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ON THE RELATIONSHIP BETWEEN ABUNDANCE, AGGREGATIONS AND "CONDITION" OF *DREISSENA POLYMORPHA* PALL. IN 36 MAZURIAN LAKES*

The present paper is a comparative study on variation in time and space of abundance, occurrence in aggregations and "condition" of individuals in the selected populations of *Dreissena polymorpha* Pall. The work was carried out in 36 lakes of the Mazurian region. Attempts were made to find the degree of dependence of these phenomena on certain morphometric and environmental characters of lakes as the area, maximal depth, visibility, pH, oxidization and Ca content; and on the environmental features of lakes taken as a whole. On the basis of field and laboratory investigations the three mentioned features of populations were compared to determine whether the abundance of molluscs in a water body influences the clumping tendency and size of aggregation, and how far is it related to the "condition" of individuals.

Literature concerned with *Dreissena polymorpha* Pall. is very abundant. Toward the enu of the last century and at the beginning of the present one, interest was taken in this species primarily because of its tremendous expansion from the Black and Caspian Seas into rivers and lakes of Eastern and Central Europe. Main concern was given to the appearance of *D. polymorpha* in more and more water bodies, to its distribution and settling in different localities. These problems were the topic of a few monographs and were often mentioned in textbooks on the fauna in various water bodies.

Biological and ecological aspects of this species, its growth and development, nutrition and social behaviour in respect to other species were of much less concern.

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Recent studies on *D. polymorpha* are aimed to solve two essential problems: the control of this mollusc, and its utilization as food for fish.

Rapid increases in the numbers of *D. polymorpha*, especially in newly established dam reservoirs, and above all its growing over of waterworks, which lowers their performance, impose a necessity of planned control of this species. These problems gain importance with the present-day development of waterworks and the use of water for industrial purposes. Studies on the control of *D. polymorpha* are most intensive in USSR and Germany.

The other aspect of the problem, viz. the role of *D. polymorpha* as a food for fish, is of an economic importance. Because of its large numbers and high biomass, *D. polymorpha* is an important component in the biocenoses of lakes and lagoons. In several reservoirs it constitutes from 80 to 90 per cent of the total animal biomass (Berg 1938, Żmudziński 1958, Sokolova 1961, Wiktor J. 1961, 1963). *D. polymorpha* is of importance in biocenoses of lakes and lagoons mainly as the food of mature roach. In Węgorzewo lakes, the development of roach is noticed to be related with the abundance of molluscs, in the first place of *D. polymorpha* (Zawisza 1961). According to Žadin (1946), *D. polymorpha* in the Caspian and Black Seas is fed upon by several other fish species, among others by sturgeon, bream and ide. Wiktor K. (1958) found *D. polymorpha* larvae in the Szczecin Lagoon to be preyed upon by smelt, pope perchpike and roach fry.

Comprehensive monographs on the biology and ecology of *D. polymorpha* are rare.

Studies carried out in the Szczecin Lagoon are concerned with the distribution of this species, its abundance and biomass in different places of the Lagoon, problems related to its growth, mortality rate and its role in the water body including its role in the forming of sea deposits (Wiktor K. 1958, Wiktor J. 1960, 1961, 1963). Similar problems are included in a narrower scope in Żmudziński's (1958) study on the zoobenthos of the Vistula Lagoon (Wislinskiy Zaliv).

The present work was intended as a comparative study of some of the characters of *D. polymorpha* populations in 36 Mazurian lakes. The four studied characters are: the distribution of *D. polymorpha* in lakes, its abundance, the distribution and sizes of aggregations and "condition". Under the term "condition" I ment the size and weight of individual specimens of *D. polymorpha*. Attempts were made to find out whether these characters undergo variation, and if so, how far does the variation range extend in the studied lakes. Is the variation related to the character of a certain locality in the lake or is it a feature typical of the lake as a whole. Beside an analysis of spacial differentiation of the examined features of *D. polymorpha* populations, the variation during different seasons and years was examined. Apart from the above, studies on *D. polymorpha* were broadened to find whether variability in the examined features is affected by the abiotic environmental factors, and if so, to what extent; and how far is it related to some of the properties of the population. Finally, the mutual relationships between the abundance, occurrence in aggregations and condition of individual specimens were given consideration.

DESCRIPTION OF THE STUDY AREA

The investigations were carried out in the Mazurian Lake District. In spite of a mass occurrence of *D. polymorpha* in Mazurian lakes, respective data are scarce in comparison with the general knowledge on this species in different regions of Poland. These data are limited to short references in some of the pre-war German papers, mainly Hilbert's; and to mentions in Polish, post-war papers (Tarwid et al. 1953, Zawisza 1961).

The study area included 36 Mazurian lakes belonging to two main drainage areas: the basin of Narew (Pisa), and that of the Baltic (Pregoła, Węgorapa). The study lakes differ from one another by their areas, morphology of the lake basin, circulation of the water masses, chemical composition of the water connected with the degree of the lake trophy.

Only one of the studied reservoirs, viz. the lake Śniardwy, exceeded 10,000 ha in surface area. (Lakes belonging to the Mamry complex, the so-called Niebolskie lakes, are regarded as separate units). Ten lakes are more than 1,000 ha, 18 lakes range between 1,000 and 100 ha, and 7 below 100 ha.

Maximum depths of the studied lakes range between 1.5 m in shallow lakes (e.g. Kotek, Przyleśne, Szymońskie) and 47 m, 42.5 m or 40 m in very deep lakes (resp. Ryńskie, Żabinki and Mamry).

The chemical and physical characteristic of the studied lakes included: visibility, pH, oxygen level, contents of H_2S and Ca, which all belong to the basic environmental factors determining the occurrence of molluscs. Data concerning the environment were based on the papers of Olszewski (1951, 1953), Gieysztor and Odechowska (1958), Olszewski and Paschalski (1959), Patalas (1960a, 1960b).

Visibility during the period of summer stagnation ranges in the studied lakes between 0.9 and 5.3 m, with a mean of 2 m.

The pH values of the surface layers range from 7.5 to 8.5, while in the bottom layers from 6.6 to 7.6.

Oxygen contents during the summer stagnation greatly vary. In some cases an oxygen deficit was noticed at the bottom. In a few lakes H_2S was found near the bottom. The majority of lakes however were well oxygenated right down to the bottom. The calcium contents remained on average levels, ranging from 70 to 112 mg/l CaO.

Most of the studied lakes belong to the eutrophic type, in the broad sense of the word, while five lakes represent the β-mesotrophic type.

METHODS

The studies took place in 1960 and 1961. Primary analyses were carried out in 1958 and 1959, while some of the supplementary data were obtained in 1962.

Samples (in 1960 and 1961) were taken in all lakes mainly in July and August, during the summer stagnation. In 8 lakes observations took place in spring and autumn.

In the large, differentiated lakes, samples of *D. polymorpha* were collected at three permanent stations (each year at the same ones), in the smaller lakes at two stations. In selecting the permanent stations, 1) the topography was determined alongside with the plant overgrowth, type of the bed and character of the littoral slope, 2) several control observations were made on more or less 15 other stations to find whether relations at the chosen ones are sufficiently characteristic of the given water body.

Samples of *D. polymorpha* were taken by means of: 1) boxes for quantitative catching (Stańczykowska 1961), 2) an Ekman-Birge sampler, 3) a dredge.

The box for quantitative gathering of molluscs is a modification of the frame used by Žadin (1938) for assays of the malacofauna occurring at small depths. A bottomless box, 22×22×20 cm in size, is placed on the lake bottom. All the *D. polymorpha* specimens are gathered and their number to 1 m² calculated.

At greater depths Ekman-Birge sampler was used. On hard lake beds, especially in sublittoral zones abundant in molluscs, stones and twigs, it failed to close completely, so that the samples could not be regarded as quantitatively representative. They provided a rough estimate of *D. polymorpha* abundance in the given locality.

In order to obtain larger numbers of specimens and whole colonies of *D. polymorpha* a dredge was used. It was dragged along a 5 m long section of the bottom. This technique yielded animals from a determined surface of the bottom more or less alike in all cases. Samples obtained with the use of a dredge were a completion of those taken with the Ekman-Birge sampler.

On the basis of materials gathered from the different lakes, the distribution of *D. polymorpha* was estimated, as well as its abundance, occurrence in aggregations and "condition" – separately for each study area.

At each of the stations samples were collected each time in two replicates from three different depths:

a. shallow littoral zone, from 0.2 to 0.5 m deep,

b. mid-littoral zone, just beyond the reed belt, usually from 1 to 2 m deep,

c. sublittoral sone, from 4 to 12 m deep (in dependence on the slope angle).

In 1960 and 1961, 1,488 samples were taken at permanent stations. By the same methods 1,250 samples were taken at "control" stations.

Beside this, in order to gain more precise data on the distribution, numbers and age structure of populations, ten lakes were studied in detail. Five draggings, of 10 samples each, were performed along the shore at different depths, alongside so-called cross-sections or draggings performed in a direction perpendicular to the shoreline, from shallow littoral to the bottom sublittoral in all, some 1,800 samples.

Aggregations of *D. polymorpha* were characterized on the basis of analyses of collected individual aggregations (20 per site) wherein the numbers, positions and age of individual specimens were determined.

The "condition" of *D. polymorpha* was estimated on grounds of measurements of length, breadth and height of shells, as well as of their weight. A detailed description of the applied methods is given in a separate chapter on the subject.

Age appraisals of *D. polymorpha* were based on the numbers of the annual rings. A detailed analysis of 3,205 specimens (Stańczykowska 1963) showed a single ring to be formed yearly on a shell of this mollusc, so that the number of rings corresponds with the age.

DISTRIBUTION OF *D. POLYMORPHA* IN THE STUDIED LAKES

D. polymorpha occurs mainly in the middle and lower littoral and in the upper sublittoral. The mollusc forms a dense belt encircling usually the entire basin. Only very shallow, eutrophic bays are characteristic of less dense populations or of a complete lack of *D. polymorpha*. The abundance of *D. polymorpha* changes with the increasing offshore distance as follows: low, near the shoreline, it gradually increases reaching the maximum at a 2 to 4 m depth, whence it dwindles to zero at a depth of 11 to 12 m (Fig. 1).

All the studied Mazurian lakes are characterized by this pattern, in spite of the minor differences in the distribution curve related to the breadth of the littoral and the angle of the slope. In Tałtowisko lake, the maximum of the abundance of *D. polymorpha* was found at a 4 m depth; while in Śniardwy at 2 m in depth. The general pattern of *D. polymorpha* distribution however remained unchanged. Respective data from reference literature bring evidence in favour of an analogous distribution of *D. polymorpha* inhabiting other lakes (Lundbeck 1926, Berg 1938, Fig. 1), dam reservoirs (Sokolova 1961) and lagoons (Wiktor J. 1960, 1963). In some cases the highest frequency may occur in more shallow, or in deeper layers, as e.g. in the 8 to 10 m deep sublittoral of the lake Wdzydze (Mikulski a. Giziński 1961); in general however the distribution follows the same pattern. Maximum depth at which *D. polymorpha* was found in the Mazurian lakes did not exceed 11 or 12 m. For Danish lakes Wesenburg-Lund (1939), and Dunn (1954) give the usual depth of from 10 to 12 m; occasionally however *D. polymorpha* occurs at depths of 30 m. According to Berg (1938), *D. polymorpha* occurred in the Esrom Lake at depths of 14 m. Lundbeck (1926) encountered specimens in lakes of Northern Germany at depths of 44 m.

