

Krzysztof LEWANDOWSKI

Department of Hydrobiology, Institute of Ecology,
Polish Academy of Sciences,
Dziekanów Leśny (near Warsaw), 05-092 Łomianki, Poland

THE ROLE OF EARLY DEVELOPMENTAL STAGES,
IN THE DYNAMICS OF DREISSENA POLYMORPHA (PALL.)
(BIVALVIA) POPULATIONS IN LAKES

II. SETTLING OF LARVAE AND THE DYNAMICS
OF NUMBERS OF SETTLED INDIVIDUALS *

ABSTRACT: In field experiments the settling was analysed of D. polymorpha larvae on natural and artificial substrates, and in 26 Masurian lakes - the occurrence of settled D. polymorpha on plants and elsewhere. As a result of studies continued for several years, the mortality of young generations and the dynamics of numbers of settled D. polymorpha were determined. Two moments connected with a high mortality of juvenile individuals have been found to be critical for the formation of a population. The first of these is the passing of the planktonic larvae to sedentary life and the second one - the mortality of postveligers attached to submerged vegetation.

KEY WORDS: Lakes, Dreissena polymorpha, age structure, distribution, dynamics of numbers, mortality, population, settling.

* Praca wykonana w ramach problemu międzyresortowego MR II/15 (grupa tematyczna „Ekologiczne podstawy gospodarowania jakością wód”).

C o n t e n t s

1. Introduction
2. Study area and methods
3. Results
 - 3.1. Settlement of D. polymorpha larvae
 - 3.1.1. Settlement on artificial substrates
 - 3.1.2. Settlement on natural substrates
 - 3.2. Mortality of the young D. polymorpha generation
 - 3.3. Abundance dynamics and the age structure of settled D. polymorpha
4. Discussion
5. Summary
6. Polish summary
7. References

1. INTRODUCTION

Though the mussel, Dreissena polymorpha, plays an important role in aquatic ecosystems and is the object of common interest, not all the aspects of its biology and ecology have been studied sufficiently. The transition of larvae from the planktonic to the sedentary habits is the example of a problem not yet sufficiently known. Studies of the settlement of larvae were conducted only from the point of view of protection of hydrotechnical installations, and they concerned artificial substrates (e.g., K a ě a n o v a 1961, Š e v c o v a 1968, M o r t o n 1969, W a l z 1973, 1975, S k a l s k a j a 1976). According to K i r p i - ě e n k o ' s (1965) suggestion, the settling of larvae is a critical moment in the life of D. polymorpha, at which the greatest reduction of numbers may take place. This has in principle been confirmed by later studies. By comparing the abundance of larvae in the plankton and the numbers of attached one year old individuals in the following year it was found that in the Lagoon

of Szczecin (W i k t o r 1969) and in Lake Tałtowisko (S t a n i c z y k o w s k a 1977), which represent very different environments, the mortality of D. polymorpha may at that time exceed 99%. Similar calculations have been carried out by W a l z (1978). However, no detailed studies of this critical period have so far been undertaken.

Knowing that the level of numbers of D. polymorpha is mainly affected by the mortality at early ontogenic stages, investigations were undertaken to determine the importance of this very little known life period of this mussel species for the population that is forming. It seems that although it represents a very small fraction of ontogenic life, this period may to a large degree determine the age structure and population size of this species in a water body. Particular attention was given to the settling of larvae in lakes and to the mortality of D. polymorpha at this stage of life.

This problem was approached in the first part of the study (L e w a n d o w s k i 1982) by analysing the occurrence of D. polymorpha larvae in the plankton, whereas in the present part an analysis has been carried out of: the settling of D. polymorpha larvae on natural and artificial substrates (time, distribution, growth conditions), rate of survival of settled individuals of the new generation during a growing season, and from year to year in the study years, formation of a D. polymorpha population in the lakes investigated.

2. STUDY AREA AND METHODS

The study area was the Masurian Lakeland where a total of 26 lakes were investigated. The lakes differed in size, depth and trophic value (Table I), owing to which very different conditions of occurrence of D. polymorpha could be considered. The investigations were carried out in the years 1976-1979. The intensity of studying D. polymorpha in the particular lakes varied.

Table I. Description of lakes covered by studies of sedentary D. polymorpha

No.	Name of lake	Area (ha)	Depth (m)		Limnological type	Years of studying settled <u>D. polymorpha</u>			
			maximum	average		1976	1977	1978	1979
1	Majcz Wielki	163	16.4	6.0	b-mesotrophic	+	+	+	+
2	Inulec	178	10.1	4.6	eutrophic	+			
3	Głębokie	47	34.3	11.8	eutrophic	+	+		
4	Zeźwążek	11	7.4	3.7	eutrophic	+			
5	Jorzec	42	11.6	5.5	eutrophic	+	+		
6	Ołów	61	40.1	12.9	b-mesotrophic		+	+	
7	Koźwin	78	7.2	4.0	eutrophic			+	
8	Czos	279	42.6	11.1	eutrophic		+	+	+
9	Bartağ	72	15.2	6.4	eutrophic		+	+	
10	Gim	176	25.8	7.6	b-mesotrophic		+		
11	Gromskie	240	15.8	5.8	eutrophic		+		
12	Jaśkowskie	152	16.5	7.3	eutrophic		+		
13	Juno	381	33.0	11.9	eutrophic		+		
14	Kierzlińskie	93	44.5	11.7	a-mesotrophic		+		
15	Kuc	99	28.0	8.0	a-mesotrophic		+		
16	Lampackie	198	38.0	11.9	b-mesotrophic		+		
17	Lidzbarskie	122	25.2	10.0	eutrophic		+		
18	Małszewskie	202	16.9	6.3	eutrophic		+		
19	Maróz	332	41.0	11.9	b-mesotrophic		+		
20	Piłakno	259	56.6	13.0	a-mesotrophic		+		
21	Probarskie	201	31.0	9.2	b-mesotrophic		+		
22	Rumian	306	14.4	6.5	eutrophic		+		
23	Rzeckie	56	29.0	7.0	eutrophic		+		
24	Sarż	77	15.0	5.0	eutrophic		+		
25	Skanda	51	12.0	5.8	eutrophic		+		
26	Szeląg Mały	84	15.2	5.7	eutrophic		+		

The settling of D. polymorpha larvae was studied in Lake Majcz Wielki in 1977 and 1978. Microscopic slides (7.5×2.5 cm) were used as artificial substrates. The total accessible surface of both sides (upper side and under side) of these slides was 32.5 cm^2 . On the bands of a plastics net attached to a metal frame (50×30 cm) 36 slides were fastened in 3 rows. Two such sets were immersed to a depth of 2 m in the lake littoral (Fig. 1) before the beginning of the breeding of D. polymorpha. Every several to over a dozen days throughout the breeding season of the species 3 slides were taken down from either set for analysis. The last slides were left in the lake for winter to be taken down in the spring of the following year, before the beginning of the next breeding season of D. polymorpha. Prior to their setting up the slides had been kept for 2 weeks in an aquarium to allow a layer of periphyton to develop on them. Thus the settling larvae attached themselves to the periphyton algae and not directly to the smooth surface of the glass. This behaviour has been noted by B ø h l e (1971) in an analysis of the settling of the larvae of Mytilus edulis (L.) on polystyrene plates. After being taken down, the slides, at the beginning with a thin periphyton layer, were examined directly under the microscope. Later on (end of summer-autumn) the periphyton and the settled D. polymorpha were scraped off the slides and used for analyses. The top side and the under side of a slide were analysed separately, the number of settled individuals was recorded and the individuals were measured.

In this type of studies of the settling of D. polymorpha larvae most investigators use relatively large plates, e.g., 10×10 cm (K a ř a n o v a 1961, W a l z 1973, 1975), 25×25 cm (L u f e r o v 1965), or even 0.5 m^2 (M o r t o n 1969), the plates being as a rule of rough materials (e.g. wood, concrete or asbestos). It is difficult to directly determine the exact number of settled individuals and especially of the smallest ones of $200\text{--}300 \text{ }\mu\text{m}$ in body-size, on plates of this type. M o r t o n (1969), for instance, assumes that in his studies the smallest individuals may

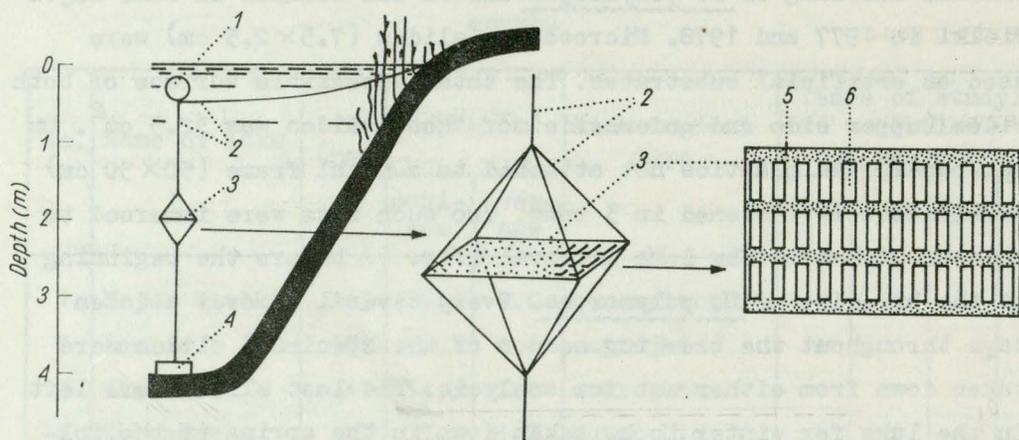


Fig. 1. Experimental setup for studying the settling of D. polymorpha larvae on slides

1 - buoy, 2 - rope, 3 - frame, 4 - brick, 5 - plastics netting, 6 - slide

have not been noticed. For this reason, settled young D. polymorpha are counted after being removed from plates, usually by scraping or washing off. These methods, are not, however, accurate and may leave out some of the settled individuals: the former by destroying some of the youngest individuals on rough surfaces, the latter - due to the impossibility of removing all settled individuals. As indicated by the investigation carried out during the present series, even the smallest settled D. polymorpha may already attach to the substrate, and even a long shaking, e.g., of plants in water, does not completely remove settled D. polymorpha from them - it leads to the falling off of 50% (from Ceratophyllum demersum L.) to 80% (from Elodea canadensis Rich.) of young D. polymorpha. The use of microscopic slides as substrates for settling larvae was in the present study chosen on account of the possibility to examine directly under the microscope and to scrape the periphyton and settled D. polymorpha off them more exactly owing to the high smoothness of the glass. As indicated by the data reported by D y g a and L u b j a n o v (1975), even rough wooden plates are colonized by settling larvae 15 days after their immersing at the

earliest, that is, only after the formation of a thin layer of periphyton.

