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ENERGY TRANSFORMATION BY *TANYPUS PUNCTIPENNIS (MEIG.)* (CHIRONOMIDAE) IN LAKE BALATON

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The chironomid larvae have an important role in the energy flow of the open water sediment of Lake Balaton. According to the first quantitative analysis (ENTZ, 1954), 60 biomass-per cent of zoobenthos comprise chironomid larvae. Besides ENTZ's later work (1965) PONYI et al. (1971) carried out quantitative investigation on the chironomid populations of the lake. It was shown already by early, semiquantitative investigation (MOON, 1934) that in the open water sediment larvae of *Tanypus punctipennis* (MEIG.) were predominant. According to the present results (PONYI and FRANKO, personal communication) covering all the lake, larvae of *Tanypus punctipennis* (MEIG.) remained predominant in the open water sediment, excluding Keszthely Bay and its surroundings where the larvae of *Chironomus plumosus* were dominant. Some places of the littoral zone are characterized by the larvae of *Cladotanytarsus mancus* and *Procladius* sp. (PONYI et al., 1971). The review of published results shows that our knowledge is very limited on the dynamics of chironomid populations especially on the energy transformation of important species.

In the years of 1973–74 in the open water sediment in front of the Biological Research Institute (Tihany) a detailed analysis was carried out on the seasonal dynamics, the age composition, the weight relation and the carbon content of the different size groups of the *Tanypus punctipennis* population for production evaluation, on the gut content for the evaluation of food consumption, and on the respiration of larval instars at different temperatures for evaluating the annual respiration at population level.

Materials and methods

The analyses were carried out on samples from the open water sediment in front of the Biological Research Institute (Tihany). The samples were collected by HARGRAVE (1969) sampler at about 500 metres from the littoral. Depending on larval density, $2-5\times225$ cm^2 sediment surface with 10 cm depth and at least 5 cm of overlying water was put in a plastic tank, diluted by filtered lake water, homogenized and screened by a 0.1 mm mesh size bronze screen. The living animals caught up on the screen after collecting and screening were selected under a microscope. The size of larvae (body length, body width,

width of head capsule) was read on an objective micrometer. All samples of every collection (altogether 9620 larvae) were selected to size groups.

The wet weight of larvae was measured by individuals blotted on-filter-paper. The dry weight was determined after a 24-hour drying at 105 °C. The carbon content was measured by bichromate wet oxidation. The gut content was washed into distilled water, analyzed under microscope then the dry matter content was measured after drying at 105 °C. The respiration of larvae was measured in a closed bottle containing filtered and aerated lake water, in each measurements 15 to 50 larvae were used depending on size. The oxygen content was measured by Winkler method in 50 ml sample. During the experiments the oxygen content in the bottles never decreased below 6 mg/l, and a complete mixing was produced by the larvae.

Results and discussion

Age composition

The most successful method for determining the age composition of chironomid populations is based on measuring the width of head capsule (Czeczuga et al., 1968). The age composition of the *Tanypus* populations was not measured earlier by this method. Prus (1969) used the length of larvae for determining the age composition of *Tanypus kraatzi* Kieff. population in Lake Wilkus. Kajak and Rybak (1966) distinguished only large, medium, and small-sized larvae in *Tanypus punctipennis* populations. In the population of Lake Balaton the larval instars are well selectable on the basis of the width of head capsule, and there are not overlappings *(Fig. 1)*. The head capsule can be used well for determining the age of this chironomid species. It was surprising that in the sediment only larvae of third and fourth instars were found. We have found only four individuals of second instar in a sample collected under ice in February *(Fig. 2)*. In the ice-free period the larvae of the first and second instars live in the plankton and it is possible that these few larvae collected under ice preferred the water-sediment surface with higher temperature. Although the planktonic life of young larval instars is known (Aleksejev, 1955; Morduhaj-Bolotskoj and Silova, 1955), the parallel quantitative analysis of planktonic and benthic samples would be very useful, especially

1. fig.