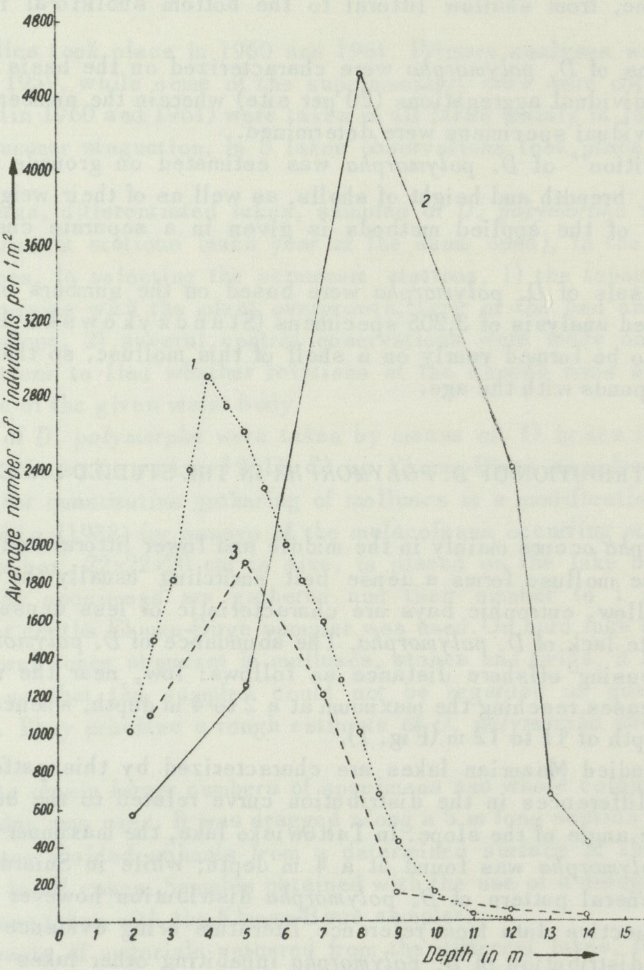

Fig. 1. Number of *D. polymorpha* individuals plotted against depth

1 — average values for the explored Mazurian lakes, *2* — average values for the Esrom Lake, after Berg (1938), *3* — average values for the east-Holstein lakes after Lundbeck (1926)

The above described distribution and range of occurrence of *D. polymorpha* in Mazurian lakes has been confirmed by direct observations made by divers. Examinations of this kind were carried out at ten stations, in four lakes: Bełdany, Śniardwy, Tałtowisko and Tyrkło. Belts from shoreline to maximum depths of 17 m were closely examined. Divers found the farthest range of *D. polymorpha* occurrence at 11 m. Their findings agreed completely with data based on the use of Ekman-Birge sampler.

Shallow littoral (20 to 50 cm deep) of the Mazurian lakes is inhabited by adult specimens at very low densities; on the other hand it is often characteristic of high numbers of young, one-year-old or two-year-old specimens, occurring both on the lake bottom and on submerged plants. In contrast to the rather equal distribution of adults round the entire lakes, young molluscs occur in patches, only in certain places of the lake; elsewhere they do not occur at all. Fejgina (1950), Tarwid et al. (1953) and Ehrenberg (1957) likewise report on the irregular occurrence of young *D. polymorpha* specimens.

In order to find whether this irregular distribution of immature specimens of *D. polymorpha* is related to the direction of winds blowing during the period of metamorphosis and settling of larvae, the problem was made subject of a study. The findings failed to reveal any correlation. Young molluscs were islanded in the shallow littoral, in the same manner however whichever the shore; on no occasion were they only found in the windward shores. The unequal distribution of immature individuals of *D. polymorpha* cannot be related to the prevailing direction of winds.

In the shallow littoral habitat *D. polymorpha* populations are characterized by a rather variable age structure related to the depth. Near the shoreline, youngest, one-year-old specimens are in majority; at rising depths the percentage of two-year-old molluscs increases; in both these cases older specimens are rare. In the mid-littoral and sublittoral i.e. within the belt of a greater density unrelated to the depths, the age structure of the population of molluscs is similar (Fig. 2). Young (one-year-old and two-year-old specimens sexually immature)

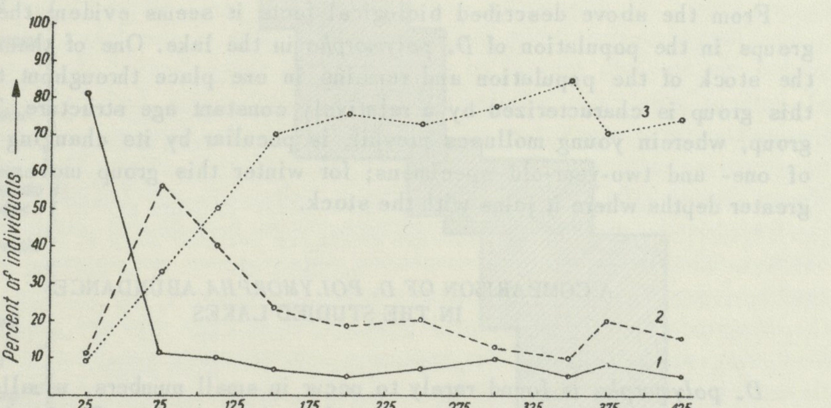

Fig. 2. Changes in age structure of populations of *D. polymorpha* plotted against depth
1 — one-year-old *D. polymorpha*, *2* — two-year-old *D. polymorpha*, *3* — older specimens of *D. polymorpha*

(Vlastov and Kačanova 1959), constitute in the main belt of occurrence a small part of the population (10 to 20 per cent). Eighty per cent is composed of older, 3-, 4-, 5- and 6-year-old specimens. Seven- and 8-year-old individuals occur at low densities; within the entire material only ten or so, 9- and 10-year-old specimens were found (Stańczykowska 1963).

The above described distribution and age structure of molluscs are characteristic of the summertime of all years of studies. In autumn, displacement was noticed in the distribution of the species. Winter migrations were observed by Schermer (1930) and Berg (1938). The abundance of *D. polymorpha* in the studied lakes of Mazuria decreases in the most shallow regions; at the same time it increases in the main belt of its occurrence. Young specimens migrate in autumn and winter deepward. In effect, the age structure in the main belt changes its proportions by a relative increase in numbers of young molluscs. The percentage of young specimens in the main belt of *D. polymorpha* occurrence, amounting in summer to 11.2 per cent, increases in the autumn to 19.8 per cent of the population.

The distribution of adults in *D. polymorpha* at greater depths is subject only to small seasonal changes. Nevertheless, according to laboratory experiments (Stańczykowska – unpublished data) and observations made at the lake Mikołajskie (Dusoge – unpublished data) adult specimens of *D. polymorpha* may likewise change place, provided they first dissolve the tufts of filaments by which they are attached to one another or to the substratum. According to Žadin (1952) and Kačanova (1963) exclusively young specimens possess the capacity to separate from the colonies and a locomotory power a situation associated with their only partial, at that period, retrogression of the foot.

From the above described biological facts it seems evident there are two groups in the population of *D. polymorpha* in the lake. One of them represents the stock of the population and remains in one place throughout the season; this group is characterized by a relatively constant age structure. The second group, wherein young molluscs prevail, is peculiar by its changing proportions of one- and two-year-old specimens; for winter this group moves offshore to greater depths where it joins with the stock.

A COMPARISON OF *D. POLYMORPHA* ABUNDANCE IN THE STUDIED LAKES

D. polymorpha is found rarely to occur in small numbers, usually its abundance is high (data from reference works). According to Wesenberg-Lund (1939) the densities in lakes amount to 30,000 specimens per 1 m^2; acc. to Lundbeck (1926) in lakes of Northern Germany, it amounts to 5,000 specimens per 1 m^2; acc. to Rzóska (1935) in Wigry lake – to 5,770 specimens per 1 m^2; acc. to Cvetkov (1957) in the lake Bełosławskie – to 7,000 per 1 m^2; and finally acc. to Wiktor J. (1963) in the Szczecin Lagoon – to 114,000 per 1 m^2.

The distribution of *D. polymorpha* followed the same pattern in all the examined lakes; its abundance however greatly varied. Seven out of the 36 tested lakes were found not to harbour *D. polymorpha*. In other lakes, the density in the main belt of its occurrence ranged between a few to several thousands of specimens per 1 m² (Fig. 3).

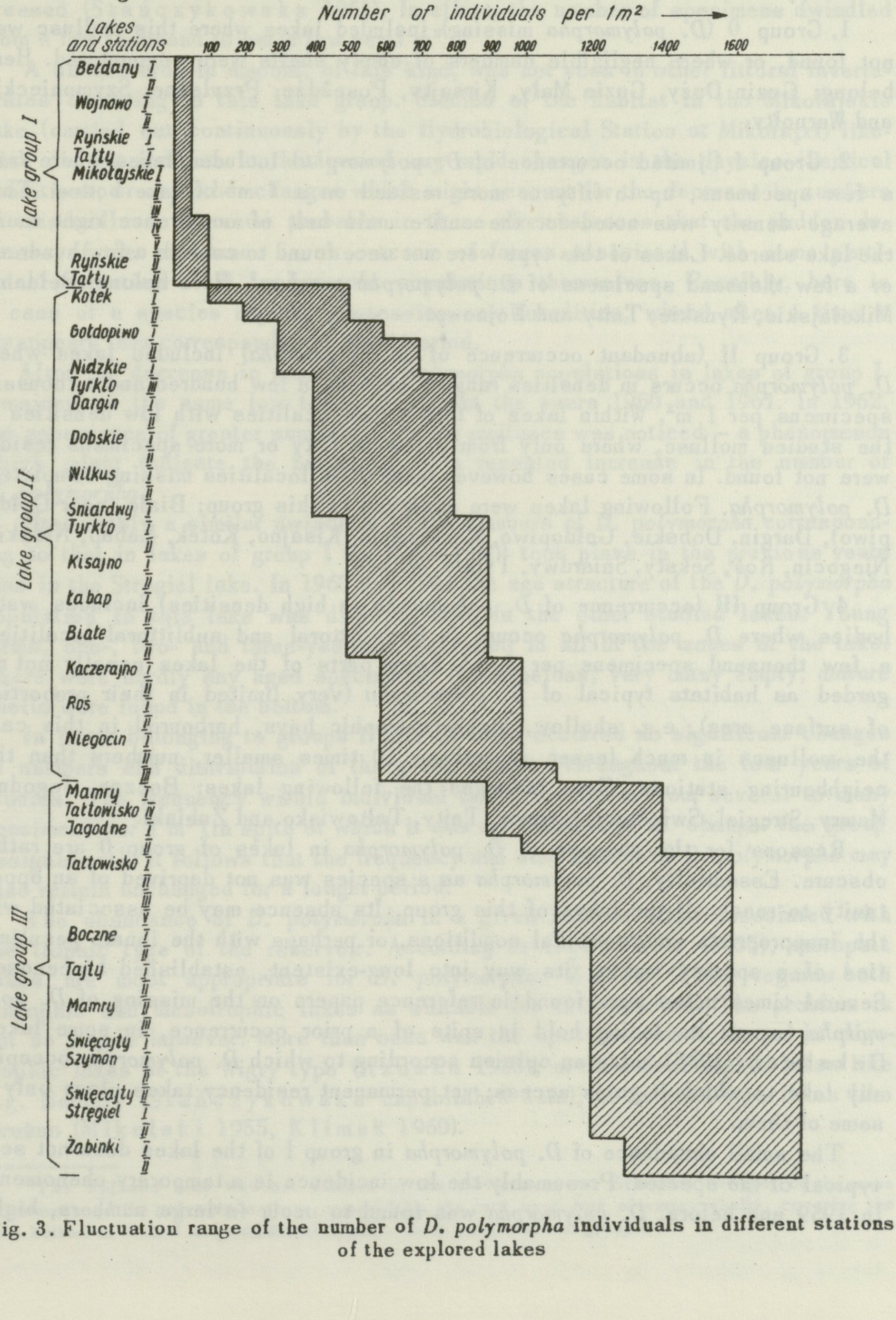

Fig. 3. Fluctuation range of the number of *D. polymorpha* individuals in different stations of the explored lakes

On grounds of the differences in *D. polymorpha* densities, the lakes were assigned to four groups (to compare the numbers in different lakes the densities in the upper border of the main belt of occurrence was considered):

1. Group 0 (*D. polymorpha* missing) included lakes where this mollusc was not found, or where negligible numbers of empty shells were encountered. Here belong: Guzin Duży, Guzin Mały, Kirsajty, Poseżdże, Przyleśne, Szymonieckie and Warnołty.