The following were used as natural substrates for settling larvae: mud, sand, stones, shoots of Characeae and colonies of adult D. polymorpha. The intended substrates were placed in plastics containers (10 cm long and 7 cm broad). Ten containers, that is, 2 with each type of substrate, represented one set (Fig. 2). Three such

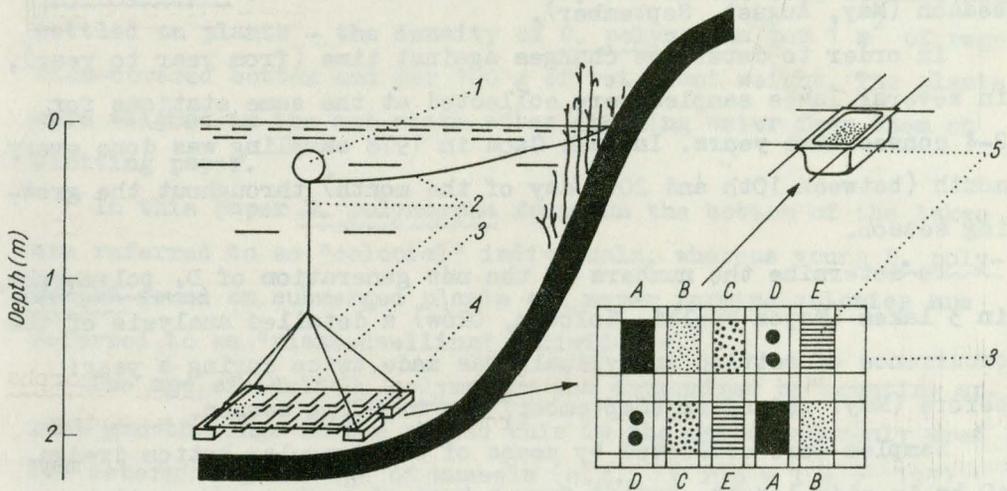


Fig. 2. Experimental setup for studying the settling of D. polymorpha larvae on natural substrates
 1 - buoy, 2 - rope, 3 - frame with containers, 4 - brick, 5 - container, A - mud, B - sand, C - pebbles, D - D. polymorpha colonies, E - plants

sets were placed at a depth of 2 m in the lake littoral in May. The experiment was terminated in September. The contents of the containers were transferred to plastics bags and preserved with 4% formalin. Settled D. polymorpha were counted by examining the material on a tray, and then under a stereoscopic microscope, to count the smallest individuals (200-300 μm long). About 4.5 thousand individuals of settled postveligers have been measured in the two types of experiments.

In 26 Masurian lakes studies of the occurrence of settled D. polymorpha were conducted for 1-4 years (Table I). In six of the

lakes (Majcz Wielki, Głębokie, Zełwążek, Jorzec, Oźów, Kołowin) a more detailed analysis has been carried out by collecting samples at 6-10 sampling stations in a lake, taking into account the whole zone of occurrence of D. polymorpha where samples were taken at one-metre depth intervals. In the remaining lakes samples were collected at 2-3 stations at depths of 1, 2, 4 and sometimes 0.5 and 6 m. Samples were collected in different periods of the growing season (May, August, September).

In order to determine changes against time (from year to year), in several lakes samples were collected at the same stations for 2-4 consecutive years. In Lake Czos in 1978 sampling was done every month (between 10th and 20th day of the month) throughout the growing season.

To determine the numbers of the new generation of D. polymorpha, in 3 lakes (Majcz Wielki, Kołowin, Oźów) a detailed analysis of the occurrence of settled individuals was made twice during a year: before (May) and after (September) the breeding season.

Samples were collected by means of a triangular bottom dredge, 40 cm in side length, hauled from a boat at anchor over a distance of 1 m parallelly to the lake shore. A similar method for collecting large mussels has been used fairly often (Starczykowska 1964, Widuto and Kompowski 1968, Lewandowski and Starczykowska 1975 among others): The contents of the dredge brought to surface from the lake bottom were transferred to a benthos sieve and live D. polymorpha, usually forming colonies, were picked from them. Samples collected at smaller depths usually contained submerged vegetation with young D. polymorpha attached to it. These were as a rule large and homogeneous samples. In such cases the whole vegetable material was spread evenly over the sieve and only part of it, e.g., 1/2 or 1/4 of the contents of the sieve, was taken for further analyses. For the preservation 4% formalin was used.

Each sample was studied by stages by examining the material part after part on a tray and picking out of it all D. polymorpha that

could be seen with the naked eye. Subsequently, to take into account the smallest, just settled, postveligers, individual plant shoots, large D. polymorpha, Unionidae, empty mollusc shells, etc., were thoroughly examined under a stereoscopic microscope. The sediment that remained in the tray and in the container was also scanned in a camera under a stereoscopic microscope. A total of over 400 samples were examined. On their basis the density was determined of D. polymorpha per 1 m² of the bottom, and in the case of individuals settled on plants - the density of D. polymorpha per 1 m² of vegetation-covered bottom and per 100 g of wet plant weight. The plants were weighed in the wet state after draining water from them on blotting paper.

In this paper D. polymorpha found on the bottom of the lakes are referred to as "colonial" individuals, whereas young D. polymorpha found on submerged plants and never forming colonies are referred to as "plant-dwelling" individuals.

The age of adult D. polymorpha was determined by counting annual growth rings on the shell. This is the method commonly used for determining the age of mussels (e.g., Crowley 1957, Ökland 1963, Negus 1966, Piechocki 1969, Wiktor 1969, Lewandowski and Stańczykowska 1975, Spiridonov 1975, Stańczykowska 1977), although it is subjective and not always certain, especially in the case of old individuals. In the present investigations the ageing was facilitated by the collecting of mussels in different periods of the growing season - the zone of this year's growth was, therefore, marked differently - and by earlier field experiments aimed at a direct determination of the growth of D. polymorpha in lakes (A. Stańczykowska and K. Lewandowski - unpublished data).

For the analysis of dead D. polymorpha larvae, in July and August 1978 bottom sediment samples were collected in three lakes (Majcz Wielki, Kołowin, Ołów). The samples were collected at 3-5 stations, where the bottom was muddy (at the depth of 5-19 m),

using Kajak's tubular bottom sampler with a catching surface area of 10 cm². For the analysis water from above the sediments, and the top (2 cm) sediment layer were used. After preservation in 4% formalin solution the whole material was scanned under a stereoscopic microscope.

3. RESULTS

3.1. Settlement of D. polymorpha larvae

3.1.1. Settlement on artificial substrates

After remaining in the plankton for several days, D. polymorpha larvae begin to fall out of the bulk of lake water and pass to the sedentary habits; colonizing various underwater objects. To determine the rate of this process, field experiments have been carried out by exposing glass substrates (microscope slides) in a lake.

In Lake Majcz Wielki throughout the growing season of 1977 D. polymorpha larvae failed to colonize the slides. This was probably due to the fact that the numbers of planktonic larvae in that year were very small (Lewandowski 1982).

An abundant colonization of slides was, however, observed in 1978, when the numbers of planktonic larvae in Lake Majcz Wielki were many times higher (Lewandowski 1982).

A detailed analysis of the body-size of planktonic larvae and of the youngest just settled postveligers has demonstrated that the transition of larvae from the planktonic to sedentary habits may occur over a fairly wide range of body-size of individuals. Most D. polymorpha larvae settled at a body-size of over 200 µm. From this size on there occurred a clear fall in the number of larvae in the plankton. Much smaller postveligers could, however, be encountered among settled individuals. The smallest post-

veligers attached to the substrate measured 140 μm (Fig. 3). Analyses of live individuals have shown that a large proportion of settled larvae do not attach to the substrate, but they actively translocate over its surface. Among such individuals D. polymorpha with a body-size of several millimetres, as well as typical planktonic larvae, even ones 80 μm long, could be seen.