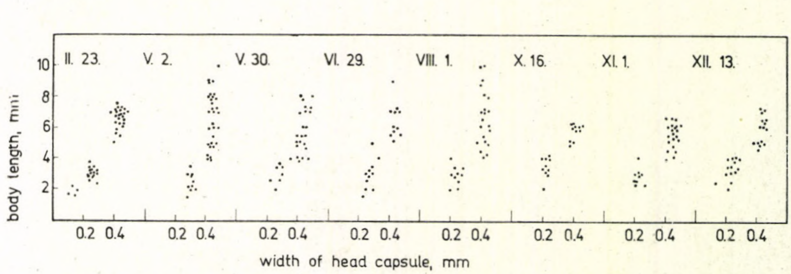

Fig. 1. Seasonal change of relationship between the width of head capsule and body length, on the basis of representative part of the total sample

at the predatory membiers of Tanypodinae subfamily. The width of the head capsule of larval instars was constant all the year round, but the length of larvae changed significantly.

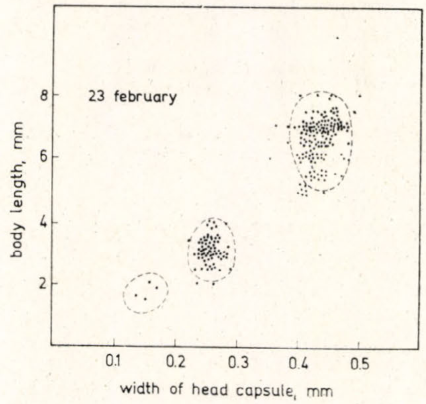

Fig. 2. Age composition of the under-ice total sample

The length of fourth instar in the autumn and winter samples showed less variation than the length of larvae collected in spring and summer times. The age composition of spring and summer populations is very complicated because there is a constant egg-laying and hatching in the entire vegetation period, and at the higher water temperature the uneven growth is more significant.

Population density

The number of larvae was highest in February in both years *(Fig. 3)*. According to KAJAK and RYBAK (1966) values higher than 1×10^4 m^{-2} characterize eutrophic lakes. In February the high larval density was connected not only with the better food condition, but also with the lower grazing activity of the fishes. The total number of larvae decreased quickly in the second half of February and in March. The under-ice decrease in absence of emerging imago could be explained by natural mortality and overgrazing. The thick diatom layer covering the sediment surface of the Lake Balaton in winter has a high daily primary production (HERODEK and OLÁH, 1973) supplying a favourable food condition for the large chironomid population. According to the gut content analyses the larvae feed actively in winter period grazing the thick diatomic carpet. Therefore the decrease of larvae in January and February can be explained by fish overgrazing and later by swarm of imagos. The summer population density compared to winter, under-ice values is very low. During the large swarm in June there are only few larvae of the last instar.

In the sediment we have found only two larval instars and so for the production estimation we had to form size-groups on the basis of body length. Larvae from 1 to 3 mm body length belong to the first size group, from 3 to

5 mm ones to the second size group and from 5 to 10 mm ones to the third size group. Larvae of the first size group appear first during the spring swarm and the larvae of this group can be found all the summer. Their highest number was found in December and in February, they practically disappeared from the sediment samples, that means they outgrew from this size group. This directly proves the active winter feeding and growing of larvae. The number of larvae of the third size group is low all the summer.

3. fig.

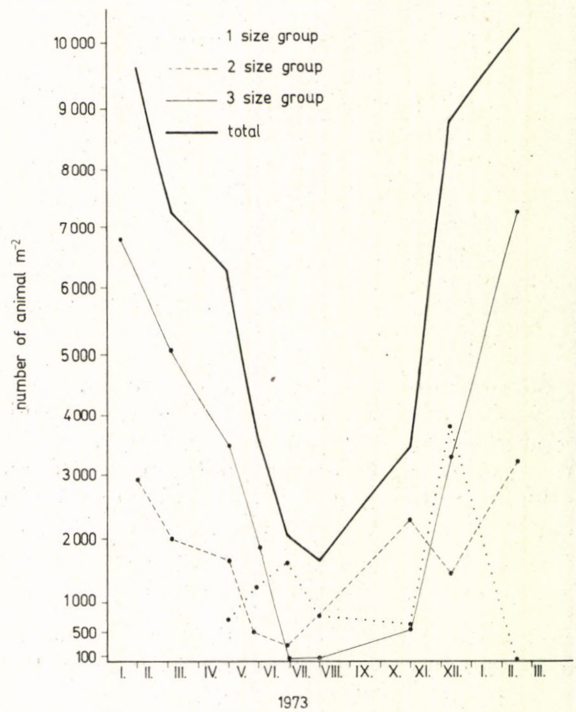

Fig. 3. Quantitative seasonal change of the size groups

Gut content

The members of Tanypodinae subfamily are generally considered as predators. ZILAHI-SEBES (1932) writing about *Tanypus punctipennis* population of Lake Balaton, stated that diatoms and plant detritus dominated in the gut of the larvae. TARWIN (1969) found a lot of plant food in the gut of the populations living in lakes of Poland. All these findings support LUFEROV's statement that the larvae of chironomids have high feeding plasticity.