2. Group I (limited occurrence of *D. polymorpha*) included lakes where from a few specimens, up to fifty or more resided on a 1 m^2 of lake bottom. This average density was noted for the entire main belt of occurrence right round the lake shores. Lakes of this type were not once found to contain a few hundred, or a few thousand specimens of *D. polymorpha* per 1 m^2. Here belong: Bełdany, Mikołajskie, Ryńskie, Tałty and Wojnowo.

3. Group II (abundant occurrence of *D. polymorpha*) included lakes where *D. polymorpha* occurs in densities ranging between a few hundred and a thousand specimens per 1 m^2. Within lakes of this group localities with low densities of the studied mollusc, where only from a few to fifty or more specimens reside, were not found. In some cases however there were localities missing completely *D. polymorpha*. Following lakes were assigned to this group: Białe (near Gołdopiwo), Dargin, Dobskie, Gołdopiwo, Kaczerajno, Kisajno, Kotek, Łabap, Nidzkie, Niegocin, Roś, Seksty, Śniardwy, Tyrkło, Wilkus

4. Group III (occurrence of *D. polymorpha* in high densities) includes water bodies where *D. polymorpha* occurs in both littoral and sublittoral localities, a few thousand specimens per 1 m^2. Even parts of the lakes usually not regarded as habitats typical of *D. polymorpha* (very limited in their proportion of surface area), e.g. shallow, highly eutrophic bays, harboured in this case the molluscs in much lesser, sometimes 10 times smaller, numbers than the neighbouring stations. Here belonged the following lakes: Boczne, Jagodne, Mamry, Stręgiel, Święcajty, Szymon, Tajty, Tałtowisko and Żabinki.

Reasons for the absence of *D. polymorpha* in lakes of group 0 are rather obscure. Essentially, *D. polymorpha* as a species was not deprived of an opportunity to reach all the lakes of this group. Its absence may be associated with the inappropriate environmental conditions, or perhaps with the innate peculiarities of a species making its way into long-existent, established biocenoses. Several times notes were found in reference papers on the missing of *D. polymorpha*, or on its losing hold in spite of a prior occurrence, in some lakes. Deksbach (1935) holds an opinion according to which *D. polymorpha* occupies any lake to which it gains access; yet permanent residency takes place only in some of them.

The small abundance of *D. polymorpha* in group I of the lakes does not seem typical of the species. Presumably the low incidence is a temporary phenomenon. In 1959 and before, *D. polymorpha* was found to occur in large numbers, higher than those in the IIIrd group, in all the lakes belonging to group I (except in Wojnowo lake)[1]. In winter of 1959–60 the density of *D. polymorpha* rapidly decreased (Stańczykowska 1961). In effect, the number of specimens dwindled from a few thousand to but a few per 1 m².

A sudden drop in amount, of this kind, was not seen in other littoral invertebrates occurring in this lake group. Studies of the habitat in the Mikołajskie lake (carried out continuously by the Hydrobiological Station at Mikołajki) likewise did not indicate at that period any rapid changes in the physico-chemical conditions, or any other changes which might account for the decrease in numbers of this mollusc. It seems probable in these circumstances that the sudden decrease of the abundance is an outcome of forces associated with some particular properties of *D. polymorpha* populations themselves. Possibly, here is a case of a species rapidly possessing new localities, where after a time it disappears in a correspondingly short period.

After the decrease in number, *D. polymorpha* populations in lakes of group I remained on the same low level throughout the years 1960 and 1961. In 1962, the appearance of greater numbers of young molluscs was noticed – a phenomenon which might indicate the beginning of a repeated increase in the number of *D. polymorpha*.

Presumably a similar dwindling of the numbers of *D. polymorpha* corresponding to that in lakes of group I (in 1959–1960) took place in the previous years also in the Stręgiel lake. In 1960 and 1961 the age structure of the *D. polymorpha* population in this lake was different than in the other studied lakes. Young forms, one-, two- and three-year-old, prevailed in all of the zones of the lake. There were hardly any aged specimens. Nevertheless, very many empty, mature shells were found in the bottom.

In lakes belonging to groups II and III there occurred no significant changes in numbers and distribution of the given species throughout the four years of studies. The frequency within individual lakes fluctuated from several to many specimens per 1 m² (in spite of which it was not necessary to change the group assignement). It follows that the frequency and distribution of *D. polymorpha* may also remain unchanged for a longer period.

The abundance of *D. polymorpha* in a given lake is often associated with the trophic type of the reservoir. According to Deksbach (1935), eutrophic lakes are most appropriate for *D. polymorpha*. Žadin (1946) regards both eutrophic and mesotrophic lakes as suitable for this species. The problem is not so simple however. More than once was the species seen to abound in oligotrophic lakes of the Wigry type (Rzóska 1935); or in α-mesotrophic lakes like e.g. Babięty (Stańczykowska unpublished data); or in pond-type lakes like Drużno (Mikulski 1955, Klimek 1960).

[1] The Wojnowo lake was not studied in the previous years. Evidence however on the mass occurrence of *D. polymorpha* there comes from the lots upon lots of empty shells, covering the lake bottom in littoral and sublittoral zones – as in other lakes of group I.

Samples collected in the Mazurian lakes also failed to reveal any direct relationship between the occurrence of *D. polymorpha* and the trophic type of the given reservoir. Lakes of group 0, not inhabited by *D. polymorpha*, are all eutrophic, and according to Stangenberg's classification (1936) most of them belong to the pond type (Kirsajty, Poseżdże, Przyleśne, Szymonieckie). Lakes of groups I and II represent eutrophic basins (with the exception of the β-mesotrophic lake Gołdopiwo of group II). In group III, characterized by an abundance of *D. polymorpha* populations, four lakes were found to be β-mesotrophic (Mamry, Święcajty, Tałtowisko and Żabinki), while five eutrophic (Boczne, Jagodne, Stręgiel, Szymon and Tajty). There seems therefore to be a certain tendency in *D. polymorpha* to occur in higher density in less eutrophic lakes.

The occurrence of *D. polymorpha* is more evidently associated with the surface of the given lakes. Lakes where this species was absent (group 0) represented small water bodies, up to 200 ha in surface area (with the exception of Warnołty, 470 ha in acreage). Low, high and very high densities of *D. polymorpha* occurred in larger lakes, above 100 ha in surface area; low and very high densities (group I and III) were found mainly in large lakes, between 100 and 1,000 ha in size; high densities occurred mostly in lakes above 1,000 ha (Fig. 4a).

A comparison of *D. polymorpha* density with the lake depths indicated a certain regularity. Lakes lacking *D. polymorpha* were usually shallow, up to 5 m deep (except for the lakes Duży Guzin and Mały Guzin). Very great numbers of this species occurred in the most deep basins (30–40 m); by no means in the most shallow units. Lakes of group II, where *D. polymorpha* was numerous, were connected with lakes of a maximum depth of 20 to 30 m, in some cases with lakes up to 10 m deep. A low density of *D. polymorpha* (group I) was a characteristic of greater depths, never of shallow waters – as in group III (Fig. 4b).

Some indistinct relationship was found between the calcium content and *D. polymorpha* abundance in the given lakes. Lakes where this mollusc occurs in great numbers (group III) are most numerous and at the same time richest in calcium. Nevertheless lakes less abundant in molluscs are rather similar in their calcium content to lakes of group III (Fig. 4c).

The very abundant occurrence of *D. polymorpha* in lakes of group III and the limited frequency in group I, similar in depth and calcium level to the former group, indicates in this case a certain convergence of these two lake groups. A situation of this kind may be regarded as further evidence in favour of the transitory character of the scarcity of *D. polymorpha* in lakes of group I, wherein the species used to be plentiful prior to its dwindling in number. No direct relationship was found between visibility (Fig. 4d), pH and oxygen content on one hand and the abundance of *D. polymorpha* on the other.

Large fluctuations in the densities of *D. polymorpha* in the studied lakes cannot, on grounds of the present findings, be attributed to the direct influence of the mentioned environmental factors. There was noticed a certain tendency in *D. polymorpha* to occur in larger numbers in lakes characterized by a lower degree of eutrophy, by greater depths, larger acreages and a higher content of

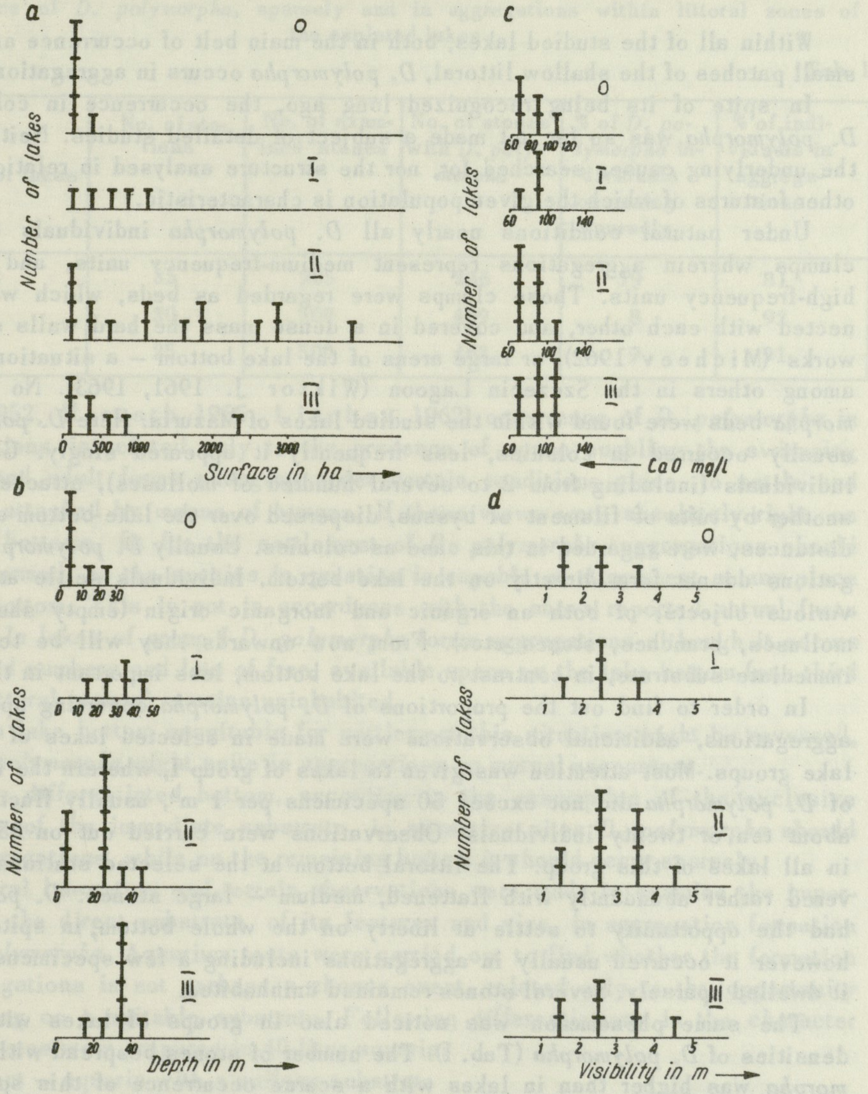

Fig. 4. Relationships between lake groups (0, I, II, and III) characterized by determined numbers of *D. polymorpha* and some of their physico-chemical properties

a — number of lakes against surface, *b* — number of lakes against maximum depth, *c* — number of lakes against the content of Ca, *d* — number of lakes against visibility

calcium than in highly eutrophic basins, more reduced in extent, shallow and poor in calcium. There is no hard and fast rule however in this case, and the parameters in question do not account for the above described variations in *D. polymorpha* numbers.

AGGREGATIONS OF *D. POLYMORPHA*

Within all of the studied lakes, both in the main belt of occurrence and in the small patches of the shallow littoral, *D. polymorpha* occurs in aggregations.

