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EFFECT OF PREDATORS ON TUBIFICIDAE GROUPINGS AND THEIR PRODUCTION IN LAKES*

ABSTRACT: In experiments carried out in a natural habitat the Tubificidae that were attacked by fish and invertebrate predators were not usually eaten completely, but they only lost the posterior body part. Consequently, the effect observed was mainly a decrease in the average body weight and in the biomass of the Tubificidae, and to a lesser extent a reduction in their numbers. In the lakes of central and northern Poland, individuals were found whose bodies, having been damaged by predators, were later on regenerating the parts lost. In the littoral, where their proportion was the largest, they represented up to 80% of all the Tubificidae. In laboratory investigations, the increase of the body during the regeneration of the parts lost was faster than during the normal growth. As a result, predation proved to be a factor stimulating the production of Tubificidae.

KEY WORDS: Lakes, benthos, Tubificidae, predator-prey relationships, body regeneration, secondary production.

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*Praca wykonana w ramach problemu węzłowego nr 09.1.7 oraz podproblemu węzłowego nr 10.2.10.

1. STUDY AIM, MATERIAL AND METHODS

The aim of the study was to analyze the action of fish and predatory invertebrates on the density, biomass and size structure of Tubificidae groupings, to assess the rate of exploitation of the Tubificidae in lakes by predators, and the role in the production of Tubificidae groupings of the regeneration of parts lost due to the feeding by predators.

The investigations were conducted in 23 lakes of central and northern Poland (Table 1) in the years 1970–1976, most intensely in the lakes Tałtowisko, Mikołajskie and Śniardwy belonging to the Great Masurian Lakes. The distribution, species composition and the density and biomass dynamics of the benthos in these three lakes had been studied and described in detail in earlier studies (K a j a k and D u s o g e 1975a, 1975b, 1976).

The action of predators on the groupings of Tubificidae was studied experimentally in the central part of Lake Śniardwy at a depth of 7.5 m. The effect of fish feeding was determined by using two types of cage 60 × 60 cm (Fig. 1 A, B). The cages were positioned on flat bottom areas by a frog-man who pressed them into the mud so that the part surrounded by plastics foil would stick out about 2 cm above the bottom sediment surface.

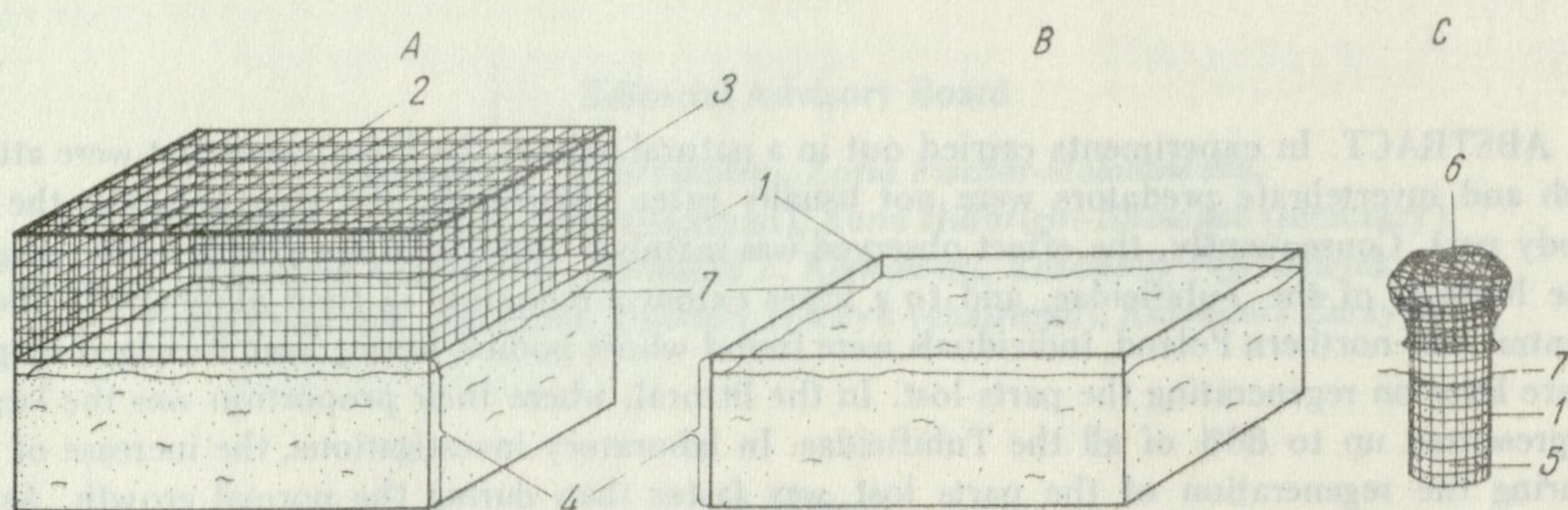


Fig. 1. Cages used in field experiments to investigate the effect of predators on Tubificidae

A — fish-inaccessible cages, B — fish-accessible cages, C — isolators used in experiments with predatory invertebrates, 1 — metal skeleton coated with water-resistant paint, 2, 3 — removable lid and lateral wall covered with VPC net of mesh size 8 × 8 mm, 4 — wall part covered with plastics foil, 5 — wall covered with steelon gauze with mesh size 0.25 × 0.25 mm, 6 — cap made of steelon net with mesh size 2 × 2 mm, 7 — sediment surface

To bait fish, in both cage types the same biomass (about 5 g in each cage) of large tubificids of the genus *Limnodrilus* derived from culture were placed. They were easy to distinguish from the only autochthonous species *Potamothrix hammoniensis* (Mich.). Moreover, as had been found in earlier laboratory investigations, in sediments from Lake Śniardwy they only survived for several days. For this reason, no effect of their increased density on the autochthonous Tubificidae populations could be observed, and no foreign faunistic element had been introduced for good into the habitat studied.

Experiments to study the effect of fish feeding on the Tubificidae were repeated four times: in August and October 1971 (9 cages of each type were exposed), and in May and September 1972 (3 cages of each type).

The effect of predatory invertebrates on the Tubificidae was investigated using cylindrical isolators about 55 cm² in surface area and 20 cm high (Fig. 1 C). They were sunk in the mud by a frog-man so that their top edge would stick out about 2–3 cm above the surface. Into some of the isolators live Pelopiinae larvae, 4–8 mm long, selected from benthos larvae collected

Table I. Description of the lakes under study

| Lake | Geographic position | Area (ha) | Max. depth (m) | Average depth (m) | Mixis type | Trophic type |
|----------------------|------------------------|-----------|----------------|-------------------|------------|-----------------------|
| Tałtowisko | Masurian Lakeland | 326.9 | 39.5 | 14.0 | dimictic | β -mesotrophic |
| Mikołajskie | " | 460.0 | 27.8 | 11.0 | " | eutrophic |
| Śniardwy | " | 10,598.4 | 25.0 | 5.9 | polymictic | " |
| Mamry Północne | Masurian Lakeland | 2,504.0 | 43.8 | 11.7 | dimictic | α -mesotrophic |
| Święcajty | " | 869.4 | 28.0 | 8.7 | " | β -mesotrophic |
| Dargin | " | } 3,030.0 | 37.6 | } 10.6 | " | " |
| Łabap | " | | 13.4 | | " | " |
| Dobskie | " | 1,776.0 | 22.5 | 7.8 | " | " |
| Kisajno | " | 1,896.0 | 25.0 | 8.4 | " | " |
| Żarnowieckie | Cassubian Coast | 1,431.6 | 19.4 | 8.4 | polymictic | " |
| Wąsosko—Mikorzyńskie | Complex of Konin lakes | 245.3 | 38.0 | 11.9 | dimictic | " |
| Tały | Masurian Lakeland | 1,162.0 | 44.7 | 13.6 | " | eutrophic |
| Ryńskie | " | 620.0 | 50.8 | 13.6 | " | " |
| Tajty | " | 265.1 | 34.0 | 7.5 | " | " |
| Niegocin | " | 2,416.7 | 39.7 | 10.0 | " | " |
| Wojnowo | " | 176.3 | 14.2 | 6.3 | " | " |
| Boczne | " | 183.3 | 17.0 | 8.6 | " | " |
| Jagodne | " | 942.7 | 37.4 | 8.7 | " | " |
| Beldany | " | 940.6 | 46.0 | 10.0 | " | " |
| Guzianka Wielka | " | 59.6 | 29.4 | 6.5 | " | " |
| Nidzkie | " | 1,818.0 | 23.7 | 6.2 | " | " |
| Ślesińskie | Complex of Konin lakes | 148.1 | 25.7 | 7.5 | " | " |
| Licheńskie | " | 155.6 | 13.3 | 4.9 | monomictic | " |

in the vicinity of the experimental area, were let (a specified number of them) into each isolator. To prevent fish from entering, the isolators were covered with a light cap made of a steelon net. An experimental series consisted of 20 isolators with an increased density of Pelopiinae larvae and 20 controls. The experiments were repeated twice: in August 1971 and in May 1972.

The exposure time for the cages and the isolators, in all the replications of the experiment, was 9 days. The aim of using short exposure times was to cause the least possible changes in the benthos due to the isolation of sections of the bottom. In earlier researches, based on a similar procedure and carried out in the same habitat (K a j a k 1963, 1964), experiments were conducted for several weeks, during which an increase in the density of benthos, therein also of predatory Chironomidae, could be observed as a result of the changed environmental conditions within the cages.

