With best Regards
Kamler

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E. KAMLER

DISTRIBUTION OF *PLECOPTERA* AND *EPHEMEROPTERA* IN RELATION TO ALTITUDE ABOVE MEAN SEA LEVEL AND CURRENT SPEED IN MOUNTAIN WATERS

Department of Experimental Hydrobiology, Nencki Institute, Polish Academy of Science, Warszawa 22, 3 Pasteura St., Poland

ABSTRACT

Investigations concerned the distribution (number of species and density of larvae per m^2) of *Plecoptera* and *Ephemeroptera* in the Tatra Mts. and the Bieszczady Mts. (the Carpathian Mts.). It was found that distribution varies with altitude above m.s.l. changes. The distribution of larvae is also variable in different conditions of water current speed.

CONTENTS

1. INTRODUCTION

Data on the vertical range of individual *Plecoptera* and *Ephemeroptera* species in mountain waters are contained in numerous faunistic papers. Recently, the interest of some investigators has been focussed on the problem of species succession along the course of the stream (e.g. ILLIES 1952, BERTHÉLEMY 1964). The classification, by ILLIES (1953) and ILLIES, BOTOSANEANU (1963), of running waters into limnological zones, was based, precisely, on the phenomenon of the *Invertebrata* species, broadly including *Plecoptera* and *Ephemeroptera*.

The present observations on the occurrence of *Plecoptera* and *Ephemeroptera* in relation to the altitude above m.s.l. are based on the material collected from two areas in the Carpathian Mountains. Special attention was devoted to the changes in species number as well as larvae density per m^2 relative to altitude changes. The vertical range of individual species was treated only as the starting point for considerations, while the question of the vertical zonation of species was entirely omitted. Use was also made of additional data provided by recent, fairly numerous publications dealing with the

Carpathian fauna*, excluding, however, as inconsistent with the scope of this work, areas situated outside the Carpathian Mountains.

Some essential changes of the abiotic factors in mountain waters occur together with altitude changes. The influence of thermal conditions on the distribution of *Plecoptera* and *Ephemeroptera* has been discussed in an earlier paper (Kamler 1965). At present, attention was given to the importance of the current speed of water. The opinion as to the importance of water current for stream fauna is shared by numerous authors. Hynes (1941) and Brinck (1949) placed water current first among the factors they enumerated as influencing the stream fauna. Illies (1955) reports that the occurrence of *Plecoptera* shows a close relationship with water flow conditions, and Phillipson (1956), basing on investigations of factors conditioning the distribution of *Simulium ornatum* MG larvae, states that water flow is more important than oxygen concentration.

Among the various problems concerned with the importance of water current speed in relation to water fauna, only one was chosen, viz. the changes of species number and density of *Plecoptera* and *Ephemeroptera* with different current speeds.

2. THE TERRAIN AND METHODS

Investigations covered the Tatra and Bieszczady areas of the Carpathian Mts.

The Tatra Mts. consist of crystal and sedimentary rocks. Their glacier formed relief is typical for high mountains, with glacial cirques, lakes, U-shaped valleys and glacial thresholds, and with moraine ridges heaped at the foot of the mountains. In the Polish region of the Tatra the highest peak Rysy rises 2499 m above m.s.l. Only in some places forests form compact areas. Investigations were performed over the entire Polish area of the Tatra, viz. the High Tatra Mts. (with main attention devoted to the Roztoka stream basin), and the Western Tatra Mts. (with particular consideration given to the Olczyski stream basin).

The Bieszczady Mts. were formed out of sandstone and slate banks. The relief-forming process produced mountain chains with moderately steep slopes and a gentle ridge line. The Quaternary did not essentially affect the Bieszczady relief. The mountains are not high: in the Polish region, their highest peak Tarnica rises 1348 m above m.s.l. Large areas of the Bieszczady are covered with forest. Investigations were centred in three places: the vicinities of Duszatyn (western part of the Polish Bieszczady), Kalnica (central part), and Ustrzyki Górne (eastern part).

In consideration of the above differences between the Tatra and the Bieszczady, the respective differences of their hydrologic conditions are evident. Bieszczady have no high mountain lakes, of which there are many in Tatra. In comparison with Tatra, the streams in Bieszczady form more numerous stagnant waters, of larger surfaces and finer grained bottom. Maximum speeds of water flow at the places of quantitative sampling from stony habitat were found 1.41 m/sec. in Tatry, and 0.50 m/sec. in Bieszczady.