In spite of its being recognized long ago, the occurrence in colonies of *D. polymorpha* was so far not made a subject of detailed studies. Neither were the underlying causes searched for, nor the structure analysed in relation to the other features of which the given population is characteristic.

Under natural conditions nearly all *D. polymorpha* individuals occur in clumps wherein aggregations represent medium-frequency units, and beds – high-frequency units. Those clumps were regarded as beds, which were connected with each other, and covered in a dense mass the hard walls of water-works (Micheev 1962), or large areas of the lake bottom – a situation noticed among others in the Szczecin Lagoon (Wiktor J. 1961, 1963). No *D. polymorpha* beds were found within the studied lakes of Mazuria. Here *D. polymorpha* usually occurred in colonies, less frequently it appeared singly. Groups of individuals (including from 2 to several hundred of molluscs), attached to one another by tufts of filament of byssus, dispersed over the lake bottom at certain distances, were regarded in this case as colonies. Usually *D. polymorpha* aggregations do not form directly on the lake bottom. Individuals settle at first on various objects, of both an organic and inorganic origin (empty shells, live molluscs, branches, stones etc.). From now onwards they will be termed the immediate substrate, in contrast to the lake bottom, less important in this case.

In order to find out the proportions of *D. polymorpha* occurring sparsely in aggregations, additional observations were made in selected lakes of all three lake groups. Most attention was given to lakes of group I, wherein the incidence of *D. polymorpha* did not exceed 50 specimens per 1 m^2, usually fluctuating at about ten or twenty individuals. Observations were carried out on 35 stations in all lakes of this group. The littoral bottom at the selected stations was covered rather abundantly with flattened, medium – large stones. *D. polymorpha* had the opportunity to settle at liberty on the whole bottom, in spite of this however it occurred usually in aggregations including a few specimens; seldom it dwelled sparsely. Several stones remained uninhabited.

The same phenomenon was noticed also in groups of lakes with higher densities of *D. polymorpha* (Tab. I). The number of stones bespread with *D. polymorpha* was higher than in lakes with a scarce occurrence of this species. In these lakes there was a much smaller proportion of *D. polymorpha* specimens occurring sparsely, than in lakes of group I. On the other hand, the proportion of specimens occurring in aggregations in groups II and III of the explored lakes is similar and large, irrespectively of the different density of *D. polymorpha* in the two groups.

On taking into account the universality of aggregatory occurrence in *D. polymorpha* within the explored lakes (81–95%) it seemed advisable to investigate more closely some of the questions related with this problem.

According to the orthodox views (among others Behning 1928, Žadin

Occurrence of *D. polymorpha*, sparsely and in aggregations within littoral zones of the explored lakes

Tab. I

Group of lakes	No. of stations	No. of examined stones	No. of stones with *D. polymorpha*	% of *D. polymorpha* individuals occurring sparsely	% of individuals in aggregations
I	35	925	336	19	81
II	30	500	459	8	92
III	25	500	463	9	91

1946, 1952, Horvath 1955, Ljachov 1962) occurrence of *D. polymorpha* in aggregations is related only to the presence of space enabling the swimming larvae and adult forms changing under certain conditions place, to settle and become attached by means of bysses. If these views were absolutely right, on uniform bottoms, fit for the settlement of *D. polymorpha*, aggregations should not be formed, as the species in question is capable of attachment at any place of the bottom. This is not in accordance with the above reported actual facts (Tab.I). In lakes of group I *D. polymorpha* forms aggregations although it occurs in limited numbers and lots of free, available space on the lake bottom (one-third of the littoral stones) remains uninhabited.

On a lake bottom unsuitable for settlement this situation might be reversed, viz. *D. polymorpha* might unite in aggregations on mutual encounters.

On a differentiated bottom, according to the assumption of the exclusive influence of the immediate substrate, in attractive sites *D. polymorpha* should form aggregations, while on the remaining bottom it should occur sparsely.

Several laboratory and terrain observations were made to examine the importance of the direct substrate, of its features and size, in aggregation formation of *D. polymorpha*. Aquarium tests were carried out to find whether the formation of aggregations is not perhaps a chance event, related only to the opportunity of settling on a suitable substrate. Following differentiations in the character of substrates were prepared in 40-liter aquaria:

1st variant – aquaria with a uniform substrate

a. soft, unfit for settlement (sand covered with a 1 cm layer of mud),

b. hard, suitable (aquaria with a glass bottom),

2nd variant – aquaria with a differentiated bottom

a. single stones overstrewn on a sandy bottom,

b. single stones overstrewn on a muddy bottom,

c. single stones placed directly on the glass bottom,

d. half of the aquarium bottom covered with a sandy and muddy bottom, the other with stones.

Each of the variants was divided into three subvariants with different numbers of *D. polymorpha*, namely 120, 240 and 400 specimens per aquarium.

Each of the variants had 3 replications. All the aquaria were filled with equal quantities of lake water. Every second day *D. polymorpha* were fed with an equal amount of condensed plankton cultured in aquaria, and of lake plankton or seston. For the tests a choice was made of adult specimens collected from a single station. The aggregations were transported to the laboratory, where the specimens were separated from one another by cutting through the bysses, and placed uniformly in aquaria. A uniform distribution was secured by dividing the bottom of each aquarium, by means of a 5 by 5 cm rack placed on the bottom for the time of investigations, into 40 squares.

At a density of 120 specimens per aquarium there occurred 3 individuals per a 5 by 5 cm square, at 240 – 6 individuals, at 400 – on the average 10 individuals per square.

Every 3 days, through a period of 35 days, observations were made of the distribution of *D. polymorpha* within the different squares. As early as on the 3rd or 4th day of testing *D. polymorpha* specimens were seen to move and definitely draw together. The latter tendency persisted until the 28th day, since when no further changes were observed.

The obtained data were tested by means of a statistical analysis. The initial distribution of *D. polymorpha* was assumed to be uniform, so that the relation

$$V = \frac{\sigma^2}{\bar{x}} \leqslant 1$$

At a Poisson's distribution, where the animals are distributed at randon, $V = 1$. In the aquaria, in all cases $V > 1$, which indicates an aggregated distribution.

Variance was calculated by the formula:

$$\sigma^2 = \frac{1}{n} \cdot \sum_{k=1}^{n} \cdot (x_k - \bar{x})^2$$

wherein:

n – number of samples, x_k – value of the k-th sample,

$\bar{x}$ – mean.

The difference of calculated V from 1 indicates the deviation from Poisson's random distribution.

Index V, calculated for the 12th and 28th day of testing, indicates in *D. polymorpha* a markedly increasing tendency to aggregate. The significance of differences between the aggregation indexes $V_1 = 1.91$ (12th day) and $V_2 = 2.36$ (28th day) was determined by the formula:

$$t_e = \frac{V_1 - V_2}{\sqrt{\frac{2}{n_1 + n_2 - 2}}}$$

where

V_1, V_2 — aggregation indexes,

n_1, n_2 — number of samples on the 12th, and 28th day, respectively.

Empirical values t_e were compared with theoretical t_t on the basis of Student's t distribution at a significance level $\alpha = 0.05$, and a number of degrees of freedom $k = n_1 + n_2 - 2$. In all cases the t_e values were very high, the differences between t_e and t_t being significant. It follows that differences between V_1 and V_2 are likewise significant, which in turn indicates a definite tendency in *D. polymorpha* to aggregate in aquaria.

In the first variant, wherein the total bottom was uniform, an aggregation of test animals took place on both types of the substrate, whether hard (glass), suitable for settling, or soft, unfit to be inhabited. For cases of differentiated, non uniform bottoms, a comparison was made between the number of the specimens on bottoms representing: sand, mud, glass, glass overstrewn with stones. Average numbers of *D. polymorpha* per square were compared on stony bottoms against the remaining types; no significant differences were found. It follows that *D. polymorpha*, where given choice of suitable and unsuitable substrate, showed a similar rate of aggregation in both cases.

Tests with the use of aquaria proved the tendency in *D. polymorpha* to form aggregations, both on uniform and differentiated bottoms, whether fit on unfit for the settlement.

Under natural conditions *D. polymorpha*, whether occurring in aggregations or sparsely, is usually associated with some particular substrate, and not with the immediate bottom of the lake. A particular substrate may consist of various objects including stones, branches, reed stems, shells of dead or live molluscs. Possibly the associations of *D. polymorpha* with these types of substrates stem from its requirement of being situated at a certain distance from the bottom in order to ensure a regular filtering (Ljachov 1961). Presumably this factor was out of action in the aquaria, where water movement was negligible, and the bottom, even when soft, remained undisturbed.

Variability of the substrate, whereupon *D. polymorpha* aggregations settle, indicates a lack of preference of this species.

For the purpose of determining the association between the aggregation density and the size of the substrate, 900 aggregations from lakes Śniardwy, Święcajty and Tyrkło have been explored. The number of specimens in each aggregation was counted and the surface, occupied by the respective aggregation, measured. Notice was also taken of the shape of objects forming the substrate, and of their position on the lake bottom. The density of *D. polymorpha* occurring on all the substrates was related to 1 cm^2 of the substrate, so that comparable values were thus obtained.

Data obtained on these grounds indicate a regularity wherein the density of *D. polymorpha* in aggregations is unrelated to the surface up to a certain limit, beyond which there occurs a proportionality (Fig. 5).

In the Tyrkło lake, where the average aggregation density in both stations amounted to 19 and 21 individuals, from 85 to 90% of the aggregations were formed on a substrate surface ranging from 2 to 40 cm^2. Within these limits the surface of the substrate was not directly related to the aggregation density. Above the surface limit 40 cm^2 the density increased in proportion with the

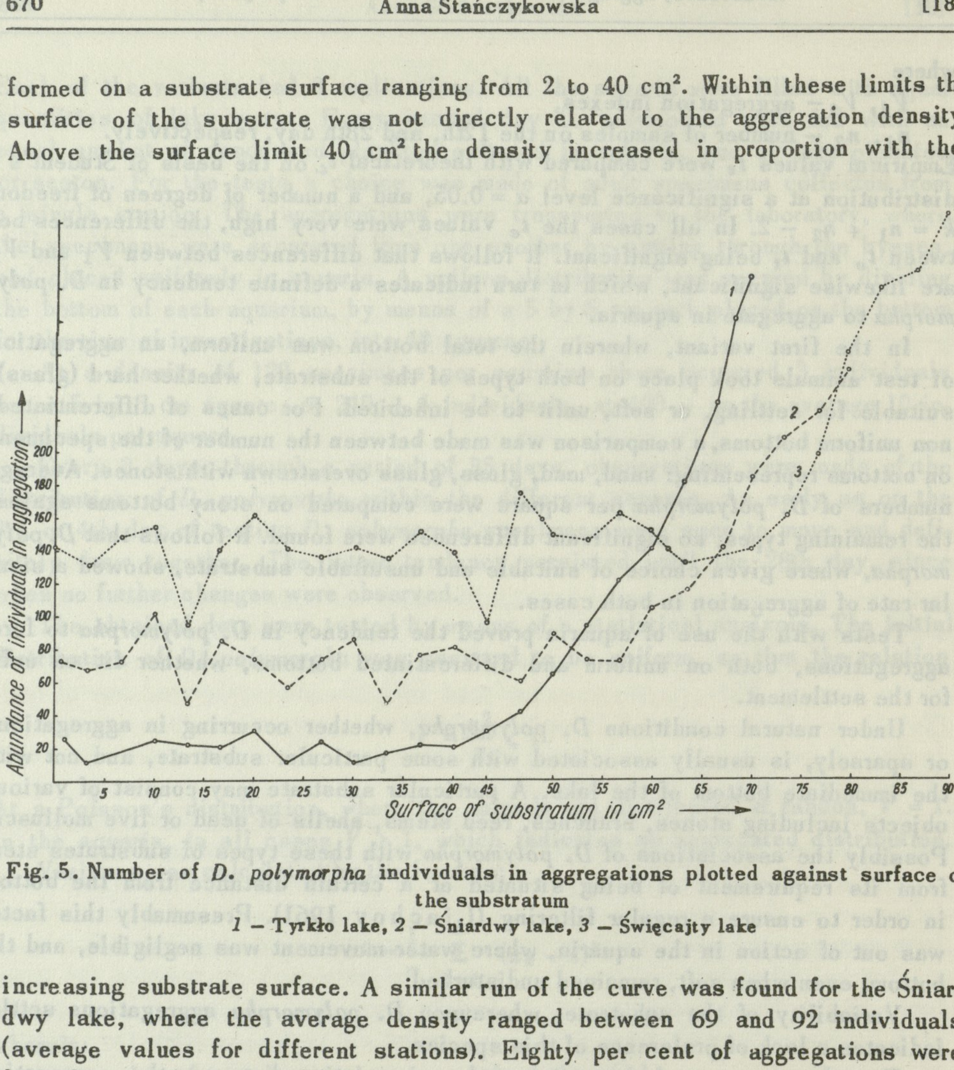

Fig. 5. Number of *D. polymorpha* individuals in aggregations plotted against surface of the substratum
1 — Tyrkło lake, *2* — Śniardwy lake, *3* — Święcajty lake

increasing substrate surface. A similar run of the curve was found for the Śniardwy lake, where the average density ranged between 69 and 92 individuals (average values for different stations). Eighty per cent of aggregations were formed on a substrate surface below 60 cm^2, in which cases no direct relationship was found between the aggregation density and the substrate surface. At larger surfaces only both parameters exhibited a parallel increase. Likewise for the lake Święcajty, the run of the curve was similar at a higher density in the *D. polymorpha* aggregations, amounting to 130 and 147 individuals (average values of both stations). The frequency increased with increasing substrate surface only above 70 cm^2 of the latter.

