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INVESTIGATIONS INTO THE REPRODUCTION AND MORTALITY OF TUBIFICIDAE IN LAKES*

ABSTRACT: With increasing depth the indices of daily egg production decreased, while the breeding periods elongated. Consequently, the fecundity of groupings did not show any clear relationship to depth. The rate of elimination during embryonic development and immediately after hatching attained 59–72% of the total number of eggs laid. In the study environments tubificid cocoons were found in the sediment layer 0– > 15 cm deep. In laboratory experiments, with no predators present, the highest mortality of embryos was recorded for the surface sediments and the lowest for the depth of 2–5 cm. The mortality of newly hatched individuals depended on the depth at which the cocoons were incubated in the sediments, the greater the depth the higher the mortality. For development of eggs of Tubificidae derived from the profundal the optimum temperature was about 12°C.

KEY WORDS: Lakes, benthos, Tubificidae, breeding periods, reproductiveness of groupings, mortality.

Contents

1. INTRODUCTION

Although for the last several years there has been a considerable growth in the researches into the ecology of Tubificidae, including their life cycles and reproduction

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(Poddubnaja 1958, 1972, Kennedy 1966, Timm 1968, 1972, 1974, Jonasson and Thorhauge 1972, Kosiorek 1974, Thorhauge 1975, 1976), certain important problems relating to density regulation and productivity of Tubificidae have not so far been studied sufficiently. Apart from this, because of the use of different study methods, the comparability of the results obtained by different authors, especially those dealing with the assessment of the fecundity and mortality of Tubificidae at various ontogenetic growth stages, is poor.

The aim of the present investigations was to determine the length of the breeding periods, to analyse the reproductiveness of tubificid groupings in different zones of a lake and to establish the death rate of tubificid embryos during development and of young individuals immediately after emergence from the cocoons.

2. MATERIAL AND METHODS

The investigations were carried out in the lakes Tałtowisko, Mikołajskie and Śniardwy (Table I) belonging to the Great Masurian Lakes. The regularities of occurrence and production of benthos in these lakes have been studied for many years and they are well known (Prejs 1969, Kajak and Dusoge 1975a, 1975b, 1976).

Table I. A short description of the lakes studied

Parameters	Tałtowisko	Mikołajskie	Śniardwy
Area (ha)	326.9	460.0	10598.4
Average depth (m)	14.0	11.0	5.9
Max. depth (m)	39.5	27.8	25.0
Limnological type	mesotrophic	eutrophic	eutrophic
Mixis	dimictic	dimictic	polymictic
Oxygen deficit during stagnation	absent	present	absent
Content of organic matter in bottom sediments of profundal (per cent d. wt sediments)	23*	29	38*

*According to Rybak (1969).

The length of breeding periods and egg production of Tubificidae were estimated on the basis of benthos material collected from the study lakes in the years 1970–1972. Benthos samples were collected with a tubular bottom sampler 43 cm^2 in area (Kajak, Kacprzak and Polkowski 1965). In Mikołajskie Lake samples were collected from a transect at depths 11, 16 and 25 m, in Lake Tałtowisko also from a transect at depths 6, 11, 16, 25 and 37 m, in Lake Śniardwy at a mid-lake site 7.5 m deep. At shallower sites (up to 11 m inclusive) 10 samples were taken each time. Because of the fact that the variation in density decreases with the depth, at all other sites 5 samples were taken each time. In summer, samples were collected at 2–3 weeks' intervals, in spring and autumn once a month, and twice in winter: at the beginning of the freezing period and before the disappearance of the ice cover. Simultaneously with the collecting of benthos samples the water temperature near the bottom was measured with a thermistor thermometer.

To determine the vertical distribution of tubificid cocoons in the sediments, in June 1971 at all sites layer samples were collected twice, 10 samples each time, according to the method described and checked previously (K a j a k, K a c p r z a k and P o l k o w s k i 1965, K a j a k and D u s o g e 1971). The five layers distinguished were as follows: from the surface to a depth of 2 cm, 2–5 cm, 5–10 cm, 10–15 cm and over 15 cm (up to a depth of 20–27 cm, depending on the hardness of the bottom).

Immediately after their collecting all benthos samples were washed on a sieve with a metal net, 0.2 × 0.2 mm in mesh size, and preserved in 4% formalin solution. The segregation of the individuals and cocoons of Tubificidae was made in the laboratory under a stereomicroscope, using 8– and 12.5-fold magnification against a dark background. This made it possible to segregate even very small individuals. Simultaneously, the body-length of the tubificids was measured to the nearest 1 mm.

The rate of embryonic growth and the mortality of embryos and juvenile individuals immediately after their emergence from the cocoons were investigated in laboratory experiments. The experiments were carried out with newly laid cocoons with eggs at early cleavage stages, selected from benthos samples collected from the profundal of Mikołajskie Lake.

For studying the relationship between the rate of embryonic growth and mortality and the temperature, glass containers, 6 cm in diameter and 4 cm high, were used. Each of them contained a 2 cm mud layer covered with a 1 cm water layer. In the mud layer of each container tubificid cocoons were placed, at a depth of 1–1.5 cm, each containing a known number of eggs. Container series, each consisting of 4, were exposed in the dark at temperatures 3, 5, 7, 12, 17 and 25°C with an accuracy of ±1°C. Embryos kept at 12–25°C were checked every 2 days for maturation, at 7°C – every 4 days, and at 3.5°C – every week. The following times were determined: the time after which the first young individuals hatched, the time after which 50% of the cocoons were found empty, the time of hatching of the last individuals, and the numbers of non-developing eggs and dead embryos.

The relationship between the mortality of embryos during their growth as well as of young individuals after emergence from the cocoons, and the depth at which the cocoons had been deposited in the sediments was investigated by a procedure based on experimental cylinders (K a j a k, K a c p r z a k and P o l k o w s k i 1965). Plexiglass cylinders with a section area of 43 cm^2 and a height of 17.5 cm containing undisturbed mud from the profundal of Mikołajskie Lake were immersed in a water thermostat filled with lake water. Tubificid cocoons with a known number of eggs were placed, using a bent-end pipette, on the surface of the mud, at depths up to 2, 2–5, 5–10, 10–15 and over 15 cm, in separate series of experimental cylinders. The content of oxygen in the water above the mud surface in the experimental cylinders was checked. It did not fall during the experiment below 2.4 mg $O_2/1$. The experiments were conducted in the dark at a temperature of 17 ± 1°C, with no predators present.