The work was based on material of about 4500 specimens of *Plecoptera*,

* See Table I.

and about 5500 specimens of *Ephemeroptera*, contained in 176 qualitative samples, and 396 quantitative samples taken in Tatra, and in 134 quantitative samples taken in Bieszczady. A part of this material was used by KAMLER (1960, 1962, 1964) for the study of fauna distribution, and (1965), for the study of the importance of temperature conditions. Qualitative sampling was performed in the Tatra, in the months of: January, February, March, May, July, August, September and October, 1954 — 1963. Quantitative studies were carried out in Tatra in July and August 1957, in Bieszczady — in June and September 1963. Investigations covered 40 streams and 11 lakes in Tatra, and 8 streams and 12 pools in Bieszczady.

Quantitative capture of larvae was performed using methods fully described by KAMLER, RIEDEL (1960). In the stony habitat, whole stony material was twice scooped out by pulling a metal-frame sieve the required distance against the current. From detritus, gravel, sandy and muddy bottom, samples were taken using a bottom sampler pushed into the substrate; from moss, 10 x 10 cm pieces were cut out under water; from among macrophytes, larvae were collected over the determined area, using a net. Adult insects were also caught.

Investigations on the species distribution at various altitudes were performed in the 500—2039 m range. The altitude of each sampling was read from the map with up to 50 m difference accuracy.

Water current speed measurements were achieved by means of fivefold surface flow measuring using a float, then mean speeds were calculated for the particular verticals (KLIMASZEWSKI et al. 1954). Use was also made of sodium fluorescein.