In the reported cases, the surface area of the suostrate affects the aggregation density only above a certain borderline value; which in turn seems to be associated with the frequency characteristic of the given basin. Aggregations characterized by such frequencies constituted in all three explored lakes from 80 to 90 per cent of the total. It may therefore be assumed that the number of individuals in an aggregation, i.e. the aggregation density, is a feature characteristic of the given lake; to a lesser degree it seems to be related to the surface of the substrate.

Close observations of *D. polymorpha* aggregations in 29 Mazurian lakes confirmed this finding. It was shown that the average numbers of individuals in aggregation within a station, in the main belt of occurrence, differ only slightly from one another. This situation was revealed on the basis of calculations of standard deviations, carried out separately for each of the stations, by the formula

$$\sigma = \sqrt{\frac{1}{n} \sum_{i=1}^{n} x_i^2 - \bar{x}^2}$$

where

σ – standard deviation,

n – number of aggregations,

x_1 – number of individuals in aggregations,

$\bar{x}$ – average frequency.

At a normal distribution, the interval $(-\sigma + \sigma)$ should include 68.26 per cent of the studied parameters. According to the above given calculations it included from 80 to 90 per cent of the values in question, which indicates a high uniformity of the studied material.

Transverse sections, on the other hand, of each of the station, revealed certain differences in the aggregation density. The innermost aggregations consisted of smaller numbers of individuals than those situated in the center of the main belt of occurrence (Fig. 6). Differences were likewise found in the numbers of individuals in aggregations situated in the most shallow zone and inhabited mainly by immature molluscs. Here the abundance was found to be directly related to the abundance in the main belt. Where populations consisted mainly of adult specimens, aggregations within a single station were found to be similar in their age structure, which was a characteristic of the given population. Yearly proportions of individuals were similar in all aggregations of each situation, even at different depths. Only aggregations of the most shallow sphere were different in that the proportion of immature specimens amounted to 80 per cent. At similar depths however age structures of aggregations were similar.

The arrangement of differently aged specimens within an aggregation was likewise similar. In general, oldest individuals occupied the center, while towards the outermost regions the age decreased – a situation due to the successive attachment of young individuals to the older ones. From time to time, in the centers of the aggregations, there were found empty shells of aged *D. polymorpha* specimens, attached to the aggregation by means of bysses or tufts of filaments peculiar to molluscs.

Comparisons of density in aggregations at various stations of the sáme lake revealed their large similarity. Differences in the density within aggregations of different stations in the same lake were rather small. Likewise the coeffi-

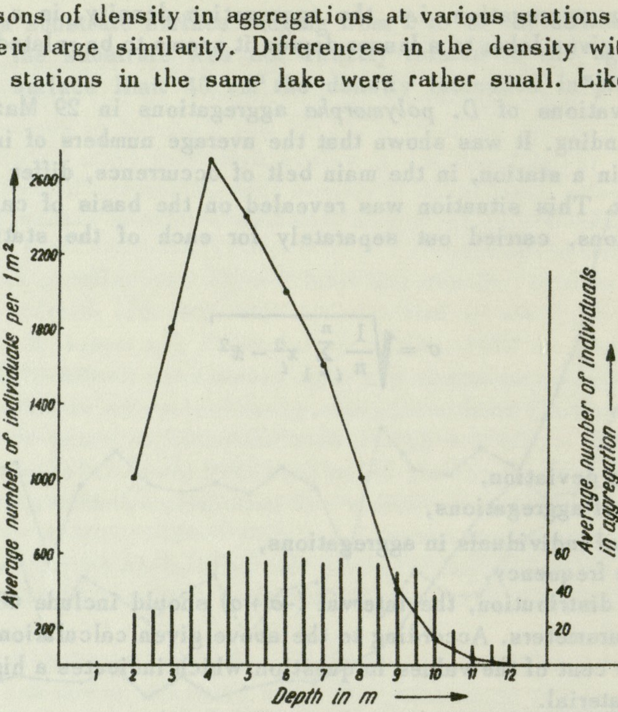

Fig. 6. Number of *D. polymorpha* individuals per 1 m² plotted against the number per aggregation with increasing depths

cients of variability: $V = \frac{\sigma}{\bar{x}}$, where σ – standard deviation, $\bar{x}$ – mean for individual stations, were largely similar. These findings however pertained only to the main belt of occurrence. Aggregations in most shallow zones varied with differing stations, both in their abundance and the age structure – a situation related to the number of immature molluscs within different littoral media, and the above described occurrence in patches.

The aggregation density within a single station, or even lake, was not found to fluctuate greatly; on the contrary, the density in aggregations belonging to different reservoirs ranged between a few and a few hundred specimens (Fig. 7). At the same time the age structure was more or less the same. The proportions of individual age groups in various lakes were similar.

Comparative tests were made of aggregation density and abundance of *D. polymorpha* on a 1 m², with different lakes – a marked correlation was found between the two parameters. In lakes containing larger numbers of molluscs, aggregations were more numerous than in reservoirs where *D. polymorpha* was scarce (Fig. 7).

In lakes of group III, characterized by largest numbers of *D. polymorpha*, the aggregations consisted of from 50 to 147 individuals (on the average 82). In

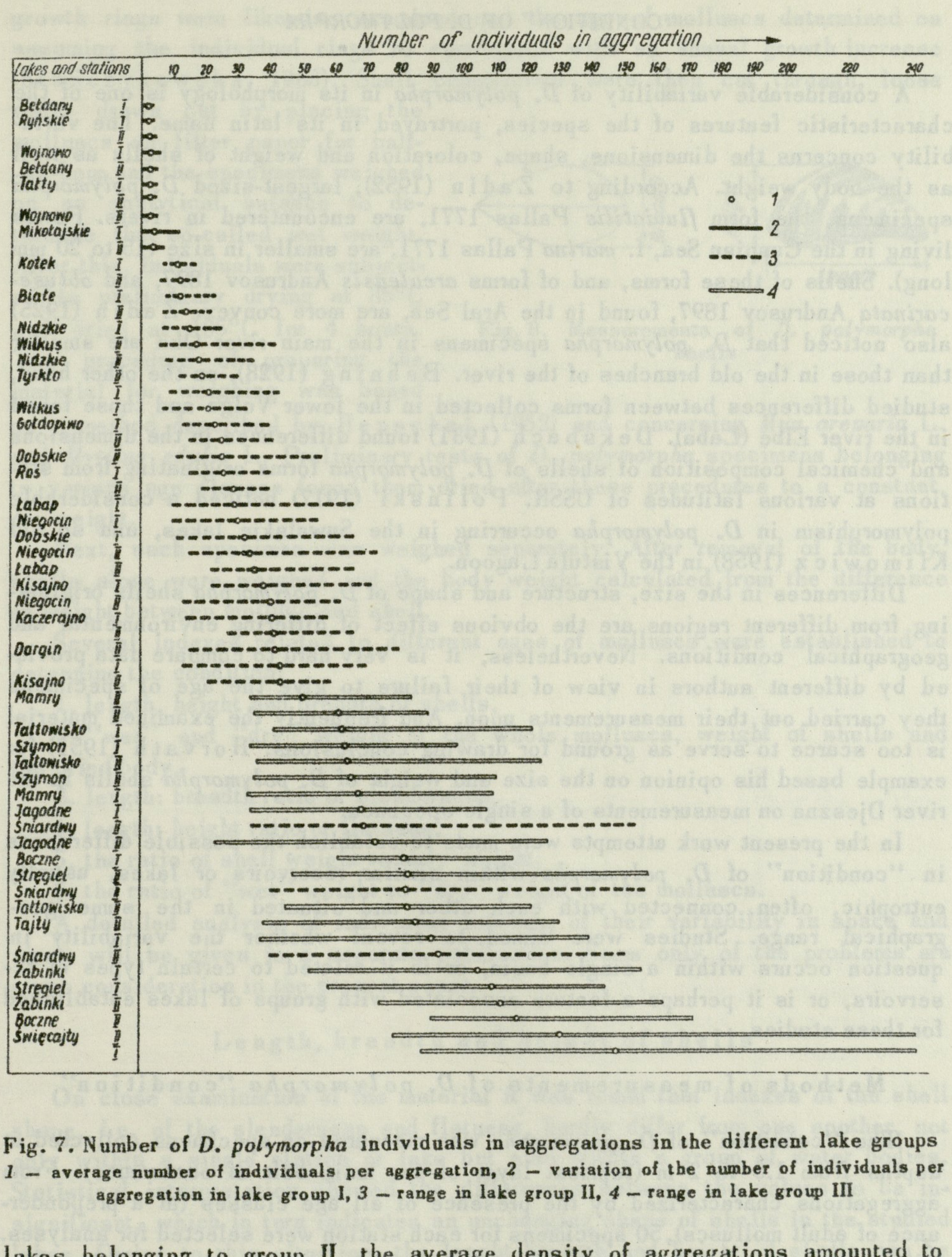

Fig. 7. Number of *D. polymorpha* individuals in aggregations in the different lake groups
1 — average number of individuals per aggregation, *2* — variation of the number of individuals per aggregation in lake group I, *3* — range in lake group II, *4* — range in lake group III

lakes belonging to group II, the average density of aggregations amounted to 41 individuals, while in those belonging to group I, where the numbers of molluscs were smallest, on the average 2.9, at the most 12 individuals were found on a 1 m^2.

"CONDITION" OF *D. POLYMORPHA*

A considerable variability of *D. polymorpha* in its morphology is one of the characteristic features of the species, portrayed in its latin name. The variability concerns the dimensions, shape, coloration and weight of shells as well as the body weight. According to Żadin (1952), largest-sized *D. polymorpha* specimens, the form *fluviatilis* Pallas 1771, are encountered in rivers. Forms living in the Caspian Sea, f. *marina* Pallas 1771, are smaller in size (15 to 20 mm long). Shells of these forms, and of forms *arealensis* Andrusov 1897, and *obtuse-carinata* Andrusov 1897, found in the Aral Sea, are more convex. Žadin (1925) also noticed that *D. polymorpha* specimens in the main river Oka are smaller than those in the old branches of the river. Behning (1928), on the other hand, studied differences between forms collected in the lower Volga and those found in the river Elbe (Łaba). Deksbach (1931) found differences in the dimensions and chemical composition of shells of *D. polymorpha* forms originating from stations at various latitudes of USSR. Poliński (1917) noticed a considerable polymorphism in *D. polymorpha* occurring in the Suwalskie lakes, and so did Klimowicz (1958) in the Vistula Lagoon.