At the end of the exposure, cage and isolator benthos samples were collected by a frog-man into small plexiglass cylinders 43 cm² in surface area and 17.5 cm high. From each cage 10 samples were collected and only one from each isolator. For the assessment of the benthos changes that had taken place in each of the cages, on the termination of the experiment 20 control samples were collected in the vicinity, using a tubular sampler 43 cm² in surface area (K a j a k, K a c p r z a k and P o l k o w s k i 1965), and 10 control samples for all isolators. Immediately on their collecting all the benthos samples were washed on a screen with a metal net of mesh-size of 0.2 × 0.2 mm, and preserved in 4% formalin solution. Sorting of the organisms was performed in the laboratory under the stereoscopic microscope, using 8-fold or 12.5-fold magnification and a dark background. At the same time the body length of the benthos organisms was measured to the nearest 1 mm. The biomass of Tubificidae was determined to the nearest 0.1 mg by joint weighing of all the individuals of one sample after superficial drying on filter paper; the biomass of Chironomidae was calculated from the body lengths of the individuals (K o n s t a n t i n o v 1969).

The size-structure of the Tubificidae groupings was determined on the basis of the presence of individuals of different body sizes in the groupings. Four classes of undamaged individuals have been distinguished with the following body lengths: 2–4, 5–8, 9–15 and above 15 mm. Individuals of various body sizes but without the posterior part of the body were placed in a separate group, group 5.

The significance of the differences in density, biomass and individual weight of the Tubificidae between the cages that were inaccessible and those that were accessible to the fish, and between the isolators with the normal and those with an increased density of predatory invertebrates, was checked by Student *t*-test.

The rate of exploitation of the natural Tubificidae groupings by predators was established on the basis of the percentages in the benthos material of Tubificidae individuals regenerating parts of body lost due to damage (K a j a k and W i ś n i e w s k i 1966). In the Mikołajskie Lake, benthos samples were collected along a transect at depths 11, 16 and 25 m, in Lake Tałtowisko also along a transect at depths 6, 11, 16, 25 and 37 m, and in Lake Śniardwy at one mid-lake station at a depth of 7.5 m. At shallower stations (up to 11 m), 10 samples were collected each time, and at the remaining stations 5 samples each time, because diversity usually decreases with the depth. In summer, samples were collected at 2-3-week intervals, in spring and autumn once a month, and in winter – at the beginning of the freezing-over and then before the disappearance of the ice. In the remaining lakes 5 samples were collected once, during the summer stagnation (in August), in each of the following parts of a lake: in the littoral (at a depth of 1.5–4 m), sublittoral (5–8 m) and in shallow (9–15 m) and deep (over 15 m)

profundal. Benthos samples from all the lakes, collected with a tubular sampler 43 cm² in surface area, were examined using the methods discussed above.

The rate of growth of the individuals growing normally and of those regenerating body losses was examined by using the small-cylinder technique (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, 43 cm² in surface area and 17.5 cm high, containing an amount of undisturbed sediment from the profundal of Mikołajskie Lake, were in the laboratory submerged in tanks filled with filtered lake water. From the benthos samples collected at the same habitat as the sediment undamaged and non-regenerating *Potamothrix hammoniensis* individuals were selected according to the three size classes: about 10, 15 and 20 mm in length. The mean body weight of the individuals in each size class was determined on the basis of a random sample of 50 individuals. After being kept in pure water for 30–40 minutes, to clean their alimentary tracts, these individuals were killed with 4% formalin solution. After the fixation of their body covers they were superficially dried and then weighed singly, on an analytical balance with a sensitivity of 0.01 mg.

The experiment consisted of four parallel series. In one of them the growth rate was studied of the undamaged individuals, in the remaining ones – the body increase of different size class individuals, whose posterior body part had been amputated in 1/3, 1/2 and 2/3 body length. Into each experimental cylinder 15–20 individuals of each size class were introduced. The cylinders were exposed at 15 ± 1°C. The content of oxygen above the mud surface in the experimental cylinders was checked. It did not drop below 2.4 mg O₂/l. In 11, 24, 39, 50 and 70 days, from the setting-up of the experiment, 2–3 cylinders of each series were examined. Their contents were washed in parts on a sieve with a mesh-size 0.2 × 0.2 mm. The Tubificidae were sorted by size classes and weighed according to the method given above. The body weight increment of the undamaged individuals was calculated by subtracting the initial weight from the current average weight at a given point of time. The regenerating individuals were weighed twice: in their entirety and then after the cutting-off of the regenerated portion. This procedure was used in order to determine the increment, i.e., the difference between these two weights.

2. RESULTS

2.1. COMPOSITION OF TUBIFICIDAE

The specific composition of the Tubificidae groupings found in the lakes studied was poor. The dominating species in all the zones of the lakes was *Potamothrix hammoniensis*. In the littoral and in the sublittoral it represented about 40–60% of the Tubificidae present there, the codominating species being *Limnodrilus hoffmeisteri* Clap. and *Psammoryctides barbatus* (Grube). Sporadically found were also *Psammoryctides albicola* (Mich.), *Tubifex tubifex* (Müll.), *T. ignotus* (Stolc) and *Peloscolex ferox* (Eisen).

In the profundal of most lakes, and in the central part of Lake Śniardwy, where predator feeding was investigated experimentally, *P. hammoniensis* was the only representative of Tubificidae. In some mesotrophic lakes *P. barbatus*, *L. hoffmeisteri* and *P. ferox* were also found to be present, but even then *P. hammoniensis* represented over 80% of Tubificidae.

On account of the important role played by the latter species in the Tubificidae groupings of the habitats under study, it was the only object of the laboratory experiments.

2.2. EFFECT OF FISH FEEDING ON TUBIFICIDAE

The effect of fish feeding on Tubificidae was investigated at various densities and size structure of their groupings. The similarity of the density and biomass of the Tubificidae near the experimental cages and in the cages inaccessible to fish (Table II) indicates that a short-lived change in the environmental conditions, caused by enclosing part of the bottom and introducing additional biomass of Tubificidae into the cages, in order to bait fish, had no significant effect on the condition of the autochthonous groupings of Tubificidae.

Table II. Effect of fish on the density (N), biomass (B) and average body-weight of individuals (W_i) of autochthonous groupings of Tubificidae (Lake Śniardwy – depth 7.5 m, end results after 9-day exposure)

n.s. – insignificant difference: $\alpha > 0.05$, * – significant difference: $\alpha = 0.05$, ** – very significant difference: $\alpha \leq 0.01$

| Dates | Parameters | Vicinity of cages | Fish-inaccessible cages (a) | Fish-accessible cages (b) | Significance of difference a and b |
|------------------|----------------------------|-------------------|-----------------------------|---------------------------|------------------------------------|
| Aug. 19–28, 1971 | N (ind./m ²) | 5,802±516 | 6,135±295 | 4,244±223 | ** |
| | B (g/m ²) | 2.74±0.31 | 2.77±0.20 | 1.33±0.10 | ** |
| | W_i (mg wet wt) | 0.47±0.07 | 0.45±0.03 | 0.31±0.02 | ** |
| Oct. 6–15, 1971 | N (ind./m ²) | 3,453±388 | 3,353±181 | 3,146±200 | n.s. |
| | B (g/m ²) | 1.49±0.20 | 1.65±0.12 | 1.14±0.08 | ** |
| | W_i (mg wet wt) | 0.43±0.04 | 0.49±0.03 | 0.36±0.02 | ** |
| May 20–29, 1972 | N (ind./m ²) | 2,117±239 | 2,063±221 | 1,484±136 | * |
| | B (g/m ²) | 2.02±0.25 | 1.69±0.22 | 0.99±0.16 | ** |
| | W_i (mg wet wt) | 0.96±0.16 | 0.82±0.07 | 0.63±0.05 | * |
| Sept. 8–17, 1972 | N (ind./m ²) | 1,565±217 | 1,644±171 | 1,369±124 | n.s. |
| | B (g/m ²) | 1.17±0.27 | 1.30±0.21 | 0.58±0.12 | ** |
| | W_i (mg wet wt) | 0.75±0.07 | 0.79±0.08 | 0.44±0.04 | ** |

An effect of fish feeding found in all the experimental series was a statistically significant decrease in the biomass and mean body weight of the Tubificidae in the fish accessible cages, relative to the inaccessible ones, while the effect of fish on the density of Tubificidae was less evident (Table II). In August 1971 and in May 1972, the Tubificidae present in the fish accessible cages showed a significant decrease in numbers. In October 1971 and in September 1972, in spite of a certain decrease, the density differences between the two cage types were statistically insignificant.