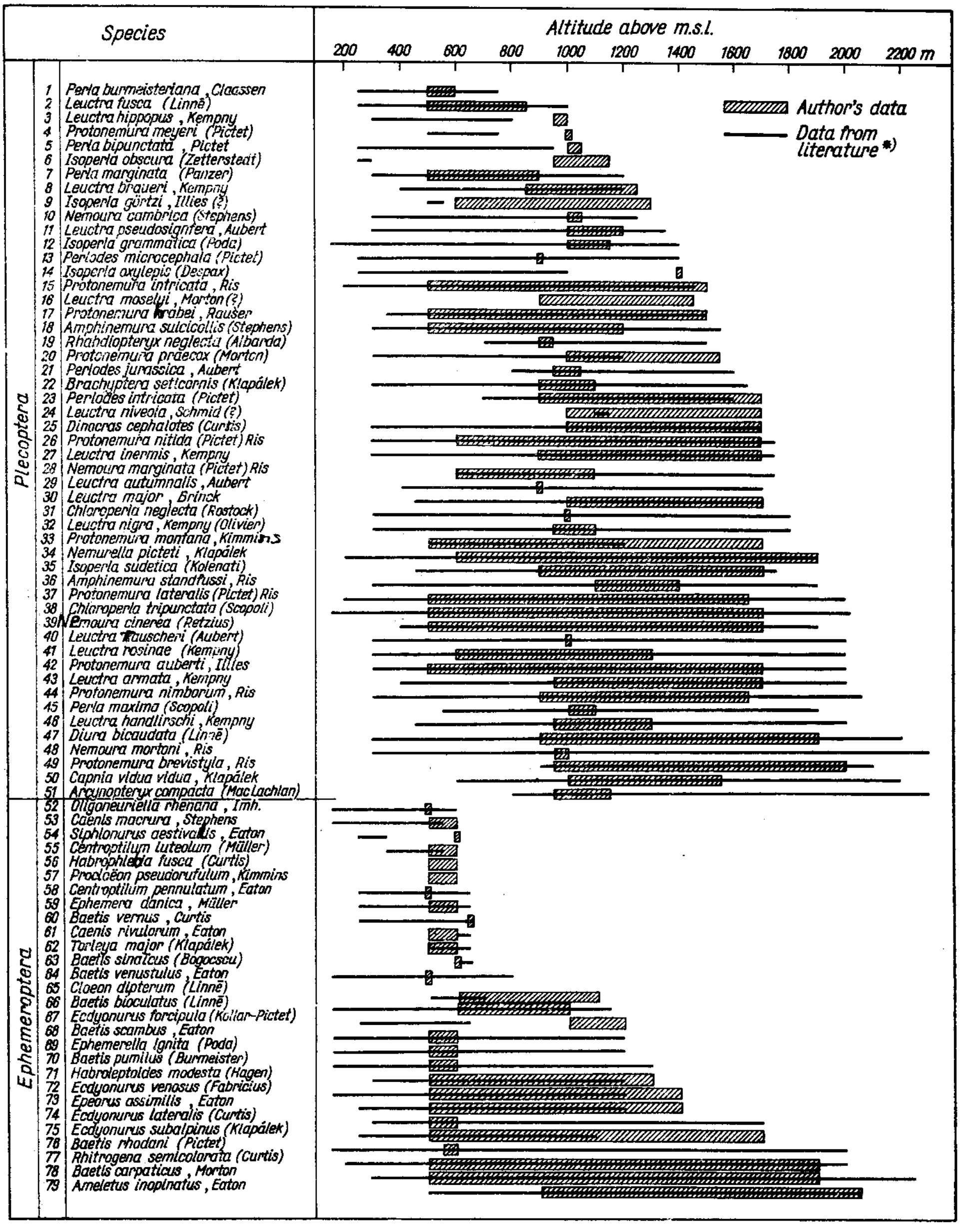
3. RESULTS

Data on the vertical distribution of *Plecoptera* and *Ephemeroptera* species found by the author in Tatra and Bieszczady are shown in Table I. Complimentary data for the entire Carpathian area reported by other investigators are also included. As it can be seen, the occurrence of some species is limited to low and medium levels, while others, characterized by a wide range of vertical distribution, are found at low, medium and high levels. Among these latter, some species count a considerable number of specimens. This refers to the species No. 26, 27, 33, 34, 35, 37, 39, 42, 43, 47, 49, 77, 78, 79, in Table I. It is interesting to note that no species were found occurring exclusively at high altitudes. At these, the existance was stated only of the vertically wide distributed forms. The above observations apply to both *Plecoptera* and *Ephemeroptera*.

Most *Plecoptera* species (Fig. 1Aa) were found in the areas situated at 800—1700 m. Most of the *Ephemeroptera* species (Fig. 2Aa) were observed below 700 m. Above 1700 m, the numbers of *Plecoptera* and *Ephemeroptera* species are small and rather similar. Changes in *Plecoptera* (Fig. 1Ab) and *Ephemeroptera* (Fig. 2Ab) density are highly similar to the changes in the number of species.

Investigations covered the changes in density of larvae per m^2 of various *Plecoptera* and *Ephemeroptera* species inhabiting boulders, stones, gravel, sand, mud and detritus in streams, relative to changes in water current speed. Moss environment was omitted, in consideration of its specific flow condi-

Table I



* Data on the vertical distribution of species, taken from: Bogoescu (1958), Bogoescu, Tabacaru (1957), Botosaneanu, Tabacaru (1963), Ciszek, Sosińska (1965), Despax (1935), DzięDzielewicz (1917, 1918), Hrabě (1942), Klapálek (1904), Kownacka, Kownacki (1965a, 1965b), Kownacki, Kownacka (1965), Mikulski (1935, 1937), Miron (1964), Mocsary (1899), Nowacka (1965), Obr (1955, 1956, 1963), Pawłowski (1959), Pongrácz (1919), Raušer (1956a, 1956b, 1957a, 1957b), Schoenemund (1930), Sowa (1961a, 1961b, 1962, 1965), Winkler (1957), Wojtas (1964), Zelinka (1953, 1959).