According to our own gut content analyses the larvae of *Tanypus punctipennis*, especially the winter population consumes mainly diatoms in Lake Balaton. A population transforming the larger part of energy in the benthic community must be fed on plant food basis. According to our measure-

TABLE I

Weight, carbon content and gut content of the different size groups μg/individual (average)

	1. (1—3 mm)	2. (3—5 mm)	3. (5—10 mm)
	Size groups		
Wet weight	122	407	2270
Dry weight	20	64	392
Organic C	11	35	199
Gut content			
Dry weight	4	15	48

ments the ratio of gut content compared to body weight is different at the larval instars. On the basis of average data *(Table I)* the gut content is 4/8 part of body weight. The daily ratio of food consumption of chironomids is generally higher than 100 per cent and at higher temperature they can reach several hundreds per cent (Pchelkina 1950; Beljavskaja and Konstantynov 1956; 1961).

On the basis of measured gut content and the generally high daily ratios of chironomids the digestion time is very short, in water of 20 – 25 °C it is about two hours. On the basis of all these we can be informed only about the magnitude of food entering the digestive tract of *Tanypus punctipennis*.

Respiration

For the estimation of total respiration of the population we had to measure the respiration of larvae of different size groups at different temperature values. The relationship between the body length and respiration of

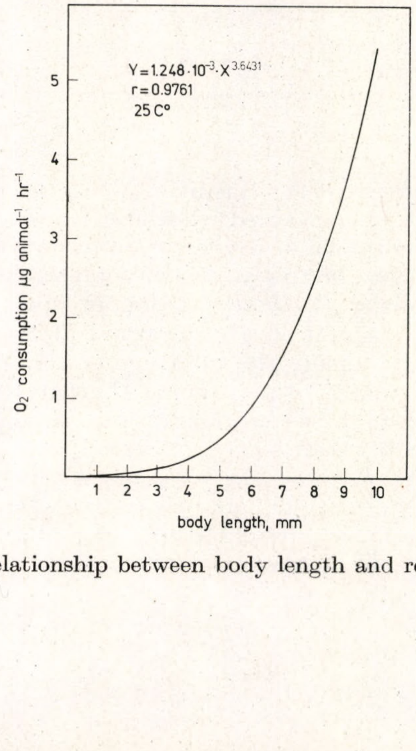

Fig. 4. Relationship between body length and respiration

larvae is followed by power function *(Fig. 4)*. This relationship was analyzed by ERMAN and HELM (1970) in several species of chironomids with the aim to determine the oxigen consumption of larvae only from the body length. The respiration of different body length larvae increased when the temperature had been increased up to 25 °C *(Fig. 5)*. At 30 °C the respiration of the second

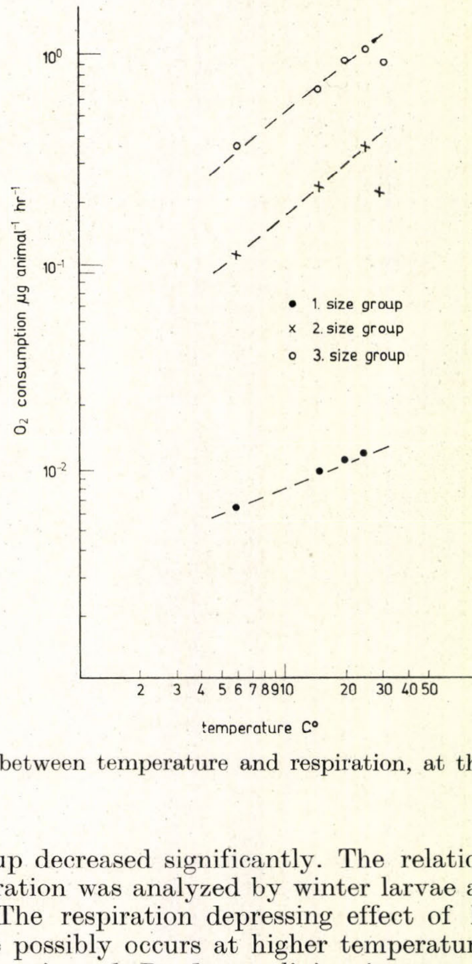

Fig. 5. Relationship between temperature and respiration, at the different size groups