The exploitation of the individual size groups of Tubificidae, expressed as the per cent loss of individuals of the given group in the fish accessible cages, relative to the inaccessible ones, was found to vary (Fig. 2). In all cases the least exploited were the smallest individuals (5–41% loss), and the most exploited were the largest individuals (71–87%). This does not mean that this group of individuals was completely eliminated, for at the same time in the fish accessible

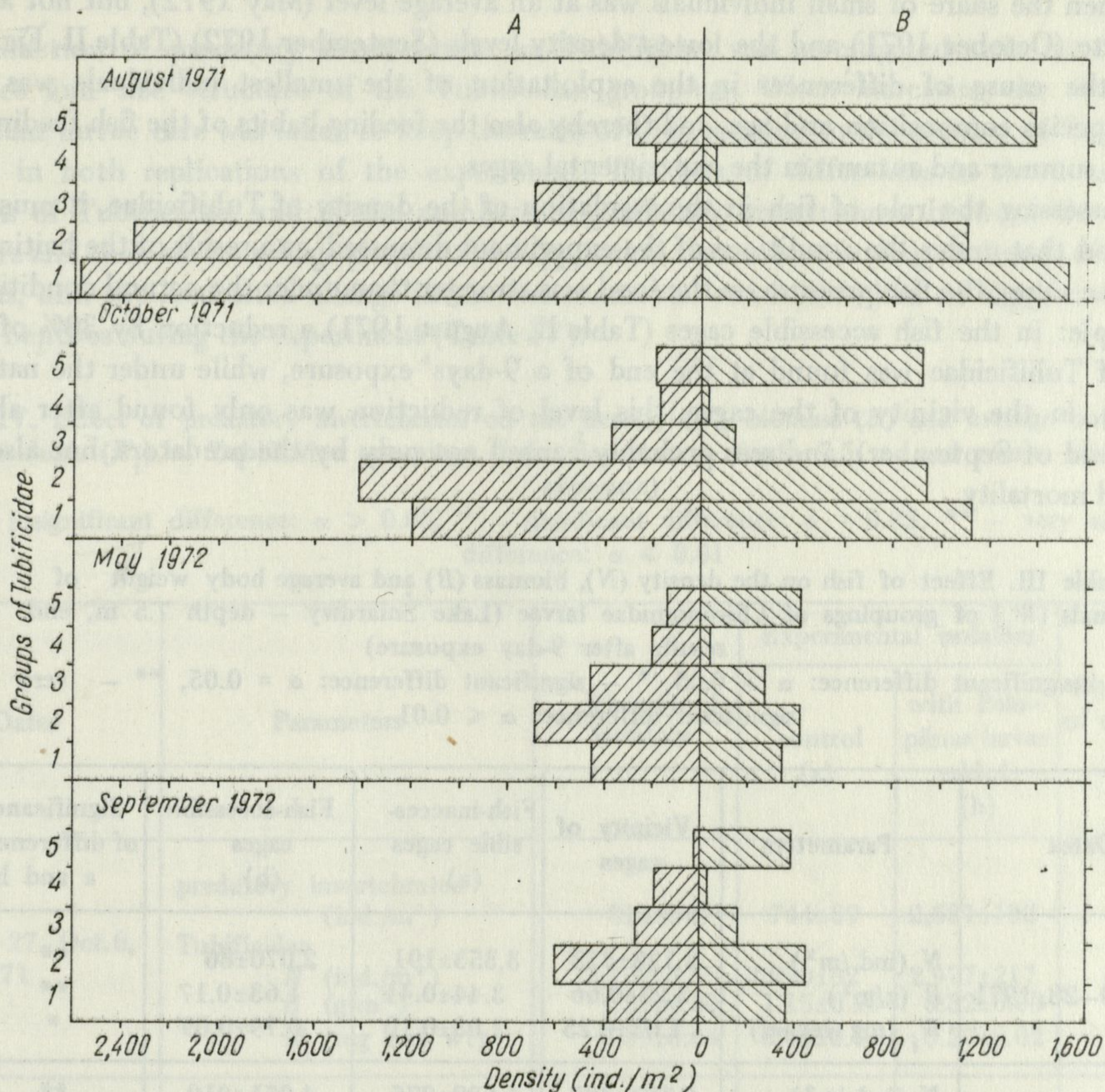


Fig. 2. Effect of fish feeding on the size structure of Tubificidae groupings

A — fish-inaccessible cages, B — fish-accessible cages. Tubificidae groups: 1 — 2–4 mm in body-length, 2 — 5–8 mm in body-length, 3 — 9–15 mm in body-length, 4 — above 15 mm in body-length, 5 — individuals without posterior body part and regenerating body losses

cages a growth could be observed of the number of individuals deprived of the posterior body part. A decreased density of the tubificid groupings in the fish accessible cages could only be seen in those replications of the experiment in which the smallest individuals were intensely exploited. It follows, therefore, that large individuals, which have more possibilities to escape into deeper sediment layers in cases of fear, were in most cases only injured (browsed) by the fish. This did not cause a decrease in the density of the tubificids, but only a decrease in the mean body weight of the individuals, and thereby a drop in the biomass of the groupings. Small individuals found in the superficial sediment layers were usually eaten in their entirety, this leading to a decrease in the density of the Tubificidae groupings.

The varying exploitation of the smallest individuals, and consequently the effect of fish on the density of the tubificids in the successive replications of the experiment was not due to the condition of their groupings. A statistically significant decrease in the number of individuals in the fish accessible cages, as compared with the inaccessible ones, was observed at both a high

density of Tubificidae and dominance of the smallest individuals (August 1971) and a low density when the share of small individuals was at an average level (May 1972), but not at an intermediate (October 1971) and the lowest density levels (September 1972) (Table II, Fig. 2). Possibly, the cause of differences in the exploitation of the smallest individuals was the different species composition and age, and thereby also the feeding habits of the fish feeding in the spring, summer and autumn in the experimental cages.

When assessing the role of fish in the regulation of the density of Tubificidae, it must be remembered that under the conditions of the experiment discussed, as a result of the baiting of fish into the cages, the fish pressure on the food was stronger than under the natural conditions. For example: in the fish accessible cages (Table II, August 1971) a reduction by 30% of the number of Tubificidae was found at the end of a 9-days' exposure, while under the natural conditions, in the vicinity of the cages, this level of reduction was only found after about 5 weeks (end of September), and was probably caused not only by the predators, but also by the natural mortality.

Table III. Effect of fish on the density (N), biomass (B) and average body weight of individuals (W_i) of groupings of Chironomidae larvae (Lake Śniardwy – depth 7.5 m, end results after 9-day exposure)

n.s. – insignificant difference: $\alpha > 0.05$, * – significant difference: $\alpha = 0.05$, ** – very significant difference: $\alpha \leq 0.01$

| Dates | Parameters | Vicinity of cages | Fish-inaccessible cages (a) | Fish-accessible cages (b) | Significance of difference a and b |
|------------------|----------------------------|-------------------|-----------------------------|---------------------------|------------------------------------|
| Aug. 19–28, 1971 | N (ind./m ²) | 3,128±373 | 3,353±191 | 2,070±86 | ** |
| | B (g/m ²) | 3.23±0.66 | 3.44±0.41 | 1.63±0.17 | ** |
| | W_i (mg wet wt) | 1.03±0.25 | 1.03±0.10 | 0.79±0.09 | * |
| Oct. 6–15, 1971 | N (ind./m ²) | 5,023±382 | 5,620±275 | 4,051±210 | ** |
| | B (g/m ²) | 4.45±0.75 | 4.54±0.36 | 2.95±0.26 | ** |
| | W_i (mg wet wt) | 0.88±0.25 | 0.81±0.10 | 0.72±0.06 | n.s. |
| May 20–29, 1972 | N (ind./m ²) | 3,477±288 | 3,860±238 | 2,519±160 | ** |
| | B (g/m ²) | 4.38±0.68 | 4.44±0.33 | 2.34±0.24 | ** |
| | W_i (mg wet wt) | 1.26±0.16 | 1.15±0.09 | 0.93±0.06 | n.s. |
| Sept. 8–17, 1972 | N (ind./m ²) | 2,325±310 | 2,670±226 | 1,756±165 | ** |
| | B (g/m ²) | 1.82±0.24 | 2.14±0.24 | 1.10±0.17 | ** |
| | W_i (mg wet wt) | 0.78±0.17 | 0.80±0.07 | 0.63±0.06 | n.s. |

A decrease in the body weight of individuals and in the biomass of the groupings exploited by fish, while density is being reduced to a lesser extent and only in some cases, is characteristic of Tubificidae. For comparison, in groupings of Chironomidae larvae – the second most important, beside Tubificidae, component of the lake benthos, fish feeding under the conditions of the experiment discussed caused a statistically significant decrease in both the number of individuals and biomass in the fish accessible cages, relative to the inaccessible ones (Table III), regardless of the differences in density and average body weight of the individuals in the successive replications of the experiment.

2.3. EFFECT OF PREDATORY INVERTEBRATES' FEEDING ON TUBIFICIDAE

The action of predatory invertebrates on Tubificidae was investigated twice at different densities and size structure of the Tubificidae groupings. When increasing the density of Pelopiinae larvae care was taken to keep the ratio of their number to the number of Tubificidae similar in both replications of the experiment. The lack of differences in the density and biomass of Tubificidae, and in the numbers of predatory invertebrates between the control isolators and their surroundings permits the supposition that a short-lasting enclosure of bottom sections, and the associated change in the environmental conditions, had no significant effect on the benthos during the experiment (Table IV).