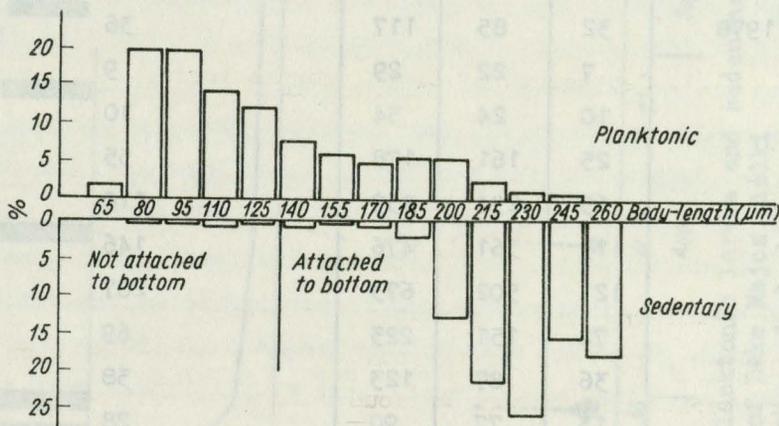


Fig. 3. Body-size of planktonic and sedentary D. polymorpha larvae (Lake Majcz Wielki, June-August 1978) (1118 planktonic and 966 sedentary larvae have been measured)

In Lake Majcz Wielki in 1978 two settling peaks were observed. The first, small, peak occurred in the second half of June, the second, much bigger, in mid-July when the largest numbers of settled postveligers were recorded (Table II). In those experiments a larger number was always found of postveligers attached to the under side of the slides than to the top side: on an average 2-6 times as many and at the most 17 times as many. Both sides of the slides were colonized by larvae directly out of the water bulk. There also occurred a crawling of settled larvae from the upper side to the under side of a slide, this being indicated by the fact that the average size of an individual was always larger on the under side than on the upper side. It seems that on the under side there existed better conditions for filtering organisms.

Table II. Average numbers of young D. polymorpha settled on experimental microscope slides in Lake Majcz Wielki (beginning of exposure 10 May 1978, slide size 7.5×2.5 cm, total accessible area of upper side and under side of a slide - 32.5 cm^2)

Date of taking-down of slide	Slide side		Total	Per 1 m^2 of glass substrate (thous. ind. $\cdot \text{m}^{-2}$)
	upper	lower		
24 June 1978	32	85	117	36
30 June	7	22	29	9
3 July	10	24	34	10
6 July	25	161	178	55
12 July	65	294	359	110
17 July	115	361	476	146
20 July	121	502	673	207
30 July	72	151	223	69
14 Aug.	36	87	123	38
10 Sept.	13	77	90	28
29 May 1979	7	24	31	9

Calculated per 1 m^2 of the glass substrate during the peak settling (20 July 1978), the results amounted on an average to over 200 thous. ind. $\cdot \text{m}^{-2}$ (Table II). The maximum value recorded for this period was 875 postveligers on a whole slide (which equals to 270 thous. ind. $\cdot \text{m}^{-2}$), as many as 776 postveligers having been found attached to the slide under side alone (= 480 thous. ind. $\cdot \text{m}^{-2}$).

The results make it possible to exactly follow the changes taking place in the plankton of the littoral, and in the settlement of larvae in Lake Majcz Wielki. Planktonic larvae were first seen on 12 June 1978 (Fig. 4). The distribution of body-size of the larvae shows that they had appeared a few days earlier, because some of them were already $150 \mu\text{m}$ long, larvae of the smallest size predominating. The culmination of this intensive appearance took

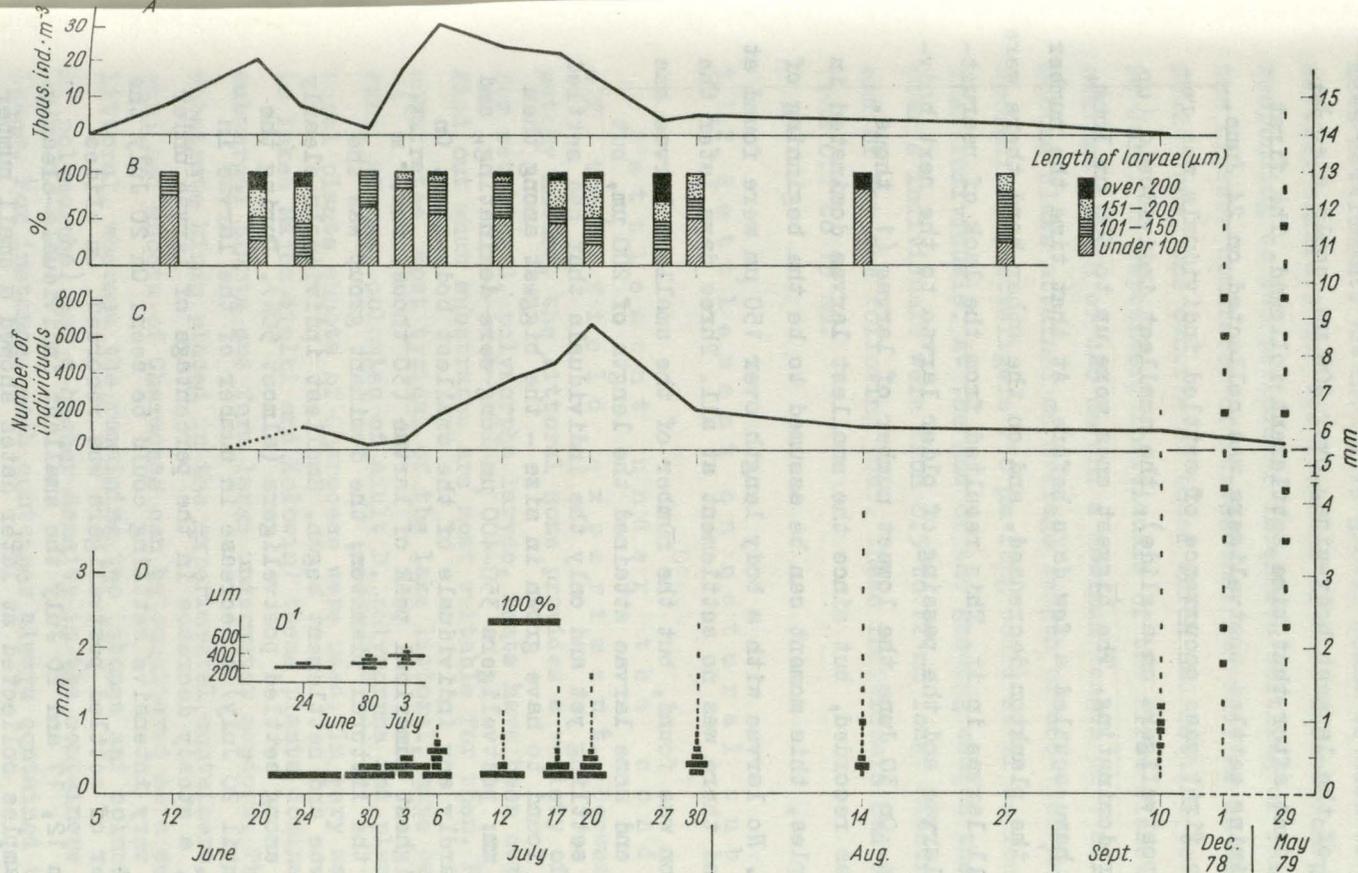


Fig. 4. Numbers and body-size of *D. polymorpha* planktonic larvae and sedentary juvenile individuals in the littoral of Lake Majcz Wielki

A - numbers of planktonic larvae, B - size structure of planktonic larvae, C - average number of *D. polymorpha* settled on experimental slides, D - body-length distribution of *D. polymorpha* settled on experimental slides, D' - body-length of *D. polymorpha* at the beginning of settling

place on 20 June (20 thous. ind. $\cdot m^{-3}$), small larvae being relatively few in number and medium-sized larvae (100-200 μm) dominating. Planktonic larvae of the largest body-size, over 200 μm , could also be already seen, and after that time settlement followed. The first sample containing settled postveligers was collected on 24 June, when also the first mass occurrence of settled individuals was recorded (117 postveligers on a slide), the smallest individuals (up to 250 μm) predominating. The biggest ones were up to 300 μm long, so they must have settled a few days before. At that time the number of larvae in the plankton decreased, and on the other hand there were very few small larvae in it. This resulted from the lack of recruitment of new larvae and the passing of older larvae to the next body-size classes. On 30 June the lowest number of larvae (1 thous. ind. $\cdot m^{-3}$) was recorded, but since the smallest larvae dominated in plankton samples, this moment can be assumed to be the beginning of another peak. No larvae with a body length over 150 μm were found at that time, and there was no settlement at all. Three days later the same situation was found, but the number of the smallest larvae was even greater and some larvae attained the length of 200 μm , but there was no settling yet and only the individuals that had settled earlier were found to have grown in size - the biggest among them measured 0.5 mm; postveligers 350-400 μm long were dominating, and there were hardly any individuals of the smallest body-size. On 6 July the highest numerical peak of larvae (30 thous. ind. $\cdot m^{-3}$) was found in the littoral plankton; the dominant group was the smallest larvae and settlement began. Smallest individuals clearly predominated among settled postveligers (almost 50%). During the next days (until 20 July) a decrease in number of the larvae in the plankton, a steady decrease in the percentage of larvae under 100 μm and a very intensive settling could be seen. On 20 July the highest number of settled postveligers was recorded. On slides taken down on 12, 17 and 20 July the smallest individuals clearly dominated. Samples collected at later dates showed a small number of larvae in the plankton, although the proportion of the smallest

larvae was sometimes large (e.g., on 14 August) and there was no mass settlement. An intensive growth could be seen of individuals settled earlier, and two dominant classes became conspicuous corresponding to two periods of intensive settling of larvae. One of the classes consisted of larvae that had settled in the period 20-24 June, the other - of those which had settled between 6 and 20 July. In September, individuals of the first class attained an average length of 4-6 mm and a maximum length of 7 mm. Those of the second class attained an average length of 600-1200 μm . In September, sporadic postveligers 250 μm long could still be found among settled individuals. At the end of the growing season the current year's individuals were from 0.5 to 12 mm long. Measured at the end of May the following year, these individuals had a body length from 0.7 to 15 mm.

