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REMARKS ON CONDITIONS INFLUENCING THE APPEARANCE OF NEW GENERATIONS OF *TENDIPEDIDAE LARVAE**

The conditions for their development are of greater importance to the appearance of young larvae of *Tendipedidae* than the mass emergence of imagines and the eggs they lay. In the majority of cases there is a certain influx of eggs (or juvenile larvae) into the bottom habitat even after the period of mass egg-laying, which facilitates rapid occupation of the habitat when favourable conditions are formed.

The opinion is often held than the appearance of a new generation of larvae of a certain species of *Tendipedidae* is conditioned by the mass emergence of the preceding generation and egg-laying by the imagines. It would however seem that too much importance is attached to this matter.

Numerical data on the emergence of imagines show that a short time mass emergence generally occurs, but both before and after this "peak" less intensive emergence continues (Miller 1941, Mundie 1957, Kajak 1958a, Zilahi-Sebess 1932, Konstantinov 1958, Sokolova 1959, Brundin 1949, Lellak 1953, Šilova 1958, Potonié 1931, Thienemann 1954 and others), and therefore the influx of a certain number of eggs also probably lasts considerably longer than the mass emergence of imagines. This presumably is of great biological importance. In view of the short life of the imaginal stages and the great extent to which they are affected by weather conditions, particularly winds (Borucki 1939, Thienemann 1954, Lenz 1954, 1962, Jonasson 1961 and others) it often happens that the mass appearance of imagines

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encounters unfavourable conditions and as a result the number of eggs laid is very small; under such circumstances the eggs laid by the succeeding, less numerous imagines may in effect produce a greater number of young larvae than the main peak of emergence.

The long-lasting influx of a certain number of eggs is therefore ensured not only by the emergence of imagines extended over a period of time from the given habitat, but also by the emergence flights occurring at a slightly different time from different habitats in a given body of water (Borucki 1939, Miller 1941, Brundin 1949, Šaronov 1951 and others), and also from other bodies of water in the vicinity. It is a known fact (Šilova 1958, Ljachov 1954, review of literature see also Konstantinov 1950, 1961, Borodič 1956) that a different number of generations occurs at different depths in the same body of water[1].

Owing to the large number of eggs in egg-masses, eggs laid even outside the period of intensive flights of the imagines can ensure the appearance of large numbers of larvae, if the latter encounter conditions favourable to their development. Situations of this kind take place, for instance, during periods of flooding dam reservoirs, when often enormous areas are abundantly settled from relatively small areas of the waters which existed in the area before the dam filled up (review of literature see Morduchaj-Boltovskoj 1961, Kajak 1962).

It would therefore seem that in the majority of cases there is a certain influx of the eggs of *Tendipedidae* throughout a considerable part of the vegetative season, also outside the mass emergence period, and to the majority of the habitats; it cannot be concluded from the absence of appearance of young larvae that there is a lack of eggs – it may equally well be due to the lack of conditions favourable to their development.

With regard to conditions for the development of larvae, the importance of the role of oxygen deficiency and temperature is generally acknowledged (Borucki 1939, 1946, Brundin 1951 and others). It would seem that there are far more factors affecting the benthos organisms, including the development of the young larvae (Kajak 1958a, Konstantinov 1958, Rybak 1963).

When analysing the variations in numbers of *Tendipedidae* and the correlation of the appearances of young larvae with the number of eggs laid in a riverside pool (Kajak 1958), I found that there is by no means a simple connection here: after mass egg-laying the juvenile forms might appear in very small numbers

[1] Probably in certain cases the authors base their conclusions on the number of generations of the given species on the basis of appearances of young larvae. In reality the appearance of young larvae is not always evidence of exchange of generations (attention was drawn to this by Potonié 1931) but only of the existence of conditions making the development of young larvae possible. The number of generations should be defined according to the full life cycles – from the time of egg hatching until transformation into an imago.

and conversely – after a long period with a very small number of eggs, numerous appearance of young larvae might take place. It must be emphasised that the oxygen supply at the bottom of the water was good (Kajak 1958).

Belavskaja and Konstantinov (1956), in interpreting different periods of the appearances of the same species in neighbouring habitats, express the opinion that the conditions of the development of the larvae are decisive here, that the larvae do not always reach the older stages, often dying in the earlier stages, which cannot be grasped by the classic benthos methods. Gurzęda and Wolny (1962) reached similar conclusions on the basis of material from fish ponds. Morduchaj-Boltovskoj (1954) also draws attention to the appearances of young larvae and their death in the early stages of development as the result of the lack favourable conditions.