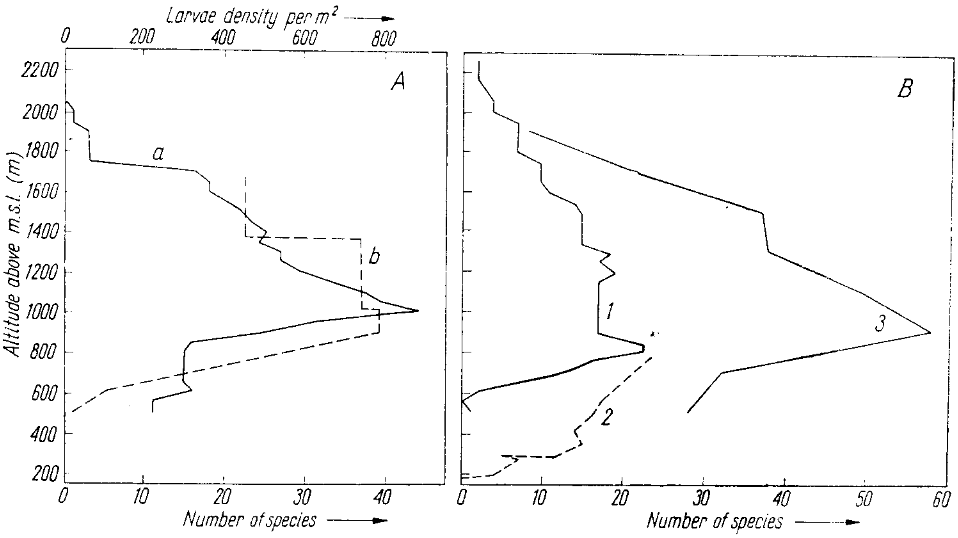


Fig. 1. *Plecoptera* distribution at various altitudes above m. s. 1
A — data based on the present work, from the Tatra and the Bieszczady: number of species (a), larvae density per m² (b], B — number of species in the Carpathian Mts., basing on literature: BOTOSANEANU, TABACARU (1963), from the Fagarasch Mts. (1), NOWACKA (1965), from the Dunajec River (2), WOJTAS (1964), from the Tatra Mts. and Podhale region (3).

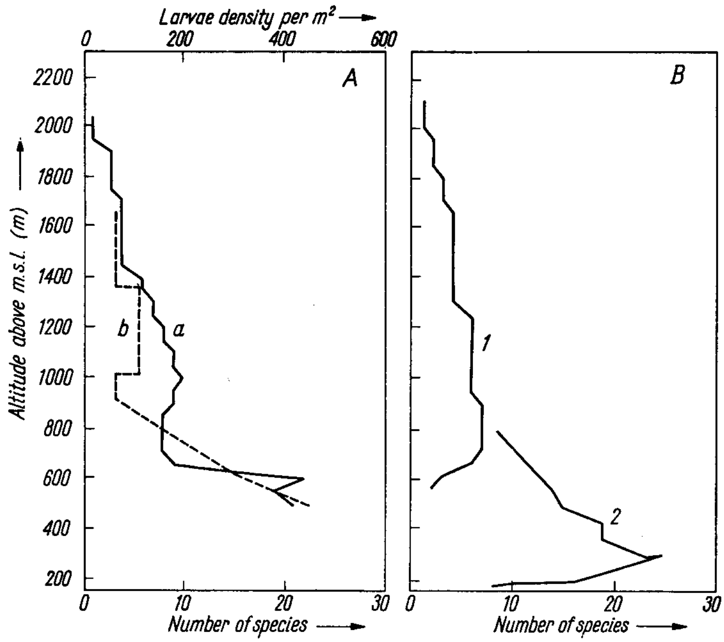


Fig. 2. *Ephemeroptera* distribution at various altitudes above m. s. 1
A — data based on the present work, from the Tatra and the Bieszczady: number of species (a), larvae density per m² (b), B — number of species in the Carpathian Mts., basing on literature: BOTOSANEANU, TABACARU (1963), from the Fagarasch Mts. (1), CISZEK, SOSIŃSKA (1965), from the Dunajec River (2).

tions. Histograms illustrating the above changes are shown in Fig. 3. The results obtained with regard to species listed in brackets should be understood as uncertain being based on unsufficient number of tests (< 9). The figures denote weighed averages of water current speeds (m/sec.), calculated using the formula:

$$X = \frac{n_1x_1 + n_2x_2 + \dots + n_sx_s}{n_1 + n_2 + \dots + n_s}$$

where $x_1, x_2 \dots x_s$ denote classes of water current speed (0,0, 0,1 . . . > 1,0 m/sec), $n_1, n_2 \dots n_s$ denote density of larvae in respective classes of water current speed.

As it is seen from Fig. 3, both *Plecoptera* and *Ephemeroptera* species are grouped under four types, characterizing their different patterns of attachment to water current speed.

Type I. Stagnant water species, mostly found, as regards the investigated area, in lakes and pools. Exceptionally occurring in streams, avoiding, however, fast water current speeds.

Type II. Species of which a small number of specimens was found in narrow range of slow water current speeds.

Type III. Species inhabiting slow and moderate current speeds. In general, the density of larvae is medium, excepting for the *Habrophlebia fusca* which occurred in great abundance in the current speed class of 0,1 m/sec.

Most of the *Plecoptera* and *Ephemeroptera* species are grouped in the above type. The density of some species decreases with the increase of water current speed (e.g. *Leuctra braueri, Habrophlebia fusca, Ecodyonurus lateralis, Ephemera danica*), while that of other species increases (e.g. *Ephemerella ignita, Baetis scambus, Caenis macrura, Baetis rhodani*) — Fig. 3. No directional changes in density relative to the water current speed increase were observed for some of the species (e.g. *Perla burmeisteriana, Leuctra fusca, Perlodes intricata, Ecodyonurus venosus, Torleya major, Caenis rivulorum, etc.*).