To extimate the mortality of embryos in cocoons placed in the sediments at different depths, 6 cylinders of each series were exposed for 18 days. After the exposure the contents of the cylinders were washed in small amounts on a sieve 0.2 × 0.2 mm in mesh-size. The cocoons were removed and examined under the stereomicroscope to determine the number of living embryos and dead eggs in them.

A similar procedure was applied in order to assess the mortality of juvenile tubificids immediately after their emergence from the cocoons, but in this case the exposure time allowed was 25 days. After this period the mud from the cylinders was washed in small amounts on a sieve of a mesh-size 0.15 × 0.15 mm. The aim of this procedure was to collect all the juvenille individuals.

3. RESULTS

3.1. QUALITATIVE DESCRIPTION OF THE TUBIFICID GROUPINGS UNDER STUDY

The qualitative diversification of the tubificids found in the habitats studied was relatively small. The most diverse, in respect of the number of species, tubificid groupings in Lake Tałtowisko at depths of 6 and 11 m consisted of 6 and 5 species, respectively, and in Mikołajskie Lake at a depth of 11 m – 3 species (Table II). The dominant species was *Potamothrix hammoniensis*, widely spread in the lakes of moderate climatic zone. Of the other species occurring in Lake Tałtowisko only *Tubifex tubifex* and *Limnodrilus hoffmeisteri* at a depth of 6 m, and *Psammoryctides barbatus* at a depth of 11 m were recorded regularly, each of them representing over 10% of total Tubificidae. The remaining two species were encountered sporadically.

Table II. Species composition and dominance structure of tubificid groupings in the lakes under study

Species	Percentage in total numbers of Tubificidae in the study lakes and at different depths (m)					
	Tałtowisko			Śniardwy	Mikołajskie	
	6	11	16–37	7.5	11	16–25
Psammoryctides barbatus (Grube)	8.6	10.2			5.2	
P. albicola (Mich.)	6.0					
Tubifex tubifex (Müll.)	12.2	8.2				
Limnodrilus hoffmeisteri Clap.	10.8	8.4				
Peloscolex ferox (Eisen)	6.6	6.4			2.2	
Potamothrix hammoniensis (Mich.)	55.8	66.3	100.0	100.0	92.6	100.0

In the central part of Lake Śniardwy and in the profundal of lakes Tałtowisko and Mikołajskie, from a depth of 16 m the only representative of Tubificidae was *P. hammoniensis*.

3.2. BREEDING PERIODS AND THE FECUNDITY OF TUBIFICIDAE

The duration of the breeding periods was determined on the basis of the presence in tubificid groupings of sexually mature individuals with clitella and eggs in egg sacs, and of tubificid egg cocoons with early growth stage embryos in the sediments.

The length of the periods of embryonic growth and of maturation of the young in most cases exceeded the time interval between the successive dates of sample collecting. As a result, some cocoons and juvenile individuals were encountered several times, at different growth stages, in the series of samples collected on different dates. For this reason, only those cocoons and juvenile individuals were taken into account which appeared in the habitat between two successive sampling dates.

The growth stages attained by the eggs laid in this period and the growth of the young emerging from the cocoons at this time were established on the basis of the results from laboratory studies of the relationship between the rate of embryonic development and growth of young individuals, and temperature. Five easily recognizable embryonic stages were distinguished: (1) the egg at the initial cleavage stage, (2) the gastrula, (3) the horseshoe-shaped embryo, 4–5 times as long as it was thick, (4) the elongate embryo with a body-length 6–10 times as large as the breadth and (5) the completely formed individual prior to its emergence from the cocoon.

The age of young individuals was estimated on the basis of body length. The above-described way of analysing the field material made possible a relatively accurate determination, in the habitats studied, of the production of eggs in different stages of breeding periods and of the recruitment of young individuals to the tubificid groupings.

The length of the periods of sexual reproduction (egg laying), the occurrence of sexually mature individuals and the production of eggs by Tubificidae varied with the depth.

In shallower habitats, in the sublittoral of Lake Tałtowisko (depth 6 m) and the central part of Lake Śniardwy (depth 7.5 m), the breeding periods were comparatively short. Sexually mature individuals with clitella occurred almost exclusively in spring and in summer (Fig. 1). The first cocoons with eggs appeared in spring – in March and April with an increase in the temperature of the near-bottom water to about 4–5°C (Fig. 2). A distinct peak fecundity period occurred at the end of the spring – in May or June. Then the daily egg production attained a rate of 1.5–1.9 eggs per one sexually mature individual with a clitellum. In summer when the temperature of the near-bottom water exceeded 15–17°C the egg production decreased. The last cocoons were deposited in August and at the beginning of September when the temperature of the near-bottom water was 17–19°C. In autumn and in winter the sexual reproduction of Tubificidae was interrupted.

At sites in the upper part of the profundal (depths 11 and 16 m in lakes Tałtowisko and Mikołajskie) sexually mature individuals with clitella were found almost throughout the year

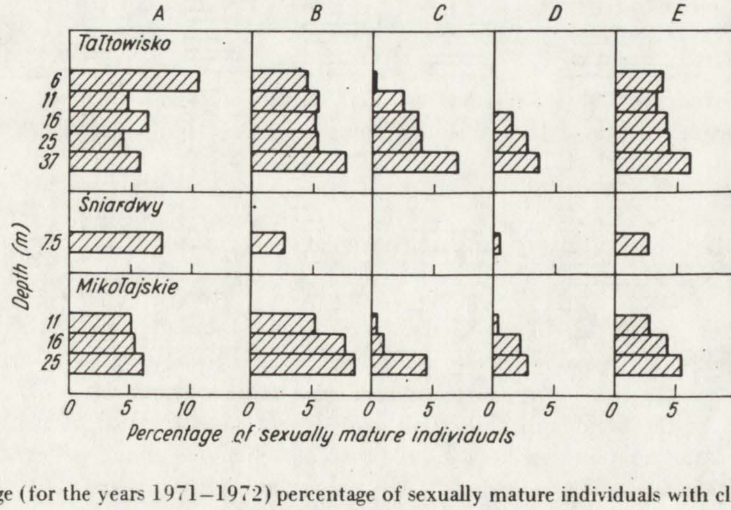

Fig. 1. Average (for the years 1971–1972) percentage of sexually mature individuals with clitella in tubificid groupings in the study environments