Differences in the size, structure and shape of *D. polymorpha* shells originating from different regions are the obvious effect of differing environmental and geographical conditions. Nevertheless, it is very hard to compare data provided by different authors in view of their failure to give the age of specimens they carried out their measurements upon. And frequently the examined material is too scarce to serve as ground for drawing conclusions. Horvath (1951) for example based his opinion on the size and weight of *D. polymorpha* shells in the river Djeszna on measurements of a single specimen.

In the present work attempts were made to establish the possible differences in "condition" of *D. polymorpha* within similar reservoirs or lakes, usually eutrophic, often connected with each other and situated in the same geographical range. Studies were aimed to reveal whether the variability in question occurs within a single basin, or is it related to certain types of reservoirs, or is it perhaps a feature associated with groups of lakes established for these studies.

Methods of measurements of *D. polymorpha* "condition"

The "condition" of *D. polymorpha* was measured on specimens collected at depths from 1.5 to 2 m (topmost layer of the main belt of occurrence). From aggregations characterized by the presence of all age classes (at a preponderance of adult molluscs), 50 specimens for each station were selected for analyses. The collected samples were preserved in a 2 to 3 per cent solution of formalin. On taking out, the molluscs were placed for some time in water, cleaned and then handled. Measurements of the length, breadth and height of shells were taken separately from each individual (Fig. 8). The number and distribution of growth rings were likewise examined and the age of molluscs determined on assuming the individual rings to correspond with an annual growth increase (Stańczykowska 1963). Shell constrictors were then cut through, loose water drawn out by placing the molluscs on filter paper for half-an-hour, and the specimens weighed on an analytical balance to determine the so-called wet weight. After this, individuals were subjected to preliminary drying at 85°C and dried at 105°C for 4 hours. The procedure of preparing the material for weighing was based on a method described by Henschel (1952) and concerning *Mya arenaria* L. and *Mytilus edulis* L. Preliminary tests of *D. polymorpha* specimens belonging to various age classes found them dried after these procedures to a constant, dry weight.

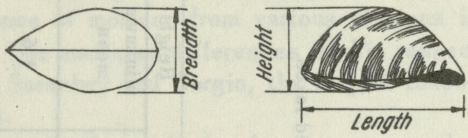

Fig. 8. Measurements of *D. polymorpha* shells

Next, each specimen was weighed separately. After removal of the body, shells alone were weighed and the body weight calculated from the difference in weight between mollusc and shell.

Several indexes related to different ages of molluscs were established to determine the condition:

1. length, height and breadth of shells,
2. "wet" and "dry" weight of the whole molluscs, weight of shells and the dried body,
3. length: breadth ratio or slenderness,
4. length: height ratio or flatness,
5. the ratio of shell weight to body weight,
6. the ratio of "wet" weight to "dry" weight of the molluscs.

A detailed analysis of individual indexes, of their variability in space and time, will be given in a separate publication. Some only of the problems are given consideration in the present paper.

Length, breadth and height of shells

On close examination of the material it was found that indexes of the shell shape, i.e. of the slenderness and flatness, hardly differ from one another, not only within a single station or lake but also within a group of water bodies. Statistical interpretation showed the differences between the values to be insignificant, which in turn indicates an unchanging shape of shells in the studied lakes. Owing to this situation, the lenght, breadth and height of shells can be discussed together as the shell size.

The size of *D. polymorpha* shells were found to be greatly different in the various lakes (Tab. II). Within some of the studied basins, e.g. in the Boczne, Maximum, minimum and average shell sizes (in mm) of *D. polymorpha* in the explored lakes

Tab. II

Age groups (years)	Length			Breadth			Height		
	total mean	minimum mean	maximum mean	total mean	minimum mean	maximum mean	total mean	minimum mean	maximum mean
1	4.9	3.0	8.5	0.9	0.6	2.6	2.4	1.6	4.6
2	8.2	5.0	12.0	2.0	1.0	3.3	4.2	2.7	6.0
3	11.1	9.0	14.2	2.9	1.8	4.2	5.5	4.8	7.2
4	14.3	10.5	18.0	3.8	2.4	4.9	7.0	5.2	7.9
5	17.2	14.0	21.0	4.7	3.2	5.5	8.2	6.9	9.1
6	20.3	15.5	24.1	5.4	3.5	6.5	9.4	7.5	11.5
7	22.4	19.4	26.0	6.3	4.5	7.2	10.2	8.5	12.0
8	24.3	21.0	28.1	6.8	5,0	8.0	10.4	9.0	12.0
9	25.4	23.1	30.0	7.0	5.6	8.0	11.1	10.1	12.3
10	26.0	24.1	30.2	8.1	7.0	9.1	12.0	11.0	13.0

Tajty, Stręgiel and Święcajty lakes, *D. polymorpha* are smaller than e.g. in the Bełdany, Gołdopiwo, Wilkus, Tyrkło and Tałty lakes.

The average size of shells of individual *D. polymorpha* specimens collected at different stations of the same lake is very similar, not to the same degree however in all reservoirs. In some of the lakes, e.g. in the lake Jagodno (Fig. 9), Święcajty and Szymon, the size difference of mollusc from various stations is small, while in other lakes it is greater. The maximum differences in this respect were found in the lakes Mamry (Fig. 9), Śniardwy and Dargin, the largest lakes, most varied in their environmental aspect.

A close statistical analysis, carried out by the analysis of variance, revealed significant differences in respect to the length of mollusc collected from various lakes. The variance between lakes, and between stations within the same lake, was verified by Fisher's statistics wherein the appropriate values were calculated according to the following formula:

For different lakes $z = \frac{1}{2} \ln \frac{S_3^2}{S_1^2}$

For different stations within the same lake $z = \frac{1}{2} \ln \frac{S_2^2}{S_1^2}$

On comparing various lakes, at a significance level $a = 0.01$, the value z definitely surpassed the critical point

$$P\,(z \geqslant 2.38108) < 0.01$$

on comparing different stations within the same lake it fell below the critical point

$$P\,(z \geqslant 0.2883) > 0.01$$

Hence the differences in mollusc lengths between various lakes are significant; while between various stations within the same lakes they are insignificant.

A comparison of the size of *D. polymorpha* specimens within individual stations indicated a relative uniformity of the studied material. Most of the specimens were characterized by a length not differing much from the average; only a few individuals deviated in a more marked manner (Fig. 10).

These deviations were not similar in all lakes. In some reservoirs the fluctuations in length, breadth and height of shells of specimens collected from the same station were negligible; in others their range was larger.

Analyses of the weight of *D. polymorpha* specimens

Analyses of the "wet" weight, "dry" weight, weight of shells and of bodies in *D. polymorpha* showed there existed in these cases similar relations as were

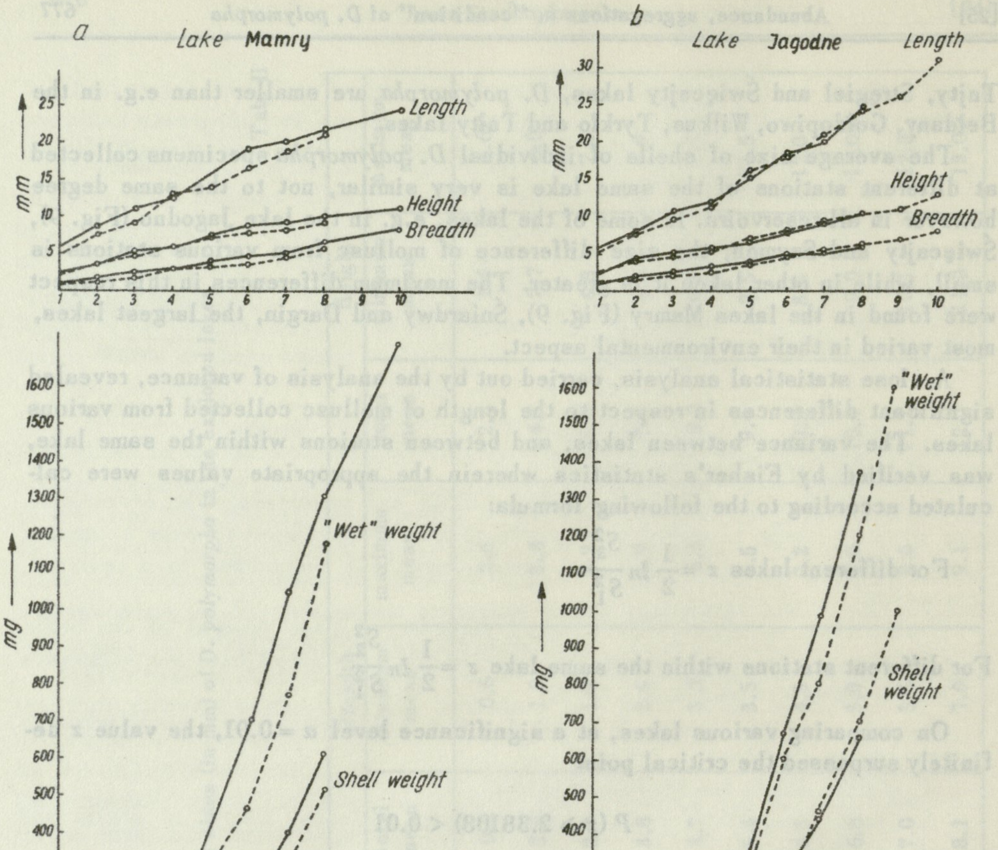

Fig. 9. Comparison of the "condition" of *D. polymorpha* individuals from two stations of the same lake

Examples of lakes characterized by: *a* — greatest differentiation of the two localities, *b* — least differentiation of the two localities, station I — full line, station II — broken line

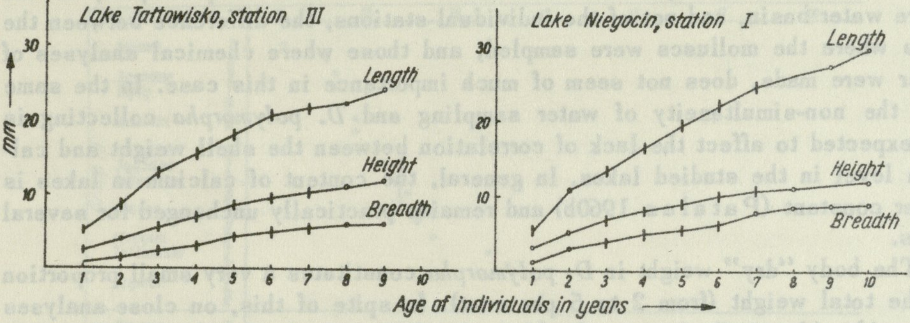

Fig. 10. Differentiation of size of *D. polymorpha* shells within the different stations exemplified by two lakes

Vertical sections – variation of the number

found in determining the shell dimensions. The greatest differences in weight were associated with different lakes. Within the same lake or station the mollusc weights differed to a lesser extent.

The "wet" weight was most differentiated. The ratio however of "wet" weight to "dry" weight remained more or less unchanged, on the level of 2:1.

A very large proportion of the "dry" weight (from 95 to 98 per cent) consisted of the shell weight, which changed little within individual stations of individual lakes, but greatly differed in the different reservoirs.

To elucidate this problem a comparative analysis was made of the shell weights and calcium contents in water. Chemical data, concerning the content of calcium in the various lakes, were based on papers of Gieysztor and Odechowska (1958) and Olszewski and Paschalski (1959). The comparison of data indicated a lack of correlation among these two parameters. Lakes similar in their calcium level were found to harbour molluscs completely different in weight (Fig. 11).