Type IV. Species represented by high numbers of specimens over the wide range of current velocities. Only *Protonemura nitida* was found to comprise a small number of specimens. This species emerges in late autumn. In the summer period, when quantitative investigations were performed, it occurred as very young larvae, which, at this stage of their development, were found in considerable quantity in moss environment unaccounted for in the present considerations. Moreover, part of the larvae, considering their small size, could have escaped attention in the course of sampling. In this type, similarly as in the previous one, for some species, the density of larvae decreased with the increase of water current speed (*Rhitrogena semicolorata*), for some others it increased (*Protonemura montana* and *Baetis carpaticus*), and for still others it was not susceptible to any directional changes (*Leuctra armata, Leuctra inermis, Isoperla sudetica, Protonemura nitida*).

Closer attention was devoted to the distribution, under various current speed conditions, of the Type III and IV species of which the density neither decreased nor increased directionally relative to the increase of current speed. It was observed that for most of these species, the density is lower in the range of moderate current velocity as compared to that encountered in faster and slower current conditions. Thus, e.g. in the case of *Leuctra armata*

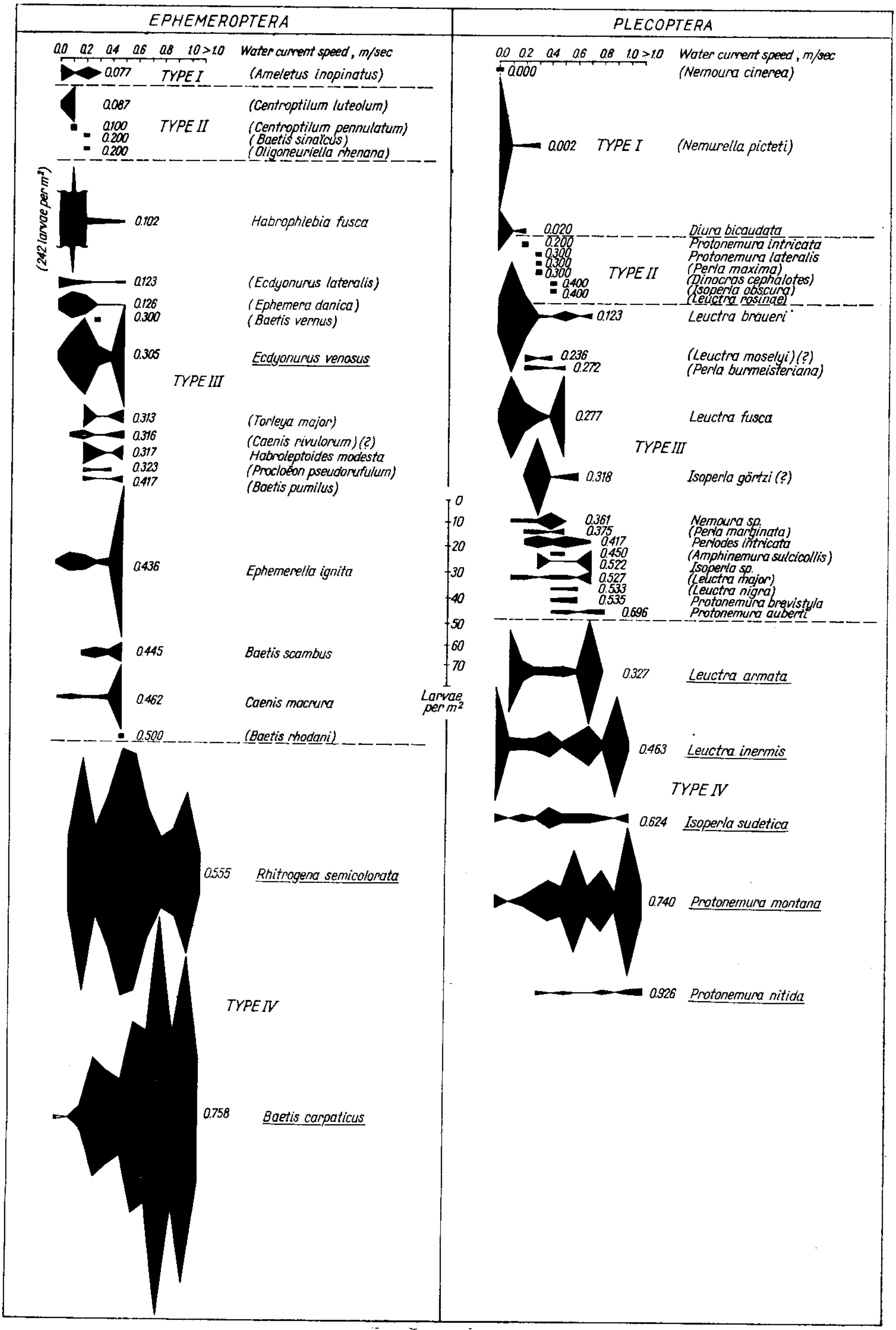


Fig. 3. Density changes of *Plecoptera* and *Ephemeroptera* species, relative to changes in water current speed. The figures denote weighed averages of water current speeds, m/sec. The species listed in brackets were found in < 9 samples. The species found in > 30 samples are underlined

with current speed of m/sec: 0,1 0,2 0,3 0,4 0,5 0,6 0,7 0,8 the average number of larvae density per m² was: 32 7 2 3 3 1 40 1, respectively.