A – spring circulation. B – summer stagnation. C – autumn circulation. D – winter stagnation. E – average for the year. For the polymictic Lake Śniardwy the same periods are given for the purpose of comparison

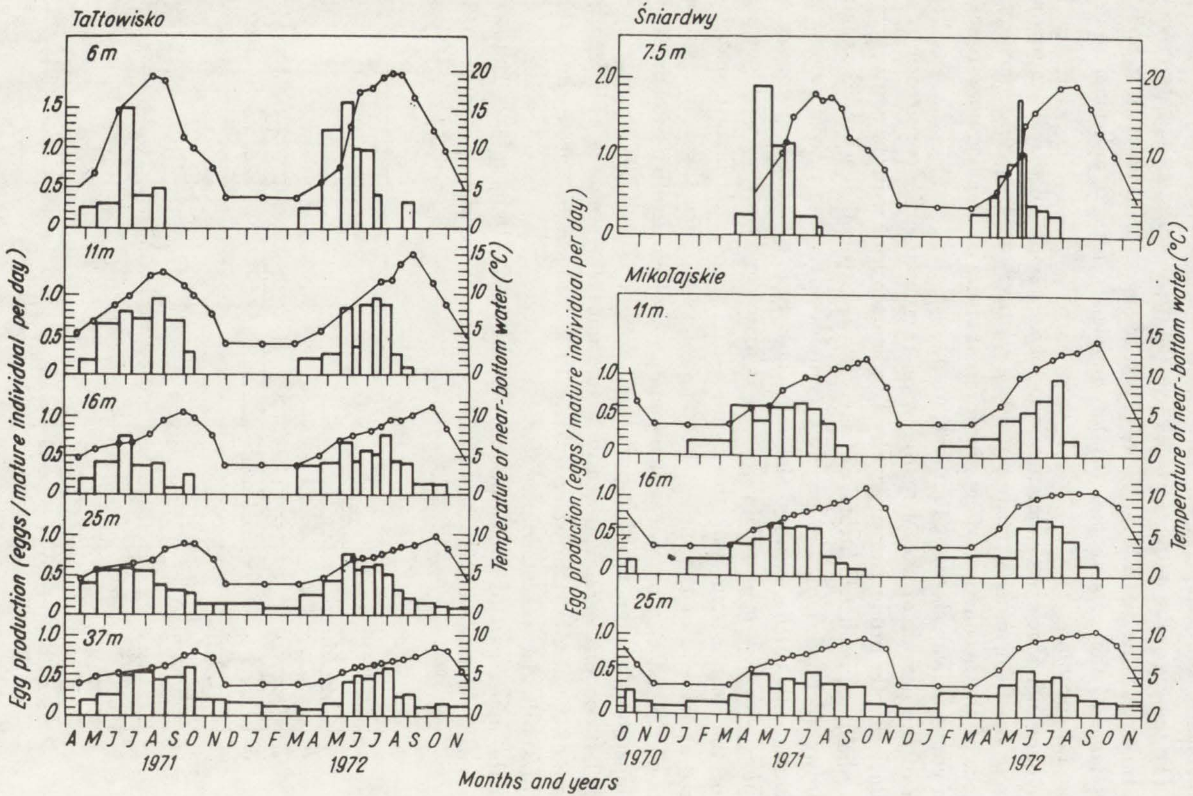

Fig. 2. Variations in egg production by Tubificidae in the habitats studied (columns) against temperature changes in the near-bottom water (continuous line)

(Fig. 1), their percentage in the tubificid groupings being the highest in spring and summer. The first cocoons with eggs appeared in winter and spring when the near-bottom water temperature was 3.5–5°C, at an earlier date in Mikołajskie Lake than in Lake Tałtowisko (Fig. 2). Periods of intensive egg deposition in the upper part of the profundal, more drawn out in time than at shallower sites, lasted from spring until the end of summer. Daily egg production then attained the level of 0.4–0.9 egg per one sexually mature individual with a clitellum. The last cocoons were deposited in autumn – at the end of September and in October. At the end of autumn and at the beginning of winter there followed an interval in the sexual reproduction.

In the deep profundal (Mikołajskie Lake – 25 m, Lake Tałtowisko 25 and 37 m) a high percentage of sexually mature individuals with clitella in the total number of Tubificidae was maintained from spring until autumn, the highest percentage occurring in summer (Fig. 1). In winter the proportion of these individuals decreased, but was still greater than at shallower sites. Deposition of cocoons took place throughout the year. The highest values of daily egg production, 0.4–0.7 egg per a sexually mature individual with a clitellum, were recorded from April to October at water temperatures of 5–10°C (Fig. 2). In winter, when the temperature of the water dropped below 4°C, egg production was much lower – 0.05–0.1 egg per one sexually mature individual with a clitellum per 24 hours.

The average percentage of sexually mature individuals with clitella in the tubificid groupings increased with the depth (Fig. 1). This probably resulted from the slowing down of the life processes and the associated elongation of the periods of sexual maturity of the individuals as the temperature of the water decreased.

Table III. Description of the reproductiveness of Tubificidae in the environments studied (average for the years 1971–1972)

Lake	Depth (m)	Egg production (eggs/m^2 per year) A	Abundance of the youngest generation replenishing the grouping in the given year (ind./m^2) B	Average density of other generations (ind./m^2) C	Reproductiveness of grouping A/C	Index of grouping renewal B/C
Tałtowisko	6	11420	3840	1320	8.6	2.9
	11	10740	3840	1970	5.4	1.9
	16	9390	2980	1800	5.2	1.6
	25	20530	6220	4290	4.8	1.4
	37	13290	3740	2740	4.9	1.4
Śniardwy	7.5	10740	3490	1780	6.0	2.0
Mikołajskie	11	22640	9290	4130	5.5	2.2
	16	32200	10030	4340	7.4	2.3
	25	20050	5530	2820	7.1	2.0

The decrease in the daily egg production with depth and with the fall of the average temperature of the near-bottom water was partially compensated for by the elongation of the periods of sexual reproduction and an increased percentage of sexually mature individuals in the tubificid groupings. As a result, the reproductiveness of the grouping, calculated as a ratio of the number of eggs laid during the whole season of sexual reproduction (year) to the average numbers of Tubificidae, except the youngest generation hatching from eggs laid during the current year, did not show a clear dependence on the depth (Table III). The highest fecundity, 7.1–8.6 eggs per an individual, was recorded for tubificid groupings in the sublittoral of Lake Tałtowisko and in the profundal of Mikołajskie Lake at depths 16 and 25 m, the lowest – 4.8–4.9 eggs per an individual was recorded for the deep profundal of Lake Tałtowisko (depth 25 and 37 m).

