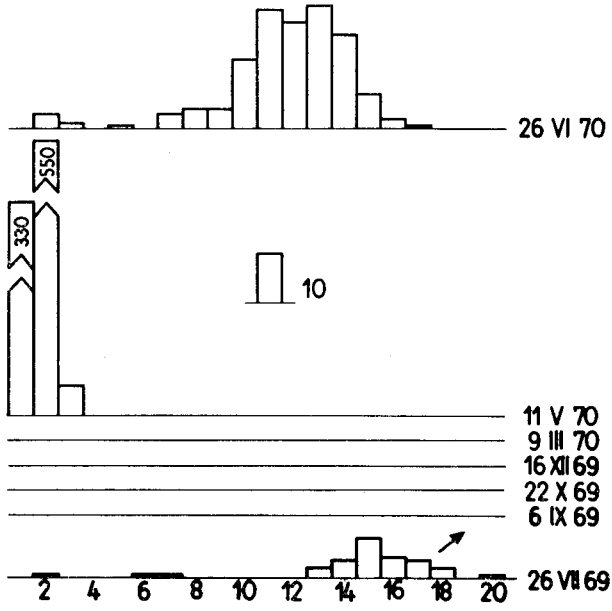
2.4.7. Other representatives of *Baetidae*

Pseudocloeon inexpectatum Tshern. probably overwinters in the investigated streams as eggs. Young nymphs appear as late as in spring; considering their growth and a break in the emergence of subimagines during the summer, it may be supposed that there are two generations in a year. *Procloeon bifidum* (Bgtss.) and *P. ornatum* Tshern. have two generations in a year. Nymphs in various size classes are encountered from spring till the middle of autumn, when the emergence of the second generation comes to an end. In late autumn and winter no nymphs of these species are found, hence they most probably overwinter as eggs. In these two species the second generation is numerically stronger. *Centroptilum pennulatum* Etn. and *C. pulchrum* Etn. behave in the investigated territory in a similar way, having here two generations in a year. Nymphs of *C. nemorale* Etn. (?) — for which however the number of generations in a year was not determined — were not found in winter either. *Centroptilum luteolum* (Müll.) has two generations in a year in the Polish part of the Carpathian Mts and its nymphs are present in suitable biotopes practically the whole year round. In winter these are mostly young nymphs. The growth of the nymphs of this species is similar to that of *Baetis muticus* nymphs (2.4.4). The fact of catching nymphs of *Baetopus tenellus* (Alb.) ready to emerge in the lower course of the San both in spring and autumn suggest the existence of two generations in this species in a year. *Cloeon cognatum* Steph., *C. dipterum* (L.) and *C. inscriptum* Bgtss. are ovoviviparous. The larvulae hatch from the eggs immediately after oviposition in the water. The growth of nymphs is directly dependent on water temperature, the development being almost arrested in winter and very rapid in summer. Observation of their life cycle in rivers is very difficult because at any time of the season the local population of nymphs can be enriched in number by adult females migrating from the neighbouring stagnant waters. In the ponds in the vicinity of Cracow all the three species are polycyclic and can with favourable thermal conditions in summer have even three generations in a year, the first emerging already at the beginning of May and the last one till the end of October. For similar reasons it is also difficult to determine in the rivers the life cycle of the oviparous *Cloeon simile* Etn. In the ponds in the vicinity of Cracow it has two generations in a year, the first overwintering as young nymphs.

2.5. Family *Oligoneuriidae*

2.5.1. Species of *Oligoneuriella* Ulm.

The growth of nymphs of *O. rhenana* (Imh.) was examined at station 6 and 7 in the Raba (fig. 10). Owing to the absence of any other species of *Oligoneuriella* even very young nymphs of *O. rhenana* could be determined. The species emerges at these stations from the middle of July to the middle of August. In 1969 a mass emergence took place on July 26th but a number of mature nymphs and ones ready to emerge still remained in the river. Young nymphs of the next generation appeared only in May 1970. These developed rapidly and by the end of June some of them attained nearly maximum size. Differentiation of nymphs in this month with respect to size



Ryc. 10. Rozkład klas wielkości larw *Oligoneuriella rhenana* na stanowiskach 6 i 7 łącznie w Rabie w roku 1969/1970. Strzałka oznacza wylot subimagines, izolowany słupek określa liczbę larw