Reference was made above to the high degree of capacity for survival and the rapidity of development of *Tendipedidae* larvae in freshly flooded dam reservoirs. This also applies to the development of *Tendipedidae* on green fertilizers (Ioffe 1957, Pankratova 1957 and others). The great capacity for survival of the young larvae connected with the change in habitat conditions should probably form the explanation of the numerous appearances of *Tendipedidae* after rises in water level (Kajak 1958b, 1959); as has been shown (Kajak 1959a) the amount of larvae carried into the reservoir by the water was not of any great significance.

Lundbeck (1926) and Borucki (1939) draw attention to the very high rate (over 90%) of mortality among the juvenile stages in the profundal conditions of lakes. There are however habitats in which mortality is negligible (Levanidova 1959). Konstantinov (1958) demonstrated the great differences existing in capacity for survival and rate of development under different breeding conditions.

The phenomenon discussed above of the long-lasting emergence of imagines (and therefore of long-lasting egg-laying) is undoubtedly of great importance, not only account of the survival conditions of the imagines, but also on account of the conditions for the development and capacity for survival of the larvae. This to say that it constitutes a form of insurance against the possibility of unfavourable conditions occurring for the development of the young larvae during the egg-laying period: the longer the period over which egg-laying continues, the greater the probability that part of the eggs will encounter conditions favourable for their development.

I encountered cases of divergence between the potential appearances of the young larvae of *Tendipes plumosus* (in the sense of the occurrence in the given time and habitat of eggs capable of development) and the factual appearances, in my experimental work on benthos, which was carried out on Lake Śniardwy. This is a polymictic lake, the whole of the bottom of which lies within the epilimnion area and therefore oxygen supply is always good (Olszewski and Paschalski 1959, Kosicki 1961).

Experiments were made using cages measuring 30×30×30 cm made of nylon gauze with meshes 0.5×0.5 mm. The contents taken from a given habitat, of 4 Ekman dredges (mud together with the fauna) were placed in control cages, care being taken to disturb the structure of the mud as little as possible. In one of the variants of the experiment the mud deprived of its macrofauna by straining it through a sieve, was placed in a cage, and in another experiment – the mud with the fauna which was dried slightly in the air for 2 days. The cages were sunk on to the bottom of the lake, at a depth of 7–8 m (for more exact data see Kajak 1964).

A general tendency to more numerous occurrence of young forms was found in the cages than in the lake habitats adjoining them (Kajak 1964).

In addition, several cases were found of numerous appearances of young larvae of different species in experimental cages, while they were completely absent in the lake throughout the whole duration of the experiment or during the final period of the experiment (Tab. I).

Appearances of young larvae of *Tendipedidae* in experimental cages, despite their absence in the lake in the neighbourhood of the cages. State existing at the end of the experiments

Tab. I

Species	Period of experiment	Number of larvae per 1 m²	
		near the cages	in the cages
Tendipes plumosus L. ⩽ 15 mm	27.6 – 29.7.60	0	389
Microtendipes chloris Mg.	"	0	155
Limnochironomus tritomus Kieff.	"	0	78
Tendipes plumosus L. ⩽ 15 mm	11.9 – 22.10.60	0	133
Einfeldia carbonaria Mg. ⩽ 6 mm	"	0	45
Procladius sp. ⩽ 8 mm	1.7 – 3.8.61	0	45

In one of the series of experiments (Tab. II) the young larvae of *T. plumosus* did not occur in the lake during the final period, and occurred in small numbers only in the control cages, while they were numerous only in one variant – in the cage with mud dried at the beginning of the experiment.

A similar case – the numerous appearance of young larvae only in one variant of the experiment – was found in the case of *Tendipes anthracinus* (Tab. II). This species did not appear throughout the whole period of the experiment in the lake, nor in the control cages, while it occurred in large numbers in the cage containing mud deprived of its macrofauna at the beginning of the experiment.

Facts of considerable differences in the capacity for survival of the young larvae of *T. plumosus* in analogical and adjacent stations are worthy of attention (Tab.III). Both habitats were situated right in the middle of the lake, at a depth of about 7 m, and the character of their sediments was analogical. They were

Comparison of the number of young (≤ 10 mm) larvae of *Tendipes plumosus* and *Tendipes anthracinus* in experimental cages and their neighbourhood at the end of the experiment. 1960.

Tab. II

Species	Period of experiment	Number of larvae per 1 m²		
		near the cages	in the cages	
			control	experi-ment
Tendipes plumosus L.*	11.9 – 22.10.	0	11	78[1]
Tendipes anthracinus Zett.	27.6 – 29.7.	0	0	111[2]

[1] Cage containing mud slightly dried at the beginning of the experiment.
[2] Cage containing mud deprived (by sieving) of macrofauna at the beginning of the experiment.
*The data refer to a different station than the data in Tab. I from the same period.