Density drops in medium current are exemplified by histogram contractions in Fig. 3. For 16 species, a comparison was made of current speeds at which density drops were observed. Most frequently, the drop occurs at 0.2—0.5 m/sec. current speed (Fig. 4 a). It is interesting to note that most of all *Ephemeroptera* and *Plecoptera* species were, simultaneously, found in precisely the same current speed range (Fig. 4 b and c).

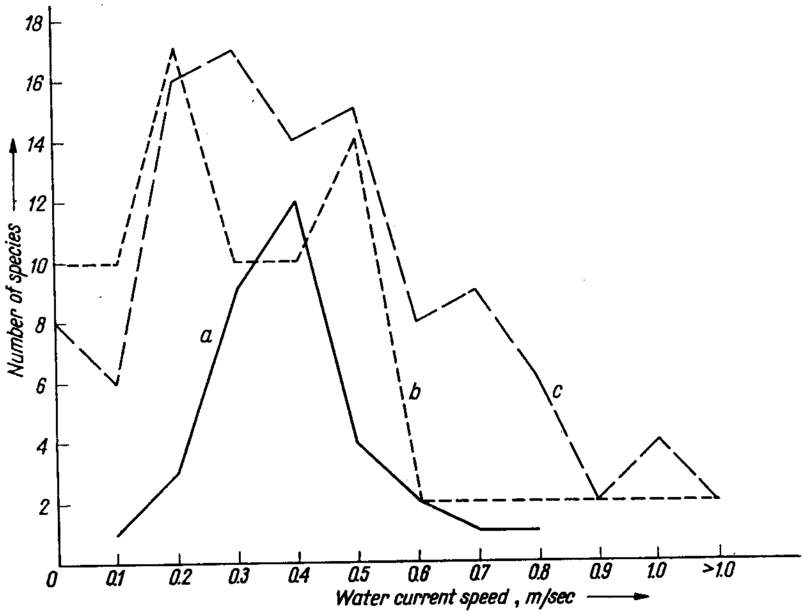


Fig. 4. Number of species in relation to water current speed in Tatra and Bieszczady streams

a — number of *Plecoptera* and *Ephemeroptera* species from type III and IV, of which the density, in the particular, moderate current speed class, is inferior to that in slower and faster current, b — total number of *Ephemeroptera* species, c — total number of *Plecoptera* species.

Most of the larvae found in Tatra streams belonged to type IV: among *Plecoptera*, these amounted to 86% of the total number of collected larvae; among *Ephemeroptera* — to 99.3%. In Bieszczady streams, however, type III species were predominant: *Plecoptera* — 89%, *Ephemeroptera* — 83.5%.

The above data are based on material collected from streams. The Tatra lakes are mainly inhabited by species accounted within type I. *Nemurella picteti* amount to 40%, *Diura bicaudata* to 16% of *Plecoptera* larvae collected from lakes, while *Ameletus inopinatus* — to 84% of *Ephemeroptera* larvae. All the above species are also occurring in streams, being, however, restricted to slow water speed habitats. Average values of current speeds at which the species were found are low (Fig. 3). In streams, slow speed areas are rare. The said species represent a small percentage of the fauna collected from streams which do not outflow from lakes: *Nemurella picteti* 6.9%, *Diura bicaudata* 3.1%, *Ameletus inopinatus* 0.9%.