3.3. MORTALITY OF TUBIFICIDAE AT EARLY STAGES OF ONTOGENETIC GROWTH

The considerable difference between the number of eggs laid during the whole period of sexual reproduction (year) and the number of individuals in the youngest generation, recruited to the tubificid groupings in the given year (Table III), indicates a high rate elimination of embryos during their development, and of young individuals immediately after their emergence from the cocoons. This elimination, defined as a per cent ratio of the above difference to the total number of eggs, varied in the habitats studied, in average values for both study years, between 59.0 and 72.4% (Table IV); it was the highest in the deep profundal of the lakes Tałtowisko and Mikołajskie, and the smallest in Mikołajskie Lake at a depth of 11 m.

Table IV. Elimination of Tubificidae during embryonic growth and immediately after emergence from cocoons (in per cent of total number of eggs; average for the years 1971–1972)

Elimination	Lake and depth (m)								
	Tałtowisko					Śniardwy	Mikołajskie		
	6	11	16	25	37	7.5	11	16	25
On the basis of field studies of benthos	66.4	64.2	68.3	69.7	71.8	67.5	59.0	68.8	72.4
Calculated on the basis of cocoon distribution in the sediments by using the coefficients obtained from laboratory experiments	66.1	62.1	61.5	64.4	60.8	56.1	51.0	63.5	60.2

Among the probable causes of the elimination of Tubificidae during the embryonic growth and immediately after emergence from the cocoons special attention was paid to the distribution of cocoons with eggs in the sediment layer, and the effect of temperature.

In the habitats studied, tubificid cocoons with eggs were found in the sediment layer from the surface down to a depth of over 15 cm (Fig. 3). The cocoons were unevenly distributed in the sediments. In the surface sediment layers, to a depth of 2 cm, 5.1% (Tałtowisko – 25 m) to 12.6% (Tałtowisko – 37 m) of eggs occurred, no cocoons being found on the surface of the sediments. The main bulk of the tubificid eggs (from 64.5% in Lake Śniardwy at the depth of 7.5 m, to 83.3% in Mikołajskie Lake at the depth of 11 m) was accumulated in the sediment layer at a depth from 2 to 10 cm. The presence of cocoons in deeper layers depended on the structure of the sediments. In soft, thick sediment layers (the deep profundal of the lakes Tałtowisko and Mikołajskie) and in porous sediments with a high content of shells (Lake

Tałtowisko – 6 m) 3.5–8.4% of eggs were still found at depths below 15 cm. In thin sediment layers, overlying compact sand with loam, the occurrence of cocoons was limited to the depth of 10 cm (Mikołajskie Lake – 11 m).

Because tubificids deposit cocoons with eggs at various depths in the thickness of the sediments, in different environmental conditions, the chance of the eggs to successfully complete their development varies. Furthermore, this makes it necessary for the young individuals, which usually live in the surface sediment layer (P o d d u b n a j a 1962, K a j a k and D u s o g e 1971), to migrate towards the surface immediately after their hatching.

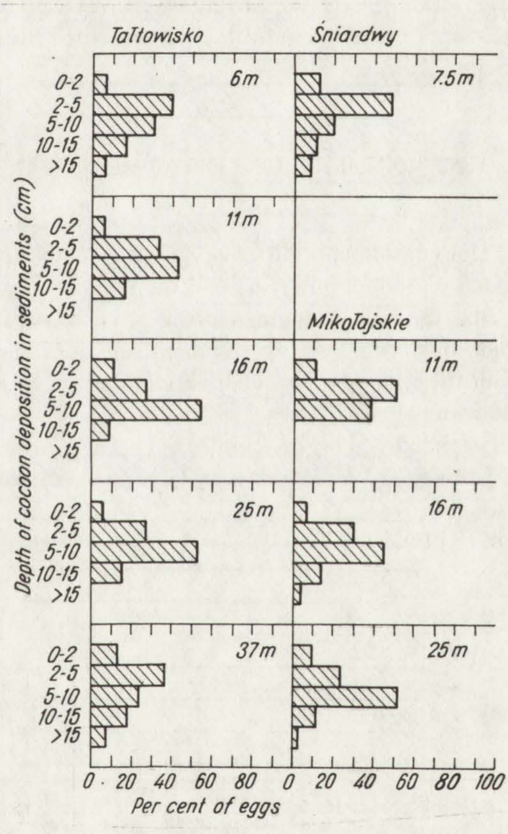

Fig. 3. Vertical distribution of egg cocoons in bottom sediments in the habitats studied (June 1971)

Laboratory investigations without predators have shown that there was some relationship between the depth at which cocoons with eggs were deposited and the death rate of embryos during development and of juvenile individuals immediately after their emergence from the cocoons (Fig. 4). In cocoons placed on the surface of the sediments embryo mortality was 100% (Fig. 4 A). This was caused by the microorganisms that attacked the cocoons, which led to the death of the eggs. The same was the cause of the considerable mortality (39.6%) of embryos in the cocoons deposited in a sediment layer at depths down to 2 cm. The smallest number of dead embryos was found in cocoons at depths of 2–5 cm (22.4%). A further growth of the incubation depth resulted in a gradual increase in the mortality of embryos, up to a maximum of 72.7% in the sediment layer at a depth below 15 cm.

The mortality of the young individuals immediately after their emergence from the cocoons was directly proportionate to the depth at which the cocoons were deposited (Fig. 4 B). An average of 6.7% of the young emerged from cocoons incubated at the depth of 2 cm died, the death rate increasing with the depth. Individuals emerged from cocoons deposited at a depth greater than 10 cm did not practically reach the surface of the sediments; the mortality rate during the migration from depth 10–15 cm was 94.3%, and from depths greater than 15 cm – 100%.