Comparison of total abundance and the abundance of different classes of size of *Tendipes plumosus* in experimental control cages and their neighbourhood on two adjacent stations Sept 11 – Oct 22 1960

Tab. III

Station	Length of larvae	Number of larvae per 1 m²		
		near the cages start – end of experiment		in the cages (end of experiment)
I	older > 20 mm	36	266	204
	younger ≤ 20 mm	35	18	369
	total	71	284	573
II	older > 15 mm	116	189	166
	younger ≤ 15 mm	71	22	11
	total	187	211	178

about 200 m apart, which in view of the great extent of the lake is a very small distance. On one of these stations a considerable number of young larvae were found in the control cage, while there was only a very small amount in the adjacent habitat. The number of larvae in the control cage on the second station was very small (Tab. III), despite the fact that there had been an influx of young larvae or eggs; this is borne out by the large amount of young larvae in the cage containing slightly dried mud (Tab. II).

It is worthy of notice that in the first of the above stations, immigration of large larvae of *T. plumosus* into the habitat adjoining the cages took place during the experiment (Tab. III). The large larvae could not get into the experimental cages on account of the fine mesh (a larger number not only of small but also of large larvae in the cages towards the end of the experiment in comparison with the start of same, is the result of the growth of part of the young larvae). Presumably some change in the habitat conditions took place which enabled a larger number of larvae to live in it. In view of the polymictic nature of the lake and the inconsiderable distance between these two stations it must be assumed that this was a relatively slight change in conditions, but nevertheless of significance to the benthos, since it brought about such important changes in their numbers. The numbers of larvae in the neighbourhood of the cages increased owing to immigration and in the cages (into which the large larvae were prevented from entering by the fine mesh) the numbers increased as the result of the development of the young larvae. It is worthy of emphasis that this same effect – increase in the numbers of the larvae took place in the cages and their neighbourhood as the result of the action of completely different mechanisms.

The series of examples of considerable differences in the number of young larvae discussed above, including facts of their complete absence in the lake and numerous appearance in the cages, form evidence of the decisive influence of small environmental differences (usually incapable of being grasped by investigation) on the capacity for survival of the larvae. These were most certainly not differences in temperature, oxygen supply or the amount of organic substances, most often considered as determining the survival and abundance of benthos. The amount of oxygen and organic substances could not be greater in the cages than in their neighbourhood.

These facts are also evidence that frequently the possibility of appearance of young larvae is determined not by the exchange of generations, egg-laying by imagines which emerge in masses, but by conditions favourable to the development of young larvae. In none of the above mentioned cases of abundant appearances of young larvae was decrease found in the numbers of large larvae (Tab. I and III), which would form evidence of the mass emergence of imagines. Also the situations discussed at the beginning of this paper (Kajak 1958, 1958b, Ioffe 1957, Pankratova 1957, Morduchaj-Boltovskoj 1961 and others) point to the frequent occurrence of numerous appearances of young larvae not preceded by mass emergence of imagines.

It would therefore seem that under favourable habitat conditions not less numerous, or even more numerous appearances of young larvae can take place outside the period of mass egg-laying, than occur as the result of mass egg-laying (preceded by mass emergence of imagines) which encountered less favourable conditions for the development of the eggs and juvenile larvae.

It must be emphasised that not one species was found in the cages which did not occur in the lake, even if only sporadically (if the entire study period, not only the periods of duration of experiments, is taken into consideration). This is evidence that the conditions formed in the cages were not qualitatively different than on the bottom of the lake, but only favoured a greater capacity for survival. In fact the general similarity of the whole fauna is evidence of the very slight differences between conditions in the cages and in the lake (Kajak 1964).

In several cases (Kajak 1963) the reciprocal relations (intra- and inter-specific) of organisms were found to exert an important influence on the capacity for survival of the juvenile stages and the rate of development of the larvae. For instance the abundance of young larvae of *T. plumosus* was smaller, and their dimensions smaller with greater abundance of the large larvae of this species. The reverse proportion of abundance (in consequence of different capacity for survival) to the density of *T. plumosus* per unit of area was also exhibited by other species — e.g. *Tendipes anthracinus*, *Microtendipes chloris* (Kajak 1963). It is possible that the above-mentioned facts of more numerous occurrence of the young larvae of *T. plumosus* in the dried mud, where the number of large larvae of this species was smaller, and the fact of the occurrence of *T. anthracinus* only in the mud deprived at the beginning of its macrofauna, are also the consequence of the weaker interaction of the organisms in such circumstances (on account of the smaller numbers).

On the basis of the review of literature made and the materials discussed it seems possible to find that the situation, in which in a given habitat a certain number of eggs occur (apart from the period of mass emergence and mass egg-laying), originating either from imagines emerging from the same habitat or from imagines from other neighbouring habitats, is a common one. As a result the species is enabled to occupy the habitat at any time if only favourable conditions exist in it.