Fig. 10. Size class distribution of nymphs of *Oligoneuriella rhenana* at stations 6 and 7 jointly, in the Raba in 1969/1970. Arrow denotes emergence of subimagines, isolated column — the number of nymphs

indicates that the hatching period is extended. The species has here, similarly as in the whole investigated territory, a single generation in a year and an egg diapause of several months in the autumn-winter period. In the lower course of the San emergence starts already at the end of June. Degrange (1960) observed, in laboratory conditions, the beginning of hatching of eggs of this species after a 5 month diapause. Hatching lasted in these conditions 60 days. *O. mikulskii* Sowa and *O. pallida* Hag. also have, it would seem, egg diapause lasting some months; young

nymphs of these two species appear in the lower course of the San (Stations 24 and 25) as late as spring. The emergence of *O. pallida* takes place there earlier, beginning at the end of June and thus concomitantly with *O. rhenana*. The two last species quickly complete their emergence, in high summer only *O. mikulskii* nymphs remaining in the water.

2.6. Family *Ephemerellidae*

2.6.1. *Ephemerella ignita* (Poda)

The development of this species is presented according to the materials from stations 9 and 10 in the River Raba (fig. 5 C). *E. ignita* emerges there from the middle of June till the end of October and single nymphs ready to emerge are still encountered in some years at the beginning of November. Absence in the river of young nymphs in autumn 1969 and of any nymphs in winter 1970 corroborates the observations carried out so far (Macan 1970, Plescot 1961 a, Landa 1968, 1969, Bohle 1972) on the diapause lasting several months in the embryonal development of this species. In 1970 young nymphs of size classes 1. and 2. appeared in the river only at the beginning of May. These nymphs developed rapidly and after a month already part of the population had attained emergence ability. A great differentiation in size classes of the nymphs at the end of June indicates a prolonged hatching period of the winter generation. The presence of the summer generation can be deduced from the fairly large numbers of nymphs of classes 2. and 3. in the samples from July 1969. This generation is poorer in numbers and may be only a partial one. In the upper course of the Raba (station 11) young nymphs of *E. ignita* appear as late as June, the beginning of emergence there being delayed in relation to the lower course of the Raba by almost a month. *E. ignita* has here a single generation in a year.

2.6.2. Other species of *Ephemerella* Walsh.

In autumn and early spring no nymphs of *E. mesoleuca* Brauer were found in the lower course of the San; it is possible that this species overwinters as eggs. In spring the nymphs develop rapidly and their emergence starts already in June. This species probably has here a single generation in a year. Young nymphs of *E. krieghoffi* (Ulm.) appear in larger streams and in the Carpathian rivers in autumn and grow at a slow rate also during winter, the majority of them attaining emergence ability in May. In late spring and in summer nymphs do not occur in the biotopes. In the Kamienica Gorczańska, at an altitude of 1000 to 1100 m above sea level (region IV) nymphs are present throughout the spring, attaining emergence ability as late as July. This species, similarly as the two succeeding ones has a single generation in a year. *E. major* (Klap.) occurs in nymphal stage in suitable biotopes in the examined territory practically all the year round, the highest percentage of young nymphs

being recorded in autumn. This species has a long emergence period — from May in larger submontane rivers (middle course of the San) or from the end of June in small streams of the Beskid Mts, till July or the beginning of August respectively. *E. notata* Etn. overwinters as nymphs which appear in autumn and grow, though very slowly, also in winter. The emergence of this species takes place in spring. In summer no nymphs are found.

2.7. Family *Caenidae*

2.7.1. *Caenis pseudorivulorum* Kefferm.

The life cycle of this species was studied on the material from stations 9 and 10 in the River Raba (fig. 5 B). *C. pseudorivulorum* emerges there from the middle of June till the end of October. From late autumn until early spring no nymphs are found in the samples. This species, too, whose life cycle has not yet been studied in detail, can be assigned to the group of typical summer species with a long-lasting embryogenesis in the autumn-winter period. Similarly as *E. ignita*, this species has two generations in a year in the lower course of the Raba; the presence of the second generation can be assumed, judging from the great increase in nymphs of class 2. at the beginnig of September 1969 and from the considerable number of nymphs of class 1. The autumn generation is much more abundant.