The lowest total mortality of Tubificidae during the embryonic growth and immediately after their hatching (Fig. 4 C) was recorded for those sediment layers in which in natural environments most of the egg cocoons occur. One may, therefore, presume that the manner of distribution of the egg cocoons in the thickness of the sediments is an adaptive feature of

Tubificidae, ensuring the recruitment of young individuals, this being essential for the lasting of a population.

Values of the elimination of embryos during their growth, and of the young immediately after hatching calculated from the difference between the total number of eggs laid and the number of individuals of the generation hatched during the given year, and determined on the basis of the distribution of eggs in the thickness of the sediments (using the coefficients obtained from laboratory experiments), show a considerable similarity in most of the habitats under study (Table IV). It may thus be assumed that the manner of cocoon distribution in the sediments is the main factor determining the elimination of Tubificidae at these growth stages.

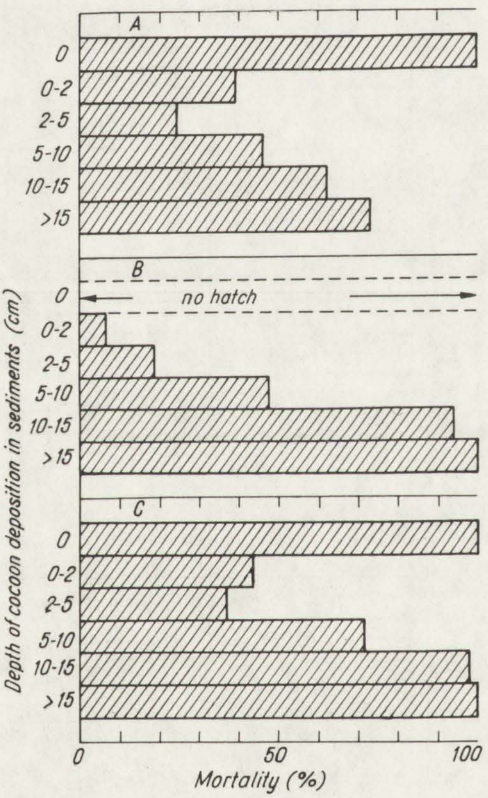

Fig. 4. Relationship between the mortality of embryos and young individuals of Tubificidae and the depth of cocoon deposition
A – mortality of embryos during growth, B – mortality of young individuals immediately after emergence from the cocoons, C – total mortality of embryos and young individuals

In the particular situations the temperature at which the embryos develop may have some effect on their mortality. Laboratory experiments have demonstrated that a temperature approaching 12°C was the optimum temperature for the growth of tubificid embryos in cocoons derived from the profundal of Mikołajskie Lake, because the growth rate was relatively fast and the mortality was low. When the temperature rose or dropped, the mortality of embryos increased, attaining a level of almost 100% at 3.5°C (Fig. 5).

In the environments studied, temperatures near the optimum existed for a longer time during the periods of sexual reproduction of Tubificidae only in the upper zone of the profundal, at a depth of 11 m, and in 1972 also at a depth of 16 m (Fig. 2). At shallower sites the embryonic growth was faster at temperatures 15–20°C, whereas in the middle and the deep zones of the profundal (16–37 m) usually below 10°C, and in winter and early spring – at temperatures 3.6–5°C. This permits the presumption that the high mortality of tubificid embryos in the deep profundal, much higher than the one calculated on the basis of the distribution of eggs in the sediments (Table IV), was to some extent caused also by the adverse thermic conditions.

Due to the low reproductiveness of the tubificid groupings and a high death rate of embryos during their growth, and of young individuals during migration from sites of cocoon deposition to the surface layers of the bottom sediments, the ratio of the number of individuals of the

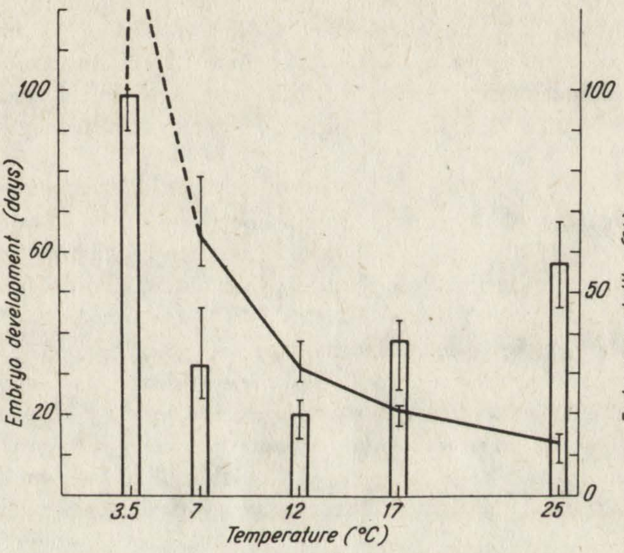

Fig. 5. Relationship between the development rate (line) and mortality of tubificid embryos (columns) and temperature. Vertical lines denote the time of hatching of the first and the last individuals, respectively, or the range of variation in embryo mortality in different repetitions of the experiment. Dashed line represents the hypothetical development rate at low temperatures

youngest generation (recruited to the grouping during the given year) to the average density of older generations was low, ranging from 1.4 (deep profundal of Lake Tałtowisko) to 2.9 (sublittoral of Lake Tałtowisko) (Table III). This ratio defines the possibility of the tubificid groupings to re-create their numbers.

4. DISCUSSION

Among the problems related to the population dynamics of tubificid groupings much attention is given to the relationship between sexual reproduction and various environmental conditions. The results provided by studies indicate considerable differences especially in the range of temperatures at which egg cocoons are deposited, and in the periods of sexual reproduction and fecundity in different habitats.

By way of experiments, K o r o t u n (1959) estimated the lower and the upper thermal thresholds of the fecundity of *Tubifex tubifex* from the lakes and rivers of the environs of Kiev at 11 and 33°C. According to B r i n k h u r s t (1964), many tubificid species in a large number of European lakes have one reproduction period in the year. It occurs in summer when the temperature is above 15°C.