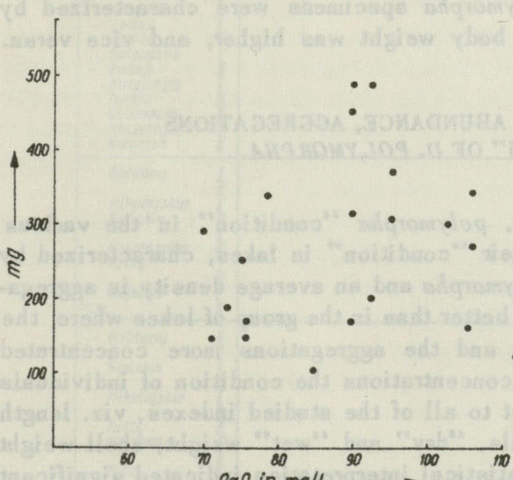

Fig. 11. Weight of shells (five-year-old individuals) of *D. polymorpha* in lakes with different calcium contents

As both the abundance and the occurrence in aggregations as well as the condition of *D. polymorpha* constitute features characteristic principally of the entire water basin, and not of the individual stations, the difference between the sites where the molluscs were sampled, and those where chemical analyses of water were made, does not seem of much importance in this case. In the same way the non-simultaneity of water sampling and *D. polymorpha* collecting is not expected to affect the lack of correlation between the shell weight and calcium level in the studied lakes. In general, the content of calcium in lakes is rather constant (Patalas 1960b) and remains practically unchanged for several years.

The body "dry" weight in *D. polymorpha* constitutes a very small proportion of the total weight (from 2 to 5 per cent). In spite of this, on close analyses a considerable similarity was found in the differentiation of the "dry" weight to other features determining the condition of *D. polymorpha* in the studied lakes. Relatively small differences in body weight were found among specimens of the same station, and also among specimens of different stations of the same lake (Fig. 9). Considerable differences were found in body weight among molluscs from different lakes.

A comparative study of the body weight and shell weight carried out successively in all the explored lakes revealed a considerable similarity in this respect. In those reservoirs wherein *D. polymorpha* specimens were characterized by a higher shell weight, likewise the body weight was higher, and vice versa.

A COMPARISON OF THE ABUNDANCE, AGGREGATIONS AND "CONDITION" OF *D. POLYMORPHA*

On comparing the indexes of *D. polymorpha* "condition" in the various groups of lakes it was found that their "condition" in lakes, characterized by an average total abundance of *D. polymorpha* and an average density in aggregations (lakes of group II), is in general better than in the group of lakes where the total number of molluscs is higher and the aggregations more concentrated (group III). It follows that at higher concentrations the condition of individuals is inferior. This holds true in respect to all of the studied indexes, viz. length (Fig. 12), height and breadth of shells, "dry" and "wet" weight, shell weight and body "dry" weight (Fig. 13). Statistical interpretation indicated significant differences between all the parameters in group II and III of the lakes.

Different relationships were found in lakes of group I. As mentioned above, in 1960, 1961 and 1962, the total *D. polymorpha* abundance in these lakes was lowest (up to 20 individuals per 1 m^2) and so was the density in aggregations (on the average 2.9 individuals). Prior to 1959 as well as in that year, within four lakes of this group the abundance of *D. polymorpha* was very high. The number of molluscs even in the shallow littoral, where in other lakes adult individuals occur sparsely, reached up to 2,000 molluscs on 1 m^2; at greater depths the abundance was even higher. In winter of 1959–1960 the abundance

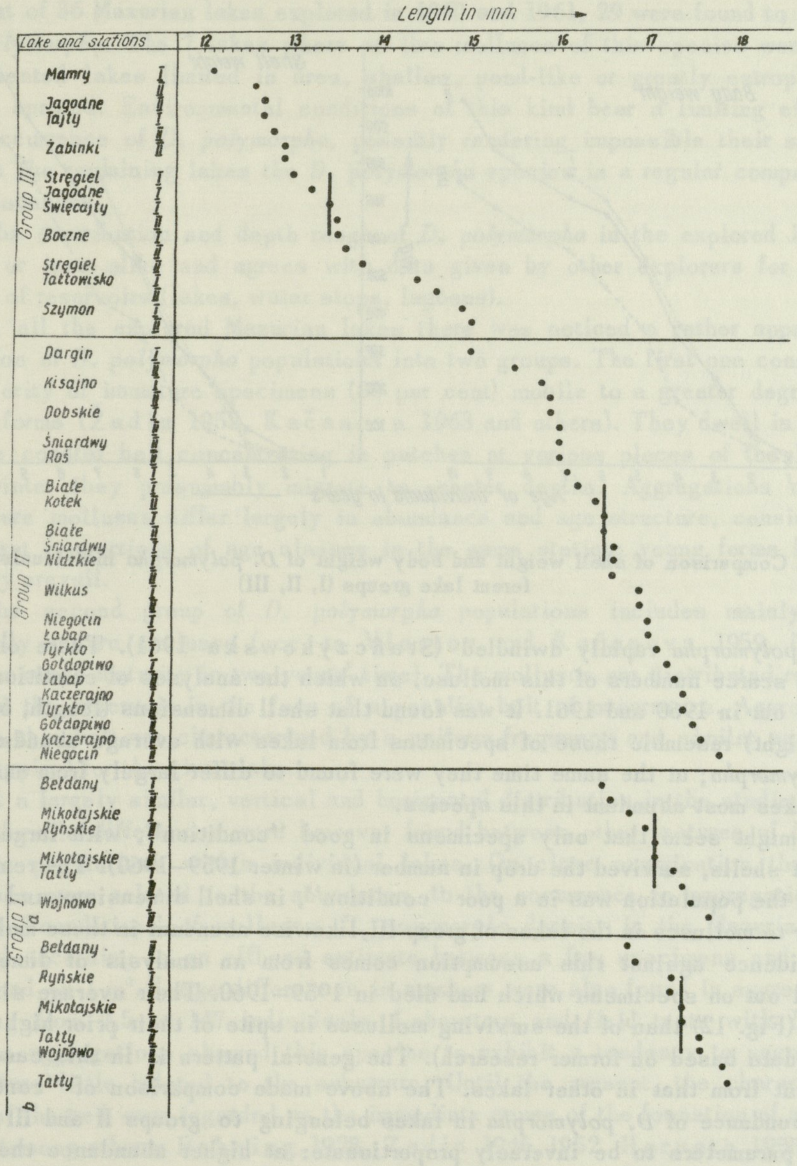

Fig. 12. Average length of *D. polymorpha* shells in different localities of the explored lakes

Black circles denote the average length of two to six-year-old individuals, vertical sections — the average length within the given lake group. Lake group I: *a* — shell length of live individuals following the reduction in numbers, *b* — shell length of live individuals preceding the reduction in numbers

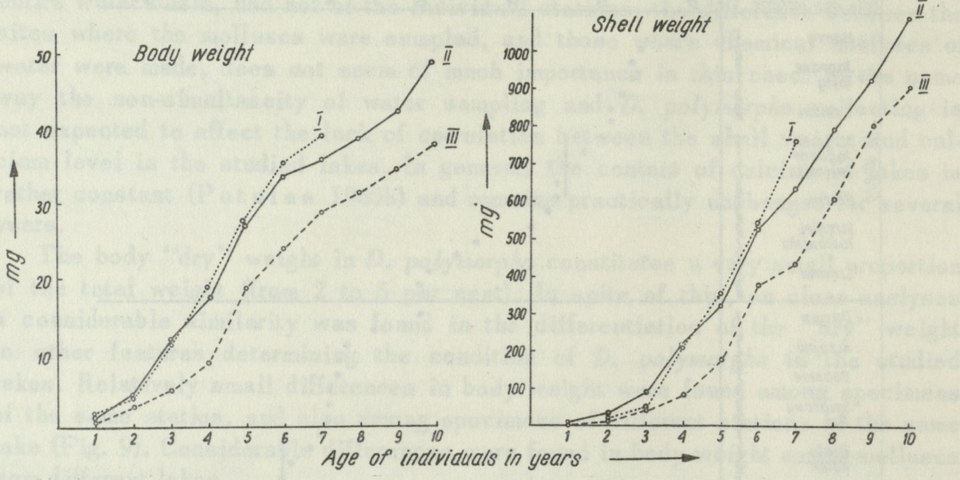

Fig. 13. Comparison of shell weight and body weight of *D. polymorpha* individuals in different lake groups (I, II, III)

of *D. polymorpha* rapidly dwindled (Stańczykowska 1961). There only remained scarce numbers of this mollusc, on which the analyses of condition were carried out in 1960 and 1961. It was found that shell dimensions (length, breadth and height) resemble those of specimens from lakes with average abundance of *D. polymorpha*; at the same time they were found to differ largely from molluscs from lakes most abundant in this species.

It might seem that only specimens in good "condition", with largest and hardest shells, survived the drop in number (in winter 1959–1960). The remaining part of the population was in a poor "condition", in shell dimensions and weight similar to molluscs in the lakes of group III, likewise abundant in these molluscs.

Evidence against this assumption comes from an analysis of dimensions carried out on specimens which had died in 1959–1960. Their average size was larger (Fig. 12) than of the surviving molluscs in spite of their prior high abundance (data based on former research). The general pattern is in this case quite different from that in other lakes. The above made comparison of "condition" and abundance of *D. polymorpha* in lakes belonging to groups II and III proves these parameters to be inversely proportionate: at higher abundance the "condition" was poor and, vice versa, at lower frequencies the "condition" was good. *D. polymorpha* in lakes of group I, occurring prior to the rapid fall in number at high abundance, was characterized by an appreciably good "condition".

DISCUSSION OF RESULTS

Out of 36 Mazurian lakes explored in 1960 and 1961, 29 were found to contain *D. polymorpha*. The 7 lakes where no live molluscs of this species were found represented lakes limited in area, shallow, pond-like or greatly eutrophic and badly aerated. Environmental conditions of this kind bear a limiting effect on the occurrence of *D. polymorpha*, possibly rendering impossible their survival. Within the remaining lakes the *D. polymorpha* species is a regular component of the biocenose.

The distribution and depth range of *D. polymorpha* in the explored lakes is more or less alike and agrees with data given by other explorers for various types of reservoirs (lakes, water stops, lagoons).

In all the explored Mazurian lakes there was noticed a rather appreciable division of *D. polymorpha* populations into two groups. The first one consists of a majority of immature specimens (80 per cent) mobile to a greater degree than adult forms (Žadin 1952, Kačanova 1963 and others). They dwell in summer in the coastal belt, concentrating in patches at various places of the littoral; for winter they presumably migrate to greater depths. Aggregations of these immature molluscs differ largely in abundance and age structure, consisting of different proportions of age classes in the same station; young forms however greatly prevail.

The second group of *D. polymorpha* populations includes mainly adult, sexually mature molluscs (acc. to Vlastov and Kačanova 1959, *D. polymorpha* reach maturity in two years' time). The molluscs are distributed regularly around the reservoir in the form of a peculiar belt of occurrence. Aggregations within this belt are characterized by a uniform frequency and similar age structure, typical for the given lake.

At a largely similar, vertical and horizontal distribution in the studied lakes, considerable differences were however found between other features of *D. polymorpha* populations within individual lakes. On close examination these differences were related to the abundance, to the occurrence in aggregations and to the "condition" of molluscs. *D. polymorpha* density in the Mazurian lakes ranged according to an offhand estimate between a few specimens and several thousand on 1 m². Large differences in numbers were also found in aggregations, ranging from 2.5 to 147 individuals. Laboratory and field tests with *D. polymorpha* aggregations showed this species to exhibit a tendency to aggregate — a feature little related to the substrate. Until the present, the character and size of the bed were regarded as the immediate cause of the formation of aggregations (among others: Behning 1928, Žadin 1946, 1952, Horvath 1955, Ljachov 1961). Studies carried out in the Mazurian lakes suggest that the tendency to concentrate in aggregations is principally related in *D. polymorpha* to biological properties of the species. On the other hand, the density in aggregations is associated with the abundance in lakes. Lakes characterized by lowest abundance include less numerous aggregations, and vice versa, so that the most numerous aggregations occur in lakes with highest abundance of molluscs.

A similar interrelationship was found in respect to the lower abundance in coastal areas and at greater depths, in spite of its not being conspicuous in some of the lakes. The aggregations were relatively less numerous than at maximal frequencies in the given lakes.