3.1.2. Settlement on natural substrates

Settlement under the conditions of the field experiment. Because of its patchy nature, the littoral zone provides a variety of possibilities for settling D. polymorpha larvae. Tests have been carried out to find out what substrates are most suitable for them. Five kinds of substrates, most typical of the lake littoral, have been chosen: mud, sand, stones, colonies of adult D. polymorpha and plants. Of the littoral plants shoots of Characeae were used. In very many lakes (e.g., in lakes Majcz Wielki and Kołowin) these plants dominate over other submerged plants and form large underwater meadows. Three of the substrate kinds placed in the experimental containers, that is, mud, sand and shoots of Characeae can be considered as a section of the littoral, whereas the remaining two (stones and colonies of adult D. polymorpha) had a higher density in the containers than in lakes. For instance, each container always contained two medium-sized colonies which jointly consisted of an average of 63 (from

53 to 68) adult D. polymorpha, that is to say, about 9000 ind. $\cdot m^{-2}$, while their density in Lake Majcz Wielki was on an average 350 ind. $\cdot m^{-2}$ in the zone of inhabitancy, and their maximum density was 750 ind. $\cdot m^{-2}$.

The settlement of D. polymorpha larvae was very similar at all the stations in Lake Majcz Wielki, where the experimental sets had been placed. Characeae shoots proved to be the best substrate for the settlement of D. polymorpha, and mass settlement was found on them (from several hundred to over 2.5 thous. individuals per a container). They were followed by formed D. polymorpha colonies (several hundred individuals per a container). Stones appeared to be a much worse substrate, whereas sand and mud were colonized at a very low rate (Table III).

Table III. Settling of D. polymorpha larvae on different natural substrates (Lake Majcz Wielki, experimental containers 7x10 cm, exposure time from May to September 1978)

Kind of substrate	Average number of <u>D. polymorpha</u> in container	Range
Characeae	1727	604-2720
<u>D. polymorpha</u> colonies	455	167-697
Stones	61	25-109
Sand	13	7-23
Mud	13	3-38

The settlement of D. polymorpha larvae on the different substrates was no doubt connected not only with the kind of substrate, but also with the degree of its complication, that is, with the really accessible surface for settlement. The greater the degree of substrate complication, the more intensive the settling of D. polymorpha larvae.

By calculating the experimental data per 1 m² of vegetation-covered bottom an average value was obtained of about 250 thous. (from about 90 thous. to almost 400 thous.) settling current year's

D. polymorpha. Much fewer larvae settle on formed D. polymorpha colonies. Under the conditions of Lake Majcz Wielki an average of 2200 and at the most 8 thous. young individuals per 1 m^2 can settle on such a substrate. Up to about 1000 current year's D. polymorpha can settle on 1 m^2 of a stony bottom, depending on the number of stones.

Settlement and occurrence of settled D. polymorpha in the littoral. In the Masurian lakes under study the density of D. polymorpha occurring in formed colonies on the bottom of the littoral was usually several hundred individuals per 1 m^2 of bottom surface in the zone of inhabitancy. Only in two out of the 26 lakes under study did D. polymorpha fail to be present (lakes Sarż and Szelaq Mały),

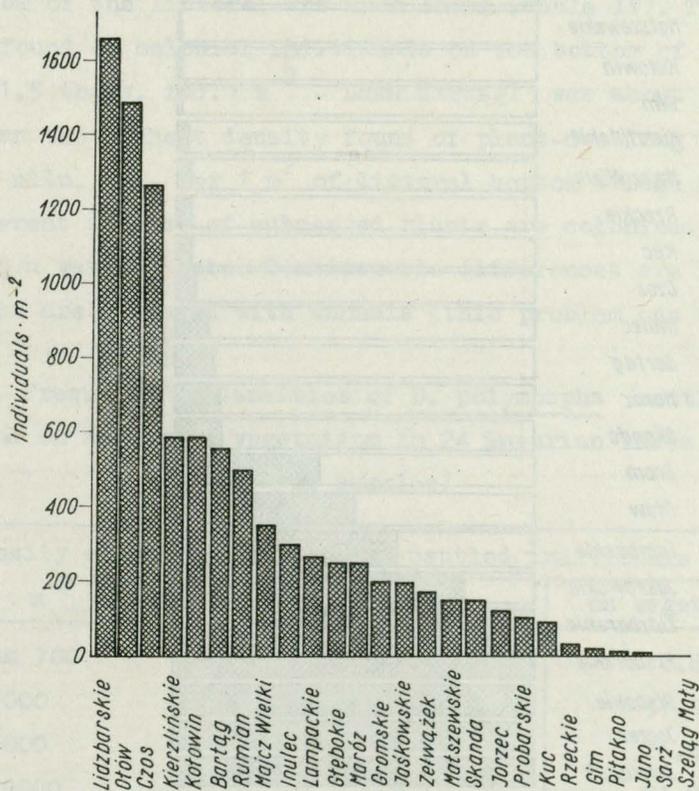


Fig. 5. Average numbers of D. polymorpha settled on the littoral bottom in 26 Masurian lakes

whereas in two others (Juno and Piłakno) their density was very low (less than $10 \text{ ind.} \cdot \text{m}^{-2}$). In three lakes (Czos, Ołów and Lidzbarskie) the average densities exceeded $1000 \text{ ind.} \cdot \text{m}^{-2}$ in the zone of inhabitancy (Fig. 5).

One of the possibilities that can be found in the littoral by the larvae passing from the planktonic to the sedentary habits and looking for a suitable substrate is the submerged plants. Almost all the littoral in most Masurian lakes is covered with vegetation. Literature data on the occurrence of D. polymorpha on plants are exceptionally scarce, while the present investigations indicate that the occurrence of D. polymorpha on submerged plants is a common and

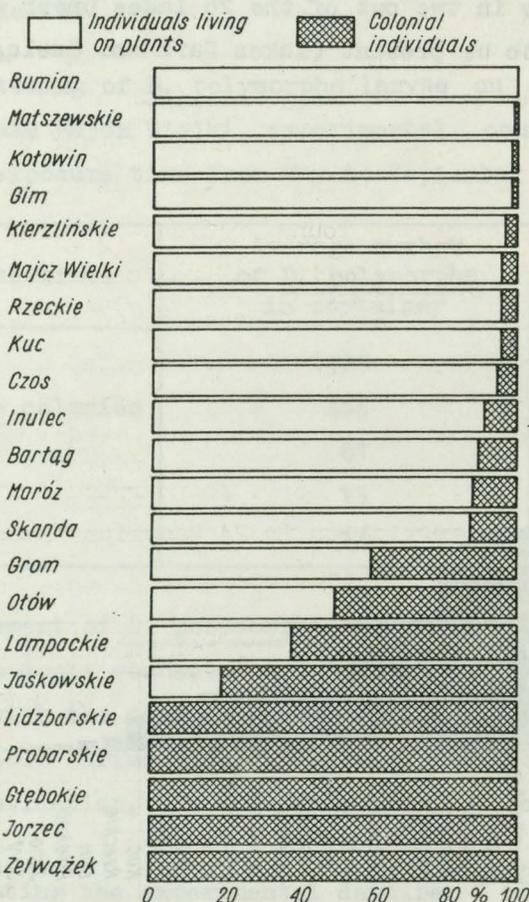


Fig. 6. Percentage of D. polymorpha individuals living on plants and in colonies in the Masurian lakes

mass phenomenon. In most of the lakes under study apart from individuals of D. polymorpha present in formed colonies on the bottom of the littoral, D. polymorpha were found on plants as a rule in densities many times exceeding the densities found on the bottom outside the plants. In 13 lakes plant-dwelling D. polymorpha represented over 85% of the whole population in the lake. Only in 5 lakes were plant-dwelling individuals found to be absent (Fig. 6) - the cause of this often was a poor submerged vegetation in the littoral, e.g., in the small but deep channel lakes Jorzec and Głębokie.

The densities of D. polymorpha found on submerged plants at the different stations and depths of the particular lakes not infrequently exceeded 100 thous. ind. \cdot m⁻² of vegetation-covered lake bottom. The density of D. polymorpha found in formed colonies on the bottom of the littoral was much lower (Table IV). The highest density found of colonial individuals on the bottom of the littoral (11.5 thous. ind. \cdot m⁻² - Lake Bartag) was about 150 times lower than the highest density found of plant-dwelling individuals (almost 2 mln. ind. per 1 m² of littoral bottom - Lake Rumian).

Different species of submerged plants are colonized by D. polymorpha at a varying rate. Considerable differences are found when perennials are compared with annuals (this problem has partially

Table IV. Frequency of densities of D. polymorpha settled on the bottom and on submerged vegetation in 24 Masurian lakes (percentage of samples)

Density classes (ind. \cdot m ⁻² of bottom)	Settled individuals	
	on bottom	on vegetation
less than 100	22.1	8.8
100-1000	36.4	31.0
1001-5000	32.4	26.6
5001-20000	9.1	21.2
20001-100000	0	8.0
over 100000	0	4.4

been described in an earlier paper - S t a ń c z y k o w s k a and L e w a n d o w s k i 1980). In the case of perennial species the percentage of samples with attached D. polymorpha is always higher than in the case of annuals (Table V).