Table IV. Effect of predatory invertebrates on the density (N), biomass (B) and average body-weight of individuals (W_i) of Tubificidae groupings (Lake Śniardwy – depth 7.5 m, end results after 9-day exposure)

n.s. – insignificant difference: $\alpha > 0.05$, * – significant difference: $\alpha = 0.05$, ** – very significant difference: $\alpha \leq 0.01$

| Dates | Parameters | Vicinity of isolators | Experimental isolators | | Significance of difference a and b |
|-----------------------|--|-----------------------|------------------------|----------------------------------|------------------------------------|
| | | | control (a) | with Pelopiinae larvae added (b) | |
| Sept. 27–Oct. 6, 1971 | predatory invertebrates (ind./m ²) | 814±349 | 744±89 | 2,581±192 | ** |
| | Tubificidae | | | | |
| | N (ind./m ²) | 3,139±577 | 2,930±82 | 2,977±217 | n.s. |
| | B (g/m ²) | 1.22±0.30 | 1.15±0.10 | 0.82±0.09 | * |
| | W_i (mg wet wt) | 0.39±0.04 | 0.40±0.04 | 0.27±0.02 | ** |
| May 20–29, 1972 | predatory invertebrates (ind./m ²) | 930±139 | 827±102 | 1,477±193 | ** |
| | Tubificidae | | | | |
| | N (ind./m ²) | 1,860±512 | 1,872±195 | 1,849±295 | n.s. |
| | B (g/m ²) | 1.99±0.56 | 1.97±0.31 | 1.51±0.27 | n.s. |
| | W_i (mg wet wt) | 1.06±0.20 | 1.05±0.10 | 0.81±0.05 | * |

Predatory invertebrates' feeding in both repetitions of the experiment resulted in an increased number of Tubificidae without the posterior part of the body (Fig. 3), and the concomitant statistically significant decrease in the average body weight of the individuals (Table IV), but no density differences could be seen between the isolators with a normal stock of predators and those with an increased stock.

By contrast to fish, the predatory invertebrates most intensely utilized young individuals of Tubificidae (Fig. 3). Their loss in the isolators with an increased density of predators, relative to the isolators with a natural density of predators, was similar in both experimental series, amounting to 35–47%. These individuals were not entirely eliminated, because at the same time the number of individuals without the posterior body part increased. The exploitation of large individuals of Tubificidae was much weaker and was different in each of the two

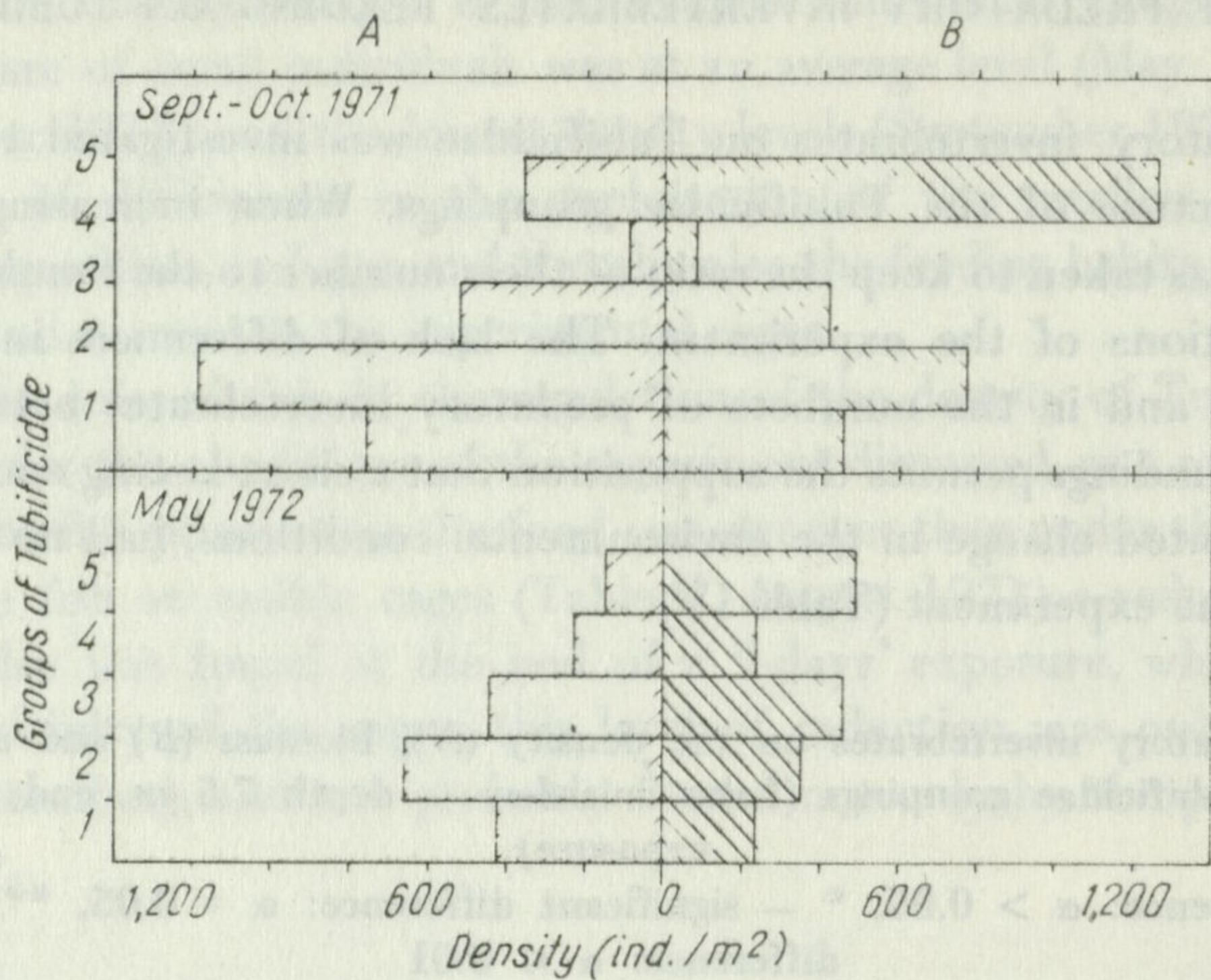


Fig. 3. Effect of predatory invertebrates on the size structure of Tubificidae groupings
 A — isolators with a natural predator density, B — isolators with an increased predator density. Tubificidae groups as in Figure 2

replications of the experiment (Fig. 3). In the autumn of 1971, when the temperature of the near-bottom water was 12°C and the density of predators exceeded 2.5 thous. ind./m², large tubificids were utilized at a higher rate (15% loss), whereas in the spring of 1972 at 9°C and a predator density below 1.5 thous. ind./m² no differences in the density of large individuals were observed between the isolators with the normal and those with an increased predator density. The higher rate of exploitation of large individuals resulted in a significant decrease in the biomass of the tubificids in the higher predatory invertebrate density isolators in autumn 1971 (Table IV).

2.4. RATE OF EXPLOITATION OF TUBIFICIDAE BY PREDATORS UNDER NATURAL CONDITIONS

In natural habitats, the feeding of fish and predatory invertebrates results in the presence of considerable numbers of individuals without the posterior body part, regenerating the lost body part (Table V, Fig. 4). Their contribution to the density of Tubificidae may be assumed to be an index of the exploitation of the groupings by predators (Kajak and Wiśniewski 1966).

The rate of exploitation of Tubificidae in the lakes under study, assessed on this basis, varied with the depth and with the seasons. The highest rates of utilization by the predators were recorded for the tubificid groupings found in shallow habitats. In the littoral, damaged and regenerating individuals represented up to 80% of all the Tubificidae. With increasing depths the exploitation of tubificids by the predators decreased gradually; in parts of the profundal deeper than 15 m the proportion of damaged Tubificidae individuals regenerating the lost body parts did not exceed 40%, being usually much less than that (Table V).

Assessed by season, the highest rate of tubificid exploitation by the predators was observed, regardless of the depth, in spring and in summer (Fig. 4). At shallower stations (up to 11 m deep)

Table V. Occurrence of damaged and regenerating individuals of Tubificidae in lakes of central and northern Poland during summer stagnation

— no data

| Lake | O ₂ content in near-bottom water (mg O ₂ /l) | Percentage of damaged and regenerating individuals in Tubificidae groupings | | | |
|----------------------|--|---|---------------------|----------------------------|-----------------------------------|
| | | littoral (1.5–4 m) | sublittoral (5–8 m) | shallow profundal (9–15 m) | deep profundal (deeper than 15 m) |
| Mamry Północne | 3.2* | 48.5 | 32.2 | 30.4 | 21.4 |
| Święcajty | 0.2* | 75.0 | — | 27.8 | 10.9 |
| Dargin | 0.3* | 75.0 | — | 28.6 | 11.1 |
| Łabap | 1.2* | — | 55.5 | 36.4 | — |
| Dobskie | 0.2* | 61.8 | 33.3 | 28.6 | — |
| Kisajno | 0.2–2.6* | 54.5 | — | 50.0 | 22.2 |
| Żarnowieckie | 7.2–7.9* | 52.8 | 36.5 | 18.6 | 15.1 |
| Wąsosko-Mikorzyńskie | 1.0** | 58.3 | — | 40.0 | 36.9 |
| Tały | 0.7* | — | 48.6 | 46.7 | 23.0 |
| Ryńskie | 0.0* | — | 69.2 | — | 0.0 |
| Tajty | 0.0* | 71.4 | — | 26.3 | 0.0 |
| Niegocin | 0.0* | 72.0 | — | 46.0 | 0.0 |
| Wojnowo | 0.1* | 80.0 | — | 14.3 | — |
| Boczne | 0.5* | — | 52.3 | 20.0 | — |
| Jagodne | 0.0* | 57.1 | — | 25.0 | 0.0 |
| Bełdany | 0.0* | 40.5 | 50.0 | 26.3 | 5.3 |
| Guzianka Wielka | 0.0* | — | 45.4 | 0.0 | 0.0 |
| Nidzkie | 0.0* | — | 52.9 | 36.8 | 0.0 |
| Ślesińskie | 0.0** | 66.7 | 48.1 | 17.6 | 0.0 |
| Licheńskie | 0.0** | 71.4 | 32.5 | 0.0 | — |

*B. Zdanowski — unpublished data. **According to Zdanowski and Korycka (1976).

it decreased in the autumn as the water temperature dropped, whereas at deeper stations it was found to fall already in summer and then grew again during the autumn circulation and dropped again in late autumn as the temperature of the water fell.