4. DISCUSSION

The vertical range of species, such, as presented in Table I (dashed rectangles) may be incomplete. It depends on the quantity of the collected material, on the uniformity of sampling at various altitudes and in various seasons and, finally, on the vastness of the area under investigation. For this reason it was considered proper to supplement it with additional data found in 35 papers of other authors, covering the Carpathian area (lines). It is interesting to note the absence in Tatra of species apparently exclusively inhabiting high altitude areas (see also Wojtas 1964). Probably, the lack of typically high mountain forms is characteristic for central and northern European mountains. According to Raušer (1962), these mountains had been, during pleistocene, under a strong glacier influence, and, contrary to the Mediterranean area mountains, the Alps and the Caucasus, include few endemic forms of local origin. Most of the species inhabiting Carpathian Mts. have reached them from the refuges lying in the south, east and west at the time of the glacier's leaving. Some of them, overcoming on their way the lower mountain parts, have reached the high mountain Carpathian area (species occurring over a wide range of altitudes — Tab. I). The post-glacier climate warming up reduced but slightly the occurrence of the most cold-water species in lower situated areas (Tab. I). The fact of the wide range species being the quantitatively predominant element of the fauna seems to speak in favour of the geohistorical interpretation of the lack of typically high mountain forms within the area under investigation. The situation is reversed in Caucasus. Martynov (1928) and Zhiltzova (1956, 1957, 1958, 1960, 1961, 1964) have discussed several *Plecoptera* species being endemic for these mountains. These species occur only in the high mountain area. One may conclude that their vertical occurrence, restricted to high mountain areas, is a characteristic feature of the endemites. The above conclusion represents a development of the theory of Martynov (1922), who, among the *Trichoptera*, distinguished lowland species of geographically broad distribution and mountain species of narrow horizontal distribution. For *Ephemeroptera*, Martynov's conception (1922) was, in broad outline, confirmed by Tschernova (1941). One should not, however, assume the occurrence of all endemites to be limited to the high mountain area. It was reported by Ikonomov (1960), investigating on *Ephemeroptera* of Macedonia, that only some of the endemites showed typically high mountain area occurrence. The vertical distribution of other species was similar to that of the non-endemic forms.

The curves of species number changes at various levels within the presently investigated area (Fig. 1 A a and 2 A a) are, in general, similar to analogical ones basing on material collected in the Carpathian Mts., as reported by other authors (Fig. 1B and 2B). As it is seen, in the Carpathian Mts., maximum occurrence of *Plecoptera* lies above 800 m, of *Ephemeroptera* below 700 m. Sowa (1965), similarly, in the Wielka Puszcza stream (Beskid Mały) flowing at 720—305 m level, observed a preponderance about 2 : 1, or 3 : 2 *Ephemeroptera* to *Plecoptera* per cent ratio, fairly constant throughout the year.

Water current has both direct and indirect effect on freshwater communities, which was stressed e.g. by Macan (1961). The direct influence of water movement is, among other effects, mechanical, by causing fauna displacement, and by affecting fauna respiration and feeding functions. Earliest attention was devoted to the mechanical influence of water movement on animals. According to Steinmann (1907), stagnant waters had been the original habitat of stream animals. After immigration into streams, the same species developed morphological adaptations involving their resistance to water movement, and, particularly, body flattening. Steinmann's opinion was broadly accepted (Brodski 1935, Steinberg, 1935, Czafik 1951). The above interpretation of animal resistance to water current was, however, critically evaluated by Popovici-Baznosanu (1928). It was demonstrated by him that the morphological adaptations, as reported by Steinmann, do not account for the resistance of animals to water current, and appear as well in organism confined to stagnant waters. Popovici-Baznosanu suggests that the resistance causes result from physiological adaptations. The latter conclusions found support in the experiments of Dorier, Vaillant (1954). Ambühl (1959) emphasizes on the hiding of animals in places of limited current speed, i.e. layers situated a few millimeters directly above the surface, and the so called dead waters, mainly situated behind an obstacle. Resistance differences of various organism to current speed consist on their different behaviour when penetrating a fast flow water area.

The results of the present work seem to confirm Ambühl's theory. The largest number of species were found, precisely, within the range of slow and moderate current (Fig. 3, Fig. 4b, c), while none were reported to inhabit, exclusively, fast current speed areas. The method applied for investigation was, however, in some degree inaccurate. The histograms (Fig. 3) of density relative to water current speed may be incomplete, particularly with respect to the sporadically occurring species. Thus, e.g. *Dinocras cephalotes* (type II) is here reported from a 0.3 m/sec. current speed class, while it was found by Sowa (1965) within the 0.4—0.5 m/sec. range, and, moreover, by Kownacka, Kownacki (1965 b), from very fast, fast and slow water current. This may suggest a shifting of the above species to type III or even to type IV. Further investigations would, therefore, probably lead to modifying the picture of species distribution in relation to flow conditions, as shown in Fig. 3, particularly in the case of type II accounted species.