As a result of long-term researches in Lake Esrom it has also been established that in the profundal at a depth of 11–20 m *Potamothrix hammoniensis* population reproduces once a year (T h o r h a u g e 1975). Cocoon deposition at a depth of 11 m lasted from April to mid-June at water temperatures 5 to 11–13°C, and at the depth of 20 m – from May to July at temperatures 7 to 8–10°C. The average water temperature during the sexual reproduction at both depths was 8–9°C.

In the lakes of Estonia, T i m m (1970) found the first cocoons of *P. hammoniensis* in April, before the disappearance of ice, at a water temperature of 2.5°C. He also observed differences in the periods of multiplication of this species at different depths in Lake Saadjärv; at the depth of 2.5 m cocoon deposition took place in April and May, while at the depth of 22 m – in July and August.

B o n o m i and R u g g i u (1966) observed reproduction of *P. hammoniensis* throughout the year in a habitat characterized by constant low temperatures of the water (Lago di Mergozzo, Italy, depth 70 m, temperature 4.5°C). Similarly, in Lake Hjälmaren, M i l b r i n k (1973) found sexually mature Tubificidae throughout the year, but, in accordance with the opinion of other authors (B r i n k h u r s t 1964, T i m m 1970), the presence of sexually mature individuals does not prove that cocoon deposition did take place.

The factor causing differences in the length of the sexual reproduction periods may also be the level of food supplies in the habitat. According to K e n n e d y (1966), the reproduction of *Limnodrilus hoffmeisteri* in richer habitats continued throughout the year, maximum sexual activity occurring in winter and spring, while in less rich habitats the reproduction was limited to the spring-summer period and the sexual activity grew with the temperature.

In the Masurian lakes under investigation, the course of sexual reproduction varied with the depth (Fig. 2). In the sublittoral of Lake Tałtowisko and in the central part of Lake Śniardwy (depths 6–7.5 m) cocoon deposition started in spring, in March or April, when the temperature of the water near the bottom was 4–5°C. In summer, when the temperature of the near-bottom water was 15–17°C, a decreased rate of cocoon deposition was recorded. With increasing depths, and as the average temperature of the near-bottom water dropped, the sexual reproduction periods elongated. In the deep profundal of the lakes studied, where the temperature of the near-bottom water was maintained in the range 3.6–10.5°C, cocoons were deposited continually throughout the year. Sexual activity depended on the temperature: the highest cocoon production was observed in summer at temperatures 6–7°C, and the lowest in winter.

The elongation of the periods of sexual reproduction with the fall of the average temperature of the water agrees with the findings reported by other authors (e.g., T h o r h a u g e 1975). This process may have been favoured by a high nutrient content in the profundal of the lakes under study.

The variable range of temperatures at which cocoons are deposited indicates a wide range of possibilities for Tubificidae to adapt to different local conditions. This may be a factor facilitating wide spreading and attaining considerable densities in diverse aquatic environments.

The available data on the fecundity of Tubificidae and on the relationship between the fecundity and the various environmental conditions come primarily from laboratory experiments. K o s i o r e k (1974) observed an almost two-fold decrease in individual fecundity of *T. tubifex* with an increase in density of an experimental population, from 1500 to 18000 ind./m^2, and a different fecundity in populations reared on different substrata. T i m m (1974) has described variations in the rate of sexual maturing, and changes in individual fecundity of some common species, depending on temperature. Analysing the deposition of cocoons by two ubiquitous species at different temperatures, A s t o n (1973) found an increased rate of cocoon deposition by *L. hoffmeisteri* with an increase in temperature over the range 5–25°C, and a lack of this relationship in *T. tubifex*. He also demonstrated that a low oxygen concentration at a high water temperature (2 mg O_2/l at 25°C) reduces the fecundity of *L. hoffmeisteri*.

Because of the favourable selection of the environmental conditions, such as temperature, substratum fertility, dissolved oxygen, population density, etc., the values of individual fecundity of Tubificidae, determined on the basis of laboratory experiments are often very high. In an extreme case this value comes up to 38 cocoons (456 eggs) per one sexually mature individual per a sexual reproduction season (M a t s u m o t o and Y a m a m o t o 1966). In natural habitats, because of a less favourable system of conditions there, a much lower fecundity of Tubificidae should be expected.

This can be exemplified by the lakes of Karelia in which the annual fecundity of *Tubifex tubifex* was estimated at 25–28 young individuals per one reproducing individual, of *P. hammoniensis* at 10–13 individuals, and of *L. hoffmeisteri* – at 52–55 individuals (P o p č e n k o 1973). Unfortunately, because of the lack of a description of the method of calculation, no comment can be made on these data.

An interesting method based on a thorough knowledge of the life cycle was used in investigations of the individual fecundity of *P. hammoniensis* in Lake Esrom (T h o r h a u g e 1975). It has been found that at depths of 11–20 m in the profundal cocoons were almost exclusively deposited by individuals with a developed reproductive system and clitellum in April and May of the current year, and that during the deposition of cocoons no young individuals hatched, due to which the maximum number of cocoons at the end of the sexual reproduction period agreed with the total number of cocoons deposited. The fecundity calculated on this basis varied with the depth from 35.7 eggs per one sexually mature individual at the depth of 11 m to 8.8 eggs at the depth of 20 m.

For the above method to be used and give reliable results three basic conditions must be satisfied: (1) during the breeding period the group of individuals depositing cocoons must not be replenished, (2) no elimination of cocoon depositing individuals by predators should take place, (3) during cocoon deposition there must not occur a simultaneous hatching of young individuals.

In natural tubificid populations the abundance of the group of individuals participating in reproduction as a rule is subject to continual variations. They are due on the one hand to the elimination by predators and loss of individuals which died after cocoon deposition, or resorbed their sexual organs, and on the other hand, to a continual recruitment of individuals beginning to deposit cocoons. The number of eggs found in the habitat is subject to similar changes as a result of the hatching of young individuals and addition of newly laid eggs. For this reason, the above-discussed method for determining the individual fecundity cannot be commonly used. Inherent in the calculations made by other methods based on field material are considerable errors, because of the difficulty to establish the real number of individuals participating in the reproduction and the total number of eggs deposited.