It would seem that on account of the importance of phenology to the abundance of fauna, two types of benthos habitats must be distinguished: habitats in which a large number of species can live owing to the favourable conditions existing in them, and habitats in which the conditions permit of a small number only of species occurring (often only 1–2) which are specially adapted to the given habitat. The role of the phenology (in the sense of the period of mass-emergence of imagines and in consequence, mass egg-laying, occur), of the "concurrence" in time of mass emergence with conditions favourable to the life of the imagines and to the development of the larvae, will be of course relatively greater in the second type of habitat than in the first type of habitat. In the second type of habitat a specially unfavourable combination of circumstances is more likely to cause small numbers of the fauna than in the first type, where the small numbers of one species may be recompensated by other species, on which the given combination of unfavourable conditions exerts a weaker influence, or the development of which species takes place at a slightly different time.

CONCLUSIONS

1. It would seem that favourable conditions for the development of young larvae is often of greater importance to the appearance of these larvae in a ben-

thos habitat than the mass emergence of imagines and the eggs they lay. This is borne out by facts of the appearances of young larvae at very different periods not preceded by mass emergence of imagines, when even very slight changes in conditions take place.

2. It is not possible to conclude that there is no influx of eggs on the basis of an absence of appearances of young larvae; the reason for this may be the existence of conditions unfavourable to the development of the larvae.

3. In many cases the capacity for survival of benthos *Tendipedidae* is determined by the interaction (intra- and interspecific) of the organisms.

4. Emergence continuing to occur over a considerable period of time characteristic to the majority of *Tendipedidae* species (combined with a large number of eggs in the egg masses) are of great importance to the species – they make survival possible in cases in which the mass appearance of the imagines encounters conditions specially unfavourable to them, or in which conditions are unsuitable for the development of young larvae during the period of mass egg-laying.

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UWAGI O OKOLICZNOŚCIACH WARUNKUJĄCYCH POJAWY NOWYCH POKOLEŃ LARW *TENDIPEDIDAE*

Streszczenie

Porównano występowanie i liczebność młodych larw *Tendipedidae* bezpośrednio na dnie jeziora oraz w klatkach eksperymentalnych o wymiarach 30×30×30 cm, obszytych gazą perlonową o oczkach 0,5 × 0,5 mm. Stosowano 3 warianty eksperymentu: klatki kontrolne z mułem i fauną z danego środowiska, klatki z mułem pozbawionym (przez odsianie) makrofauny, oraz z mułem nieco podsuszonym. Prace przeprowadzono latem i jesienią 1960 r. na terenie jeziora Śniardwy (polymiktyczne, 100 km²).

Stwierdzono, że w wielu przypadkach w klatkach kontrolnych pojawiają się licznie młode larwy różnych gatunków *Tendipedidae*, podczas gdy w jeziorze pojawy młodych nie zachodzą. Co więcej, młode larwy niektórych gatunków nie wystąpiły ani bezpośrednio w jeziorze ani w klatkach kontrolnych, natomiast pojawiły się licznie w klatce z mułem pozbawionym na wstępie makrofauny, bądź z mułem podsuszonym. Fakty powyższe, jak również inne, zaczerpnięte z piśmiennictwa świadczą, że często o przeżywalności młodych larw decydują jakieś stosunkowo drobne różnice warunków, najczęściej umykające badaniu. Z pewnością w omawianych tu sytuacjach nie były to różnice ilości tlenu bądź substancji organicznej, często uznawane za decydujące dla liczebności bentosu; te 2 czynniki mogły być bowiem raczej mniej korzystne dla rozwoju larw w klatkach niż bezpośrednio na dnie jeziora.

Na podstawie braku pojawów młodych larw nie można sądzić o braku jaj; przyczyną mogą tu być nieodpowiednie warunki dla rozwoju larw, nawet w środowiskach pozornie korzystnych pod względem termiki, ilości tlenu, substancji organicznej itp.

Z omówionych tu faktów pojawu młodych larw w mule częściowo lub całkowicie pozbawionym makrofauny na początku eksperymentu, jak również z dyskusji piśmiennictwa wynika także duża rola wzajemnych oddziaływań organizmów bentosowych dla pojawów ich stadiów młodocianych.

Rozciągnięte w czasie wyloty większości gatunków *Tendipedidae* (w połączeniu z duża liczbą jaj w kładkach jajowych) mają duże znaczenie dla gatunku — pozwalają na przeżycie w tych przypadkach, gdy masowy wylot imagines natrafia na szczególnie niekorzystne dla nich warunki, bądź też kiedy w okresie masowego składania jaj nie ma warunków dla rozwoju młodych larw. W niniejszej pracy wielokrotnie

stwierdzano liczne pojawy młodych larw, mimo że nie poprzedzał ich masowy wylot imagines i masowe składanie jaj.

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