2.7.2. Other *Caenidae* species

Nymphs of *Caenis rivulorum* Etn. appear in larger streams of the Beskid Mts in autumn and grow, though very slowly, also in winter; at the end of May some of them are ready to emerge. Emergence lasts in small streams till August. The species has a single generation in a year. Nymphs of *C. macrura* Steph. are present in the Carpathian rivers all the year round and nymphs ready to emerge are caught from the middle of May till the beginning of September. In the territory of Czechoslovakia Landa (1968, 1969) assigns them to the group of polycyclic species. Taking into consideration the presence of young nymphs in summer, this seems possible also in the Polish part of the Carpathian Mts. Because of the very scarce material the life cycles of *C. robusta* Etn. and *C. moesta* Bgtss. were not determined. Nymphs of the former species are found also in winter. In the investigated territory *C. beskidensis* Sowa has a single generation in a year. Young nymphs appear in the samples as late as spring; with a differentiated rate of growth, emergence takes place in high summer. Perhaps this species has in winter, similarly as *C. pseudorivulorum*, a long quiescent period in the embryonal development. *Brachycercus harrisella* Curt., *B. minutus* Tsher., and *B. pallidus* Tsher., in the lower course of the San, probably have a single generation in a year whose emergence takes place in spring and during the summer. In autumn the nymphs of these species are not encountered in the samples. According to Landa (1969), nymphs of *B. harrisella* appear in running waters of the Czechoslovakian territory as late as May.

2.8. Species of other families

Ephoron virgo (Oliv.) is among the species which have a long development period lasting from late summer till the end of winter. The nymphs develop rapidly in spring and emergence usually takes place in the form of mass swarming from the middle of July till September. *Isonychia ignota* Walk. is also not encountered in nymphal stage in winter. Young or half-grown nymphs are found during the spring and during the summer the population of nymphs is also differentiated in size. Nymphs of *Potamanthus luteus* (L.) are found in various stages in the investigated territory all the year round, young nymphs prevailing in number late in autumn and in winter. Emergence begins in May and lasts till July. All these species have a single generation in a year, similarly as *Ametropus fragilis* Alb., which according to Landa's data (1968, 1969) emerges in Czechoslovakian rivers in spring, young nymphs appearing already at the end of August.

Ephemera danica (Müll.), *E. lineata* Etn. and *E. vulgata* L. have in the investigated territory a single generation in the course of two years. These species emerge during the summer, nymphs of all three species, heterogeneous in size, being found all the year round. Only the life cycle of *E. danica* has been the subject of more detailed investigations (Plescot 1961, Illies 1952, Landa 1968, 1969, Jażdżewska 1971, Thibault 1971 b). According to Thibault, this species has in the Lissuraga stream in the Low Pirenees a semivoltine cycle, whereas Jażdżewska, on the example of the River Grabia in Central Poland, is inclined to ascribe to it a univoltine developmental cycle. In the streams of the Jura Krakowsko-Wieluńska, where this species lives in great abundance (Sowa 1959, Głowaciński 1968, Szczęsny 1968), the emergence lasts very regularly every year from the end of May till the middle of June. At that time numerous young nymphs are also found which attain ability to emerge only in the following year and which quite certainly do not originate from eggs laid in the current year. Emergence of *E. danica* is in the Carpathian streams prolonged till the end of July, its no special intensity being observed in June. Nymphs of *E. lineata* and *E. vulgata* grow in a similar way. According to Keffermüller (1960), the former emerge in the Polish Lowlands from the middle of June till the end of July. In the middle course of the San, where this species is fairly numerous, nymphs ready to emerge are found in high summer, besides young nymphs of various sizes.

3. Classification of Carpathian Mayflies as to their life cycles

From the attempts made so far at the division in this respect of the European mayflies Hynes's classification (1961, 1971), apart from the number of generations produced in a year, takes as the starting point above all the growth rate of the nymphs. Landa (1968) distinguishes for Middle-European mayflies 11 ways of carrying out

the life cycle taking as a basis mainly the data from Czechoslovakia. He takes into account the number of generations during a year, the course of egg development, and the appearance period and growth rate of nymphs. The following attempt at classification was carried out on the basis of the same criteria, though it differs in a fair number of cases from the hitherto presented classifications. It refers to the natural conditions and to the characteristic or other biotopes in which the particular species reach a relatively great abundance; for some species, apart from the life cycle carried out by them at the majority of stations of occurrence, the recognized variety of this cycle is also given.