The "condition" of *D. polymorpha* was studied on grounds of the analyses of abundance within individual reservoirs, associated with changes in the numbers of specimens in aggregations. Analyses of the indexes of good "condition" revealed considerable differences between individual lakes – as was the case in respect to the above discussed features. In some reservoirs the specimens were much larger (the length, breadth and height in the different age classes were measured) and heavier (weight of shell and body at different ages) than in others.

On comparing the "condition" with the abundance and occurrence in aggregations there was proved an inversely proportionate correlation. In lakes where *D. polymorpha* was found in great abundance on 1 m^2 of the bed, and in large numbers in the aggregations, its "condition" was inferior to that in lakes characterized by a smaller abundance and less numerous aggregations.

The destructive influence of overcrowding (high frequencies) on several life processes in populations accounting for the lowered fertility, delayed furrowing, lower rate of growth etc. is a well-known phenomenon (Allee et al. 1958). It was found that in populations with a higher frequency there occurs an inverse proportionality between the number of specimens and their dimensions (among others Davidson and Voughn 1941). A correlation of this kind might have occurred also in the *D. polymorpha* populations of Mazurian lakes.

It remains to be discussed however whether the explored lakes are actually overcrowded. As mentioned above, the abundance of *D. polymorpha* even where it was highest in the studied lakes when compared with reference data was not exceptionally high. Very often in other reservoirs, e.g. in lakes of Northern Germany (Lundbeck 1926), of Denmark (Berg 1938, Wesenberg-Lund 1939) or of Suwałki (Rzóska 1935) twice or three times as large numbers of *D. polymorpha* specimens were found. In the Szczecin Lagoon relative numbers of this species were as much as 20 times larger (Wiktor J. 1961, 1963). In spite of that the molluscs developed there successfully. Specimens of *D. polymorpha* from Mazurian lakes were compared with those from the Szczecin Lagoon (Wiktor J. 1963), the latter found to be larger in all age groups in spite of a maximal abundance of 114,000 individuals on 1 m^2. Overcrowding might have only reduced the life span in this case. In the Mazurian lakes of *D. polymorpha* populations live six or seven years, at the most ten years (Stańczykowska 1963), while in the Szczecin Lagoon four or five years, at the most seven years (Wiktor J. 1963).

It seems hardly acceptable to compare so different basins as the Szczecin Lagoon and Mazurian lakes. Mollusc frequencies low for the Szczecin Lagoon would be considered very high in the Mazurian lakes. All the indexes by which *D. polymorpha* populations are characterized are related to the given environmental conditions.

Variability of all three features in question (abundance, occurrence in aggregations and "condition") is in the first place associated with the lakes, less with the station within the reservoir. It seems the lakes bears an effect on the population as a whole. Attempts to relate some features to particular properties of the environment remained effectless. Certain regular relationships were only found between the abundance and the trophic type of basins, their area and maximal depth. *D. polymorpha* usually occurs in higher numbers in less eutrophic lakes which are at the same time larger and deeper.

No correlation was found between the abundance and water visibility, pH and O_2.

Comparisons of *D. polymorpha* frequencies and shell weight of individual specimens with the calcium content in water failed to yield any uniform results. It was only found that *D. polymorpha* occurs usually in greater numbers in lakes with a higher calcium content – at the same time shell weights of specimens originating from these lakes are not impressive. So far the effect of calcium content in water on the occurrence of molluscs, and in the first place on the thickness or weight of mollusc shells, is not established definitely. Several investigators found close relationships between the calcium content and development of malacofauna (Hubendick 1947, 1948, Tadajewski 1955). On the contrary, others point out a complete lack of correlation between the two phenomena (Frömming 1953, 1956, Trübsbach 1943, 1947).

Both the abundance and occurrence in aggregations as well the "condition" of *D. polymorpha* in the different lakes does not in general change year by year. These features were found to be relatively constant not only by three-year trials, but also by control estimates of frequency carried out prior to the present studies and in 1962.

These findings however do not hold true in respect to lake group I, in which at time of studies the mollusc abundance was lowest. In four of the lakes (Bełdany, Mikołajskie, Ryńskie and Tałty) the number of *D. polymorpha* rapidly dwindled in the winter of 1959–1960 (Stańczykowska 1961). Similar sudden decreases in the number of *D. polymorpha* were also found to have occurred in the lakes Stręgiel and Wojnowo in the previous years. These lakes differ from the drainage lakes of the Mikołajki district both in the morphology of the lake basin and in the position in relation to other lakes. Owing to the difference in time and large distance between the lakes wherein the reductions took place it is hard to establish any definite causes. Sudden changes in the numbers of molluscs were noticed in different lakes and in different years. Possibly therefore climatic factors are not at the immediate base of these phenomena.

It is likewise hard to relate the rapid changes in number to the particular environmental conditions in the given lakes. The phenomenon of reduction took place in one case in a connected group of lakes near Mikołajki (wherein no sudden changes in the physico-chemical conditions were found at that time), in the other two cases – in two distant lakes.

In all cases the reduction in number took place in lakes with a high frequency of *D. polymorpha*, higher than in the other lakes. At the same time the shell dimensions were much larger, whether of those specimens which survived or of those which perished. It follows that molluscs within the lakes of group I were in good "condition" in spite of the overcrowding, in contrast to the situation in other groups. At the present state of knowledge it hardly seems possible to indicate the underlying causes of the rapid decreases in number of *D. polymorpha.* Possibly they belong to phenomena observed by Chitty and Chitty (1962) and pertaining to cyclic changes in numbers of *Microtus agrestis* L. In natural populations of this species remaining for several years under observation, prior to rapid decreases in numbers, weights of the animals higher than in other years were observed each time.

Whatever the theory, long-term experiments are necessary to provide the confirming evidence. In a majority of the explored lakes studies of this kind are under way.

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ZALEŻNOŚĆ MIĘDZY LICZEBNOŚCIĄ, KOLONIJNYM WYSTĘPOWANIEM I „DORODNOŚCIĄ" *DREISSENA POLYMORPHA* PALL. W 36 JEZIORACH MAZURSKICH

Streszczenie

Badania szczegółowe prowadzono w latach 1960–1961 na 36 jeziorach mazurskich. (Orientacyjne dane uzyskano w latach poprzednich). Zbiorniki były dość zróżnicowane pod względem środowiskowym, charakteryzowały się różną powierzchnią, maksymalną głębokością, widzialnością, odczynem wody, natlenieniem i ilością wapnia. Stwierdzono, że rozmieszczenie *D. polymorpha* we wszystkich badanych jeziorach jest podobne. W płytkim litoralu występują wyspowo i nierównomiernie osobniki przeważnie młode. Głębiej, wokół całego jeziora, szeroki pas równoległy do brzegu, obejmujący litoral i częściowo sublitoral, zasiedlony jest w przeważającej części (ok. 80–90%) przez racicznice dorosłe. Największe zagęszczenie obserwowane jest na głębokości od 2 do 4 m. Maleje ono stopniowo w kierunku brzegu i dość gwałtownie w głąb zbiornika (fig. 1). Struktura wiekowa w obrębie głównego pasa występowania zmienia się tylko nieznacznie (fig. 2).

Rozmieszczenie to ulega pewnym zmianom sezonowym, związanym z jesienną migracją młodych osobników w głąb zbiornika. Poza tym, w zasadniczych ramach układ ten utrzymuje się prawie niezmiennie z roku na rok.

Mimo podobieństwa rozmieszczenia racicznicy, liczebność jej w różnych jeziorach jest różna. Pozwoliło to na podział jezior na trzy zasadnicze grupy: 1) z ubogim występowaniem racicznicy (grupa I), 2) licznym (grupa II), 3) bardzo licznym (grupa III). Siedem jezior, w których nie stwierdzono występowania *D. polymorpha*, zaliczono do grupy 0 (fig. 3).

Analiza przyczyn niewystępowania, lub różnic liczebności *D. polymorpha* w badanych jeziorach, przeprowadzona przez porównanie występowania z poszczególnymi cechami środowiska, nie dała jasnego obrazu. Udało się jedynie stwierdzić, że istnieje pewna tendencja do liczniejszego występowania w jeziorach mezotroficznych, większych (chociaż nie największych) i głębszych niż w silnie zeutrofizowanych płytkich i małych (fig. 4).

Nie udało się znaleźć bezpośredniej korelacji z widzialnością, odczynem wody i zawartością w niej wapnia.

Przy analizie tych korelacji udało się stwierdzić większe różnice między grupą II jezior (z licznie występującą racicznicą) i III grupą (z bardzo licznym występowaniem) niż między grupą III i I (małe ilości *D. polymorpha*). Pozwala to przypuszczać, że niska liczebność racicznicy (notowana w jeziorach grupy I po gwałtownej redukcji liczebności w roku 1959–1960) jest zjawiskiem przejściowym, a poprzednie wysokie liczebności obserwowane przed redukcją liczebności były dla tych jezior typowe.

We wszystkich trzech grupach jezior, jak wykazały badania, 81–95% (Tab. I) ogólnej liczby racicznic występowało w koloniach. Na podstawie przeprowadzonych doświadczeń laboratoryjnych i terenowych wydaje się, że powstawanie kolonii *D. polymorpha* związane jest nie tylko z obecnością i dogodnością odpowiedniego podłoża (fig. 5), ale również zależy od cech samej populacji. Porównywany materiał uzyskany z 29 jezior wykazuje wprost proporcjonalną zależność liczebności *D. polymorpha* w danym zbiorniku i wielkości jej kolonii (fig. 7). Liczebność kolonii, podobnie jak zagęszczenie małża w jeziorze, jest cechą charakterystyczną dla danego zbiornika. Kolonie pobierane z tej samej głębokości (fig. 6) różnią się tylko nieznacznie zarówno pod względem liczebności, jak i struktury wiekowej. Ma to miejsce nie tylko w obrębie każdego stanowiska, ale również przy porównywaniu różnych stanowisk na tym samym jeziorze.

Jako kryterium warunków życia populacji w danym zbiorniku brano również, poza liczebnością i kolonialnością, „dorodność" osobników *D. polymorpha*. Dla określenia „dorodności" prześledzono dla poszczególnych roczników małża: długość, szerokość, wysokość muszli (fig. 8), wagę „mokrą" i „suchą" (dla uzyskania stałej wagi), wagę muszli i wagę ciała.

Stwierdzono, że cechy te w obrębie poszczególnych stanowisk są mało zmienne (fig. 10). Również niewielką zmienność wykazano między różnymi stanowiskami w każdym zbiorniku (fig. 9).

Duże natomiast różnice zaobserwowano porównując materiały zebrane z różnych jezior (fig. 12, 13, tab. II). W niektórych z nich małże były dużo większe i cięższe niż w innych.

Przeprowadzono porównanie „dorodności" z liczebnością i skupiskowością. Pozwoliło to na stwierdzenie pewnych wzajemnych zależności. „Dorodność" *D. polymorpha* w jeziorach charakteryzujących się średnią liczebnością i wielkością kolonii jest przeważnie lepsza niż w grupie jezior charakteryzującej się największą liczebnością i skupiskowością, co świadczyłoby o odwrotnej proporcjonalności tych cech badanej populacji (fig. 12 i 13).

Odrębne stanowisko zajmuje tu grupa I jezior, charakteryzująca się najniższą liczebnością i wielkością kolonii. „Dorodność" osobników racicznicy zajmującej te jeziora jest zbliżona zasadniczo do małży z grupy II jezior i różni się istotnie od grupy III, lub też zajmuje stanowisko pośrednie między obu grupami. Grupa I jezior wykazuje więc dużą odrębność w porównaniu ze stosunkami panującymi w większości pozostałych jezior (grupa II i III). Analiza pustych muszli *D. polymorpha* wymarłych podczas redukcji liczebności dowodzi, iż wielkość małży w tych jeziorach była poprzednio jeszcze większa niż w grupie II, mimo bardzo dużego zagęszczenia.

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