The above-presented seasonal variations and the decrease, with increasing depths, in the rate of tubificid exploitation by predators probably resulted from changes in the activity of the predators, depending on the temperature and limited availability of Tubificidae to the predators with the deterioration of the oxygen conditions. This is indicated on the one hand by the fact that the occurrence of damaged and regenerating tubificids is associated with changes in the temperature of the environment (Fig. 4), and on the other by the different percentage of these individuals in the tubificid groupings in the deep profundal of lakes differing by the oxygen conditions (Table V). During the summer stagnation in the lakes in which oxygen was present even at the bottom, the damaged and regenerating individuals in the profundal at depths greater than 15 m represented from between 10 and 20 up to about 40% of all Tubificidae, whereas in the lakes in which oxygen was absent from the near-bottom water layer, damaged and regenerating individuals were not usually found, and only in one case (Lake Bełdany) did they represent about 5% of the total number of Tubificidae.

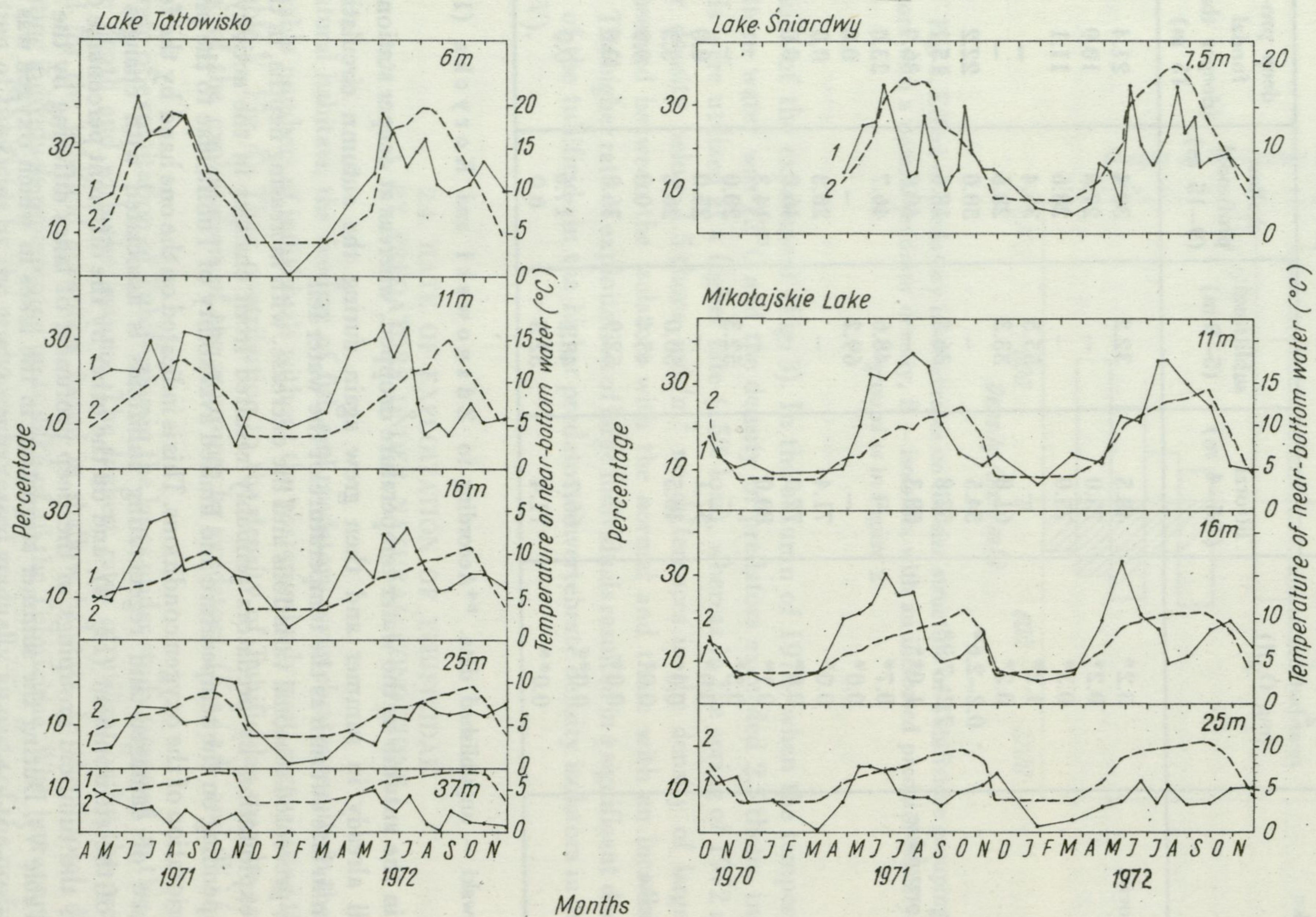


Fig. 4. Variations in the occurrence of damaged individuals regenerating lost body parts in the tubificid groupings (1) against changes in the temperature of near-bottom water layer (2)

2.5. RATE OF BODY INCREASE IN TUBIFICIDAE DURING THE REGENERATION OF LOST PARTS, RELATIVE TO NORMAL GROWTH

The relationship between the growth of undamaged individuals and the body increase during regeneration was determined on the basis of laboratory experiments. The rate of growth was investigated in three groups of individuals differing in size, the average body weights of which were about 2.4, 4.2, 6.3 mg of wet weight. Increments in body weight due to regeneration were determined in individuals of the same size groups, the posterior body part of which was cut off at about 1/3, 1/2 and 2/3 body length, due to which their average body weight became reduced by 25–30, 40–45 and 55–60%, respectively.

In the course of regeneration three phases were distinguished which differed by the rate of body increase (Fig. 5).

In the first phase, as a result of the loss of the growth zone which is found in these animals at the end of the body, the weight increase was slower than during the normal growth. During this regenerative phase there occurred a tissue reorganization at the site of damage and a new growth zone formed. In individuals differing by body size and degree of damage the duration of this phase varied. Under the conditions of the experiment it lasted the longest (about 20–30 days) in small individuals which had lost 2/3 of body, and the shortest (about 10 days) – in large individuals.

In the second phase of regeneration new segments formed intensely, and as a result, the regenerated part grew quickly. The increase in body weight was in all variants of the experiment faster than during the normal growth. This phase too was the shortest in the largest individuals with a small degree of body loss (about 30 days), and it elongated in smaller individuals with a higher degree of body loss. Because of the limited time of the experiment, the growth of some groups of individuals, e.g., small and medium-size individuals deprived of 2/3 of body, was terminated at this phase.

During the third regeneration phase a decrease was observed of the rate of body increase to the level characteristic of the normal growth. In this phase, the large and medium-size individuals damaged to a lesser degree attained a body weight similar to that of the individuals