For the above-enumerated reasons, in the Masurian lakes studied the research work was limited to the determination of the rate of egg production by sexually mature individuals and the fecundity of the tubificid groupings, as a ratio of the total number of eggs laid during the sexual reproduction season to the average density of the grouping, leaving the youngest individuals hatching from cocoons deposited in the current years.

The maximum value of the daily egg production decreased with increasing depth: from 1.5–1.9 eggs per a sexually mature individual at shallow sites (6–7.5 m) to 0.4–0.7 egg in the deep profundal (Fig. 2). The differences in daily egg production at different depths did not affect the reproductiveness of the tubificid groupings, because simultaneously with the increasing depth the periods of sexual reproduction were elongated and there occurred an increase in the percentage of sexually mature individuals with clitella (Fig. 1).

The considerable differences found between the fecundity of the tubificid groupings and the indices of recruitment of young individuals to the groupings (the ratio of the numbers of the youngest generation hatched from the cocoons during the current year to the average density of the remaining generations) (Table III) indicate that elimination at early ontogenetic stages plays an important role in the regulation of the density of this group of organisms. Elimination consits of: death of unfertilized eggs, loss of eggs and embryos due to predation, death of embryos developing under adverse conditions, and the death of young individuals immediately after emergence from the cocoons.

When analysing the production of *Isochaetides newaensis* (Mich.) in Rybinskoe dam reservoir, Poddubnaja (1972) estimated the mortality of eggs in cocoons in different study years at 0.8–2.9% (on the average 1.6%), and the elimination of young individuals immediately after emergence from the cocoons – at 95.0–97.5% (on the average 96.4%). Jonasson and Thorhauge (1976) have found that at depths of 11–20 m in the profundal of Lake Esrom 1.4–13.6% (on the average 4.9%) of *P. hammoniensis* eggs die as a result of the failure to become fertilized, whereas the mortality of young individuals during the first life year came up to from 52 ± 9% to 56 ± 13%. They have also found and proved experimentally that the cocoons of *P. hammoniensis* are attacked by the larvae of *Chironomus anthracinus* (Zett.).

In the Masurian lakes, elimination of Tubificidae in the course of the embryonic growth and immediately after hatching was 59.0–71.8% (Table IV). The most important of the possible causes is the distribution of the cocoons in the sediments. In the study periods tubificid cocoons were found in the sediment layer from the surface down to a depth of more than 15 cm (Fig. 3). As a result of the vertical distribution of the cocoons in the sediments, their embryonic growth goes on in different conditions, and besides, young individuals immediately after their emergence from the cocoons had to make migrations of variable length to reach the surface sediment layer in which they usually live.

Laboratory experiments under conditions similar to the natural ones, but with no predators, made it possible to find a relationship between the depth of cocoon deposition in the sediments and the death rate of embryos during their growth, and of young individuals immediately after emergence from the cocoons. The lowest total elimination of embryos and of young individuals immediately after emergence from the cocoons was found in cases where the eggs were deposited in the sediment layers at depths from 2 to 10 cm (Fig. 4). Because in the habitats studied it was in this layer that most of the cocoons were deposited, it may be presumed that the distribution of cocoons in the sediments is an adaptive character ensuring the essential recruitment of young individuals to the tubificid groupings.

One of the environmental factors limiting the number of embryos is temperature. A particularly high mortality (98%) was observed during an elongated growth of embryos at a temperature approaching 3.5°C (Fig. 5). The lowest death rate was recorded for embryos developing at temperature 7–12°C, that is, over a range of temperature occurring in the profundal of the lakes studied at the end of the period of an intense egg laying, at the time of maturing of most embryos.

The ratio of the numbers of the youngest tubificid generation, replenishing the grouping in the given year to the denisty of other generations in different habitats in the lakes amounted to 1.4–2.9 (Table III). Assuming, on the basis of the above-discussed literature and the author's own data, that in natural habitats individual fecundity of Tubificidae attains the level of 10–50 eggs a year, the proportion of reproducing individuals is 10–20% of the average number of individuals, and the mortality of embryos and young individuals immediately after hatching remains within the range 50–90%, it is possible to find that this ratio, which defines the possibility to replenish the numbers of the groupings, has for most aquatic environments an approximate value between 0.5 and 4.0. From this follows that in many habitats there are limited possibilities for tubificid groupings to be exploited by predators without their liquidation. At the same time a number of data indicate that tubificids are used as food by numerous invertebrate groups and by fishes. This is possible due to the fact that the manner in which predators exploit tubificid grouping differes from a simple reduction in numbers, as in a typical predator-prey system (W i ś n i e w s k i 1978).

5. SUMMARY

Studies of the reproduction and mortality of Tubificidae were carried out in lakes Tałtowisko, Mikołajskie and Śniardwy (Table I), belonging to the Great Masurian Lakes. The length of the breeding periods, egg production by sexually mature individuals and the fecundity of tubificid groupings were determined on the basis of benthos samples regularly collected in the study lakes in the years 1970–1972. The development rate of the eggs and the mortality of embryos at different temperatures, and the relationship between the mortality of embryos and of young individuals immediately after emergence from the cocoons, and the depth at which the cocoons were deposited in the sediments, were investigated in laboratory experiments using natural substrata (mud of undisturbed stratification) without predators, in the dark and under oxygen conditions similar to the natural ones.

In all the study habitats the dominant species was *Potamothrix hammoniensis* (Table II).

Deposition of tubificid cocoons in the habitats under study began at temperatures 3.5–5°C (Fig. 2).

The duration of the breeding periods varied with the depth. At shallower sites (6–7.5 m) sexual reproduction occurred only in spring and in summer; the daily egg production was fairly high, amounting to 1.5–1.9 eggs per a sexually mature individual. With increasing depths the breeding periods elongated and the daily egg production decreased. In the deep profundal of the study lakes cocoon deposition was continuous throughout the year, whereas the maximum daily egg production was 0.4–0.7 egg per a sexually mature individual.

The observed fall in the daily egg production, with the depth and rise in the average temperature of the near-bottom water, was compensated for by the elongation of the breeding period and an increase in the average percentage of sexually mature individuals in the tubificid groupings (Fig. 1). As a result, the reproductiveness of the tubificid groupings in the study habitats did not show any clear relationship to depth, and was within the range of 4.8–8.6 eggs per an average individual of a grouping per year (Table III).