3.1. Type A. Species with a semivoltine cycle

3.1.1. Group A1

The embryonal development proceeds without a quiescent period. Nymphs hatch from eggs 1 to 2 months following oviposition and develop fairly slowly during the summer. In winter their growth is arrested or very slow. They reach emergence ability as late as after about 20 months. At any date in the year the nymphal population has a heterogeneous character.

Ephemera danica, E. lineata, E. vulgata.

3.1.2. Group A2

A full embryonal development occurs, depending on the date of oviposition, after a quiescent period of many months or without one. Nymphs present in the biotopes throughout the year grow fairly slowly during the season, still slower in winter, and attain emergence ability during the following year, a small part of the population probably being able in favourable thermal conditions to carry out a full life cycle during one year.

Rhithrogena loyolaea

3.2. Type B. Species with a univoltine cycle.

3.2.1. Group B1

The embryonal development of eggs laid at the end of spring, in summer, or in autumn, proceeds with a quiescence of several months (or even diapause) and lasts till spring of the following year. Hatched nymphs grow quickly, reaching, in some species, emergence ability already from late spring on.

Ephoron virgo, Rhithrogena diaphana, Ecdyonurus submontanus, E. aurantiacus, E. insignis, Choroterpes picteti, Siphlonurus lacustris, Baetis melanonyx, B. sinaicus, Oligoneuriella mikulskii, O. pallida, O. rhenana, Ephemerella mesoleuca, Caenis beskidensis.

To this group probably also belong *Ecdyonurus fascioculatus* and *Isynochia ignota* and, according to Landa's (1968), data, also *Arthroplea congener, Habrophlebia fusca* and *Brachycercus harrisella.*

3.2.2. Group B2

Embryonal development of eggs laid in spring, summer or at the beginning of the autumn proceeds without a quiescent period. Within 1 to 2 months young nymphs appear their growth being relatively slow during the season. They still continue to grow in winter, though at a still slower rate. At a certain period of the season there are no nymphs or older nymphs in biotopes suitable for the species.

Rhithrogena germanica, R. gorganica, R. hercynia, R. hybrida, R. ferruginea, R. semicolorata, Ecdyonurus affinis, E. macani, E. quadrilineatus, E. torrentis, Heptagenia coerulans, Habroleptoides modesta, Paraleptophlebia cincta, P. submarginata, Leptophlebia vespertina, Ephemerella krieghoffi, E. notata, Caenis rivulorum.

Judging from Landa's (1968) data, to this group also belong *Heptagenia fuscogrisea, Leptophlebia marginata,* and *Ametropus fragilis.* At great altitudes *Baetis alpinus,* and in lower section of some Carpathian rivers *B. rhodani, B. lutheri,* and *B. niger* have a similar developmental character. It is possible that some species from the genus *Leptophlebia* and *Heptagenia* will in the course of further investigations be assigned to the further discussed group B5.

3.2.3 Group B3

The embryonal development is here similar to that of Group B2, the growth rate of nymphs, however, being faster in the season and practically arrested in winter when the species are present in the water in the stage of young nymphs or nymphs of various sizes.

Potamanthus luteus, Epeorus sylvicola, Ecdyonurus carpathicus, E. lateralis, E. starmachi, E. venosus, Heptagenia flava, H. longicauda, H. sulphurea, Habrophlebia lauta, Ephemerella major.

3.2.4. Group B4

The embryonal development and growth of the nymphs proceeds heterogeneically. Eggs from the spring or high summer oviposition undergo development in the course of 1 to 2 months. Young nymphs appear in autumn, also grow, though slowly, in winter, and reach emergence ability in spring or at the beginning of summer. Eggs

laid later, especially in autumn, have a longer development period with a probable quiescent period during the winter. Nymphs hatch in spring, grow fairly rapidly, and emerge from the water in summer or autumn. Nymphs are present in the biotopes practically the whole year round.

Rhithrogena iridina iridina, Ecdyonurus dispar, E. subalpinus.

3.2.5. Group B5

Eggs laid in spring or summer have a developmental cycle several months long with a possible quiescent period in summer. Nymphs hatch in autumn and also grow, though considerably slower, in the following year. At a certain period of the year no nymphs are present in the biotopes suitable for the species.