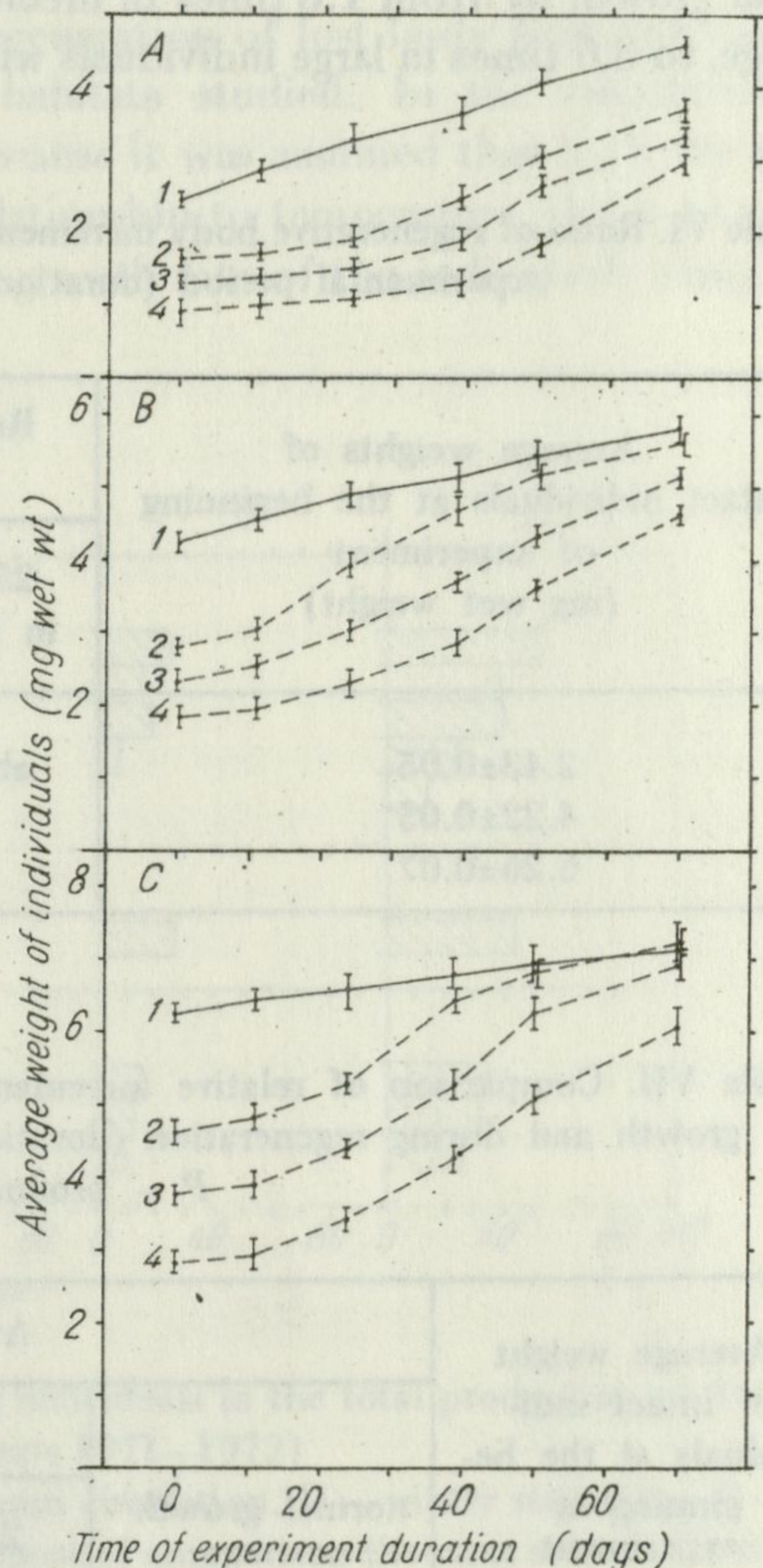


Fig. 5. Body-weight increments of *Potamothenis hammoniensis* individuals growing normally (1) and regenerating a body loss of about 25–30% (2), 40–45% (3) and 55–60% (4) body weight (temperature $15 \pm 1^\circ\text{C}$)

Average body-weight of intact individuals at the beginning of the experiment: A – 2.43 ± 0.05 mg, B – 4.22 ± 0.05 mg, C – 6.26 ± 0.07 mg wet weight (vertical lines indicate standard error of the mean)

growing normally, which indicated a complete regeneration of the lost body part. In small individuals, regardless of the degree of damage, the process of regeneration slowed down before the individuals attained the weight of the individuals growing normally, so the regeneration was incomplete.

The ratio of the absolute regenerative body weight increment to the body increment in the normal growth varied with the individuals differing in size (Table VI). The rate of regeneration and the rate of normal growth of small individuals were found to be almost the same. In the remaining groups the absolute body weight increase due to regeneration was faster than the normal growth by from 1.8 times in medium-size individuals, regardless of the degree of body damage, to 3.6 times in large individuals with a 55–60% body loss.

Table VI. Ratio of regenerative body increment to normal growth increment, on average for the whole experimental period (duration of experiment 70 days, temperature $15 \pm 1^\circ\text{C}$).

| Average weights of intact individuals at the beginning of experiment (mg wet weight) | Regenerative body increment to body increment of intact individuals | | |
|--|---|----------------------------|----------------------------|
| | 25–30% loss in body-weight | 40–45% loss in body-weight | 55–60% loss in body-weight |
| 2.43±0.05 | about 1 | about 1 | about 1 |
| 4.22±0.05 | 1.8 | 1.8 | 1.8 |
| 6.26±0.07 | 2.8 | 3.5 | 3.5 |

Table VII. Comparison of relative increments in body-weight (P/B) of Tubificidae during normal growth and during regeneration (duration of experiment 70 days, temperature $15 \pm 1^\circ\text{C}$)

P – production, B – biomass

| Average weight of intact individuals at the beginning of experiment (mg wet weight) | Average 24-hour P/B coefficients | | | |
|---|------------------------------------|-----------------------------|----------------------------|----------------------------|
| | normal growth | lost body part regeneration | | |
| | | 25–30% loss in body-weight | 40–45% loss in body-weight | 55–60% loss in body-weight |
| 2.43±0.05 | 0.009 | 0.011 | 0.012 | 0.014 |
| 4.22±0.05 | 0.004 | 0.010 | 0.010 | 0.012 |
| 6.26±0.07 | 0.002 | 0.006 | 0.008 | 0.010 |

The relative body weight increments (P/B), during both the normal growth and regeneration, were inversely proportional to the body size of the individuals; the highest values were recorded for small individuals, the lowest for large individuals (Table VII). Due to the faster regenerative body growth the 24-hour P/B ratios of the regenerating individuals in the particular size classes were greater than those recorded for normally growing individuals, and they increased with the increasing degree of body damage.

2.6. THE ROLE OF REGENERATION IN THE PRODUCTION OF TUBIFICIDAE GROUPINGS

The determination of the contribution of regeneration to the production of the tubificid groupings in the habitats studied was based on the data relating to the biomass of the individuals deprived of the posterior body part and regenerating it, and of the intact individuals (data from field studies), as well as on the P/B ratios recorded during laboratory experiments. For each of the body size and degree of body damage groups the calculations were made separately, and for each of them the appropriate P/B ratio was selected. The same data were used for the calculation of the degree to which regeneration of lost body parts increased the production of the tubificid groupings in the habitats studied. In the calculations the temperature factor was not taken into account, because it was assumed that both the regeneration and the normal growth showed the same relationship to temperature, that is to say, the ratio of regenerative body growth rate to normal growth rate of the individuals living in the same habitats is independent of the temperature.

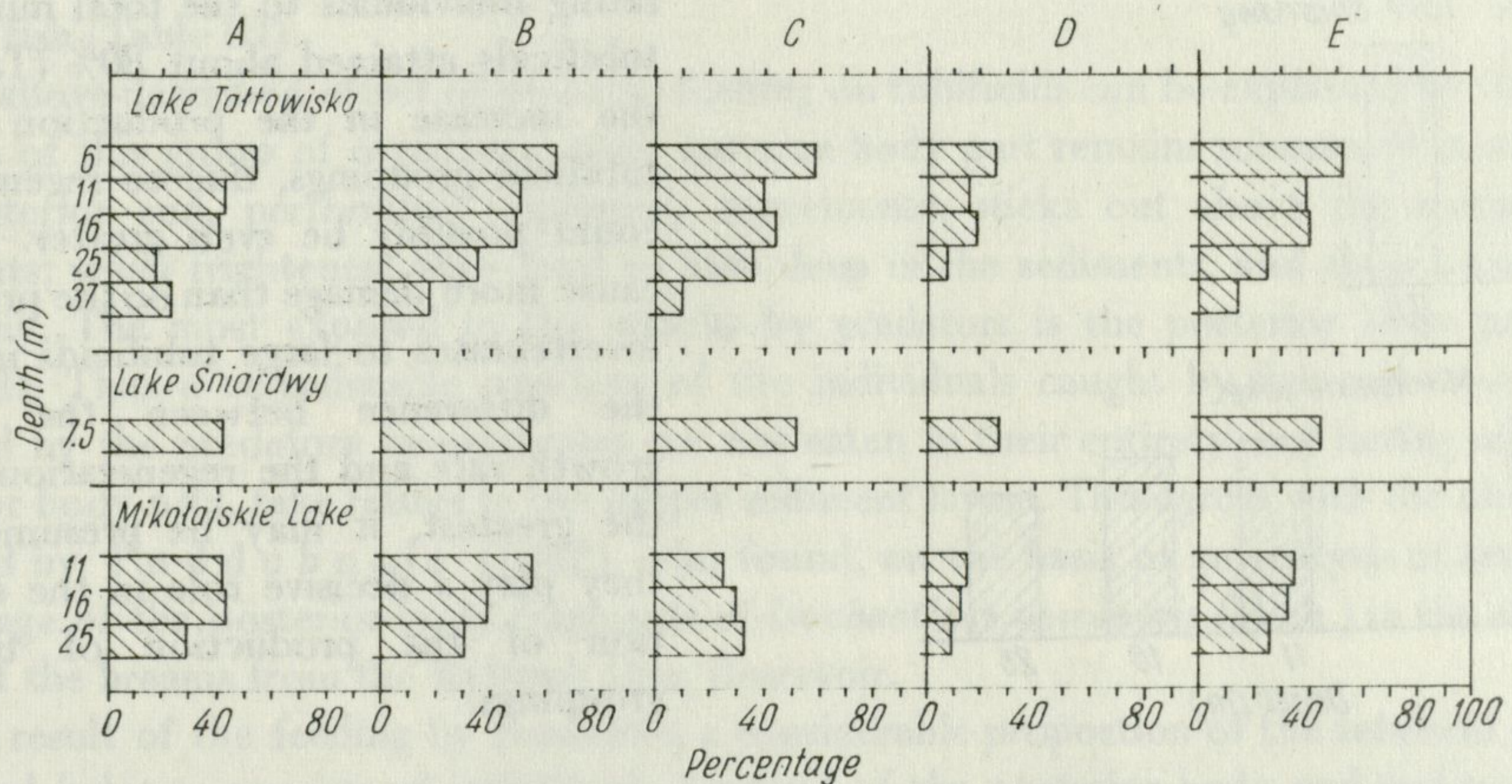


Fig. 6. Percentage of production realized by regenerating individuals in the total production of Tubificidae (on an average for the years 1971–1972)