and third size group decreased significantly. The relationship between temperature and respiration was analyzed by winter larvae after 24 hour temperature adaptation. The respiration depressing effect of high temperature at the summer larvae possibly occurs at higher temperatures. In the larvae of *Proclaudius nigriventris* and *P. choreus* living in open water sediment the decrease in intensity of respiration also occurred at 30 °C (LUFEROV, 1958). In EDWARDS (1958) experiments the intensity of respiration of *Chironomus riparius* MEIG. at 20 °C was 2.6 times higher than at 10 °C.

The estimation of total respiration of the population was lightened, because the relationship between body length and respiration was influenced slightly by temperature *(Fig. 5)*. The total respiration was evaluated from data of age composition, average monthly water temperature, population density and respiration of the different size groups at the given temperature *(Fig. 6)*. The respiration of the whole population was highest in May, and the respiration of the very high biomass at the low water temperature in February was much less. In July and August both biomass and respiration were low. According to our earlier analyses (PONYI et al., 1971) besides chironomids the biomass of most members of zoobenthos reached its minimum in August.

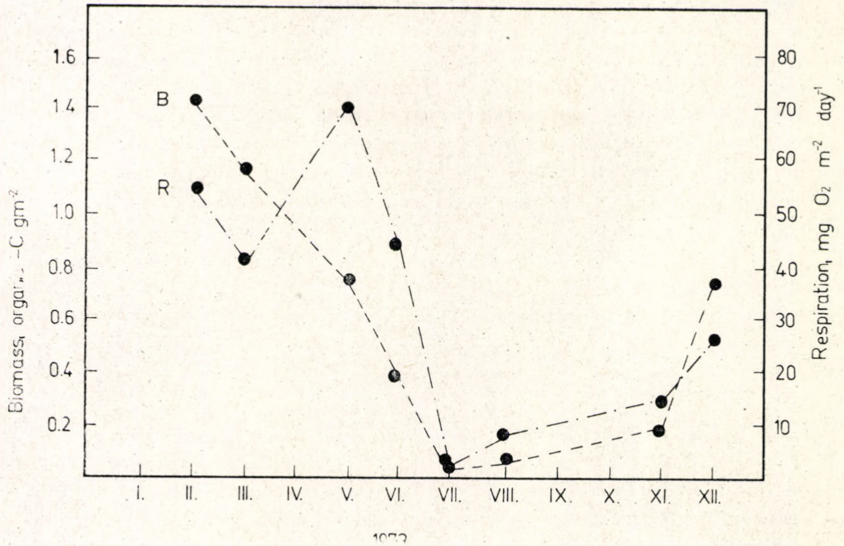

Fig. 6. Seasonal variation of the total population respiration (R) and of the average monthly biomass (B)

Growth and production

Originally we planned to estimate the production of the whole population by following detailed size groups analysis. But in summer months the age composition of the population was very complicated because of continuous egg-laying and hatching and so the selection of groups hatched at the same time was doubtful. The winter population originating from hatching after the autumn swarm forms a well-selectable size group with long, six months of growing period. After the large spring swarm (May or June) of this group the growing period was shortened very quickly. According to KAJAK and RYBAK (1966) at the northern Polish lakes the life cycle is two months in spring and one month in summer. Presumably the summer growing period at the population of Lake Balaton is less than the above-mentioned one. In autumn with decreasing water temperature the groups hatched nearly at the same time come to synchron and this results in the large autumn outswarm. The winter population with the long growing period originates from eggs of these imagos. On the basis of these in Lake Balaton annually there are at least five generations of *Tanypus punctipennis*.

The biomass of summer generations is very low, and the growing is quick, so the energy flowing through the population during a given time is approaching the other periods.