Ameletus inopinatus

3.3. Type C. Polyvoltine species

3.3.1. Group C1

The embryonal development of eggs laid in winter proceeds with a quiescent period or diapause lasting many months. Nymphs hatch in spring, grow rapidly, and at the end of spring or beginning of summer the first generation emerges from water. From the eggs laid by this generation nymphs hatch already after 2 to 3 weeks, growing rapidly, and emergence of the second generation begins at the end of summer or at the beginning of autumn. In some species of this group the first generation is more numerous, in others the second. Emergence of the two generations can in some species partly overlap while in others there is a lapse of time between the emergence of the first and second generation.

Baetis beskidensis, B. fuscatus, B. gracilis, B. scambus, Centroptilum pennulatum, C. pulchrum, Procloeon bifidum, P. ornatum, Ephemerella ignita, Caenis pseudorivulorum.

To this group also probably belong other species of the genus *Centroptilum* (except *C. luteolum*), the *Pseudocloeon inexpectatum*, and *Baetis vernus* — these last at lower situated stations.

3.3.2. Group C2

Eggs of the first generation laid by the end of summer or in autumn develop without a quiescent period, or at most a few of them may have a prolonged development. Young nymphs appear before the winter and also grow slowly during this period. This generation emerges in spring. Embryogenesis of the second generation

lasts for a short time, the hatched nymphs grow rapidly and attain emergence ability during the summer or early autumn, being of slightly smaller size. Nymphs of the species of this group are encountered in suitable biotopes practically throughout the year.

Baetis alpinus, B. lutheri, B. muticus, B. niger, B. rhodani, B. vardarensis, Centroptilum luteolum.

It would seem that *B. buceratus, Cloeon simile,* and *Caenis macrura* also belong to this group of species.

3.3.3. Group C3

Ovoviviparous species. In favourable thermal conditions these can have one winter generation, the growth of nymphs being arrested in winter, and two summer generations, emerging from spring till autumn. The growth rate of the nymphs increases during the season concomitantly with the increase in water temperature.

Cloeon dipterum, C. cognatum, C. inscriptum.

4. Discussion of results

From the results of the described investigation on the life cycles of species of mayflies, which are also partly confirmed by the data from literatutre concerning the neighbouring territories, it can be seen that majority, i. e. at least 54 species, have a single generation in a year. This number, as may be supposed from the as yet fragmentary data, will increase in future to about 60. More than a single generation in a year, at least in a larger part of the distribution area, is achieved by at least 21 species. Their number also will probably increase during the course of further investigations to 30 or 35. A single generation in the course of almost two years is produced by only 4 species. Within the monocyclic species the majority are the so-called „winter" species whose nymphs grow also in winter. To these belong the representatives of groups B2, B4, and 5B — altogether 25 species. Together with group B3, numbering 11 species, nymphs of these mayflies are present in the streams either the whole year round or their absence is limited to some spring-summer months. „Summer" species of group B1 are twice as few their nymphs being absent in the streams during the autumn-winter period. The number of „winter" species (C2) and summer species (C1) is in the case of polycyclic forms similar. The growth rate of nymphs is usually high in species from group B1 and C1, and low or variable in those of the other groups.

Polycyclic species appear above all in larger Carpathian rivers or in smaller streams situated at low altitudes. There is a correlation between the character of growth of the species and the type of streams inhabited by them. In large rivers,

i. e. in zone 5. and in zone 4. (Sowa 1975), summer species of group C1 and B1 prevail in number. In consequence of the absence of their nymphs, the winter communities of mayflies in these rivers is markedly poorer in species composition and less numerous than the summer ones.

In smaller submontane rivers and larger highland streams, i. e. in zone 3., winter species of group B2 and C2, which undergo their embryonal development before winter, prevail in number. Winter communities of mayflies are here only slightly poorer in species composition and slightly different from the summer communities. In small mountain streams, i. e. in zone 2., species of heterogeneous development of group B4, whose nymphs are present in the water all the year round, mainly occur along with other winter species of groups B2 and C2. Participation of summer species there is very small. Winter communities of mayflies are similar to the summer ones or even slightly richer in species.

In a number of species with a greater longitudinal distribution in the Carpathian streams flexibility in the way of carrying out the life cycle is observed. These species react to changes in the environmental conditions, especially in water temperature, which take place along the course of the streams, by changes in the course of particular phases or in the whole life cycle to such an extent that a polycyclic species becomes a monocyclic one or vice versa. Such changes usually take place in the case of species of groups C1 and B1, and species of groups C2 and B2. These species thus retain their attachment to summer or winter forms (Table I).