Elimination of embryos during the development and of the youngest individuals from the time of their emergence from the cocoons to their appearance in the surface sediment layers, in which they normally live, was 59.0–72.4% of the total number of eggs laid during a sexual reproduction season (Table IV). Among the causes of this high elimination of the youngest developmental stages special attention was paid to the distribution of cocoons in the sediments. In the lakes under study, egg cocoons were distributed in the sediment layer from the surface to a depth of more than 15 cm (Fig. 3).

Laboratory experiments have shown a relationship between the depth of cocoon deposition and the mortality of embryos during growth, and of young individuals immediately after hatching (Fig. 4). In cocoons placed on the surface of the sediments the mortality of embryos, as a result of the cocoons being attacked by microorganisms, amounted to 100%. The lowest mortality has been recorded for embryos developing in the sediment layer to a depth of 2–5 cm; with the increasing depth of cocoon deposition the mortality of embryos grew again (Fig. 4 A).

The death rate of young individuals immediately after hatching was directly proportionate to the depth of cocoon deposition (Fig. 4 B). An average of 6.7% of young individuals emerged from the cocoons incubated in the surface 2 cm sediment layer died; with increasing depths of cocoon deposition the mortality grew up to 100% of individuals in sediments below 10 cm.

In the particular situations the mortality of embryos may have been to some extent caused by the temperature at which they developed. For cocoons derived from the environments under study the optimum temperature, at which a relatively fast egg development and a low mortality were observed, was a temperature approaching 12°C. With a rise or fall of the temperature the mortality of embryos increased, coming up to almost 100% at a temperature of about 3.5°C (Fig. 5).

6. POLISH SUMMARY

Badania nad rozmnażaniem się i śmiertelnością *Tubificidae* prowadzono w jeziorach Tałtowisko, Mikołajskie i Śniardwy (tab. I), należących do kompleksu Wielkich Jezior Mazurskich. Długość okresów rozmnażania płciowego, produkcję jaj przez osobniki dojrzałe płciowo i płodność zgrupowań *Tubificidae* określano na podstawie próbek bentosowych, systematycznie pobieranych z badanych jezior w latach 1970–1972. Tempo rozwoju jaj i śmiertelność zarodków w różnych temperaturach oraz zależność śmiertelności zarodków i osobników młodych tuż po opuszczeniu kokonów od głębokości złożenia kokonów jajowych w osadach badano w eksperymentach laboratoryjnych na naturalnym podłożu (muł o nie naruszonym uwarstwieniu), przy nieobecności drapieżców, w ciemności i w warunkach tlenowych zbliżonych do naturalnych.

Dominantem wśród *Tubificidae* we wszystkich badanych środowiskach był *Potamothrix hammoniensis* (tab. II).

Odkładanie kokonów jajowych przez *Tubificidae* w badanych środowiskach rozpoczynało się w temperaturach 3,5–5°C (rys. 2).

Długość okresów rozmnażania płciowego była różna na różnych głębokościach. Na stanowiskach płytszych (6–7,5 m) rozmnażanie płciowe zachodziło wyłącznie wiosną i latem, dobowa produkcja jaj była stosunkowo wysoka i osiągała 1,5–1,9 jaja na dojrzałego płciowo osobnika. W miarę wzrostu głębokości następowało wydłużanie okresów rozmnażania płciowego i spadek dobowej produkcji jaj. W głębokim profundalu badanych jezior odkładanie kokonów zachodziło nieprzerwanie w ciągu całego roku a dobowa produkcja jaj osiągała maksymalnie 0,4–0,7 jaja na dojrzałego płciowo osobnika.

Obserwowany spadek dobowej produkcji jaj, wraz ze wzrostem głębokości i obniżaniem się średniej temperatury wody przydennej, był kompensowany wydłużaniem się okresów rozmnażania płciowego i zwiększaniem średniego udziału dojrzałych płciowo osobników w zgrupowaniach *Tubificidae* (rys. 1). W efekcie płodność zgrupowań *Tubificidae* nie wykazywała wyraźnej zależności od głębokości i zawierała się w badanych środowiskach w granicach 4,8–8,6 jaja na średniego osobnika zgrupowania na rok (tab. III).

Eliminacja zarodków podczas rozwoju i osobników najmłodszych w okresie od wyklucia się z kokonów do pojawienia się w powierzchniowych warstwach osadów, w których normalnie żyją, wynosiła 59,0–72,4% od całkowitej liczby jaj złożonych w okresie rozmnażania płciowego (tab. IV). Wśród przyczyn tak wysokiej eliminacji najmłodszych stadiów rozwojowych szczególną uwagę zwrócono na rozmieszczenie kokonów w osadach. W badanych jeziorach kokony jajowe były rozmieszczone w warstwie osadów od powierzchni do ponad 15 cm głębokości (rys. 3).

Badania laboratoryjne wykazały, że istnieje związek między głębokością złożenia kokonów a śmiertelnością zarodków w czasie rozwoju i osobników młodych tuż po wykluciu (rys. 4). W kokonach umieszczonych na powierzchni osadów śmiertelność zarodków, w wyniku atakowania kokonów przez mikroorganizmy, wynosiła 100%. Najniższa śmiertelność charakteryzowała zarodki rozwijające się w warstwie osadów na głębokości 2–5 cm; w miarę wzrostu głębokości złożenia kokonów śmiertelność zarodków ponownie rosła (rys. 4 A).

Wymieranie osobników młodych tuż po wykluciu się z kokonów było wprost proporcjonalne do głębokości złożenia kokonów jajowych (rys. 4 B). Spośród młodych wylęgających się z kokonów inkubowanych w warstwie osadów do głębokości 2 cm ginęło 6,7% osobników; w miarę wzrostu głębokości złożenia kokonów śmiertelność rosła aż do 100% osobników w warstwach osadów poniżej 10 cm głębokości.

W poszczególnych sytuacjach pewien wpływ na śmiertelność zarodków mogła mieć również temperatura w jakiej przebiegał ich rozwój. Dla kokonów pochodzących z badanych środowisk optymalną, ze względu na stosunkowo szybki rozwój jaj i niską śmiertelność, była temperatura bliska 12°C. Wraz ze wzrostem lub obniżaniem temperatury śmiertelność zarodków rosła osiągając niemal 100% w temperaturze ok. 3,5°C (rys. 5).

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