Table V. Degree of colonization of annual and perennial plants by D. polymorpha in the lakes under study

Plants	Percentage of samples with <u>D. polymorpha</u>
Perennials	
<u>Fontinalis antipyretica</u> (Hedw.)	87
Characeae	67
<u>Ceratophyllum demersum</u> (L.)	64
<u>Elodea canadensis</u> (Rich.)	54
Annuals	
<u>Potamogeton perfoliatus</u> (L.)	10
<u>P. pectinatus</u> (L.)	9
<u>P. lucens</u> (L.)	5
<u>Myriophyllum spicatum</u> (L.)	7

Among perennials the highest densities of D. polymorpha were found on Ceratophyllum demersum (L.), Fontinalis antipyretica (Hedw.) and Characeae, slightly lower on Elodea canadensis (Rich.). On these plants the highest densities came up to 500-800 thous. ind. $\cdot m^{-2}$ of the bottom of the littoral. The densities of D. polymorpha on annuals were lower - they did not in principle exceed 5 thous. ind. per $1 m^2$ of vegetation-covered bottom. Only in one case was a very high density found - about 300 thous. ind. $\cdot m^{-2}$ of lake bottom overgrown with Potamogeton pectinatus (L.) - this was the situation found in Lake Rumian, where, as has already been mentioned, plant-dwelling D. polymorpha were encountered in exceptionally large numbers. The time of sample collecting in this lake (beginning of August) and the body-size of plant-dwelling individuals (99.5% of plant-dwelling individuals were less than 0.5 mm long) indicate

that the situation was recorded at the point of time immediately following a mass transition of D. polymorpha larvae from the planktonic to the sedentary habits.

The number of D. polymorpha settled on 100 g (wet weight) of each plant species varies, too. Several thousand settled D. polymorpha were usually found per 100 g of perennials, the maximum number exceeding 100 thous. individuals. An exception was Characeae for which smaller numbers of D. polymorpha per 100 g of vegetable weight were recorded, because of the high weight of these plants caused by incrustation. In most cases there were several hundred individuals per 100 g of annual plant species, and the maximum numbers varied considerably from species to species, being, however, on the whole much lower than on perennials (Table VI).

Table VI. Maximum numbers of settled D. polymorpha per 100 g of plants in the lakes under study

Plants	Number of <u>D. polymorpha</u>
Perennials	
<u>Fontinalis antipyretica</u>	118000
<u>Ceratophyllum demersum</u>	110000
<u>Elodea canadensis</u>	105000
Characeae	34000
Annuals	
<u>Potamogeton pectinatus</u>	104000
<u>P. lucens</u>	19000
<u>P. perfoliatus</u>	3500
<u>Myriophyllum spicatum</u>	1200

On perennials settled D. polymorpha were encountered throughout the year, whereas on annuals only current year's D. polymorpha individuals were found settling during midsummer. The general regularity was that only the youngest D. polymorpha occurred on submerged plants. They were mainly current year's individuals (in the autumn)

and one year old individuals (in the spring). The oldest D. polymorpha encountered on plants were 3 years old. Thus there occurs a rapid decrease in numbers and percentage of the successive age-classes as they become older and older. Such a picture of the age-structure of D. polymorpha found on plants was commonly encountered in different lakes.

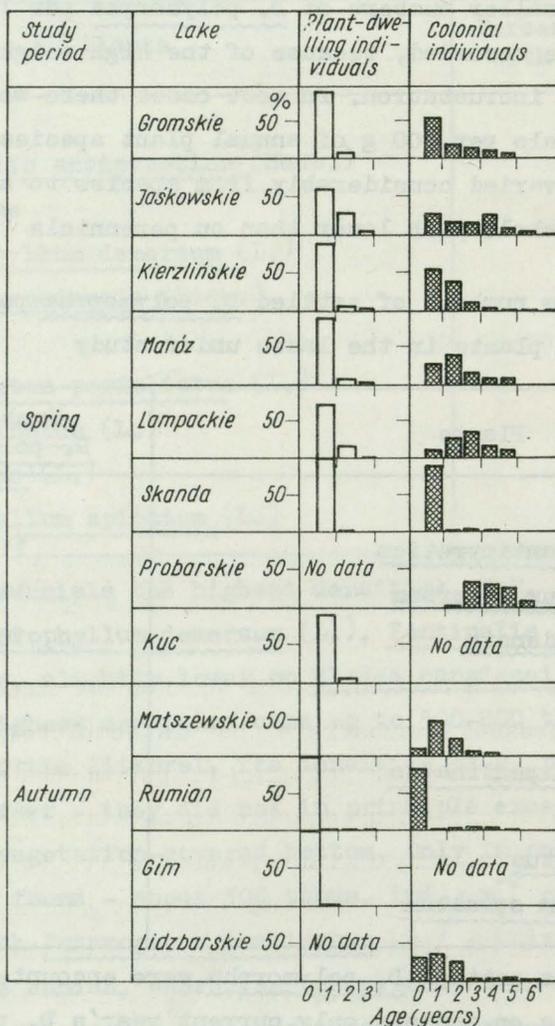


Fig. 7. Age structure of plant-dwelling and colonial D. polymorpha individuals in different lakes before breeding (spring) and after breeding (autumn) (1977)

Quite a different age-structure was observed in the case of formed D. polymorpha colonies found on the bottom not on plants. In this case all age classes were represented, that is, up to the 5th or 6th year of life, and middle-aged individuals dominated more often than the youngest ones. Among colonial individuals the distribution of numbers by age classes was much more even than among plant-dwelling individuals (Fig. 7, Table VII).

Table VII. Maximum numbers of different age classes of D. polymorpha settled on plants and on the bottom of Lake Rumian (August 1977)

Age class of <u>D. polymorpha</u> (in years)	Numbers of <u>D. polymorpha</u> (individuals per 1 m ² of littoral bottom)	
	on plants	on bottom
0	1700000	1800
1	3300	2100
2	250	1600
3	80	900
4	0	280
5	0	40

Stalks of emergent plants, and especially of the reed (Phragmites australis (Cav.) Trin. ex Steud.), abundantly occurring in the lake littoral, represent a substrate that is completely different from those discussed above for settling D. polymorpha individuals. The reed is for certain less accessible to settling D. polymorpha individuals than are submerged plants, because it grows in shallow lake zones reaching depths up to about 1.5 m at the most; the surface of the submerged part of the stalk is smaller than that of other plants, and apart from this, reed stalks have a one-year life cycle. On the other hand, however, the reed grows in close communities with large numbers of stalks (about 50 stalks per 1 m²) (S z c z e p a ń s k i 1978). Though its life is short, a reed stalk can last in the dry state for a relatively long time, not

losing its properties as a substrate, and even after its breaking off and falling on to the bottom it continues for a fairly long time to be a suitable substrate for D. polymorpha. The reed is one of few plants representing a rigid substrate, and only on it, among submerged plants, were D. polymorpha colonies found, the size of which many a time exceeded 100 individuals. The expansion of D. polymorpha into a reed bed is relatively small - they occurred in largest numbers at its edge on the side of the open water (Table VIII).

Table VIII. Range of D. polymorpha distribution into the reed bed (dry last year's reed stalks, Lake Kołowin, June 1978)

Distance from reed-bed edge (m)	Depth (m)	Numbers of <u>D. polymorpha</u> settled on 1 stalk	
		average	range
0	1.5	31	0-210
4	1.0	19	0-68
7	0.5	3	0-12
10	0.3	0	0

In Lake Kołowin, in June, before the breeding season of D. polymorpha settled individuals were found mainly on dry, previous year's reed stalks. One year old individuals dominated (86-91%), and the oldest D. polymorpha were 3-4 years old. At that time to current year's stalks that were just germinating adult D. polymorpha attached (up to 3 individuals on a stalk) and their density remained low throughout the growing season. Therefore on the reed mainly current year's postveligers are found. In July, they settled at the same rate on dry stalks as on the current year's stalks. On an average about 200 attached postveligers, 320 at the most, were recorded for single stalks.

On the reed settled D. polymorpha may in certain situations attain a level of density of up to about 20 thous. individuals per 1 m² of reed-covered lake bottom.

The horizontal distribution of settled D. polymorpha in a lake depends on the one hand on the environmental conditions in the different parts of a lake and on the other hand - on the inflow to those places in each breeding season of planktonic larvae capable of settling. Planktonic larvae present in the epilimnion are subject to the action of winds and currents. A detailed analysis of the horizontal distribution of settled D. polymorpha in several lakes has shown that the effect of these factors becomes visible in small lakes, the shoreline of which is not complicated and the littoral is homogeneous and little varied. In Lake Żelwążek, a small water body, in its windward eastern part, reached also by the current of the Jorka river, the density of settled D. polymorpha exceeded $1000 \text{ ind.} \cdot \text{m}^{-2}$, while at other places it did not attain the level of $100 \text{ ind.} \cdot \text{m}^{-2}$. A similar situation was found in Lake Kołowin, the littoral of which was uniformly covered with Characeae: in the windward eastern part the number of settled postveligers alone was at the end of the growing season five times as large as that in the western part.

In the other lakes (Głębokie, Jorzec, Ożów), the littoral of which was characterized by a great diversity and variation (dispersed submerged vegetation of an insular distribution, muddy spots, shoals of adult D. polymorpha), the effect of winds and currents on the distribution of settled D. polymorpha was not so marked.