A – spring circulation, B – summer stagnation, C – autumn circulation, D – winter stagnation, E – yearly average (for the polymictic Lake Śniardwy, for the purpose of comparison the same seasons are given)

The percentage of the production realized by the regenerating individuals in the total tubificid production of the study habitats varied with depths and with the seasons (Fig. 6). Its highest values were recorded for the sublittoral of Lake Tałtowisko and for the central part of Lake Śniardwy, where its average values for the two years were 50.3 and 42.8%. With the increasing depth the role of regeneration in the production of Tubificidae decreased, and in the deep profundal of Lake Tałtowisko (37 m deep) the average contribution of regeneration to the production did not exceed 14.3%. Analyzed in the seasonal aspect, the contribution of regeneration to the tubificid production in the lakes Śniardwy, Tałtowisko (up to the depth of 25 m) and Mikołajskie (at the depth of 11 m) appeared to be the greatest in summer, and at deeper stations – during the spring circulation (Mikołajskie Lake – 16 m and Lake Tałtowisko – 37 m), or the autumn circulation (Mikołajskie Lake – 25 m). The smallest

contribution of regeneration to the tubificid production in all the habitats studied was recorded for winter. It then ranged from 0% (in the deep profundal of Lake Tałtowisko) to 26.5% (in Lake Śniardwy).

Because regeneration accelerates the body growth, relative to the normal growth, the feeding of predators becomes a factor that stimulates the production of Tubificidae by increasing the

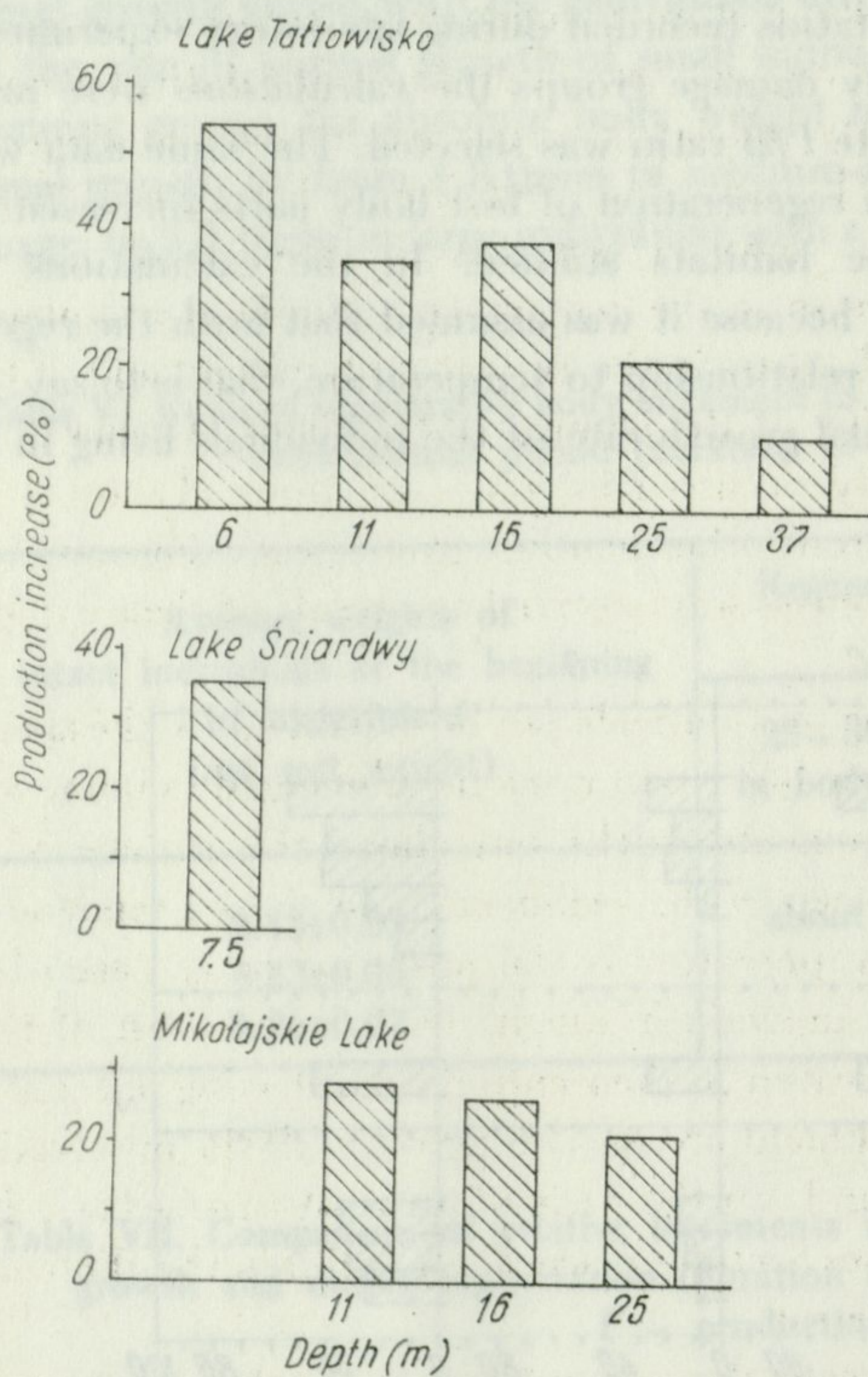


Fig. 7. Increase in annual production of natural Tubificidae groupings as a result of regeneration, relative to the production of speculative groupings of the same biomass and size structure, but not exploited by predators (average for the years 1971–1972)

1958, Lufarov 1961, 1963, Popčenko 1971, Jarošenko, Valkovskaja and Čokyrlan 1972, Monakov 1972, Nechaeva 1973, Schwüste, Cremer and Parma 1973, Loden 1974) in which the considerable importance of tubificids as the food items of these organisms has been pointed. The observations relate primarily to the food requirement and food spectra of various predator groups and species. For this reason, it is difficult on their basis to describe the effect of predators on the natural tubificid groupings. An additional difficulty in the assessment of the number and biomass of the Tubificidae used as food, in spite of the fact that more and more exact methods are used for analyzing the contents of the alimentary tracts (Galinskij and Nikitin 1972), is the lack in this animal group of hard body covers, due to which their decomposition in the alimentary tract of the predator is fast and almost complete (Jablonskaja 1935).

number of regenerating individuals. The increased tubificid production due to regeneration, relative to the production of speculative groupings of the same biomass and size structure, but not exploited by predators (all the individuals being intact) ranged in the habitats studied from 10.4%, in the deep profundal, to 54.2%, in the sublittoral of Lake Tałtowisko (Fig. 7). In shallower habitats, where the proportion of regenerating individuals to the total number of tubificids attained about 80% (Table V), the increase in the production of the tubificid groupings, due to regeneration, could possibly be even greater. As fish cause more damage than do the predatory invertebrates to large tubificids in which the difference between the normal growth rate and the regeneration rate is the greatest, it may be presumed that they play a decisive role in the stimulation of the production of tubificid groupings.

3. DISCUSSION

There have been many studies concerned with the feeding of the predatory invertebrates and fish (Žiteneva

Consequently, little is known about the effects of the exploitation of Tubificidae by the predators.

Some field studies and experimental investigations indicate that predators may affect both the biological functions of the tubificids and the condition of their groupings. K a j a k and W i ś n i e w s k i (1966) found that in the Masurian lakes intensive exploitation by predators caused a decrease in the percentage of sexually mature individuals in tubificid groupings. Likewise, a mass occurrence of *Chironomus anthracinus* Zett., a predator of tubificid cocoons, in Lake Esrom caused a decrease in the growth rate, a delay in sexual maturation and a lowering of the fecundity of *Potamothrix hammoniensis* (J o n a s s o n and T h o r h a u g e 1976).

Experiments carried out on Lake Śniardwy have shown that the feeding of fish and predatory invertebrates causes primarily an increase in the percentage in tubificid groupings of individuals without the posterior body part, a decrease in the average body weight and, if large individuals are exploited at a high rate, a lowering of the biomass of tubificids. A reduction in the density of tubificids by the predators only occurred in some situations (Tables II, IV, Figs. 2, 3). In this respect the tubificids differ from other benthos groups, e.g., Chironomidae, in which a reduction of both the density and biomass was observed as a result of their exploitation by fish (Table III).