Another weakness of the applied method lies in the impossibility to eliminate, from the results, the effect of other factors, as well as the impossibility of an authoritative evaluation of their influence. Thus, e.g., one may only suppose that larvae density drops, occurring in some species only at 0.2—0.5 m/sec. current speeds (Fig. 3, Fig. 4a), are related with the increased competition phenomenon, since, in the above zone, the number of species is the largest (Fig. 4b, c). For this reason, it was considered justified not to endeavour any detailed interpretation of the quantitative distribution of individual species, and to limit the scope of this work to a division of the species under investigation into distinctly differentiated distribution types.

The adopted division seems to be supported by the marked quantitative predominance of species accounted to type III in the slower Bieszczady streams, and that of type IV in the faster Tatry streams.

From a comparison of Fig. 3 and Table I it is evident that all species inhabiting the broad water current range (type IV), simultaneously show a broad vertical distribution. On that basis, however, one may not conclude on the homogeneous influence of the altitude and water current speed relation on fauna distribution: all of the type I species also show a broad vertical distribution range. The above species were found in high elevated Tatra lakes, but, moreover, were also met within lower situated streams, in habitats where conditions were favourable to them.

5. SUMMARY

A total of 530 quantitative and 170 qualitative samples of *Plecoptera* and *Ephemeroptera* were collected from streams, lakes and pools in Tatra and Bieszczady (Carpathian Mts.). Evaluations of altitude and of water current speed were performed simultaneously. Some of the species are occurring at low and medium altitudes. Other species inhabit both low and high altitude areas, a great many of them occurring in considerable quantities. No typically high mountain species were found (Tab. I). Maximum occurrence, both quantitative and qualitative, of *Plecoptera* was reported above 800 m (Fig. 1), of *Ephemeroptera*, however, below 700 m (Fig. 2). The larvae density per m^2 was investigated in habitats of various current speed. Four types of distribution were distinguished: I — stagnant water species, exceptionally occurring in streams, II — species sporadically encountered in slow and little differentiated current speed areas, III — medium numerous species inhabiting slow and moderate current speed ranges, IV — species found in large quantities in slow current, as well as in fast current conditions. No species inhabiting, exclusively, fast flowing waters were found (Fig. 3). Most species were encountered in the zone of 0.2—0.5 m/sec. velocities, in which range the density of some of the type III and IV species is inferior to that found in slower and faster speed areas (Fig. 4). Among the larvae collected in Bieszczady (lower mountains) most belonged to type III, in Tatra-to type IV.

6. STRESZCZENIE

Zebrano 530 prób ilościowych i 170 jakościowych *Plecoptera* i *Ephemeroptera* z potoków, jezior i małych zbiorników w Tatrach i w Bieszczadach (Karpaty). Jednocześnie dokonywano pomiarów wzniesienia i prędkości przepływu wody. Niektóre gatunki występują na wzniesieniach niskich i średnich. Inne gatunki występują zarówno na wzniesieniach niskich, jak i wysokich, wiele z nich występuje bardzo licznie. Gatunków typowo wysokogórskich nie znaleziono (Tab. I). Ilościowe i jakościowe maksimum występowania *Plecoptera* leży powyżej 800 m (Fig. 1), zaś *Ephemeroptera* poniżej 700 m (Fig. 2). Badano zagęszczenie larw/m^2 w potokach w różnej prędkości przepływu. Wyróżniono 4 typy prądolubności: I — gatunki wód stojących, w potokach występujące wyjątkowo, II — gatunki, które sporadycznie spotykano na powolnych i niezbyt zróżnicowanych prędkościach przepływu, III — gatunki średnio licznie zamieszkujące powolne i średnie prędkości przepływu, IV — gatunki bardzo licznie reprezentowane w warunkach zarówno lotycznych, jak i lenitycznych. Nie znaleziono gatunków zamieszkujących wyłącznie wody szybkopłynące (Fig. 3). Najwięcej gatunków spotykano tam, gdzie prędkość przepływu była 0,2—0,5 m/sek, w tej strefie niektóre gatunki z typu III i IV występują w zagęszczeniu mniejszym, niż na przepływach powolniejszych i szybszych (Fig. 4). W Bieszczadach (góry niższe) złowiono najwięcej larw typu III, w Tatrach — typu IV.

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