Because of complicated summer age composition, and at the same time in the knowledge of total respiration of population the equation of McNeill and Lawton (1970) was applied for the estimation of the annual production of *Tanypus punctipennis*. The ratios in the equation of the computed energy budget (A,59.3 = R,41.5 + P,17.8 Kcal m^{-2} $year^{-1}$) is similar to ratios of energy budget of *Glyptotendipes barbipes* (Staeger) gained by another method (Kimerle and Anderson, 1971). The basis of production estimation from the respiration is that the ratio of production and respiration of different invertebrate populations is fairly similar (McNeill and Lawton, 1970).

In Lake Balaton the annual energy flow through *Tanypus punctipennis* populations is about four per cent of the primary production of the lake, and the production of population is 1.2 per cent of the primary production. From the total respiration of the benthic populations 8 per cent is given for the population of *Tanypus punctipennis* (Oláh, 1975). The production of this chironomid species alone in the lake approaches the energy required for the total fish population (A, fish, Biró, 1974).

Conclusions

1. The age composition of population was determined seasonally on the basis of the width of head capsule of larvae. In the sediment there were found only the third and fourth larval instars and so it is reasonable to consider the first and second instars to be planktonic. In summer the age composition is very complicated owing to the almost continuous egg-laying and hatching.

2. The population density reached its maximum in February with a biomass higher than 1.4 g organic-C m^{-2}. In summer the biomass was very low, in July and August it was below 0.1 g organic-C m^{-2}. The high winter biomass is connected with the high, under-ice benthic primary production and the low grazing by fish.

3. *Tanypus punctipennis* considered to be predator consumes mainly diatoms in Lake Balaton. The measured gut content and the daily ratios known from the literature suggest high food consumption.

4. The relationship between body length and respiration of larvae: $y(\mu g\ O_2\ larvae^{-1}\ hour^{-1}) = 1.248 \cdot 10^{-3} \cdot \times (\text{body length, mm})^{3.6431}$.

The total respiration of population was estimated on the basis of data of age composition, average monthly water temperature, population density and respiration data of the given temperature and size group.

5. The winter population originating from hatching after the large autumn swarm has a six month long growing period. The growing period of summer populations shortens for one month. According to energy budget estimated by McNeill and Lawton equation (A,59.3 = R,41.5 + P,17.8 Kcal m^{-2} $year^{-1}$) the annual energy flow through the population is about four per cent of the primary production of the lake. The production of *Tanypus punctipennis* alone approaches the energy required for the fish population.

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A *TANYPUS PUNCTIPENNIS* (MEIG.) ÁRVASZÚNYOG ENERGIATRANSFORMÁLÁSA A BALATONBAN

Oláh János

Összefoglalás

1. A lárvák fejtok szélessége alapján évszakosan meghatároztuk a populáció korösszetételét. Az üledékben csupán a harmadik és negyedik lárvastádium él, az első és döntően a második is planktonikus életmódot folytat. Nyáron a korösszetétel a közel folyamatos peterakás és kelés miatt nagyon bonyolult.

2. A populáció-sűrűség februárban éri el maximumát, ekkor a biomassza valamivel meghaladja az 1,4 g szerves-C/m^2-t. Nyáron a biomassza nagyon alacsony, július és augusztus hónapkban 0,1 g szerves-C/m^2 alatt van. A nagy téli biomassza összefügg a Balatonra jellemző jelentős téli, jégalatti bentikus elsődleges termeléssel.

3. A ragadozónak tartott *Tanypus punctipennis* a Balatonban döntően kovamoszatokkal táplálkozik. A mért béltartalom és az irodalomból ismert napi arányok jelentős táplálékfelvételre utalnak.

4. A lárvák testhossza és légzése közötti összefüggés: Y = 1,24 × 3,64. A populáció összlégzését a korösszetétel, az átlagos havi vízhőmérséklet és populáció-sűrűség, valamint az adott hőmérséklet és méretcsoport légzés adatainak a felhasználásával számítottuk.

5. A nagy őszi rajzást követő kelésből származó téli populáció hosszú, hat hónapos fejlődési ciklussal bír. A nyári populációk fejlődési ideje egy hónapra lerövidül. A McNeil- és Lawton-egyenlettel számított energia háztartási mérleg (A,59,3 = R,41,5 + P,17,8 Kcal m^{-2} év^{-1}) szerint a populáción évente átfolyó energia a tó elsődleges termelésének mintegy 4 százaléka. Összességében a tóban egyedül a *Tanypus punctipennis* produkciója megközelíti a halállomány számára szükséges energiamennyiséget.