The above-described effect of predator feeding on tubificids can be explained by the specific features of this group of organisms: their anterior body part remains submerged in mud, while the posterior end, performing respiratory movements, sticks out above the surface of the sediments; when frightened, they tend to hide deep in the sediments, and show a tendency to autotomy. The most exposed to the attacks by predators is the posterior body part of the tubificids. Thus a considerable numbers of the individuals caught by fish and most of those attacked by the predatory invertebrates are not eaten in their entirety, but having rejected the posterior body part, take refuge in the deeper sediment layers. This agrees with the observations reported by P o d d u b n a j a (1962), who found, on the basis of an analysis of setae, a high percentage of the posterior body fragments of *Isochaetides newaensis* (Mich.) in the alimentary tracts of the breams from the Rybinsk Dam Reservoir.

As a result of the feeding by predators, a considerable proportion of the tubificid groupings in natural habitats consists of individuals deprived of the posterior body end and regenerating the part that had been lost (Table V, Fig. 4). The following question therefore arises: What is the relationship between the regenerative growth rate and the normal growth rate, and what is the role of regeneration in the production of tubificids? The existing information on the ecological effects of invertebrate regeneration is scarce, being limited to brackish and salt-water habitats. As has been demonstrated by experiments on a simple predator-prey system, in which the only predator of the bivalve, *Tellina tenuis* Da Costa, was the fry of the plaice, *Pleuronectes platessa* L. (using bivalve siphons as food), the energy of the regenerated siphon portions covered the energy requirement of the predator (T r e v a l l i o n, E d w a r d s and S t e e l e 1970). S a l z w e d e l (1974), who studied the regeneration of the rays of the ophiuroids, has found that the rate of ray regeneration was faster than the rate of ray growth, but he has not analyzed the ecological consequences of this phenomenon.

Also, laboratory investigations into the rate of regeneration in Tubificidae have shown that both the absolute body weight increments and the production efficiency during regeneration are higher than during the normal growth (Tables VI, VII). On the basis of the results of these experiments it has been estimated that in the shallower habitats (the sublittoral of Lake Tałtowisko, the central part of Lake Śniardwy) the proportion of production realized by the regenerating individuals amounted to about 50% of the total production of Tubificidae, and

that owing to the presence of the regenerating individuals in the lakes studied there occurred an increase in the production of Tubificidae by about 10% (in the deep profundal) up to over 50% (in the sublittoral of Lake Tałtowisko) (Fig. 7).

Thus, the way of feeding used by the predator, causing an increase in the number of regenerating individuals, acted as a production-stimulating factor. It may be presumed that this is a regularity of a general nature. This is confirmed by studies of the effects of phytophage grazing on vascular plants (Rafes 1971, Zlotin and Chodašova 1974), as also by the studies, mentioned in this paper, of regeneration in other invertebrates.

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4. SUMMARY

The effect was studied of predators on the tubificids in short-term (9 days) experiments in the central part of Lake Śniardwy. The effect of fish feeding was determined by comparing the density, biomass and size structure of Tubificidae in sections of the lake bottom (cages) accessible and inaccessible to fish (Fig. 1 A, B), and the effect of predatory invertebrates was determined by comparing tubificid groupings in isolated bottom sections (Fig. 1 C) with a natural and an artificially increased density of predatory Chironomidae larvae.

The rate of tubificid exploitation by the predators was assessed on the basis of the percentage in the tubificid communities of 23 lakes in central and northern Poland (Table I) of individuals damaged, due to the feeding by predators, and regenerating the lost body parts.

Body increase rates of individuals growing normally and of those regenerating body parts lost due to predation, were investigated in laboratory experiments, using a natural substratum and oxygen conditions similar to the natural ones.

It has been found that fish and predatory invertebrates do not usually eat tubificids in their entirety, but they only bite off the posterior parts of their bodies. This causes a decrease in the average body weight of individuals and in the biomass of tubificid groupings. A reduction in the density of Tubificidae was only observed when young individuals dominated in their groupings (Tables II, IV). Predation caused an increase in number of the damaged individuals regenerating the lost parts of body (Figs. 2, 3).

The percentage in lake tubificid groupings of individuals with bodies damaged due to predation, and regenerating the lost body parts was found to be the highest in the littoral (up to 80%) and in decreased with the depth (Table V). Analyzed in seasonal aspect, the damaged and regenerating individuals represented the largest proportion of tubificid groupings in the spring, and in shallow lake zones also in the summer (Fig. 4). The variations in the occurrence of damaged and regenerating individuals are probably connected with changes in the predator activity related to the temperature, and with a limited accessibility of Tubificidae to predators in deeper habitats with the deterioration of oxygen conditions during stagnation.

Laboratory experiments, the aim of which was to determine the rate of regeneration of the tubificids, have shown that in regenerating individuals the absolute body weight increments are, depending on the body size and the degree of damage to the body, up to 3.6 times as large as in the individuals growing normally (Table VI). The faster growth resulted in a better production efficiency (P/B) of the regenerating individuals of the particular body size groups, relative to the individuals growing normally (Table VII).

The average percentage of the production realized by those individuals which were regenerating the lost parts of their bodies in the total production of tubificids in the habitats under study was about 14% in the profundal up to about 50% in the sublittoral (Fig. 6).

Because of the faster (than the normal) body growth during regeneration, the feeding of predators, which leads on to increased numbers of the individuals regenerating the lost parts of their bodies, is a factor that stimulates the production of the tubificids. The increase in the tubificid production due to regeneration as estimated for the lakes under study, relative to speculative groupings of the same biomass and body size structure, but not exploited by predators (all the individuals being intact) amounted to about 10% in the deep profundal, and over 50% in the sublittoral.

5. POLISH SUMMARY

Badano oddziaływanie drapieżców na *Tubificidae* w toku krótkotrwałych (9 dni) eksperymentów w śródzieżerzu jeziora Śniardwy. Efekt żerowania ryb określano przez porównanie zagęszczenia, biomasy i struktury wielkości *Tubificidae* w wycinkach dna (zagrodach) dostępnych i niedostępnych dla ryb (rys. 1 A, B); oddziaływanie bezkręgowców drapieżnych określano przez porównanie zgrupowań *Tubificidae* w izolowanych wycinkach dna (rys. 1 C) o naturalnym i sztucznie zwiększonym zagęszczeniu drapieżnych larw *Chironomidae*.

Intensywność eksploatacji *Tubificidae* przez drapieżce oceniano na podstawie udziału w zgrupowaniach *Tubificidae* 23 jezior centralnej i północnej Polski (tab. I) osobników uszkodzonych w wyniku żerowania drapieżców i regenerujących ubytki ciała.

Tempo przyrostu ciała osobników rosnących normalnie i regenerujących ubytki ciała badano w eksperymentach laboratoryjnych na naturalnym podłożu, w warunkach tlenowych zbliżonych do naturalnych.

Zaobserwowano, że ryby i bezkręgowce drapieżne przeważnie nie zjadają całych osobników *Tubificidae*, a jedynie odgryzają tylne odcinki ich ciała. Powoduje to spadek średniego ciężaru osobników i obniżanie biomasy zgrupowań. Redukcję zagęszczenia *Tubificidae* obserwowano jedynie w tych przypadkach, w których w zgrupowaniach dominowały osobniki młode (tab. II, IV). Żerowanie drapieżców powodowało wzrost liczby osobników uszkodzonych i regenerujących ubytki ciała (rys. 2, 3).

Udział osobników uszkodzonych w efekcie żerowania drapieżców i regenerujących ubytki ciała w zgrupowaniach *Tubificidae* w jeziorach był największy w litoralu (do 80%) i malał wraz ze wzrostem głębokości (tab. V). W aspekcie sezonowym osobniki uszkodzone i regenerujące ubytki ciała osiągały największy udział w zgrupowaniach *Tubificidae* wiosną, a w płytszych strefach jezior także latem (rys. 4). Zróżnicowanie występowania osobników uszkodzonych i regenerujących ubytki ciała jest prawdopodobnie związane ze zmianami aktywności drapieżców w zależności od temperatury i z ograniczeniem dostępności *Tubificidae* dla drapieżców w środowiskach głębszych, w miarę pogarszania się warunków tlenowych podczas stagnacji.

Eksperymenty laboratoryjne nad tempem regeneracji osobników *Tubificidae* wykazały, że bezwzględne przyrosty masy ciała u osobników regenerujących są w zależności od rozmiarów i stopnia uszkodzenia ciała, do 3,6 razy większe niż u osobników rosnących normalnie (tab. VI). W następstwie szybszego wzrostu również efektywność produkcji (P/B) osobników regenerujących ubytki ciała była, w poszczególnych grupach wielkości osobników, większa niż u osobników rosnących normalnie (tab. VII).

Udział produkcji realizowanej przez osobniki regenerujące ubytki ciała w całkowitej produkcji zgrupowań *Tubificidae* w badanych środowiskach wynosił średnio od ok. 14% w profundalu do ok. 50% w sublitoralu (rys. 6).

Szybszy (niż normalny wzrost) przyrost ciała podczas regeneracji powoduje, że żerowanie drapieżców, prowadzące do zwiększenia liczby osobników regenerujących ubytki ciała, jest czynnikiem stymulującym produkcję *Tubificidae*. Zwiększenie produkcji *Tubificidae* w następstwie regeneracji, w stosunku do produkcji teoretycznie założonych zgrupowań o tej samej biomasy i strukturze wielkości, ale nie eksploatowanych przez drapieżce (w których wszystkie osobniki są całe) oceniono w badanych jeziorach na ok. 10% w głębokim profundalu i ponad 50% w sublitoralu.

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