3.2. Mortality of the young D. polymorpha generation

The mortality of the young generation was studied by a direct analysis of dead individuals. In the experiment aimed at investigating the settlement of D. polymorpha larvae on glass substrates dead individuals represented on an average 3.9% of all the individuals found on microscope slides. As the growing season passed, the percentage of dead D. polymorpha on the slides grew (Table IX).

Table IX. Percentage of dead D. polymorpha on experimental slides
(Lake Majcz Wielki, exposure from May 10, 1978)

Date of taking-down of slides	Percentage of dead individuals (average)	Size of dead individuals (μm)
24 June 1978	0.3	185-200
30 June	0	-
3 July	0	-
6 July	0	-
12 July	1.8	95-245
17 July	2.9	80-650
20 July	3.0	95-560
30 July	4.7	80-650
14 Aug.	4.9	110-825
10 Sept.	30.8	200-920

Individuals less than 250 μm long, that is, those that died at the stage of passing from the planktonic to sedentary habits, represented 41.3% of the dead individuals. These data should, however, be considered with some caution, because empty shells of dead individuals (as well as living individuals) may have come off the slides still during the exposure. This is confirmed by the slides taken down in May the following year on which no dead individuals were found.

A clear picture of mortality has been obtained from the experiment dealing with the settlement of larvae on different natural substrates. In this experiment all dead individuals remained in the experimental containers. Dead young D. polymorpha were found with all kinds of substrates, but their number on the different substrate kinds varied. In the case of plants, D. polymorpha colonies and stones, that is, substrates on which postveligers settle most abundantly (Table III), dead individuals constituted as little as several per cent. On the other hand in the case of sand and mud dead individuals made up on an average more than 30%; in some containers they came up to 67% (sand) and 71% (mud) (Table X).

Table X. Percentage of dead D. polymorpha on different natural substrates (Lake Majcz Wielki, experimental containers 7 X10 cm, exposure time from May to September 1978)

Kind of substrate	Percentage of dead individuals	
	average	range
Characeae	2.6	1.3-3.5
<u>D. polymorpha</u> colonies	3.8	2.8-6.5
Stones	6.1	1.8-16.6
Sand	31.6	4.7-66.6
Mud	46.3	13.3-70.7

Sand and mud, therefore, represent a clearly unfavourable substrate for settling D. polymorpha (poor settlement, a high mortality during the experiment that lasted only 3 months), and it may be assumed that all the individuals which have found themselves on sand or mud will die within a relatively short time.

By calculating these data per 1 m² it is possible to find out that on an average 3-4 thous. young D. polymorpha die in an area of this size of a sandy or muddy bottom.

The dead individuals examined were from 220 μm to 3 mm long, most of them were less than 1.5 mm long at the time of their death, regardless of the kind of substrate (Fig. 8).

Environmental conditions prevailing in the lake profundal, where the bottom is muddy, did not fully correspond with the experimental conditions created in the case of muddy bottom. Under the experimental conditions settling larvae could find a better substrate over a small area, as indicated by the high preference (Table III). The lake profundal does not provide such a possibility, and all the larvae that fall from the pelagial die at a much higher rate. This has been confirmed among other things by analyses of mud samples from the profundal which have shown that in this zone in Lake Majcz Wielki there were on an average 130 thous. dead postveligers on 1 m², the maximum being 400 thous. Smaller numbers of dead postveligers (up to 4 thous.) per 1 m² of muddy bottom were found in

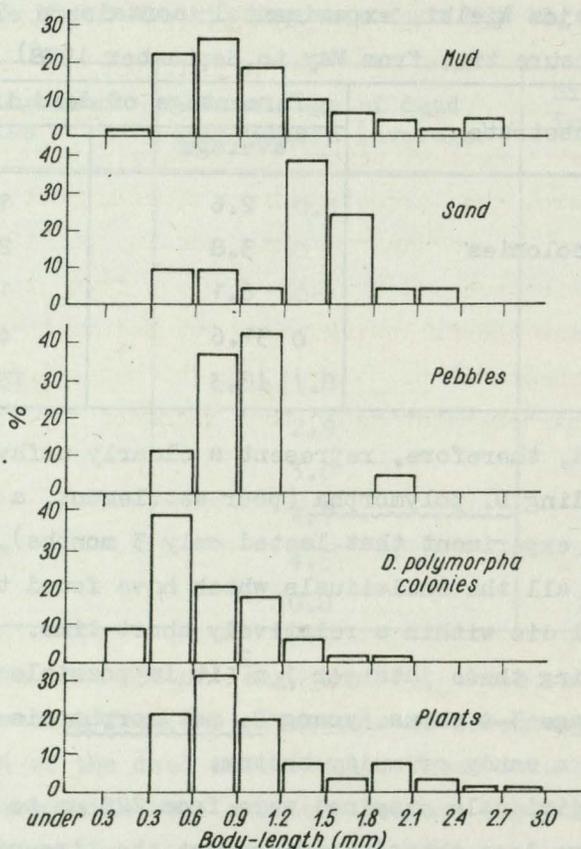


Fig. 8. Body-size of dead *D. polymorpha* on different substrates

Lake Kołowin and Lake Ożów, where the numbers of planktonic larvae were, however, smaller than in Lake Majcz Wielki.

The size of dead *D. polymorpha* varied over a fairly wide range - between lengths characteristic of typical planktonic larvae (110 μ m) to 1400 μ m, which indicates that some individuals had died still in the plankton, others - at the stage of passing from the planktonic to sedentary habits. However, a large proportion showed some growth after falling on to an unfavourable substrate and died only some time later.

A great variation of the mortality picture has been found in the submerged vegetation of the littoral zone of the lakes where

most postveligers settled. In the autumn, that is, after the completion of settling, dead postveligers in all the lakes under study represented on an average 4.4%¹ (= 2700 ind. per 1 m² of littoral). The range of the results was from 0.2 to 56.0%, from which follows that in some situations dead postveligers were more numerous than living postveligers. The largest numbers of dead postveligers were found in Lake Czoz, where their maximum density per 1 m² of bottom surface covered with submerged vegetation was found to be about 22 thous. In spring the following year, but before the beginning of the breeding season of D. polymorpha, the percentage of dead individuals was higher relative to that recorded for the autumn (on an average 13.9%).

A detailed analysis of these dead individuals has shown, however, that most of them (59-85%) had died before the beginning of winter - for the ring that forms on the shells at the time of the winter stoppage of growth was absent. Other individuals had died during winter (a faintly marked winter ring) or in early spring (with the current year's increment clearly marked). In Lake Majcz Wielki, for instance, 70% of the dead young D. polymorpha analysed in spring had died in late autumn, 23% - in winter and 7% in early spring. Shells of the smallest postveligers that die in summer and early autumn are never preserved in the sediments of the littoral till the spring of the next year. In spring, the smallest shells were about 1 mm long, and only sporadically - 400 µm, while during the preceding autumn individuals 200 µm long were often found among dead postveligers.

The results indicate a very high mortality of D. polymorpha at early stages following the transition from the planktonic to sedentary habits.

¹ 100% = living + dead postveligers.

3.3. Abundance dynamics and the age-structure of settled

D. polymorpha

The age-structure of a D. polymorpha population in a body of water is primarily affected by the reproduction which varies from year to year, and by the mortality at the different developmental stages of D. polymorpha. A certain role may in this case be played also by migration.

A very marked effect of the young generation on the age-structure of D. polymorpha and a great variation of this structure in different years was observed in Lake Majcz Wielki. In 1976, the numbers of planktonic larvae were in this lake very high (Lewandowski 1982), due to which in the June of the following year one year old individuals predominated. In 1977, the number of larvae in the plankton was very small (Lewandowski 1982) and practically no settlement was seen. Consequently, there were hardly any one year old individuals in the next year, and in June two year old individuals (settled in 1976) dominated. Due to the production of large numbers of larvae in 1978, in September the most numerous among D. polymorpha settled on submerged vegetation and in colonies on the bottom not on plants were the current year's individuals, and in June 1979 - one year old individuals (Fig. 9).

Examples of a little varying, from year to year, age-structure of settled D. polymorpha in different lakes are given in Figure 10. In lakes Jorzec and Głębokie, where the number of planktonic larvae in two consecutive years was very small (Lewandowski 1982), a very low proportion of the youngest classes was found in the age-structure of settled individuals. In two other lakes (Bartąg and Ołów) a converse situation was found. In both study years the youngest D. polymorpha dominated in them. A growth of the percentage of the youngest individuals in these lakes in 1978 relative to 1977 resulted in an increase in the total density of settled D. polymorpha in the zone of their inhabitancy: from 720 to 3000

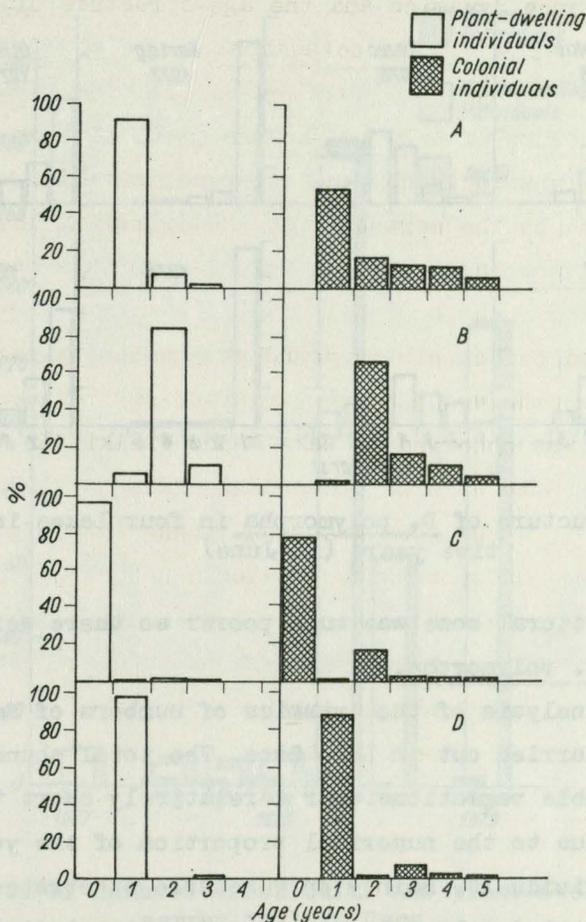


Fig. 9. Age structure of sedentary D. polymorpha in Lake Majcz Wielki on submerged vegetation and on the bottom (in colonies) in different periods