Protective mechanisms within the life cycle, permitting the species to survive unfavourable periods and assure their permanent existence in the biotope, concern, it seems, mainly the way of egg development. In this respect, both in small mountain streams and in large submontane rivers, there are species whose egg development proceeds in a different way. Among the former, however, almost no species undergoing a deep winter diapause in the embryonal development are encountered. This, on the other hand, is frequent among species living in large Carpathian streams and permits them to survive the unfavourable winter period (low oxygen content, very low temperature, increased shading of the bottom) and is the cause of a more synchronous growth of nymphs and their emergence, which facilitates reproduction.

The smallest number of species living in nymphal stage is observed in streams in the investigated territory from November till February. It does not then exceed 60. From March on an increase in the number of species takes place, which continues until June, slightly more than 80 then being found in the water. In the following months the number of species somewhat decreases, becoming markedly lower only in October when the presence of 68 species was recorded.

In the period from the middle of November till the middle of February no adults of mayfly are encountered in the investigated territory. Emergence of *Baetis rhodani* starts the earliest and finishes the latest (end of February of beginning of March — beginning of November) a considerable increase in the number of emerging species being marked only from the middle of April (21 species). The peak of emergence occurs in June (73 species) and in July (70 species). In the following months the number of emerging mayflies decreases gradually to 35 species in October. In the

middle of this month a more intensive emergence of almost all species is completed and at the beinning of November the adult representatives of only 2 species were caught as single specimens.

STRESZCZENIE

Przebadano wzrost i cykle życiowe 21 gatunków jętek karpackich w systemie wodnym Olszowy-Koninka-Porębianka-Raba oraz w górnej części potoku Wielka Puszcza w Beskidzie Małym. Cykle życiowe 54 innych gatunków rozpoznano według proporcjonalnej obecności w wodach bieżących larw w różnych stadiach wzrostu oraz według pojawu postaci uskrzydlonych, na całym obszarze badań w polskiej części Karpat. Charakterystykę terenu, terminy i sposób zbierania materiału oraz ogólną charakterystykę ekologiczno-biogeograficzną 97 odszukanych gatunków omówiono w pierwszej części pracy (Sowa 1975). 54 gatunki ma na obszarze badań jedno pokolenie w roku. Co najmniej 21 gatunków ma, przynajmniej na większości stanowisk występowania, dwa pokolenia w roku (u 3 gatunków możliwe jest także trzecie pokolenie). Tylko 4 gatunki realizują swój cykl życiowy w okresie prawie dwóch lat. W obrębie monocyklicznych najwięcej stwierdzono tzw. zimowych gatunków, których larwy obecne są i rosną także w zimie. Na podstawie ilości pokoleń w roku, okresu pojawu larw i tempa ich wzrostu oraz według charakteru rozwoju jaj dokonano klasyfikacji jętek karpackich, wyodrębniając 9 grup gatunków, o różnych cyklach życiowych. U niektórych gatunków, o większych zasięgach wzdłuż biegu wód, zaobserwowano plastyczność w sposobie realizacji cyklu życiowego. W niektórych wypadkach może ona być tak duża, że gatunek zmienia liczbę pokoleń w roku. Zaobserwowano związek między sposobem wzrostu gatunków a wielkością i położeniem zasiedlanych przez nie wód płynących. W ugrupowaniach jętek dużych rzek, tj. w strefie 5. i 4. według klasyfikacji Sowy (1975), przeważają liczbowo gatunki, mające w rozwoju embrionalnym długi okres spoczynku zimowego; ugrupowania larw jętek tych rzek są w zimie wyraźnie uboższe w gatunki od ugrupowań letnich i mniej liczebne. W ugrupowaniach mniejszych rzek podgórskich lub dużych potoków, tj. w strefie 3., przeważają gatunki, których larwy wykluwają się z jaj przed nadejściem zimy; ugrupowania zimowe larw są tu tylko nieznacznie różne i uboższe w gatunki od ugrupowań letnich. W ugrupowaniach mniejszych potoków górskich, tj. w strefie 2., liczebniejsze są gatunki, u których rozwój jaj w zależności od terminu złożenia, przebiega z okresem lub bez okresu spoczynku, w konsekwencji także tempo wzrostu larw nie jest jednakowe. Ugrupowania larw jętek w zimie nie odbiegają tu składem gatunkowym od ugrupowań letnich lub nawet są od nich nieco obfitsze w gatunki.

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