A - June 1977 (after a high level of numbers of planktonic larvae in 1976), B - June 1978 (after a very low level of numbers of planktonic larvae in 1977), C - September 1978 (after a high level of numbers of planktonic larvae in 1978), D - June 1979 (after a high level of numbers of planktonic larvae in 1978)

ind. · m⁻² in Lake Bartąg, and from 1500 to 2100 ind. · m⁻² in Lake Oków. These two lakes clearly differed in the proportion of one year old individuals in the age-structure. This proportion was much larger in Lake Bartąg as a result of the dominance of plant-dwelling D. polymorpha (Fig. 6); in Lake Oków the submerged vege-

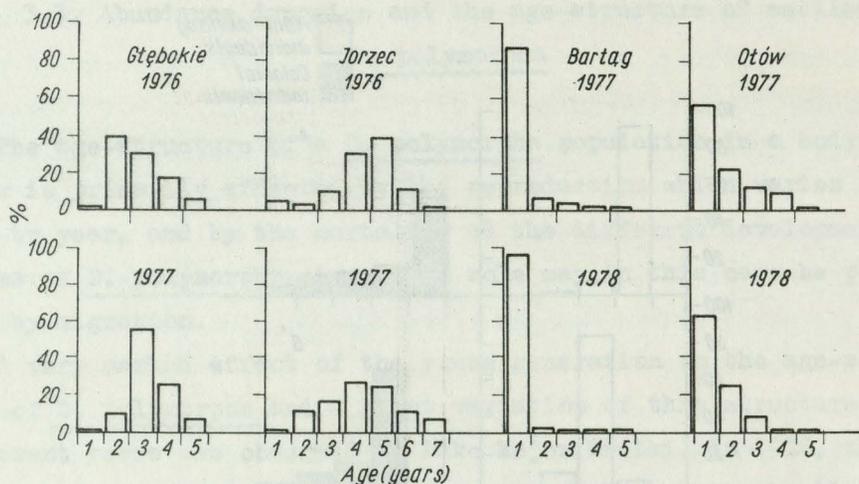


Fig. 10. Age structure of D. polymorpha in four lakes in consecutive years (in June)

tation of the littoral zone was much poorer so there were fewer plant-dwelling D. polymorpha.

A detailed analysis of the dynamics of numbers of settled D. polymorpha was carried out in Lake Czoz. The total abundance showed considerable variations over a relatively short time (Fig. 11), which was due to the numerical proportion of the youngest, just settled individuals, mainly on vegetable substrates. The age-structure of settled colonial and plant-dwelling individuals in different periods was similar to the structures discussed earlier on for other lakes (Fig. 7), that is, in the case of a vegetable substrate before the breeding season of D. polymorpha one year-old individuals positively dominated, and after the breeding season - the current year's individuals, aged from several to over a dozen weeks. A certain deviation from this pattern was found in July, that is, in the middle of the breeding season when the settling had just begun and the current year's individuals were still less numerous than one year old individuals (Fig. 12).

The data obtained from the study make it possible to trace the fate of settled D. polymorpha of the different age groups in

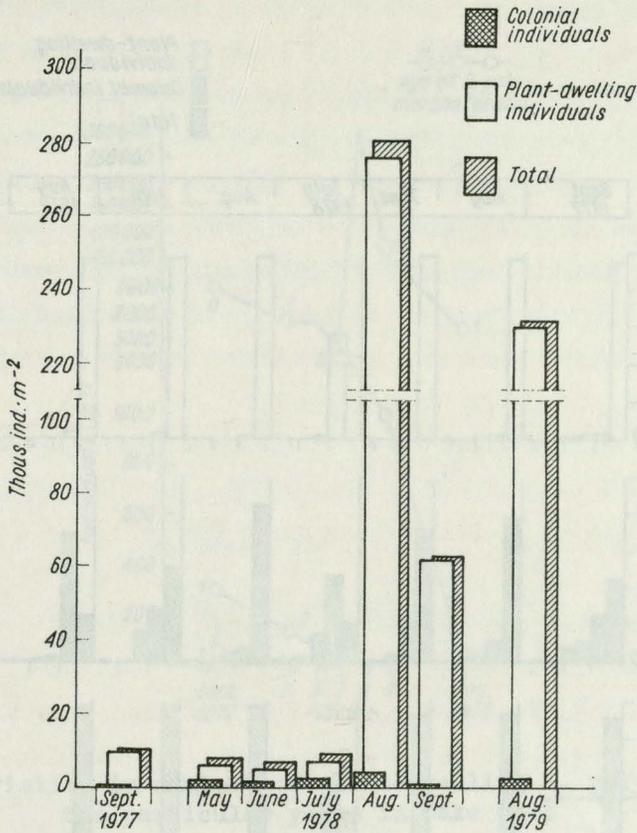


Fig. 11. Dynamics of numbers of colonial and plant-dwelling D. polymorpha in Lake Czos

Lake Czos. Plant-dwelling individuals show an intensive decrease in numbers from year to year. Between September 1977 and September 1978 there occurred a decrease of 89% of individuals almost one year old. Between August 1978, with a high initial density of post-veligers (280 thous. ind. · m⁻² of the littoral), and August 1979 there occurred a 98% fall in numbers, this decrease being very high already in the first month (between August and September 1978 - 78%). A rapid, too, decrease in numbers - often as high as 100% - was observed in the case of older age classes, e.g., between the 1st and 2nd years of life - as was the case in the years 1977-1978 and 1978-1979, or between the 2nd and 3rd life years - as was the case

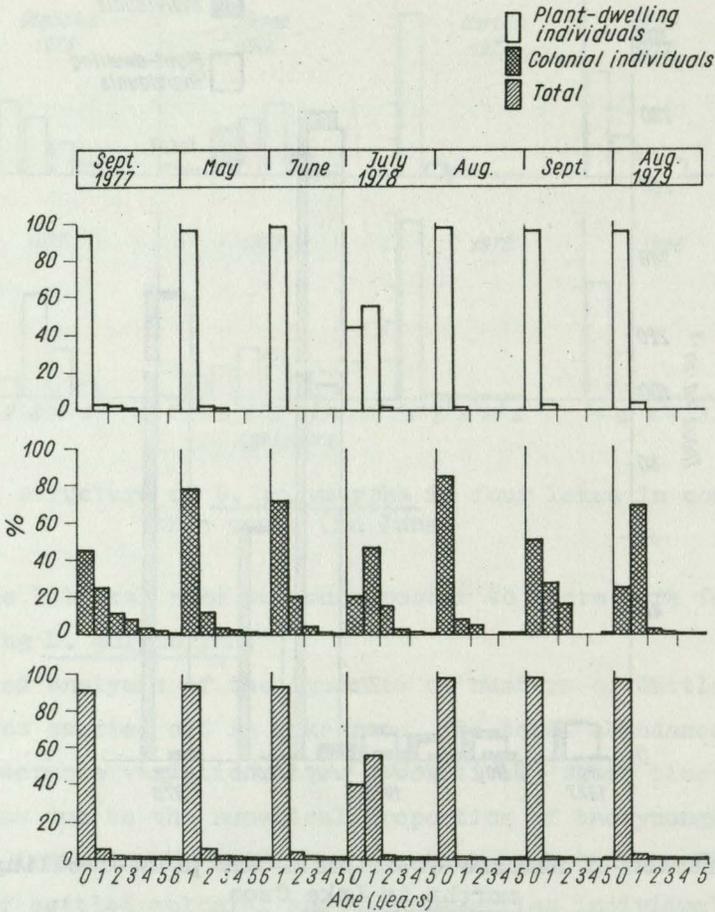


Fig. 12. Age structure of plant-dwelling and colonial *D. polymorpha* in Lake Czos

in the years 1977-1978. On submerged plants individuals aged over 3 years were never encountered (Fig. 13).

A very similar situation was found in Lake Majcz Wielki where 98% of plant-dwelling postveligers that settled in 1978 disappeared within a year. A 100% reduction in numbers on plants is always found to occur between 3rd and 4th year of life, but it was observed also at an earlier stage (between 1st and 2nd year of life) in the case of a very small *D. polymorpha* age group of the same year settling in 1977.

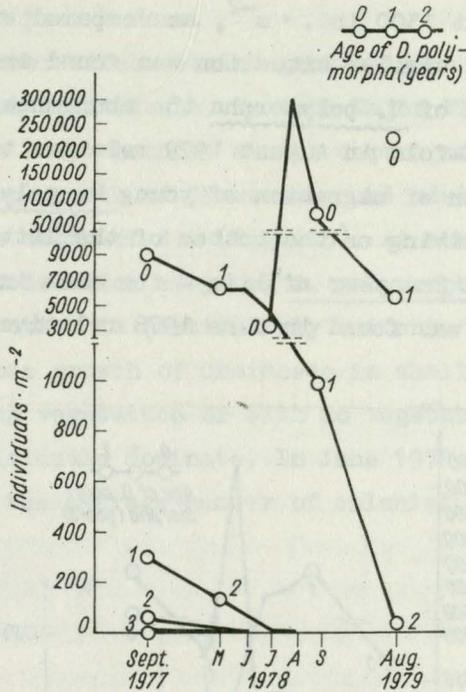


Fig. 13. Variation in numbers of plant-dwelling *D. polymorpha* of the particular years in Lake Czos

In Lake Bartag there occurred a 99% reduction in the number of one and two year old *D. polymorpha*, and a 100% reduction of individuals two and three years old, between June 1977 and June 1978.

A reduction in the number of plant-dwelling *D. polymorpha* is caused primarily by the mass mortality of the youngest individuals, but there is also some migration. Migration, more often passive than active, takes place mostly in the autumn when plant shoots die and break off, especially shoots of annuals, and when those young *D. polymorpha* which fall on to the bottom must look for a new substrate. In such a situation it is the formed *D. polymorpha* colonies on the bottom of the littoral that are most frequently colonized. This was observed, for instance, in Lake Czos where there occurred an increase in the number of one year old individuals within colonies in spring relative to the numbers of 0 class

individuals in autumn the preceding year. In May 1978, the density increased up to about $1300 \text{ ind.} \cdot \text{m}^{-2}$, as compared with $370 \text{ ind.} \cdot \text{m}^{-2}$ in September 1977. A similar situation was found in the case of the successive age class of *D. polymorpha* the abundance of which increased almost three-fold in August 1979 relative to September 1978. This phenomenon of migration of young *D. polymorpha* from plants to colonies living on the bottom of the littoral takes place also between 1st and 2nd year of life - for also in this case an increase in numbers was found in June 1978 relative to September 1977 (Fig. 14).

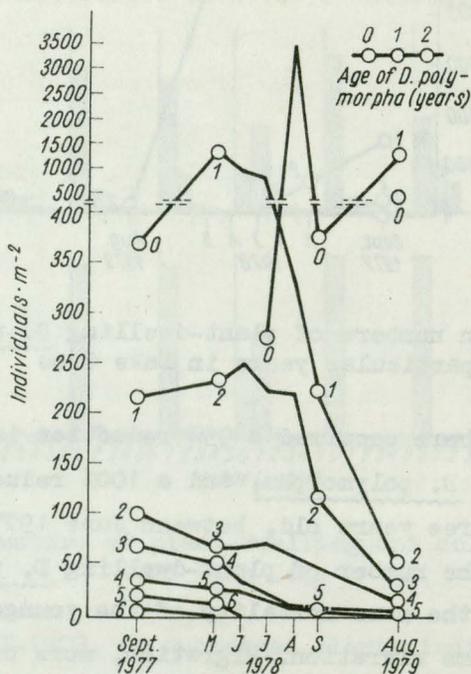


Fig. 14. Variation in numbers of colonial *D. polymorpha* of the particular years in Lake Czos

In Lake Majcz Wielki, as in Lake Czos, in spring a growth in numbers of one year old individuals occurred relative to settled postveligers in the previous year (by 69%), and of two year old individuals (by 14%) relative to one year old individuals in the previous year, and in Lake Bartag where two year old individuals

in colonies were found to be more numerous by 55% than one year old individuals a year before.

In shallower sites settled postveligers are more abundant than adult colonial individuals. In Lake Majcz Wielki, for example, postveligers were most abundant at the depths of 1.0-2.5 m, that is, within a close growth of Characeae, and adult individuals - on the bottom at the depth of 4 m (Fig. 15). At the depth of 4 m in this lake the translocation of young D. polymorpha from plants to colonies on the bottom is particularly evident. This is the border zone between a close growth of Characeae in shallower sites and areas with declining vegetation or with no vegetation at all, and where colonial individuals dominate. In June 1978, in this lake at the depth of 4 m the average number of colonial D. polymorpha was

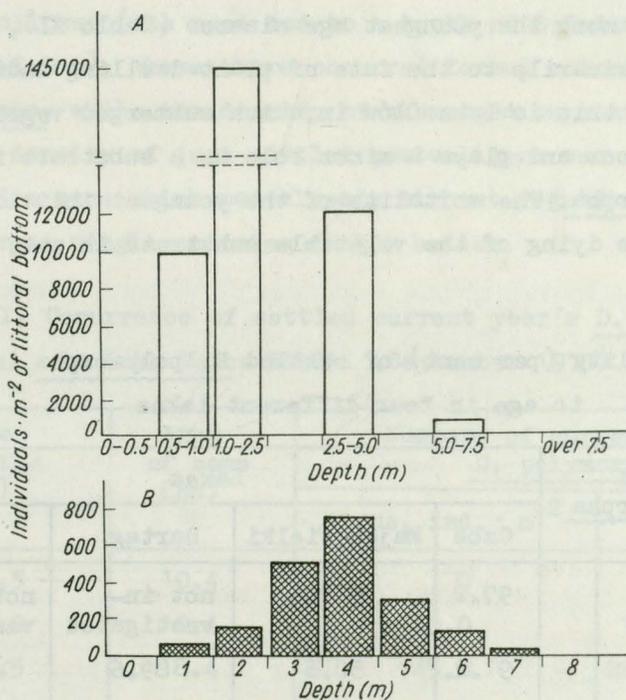


Fig. 15. Occurrence of D. polymorpha at different depths in Lake Majcz Wielki

A - postveligers (September 1978), B - colonial individuals (June 1978)

750 ind. · m⁻². In September, that is, after the termination of breeding and settling the numbers increased to 3300 ind. · m⁻². The next year, but still before the next breeding season (June 1979), the number of colonial D. polymorpha at that depth increased to 8800 ind. · m⁻², that is, by 168% relative to the numbers found in September 1978.

The translocation of young D. polymorpha from plants to colonies is confirmed by a frequent presence of plant remains in the byssuses of one and two year old individuals found within the colonies on the bottom.

Mortality of settled D. polymorpha from year to year can only be discussed by jointly considering changes in the numbers of individual age classes of colonial and plant-dwelling individuals. An analysis of the results obtained shows that there is a very high mortality among the youngest age classes (Table XI), this being related primarily to the fate of plant-dwelling individuals. An exception to this is Lake Ołów in which submerged vegetation is relatively poor and plays a minor role as a substrate for settling D. polymorpha. The mortality of the youngest individuals there due to the dying of the vegetable substrate is not, therefore, so rapid.

Table XI. Mortality (per cent) of settled D. polymorpha in relation to age in four different lakes

Life period of. <u>D. polymorpha</u> (years)	Lakes			
	Czos	Majcz Wielki	Bartag	Ołów
0-1	97.2	96.0	not investigated	not investigated
1-2	91.2	50.6	89.6	37.5
2-3	78.7	28.2	39.5	48.6
3-4	85.0	53.5	25.0	74.2
4-5	84.6	65.6	77.8	86.2
5-6	100.0	100.0	100.0	100.0

In the lakes under study a decrease in mortality is observed when D. polymorpha are at the age of 2-4 years, but it increases again as they grow older, and usually between 5th and 6th year of life it is already 100% (Table XI).

The data collected in 1978 from Lake Majcz Wielki make it possible to estimate the total number of young D. polymorpha which settled that year throughout the lake. Six zones differing in the number of settling postveligers have been distinguished in this lake. Settling postveligers have been found to be absent from two zones: from the shore part of the reed bed (up to a depth of about 0.5 m) and from the profundal part of the lake to a depth of about 7.5 m. The highest numbers of just settled individuals were recorded for the zone of close growth of submerged vegetation, mainly Characeae (depths of 1.0-2.5 m). Much smaller numbers were found in both shallower (the reed bed to a depth of 0.5-1.0 m) and deeper sites (2.5-5.0 m), where there occurred formed colonies of adult D. polymorpha, while the density of submerged vegetation decreased. The lowest density of just settled postveligers was recorded for the 5.0-7.5 m zone which was already without vegetation, and where there occurred single colonies on the bottom.

Table XII. Occurrence of settled current year's D. polymorpha in Lake Majcz Wielki (September 1978)

Zone (depth) (m)	Area of zone (ha)	Numbers of current year's <u>D. polymorpha</u>	
		thous. ind. · m ⁻²	in zone
0-0.5	10.4	0	0
0.5-1.0	10.4	10.0	1.0 · 10 ⁹
1.0-2.5	18.4	145.0	26.7 · 10 ⁹
2.5-5.0	32.3	12.0	3.9 · 10 ⁹
5.0-7.5	31.1	0.6	0.2 · 10 ⁹
Over 7.5	60.9	0	0
Total in lake			31.8 · 10 ⁹

Taking into account the surface areas occupied by these zones in the lake, it has been estimated that on the termination of the breeding season of D. polymorpha (mid-September) there were $31.8 \cdot 10^9$ settled current year's individuals in the whole Lake Majcz Wielki (Table XII).

The initial quantity for this settlement was the total number of planktonic larvae that occurred in the lake during the breeding season of 1978 (L e w a n d o w s k i 1982). The growing season lasted then from 8 June to 27 August 1978 (81 days), and there were each day on an average about 15000 planktonic larvae per 1 m^3 in the epilimnion. Assuming a 10 days' occurrence of larvae in the plankton, the daily production of larvae is estimated at $1500 \text{ ind.} \cdot \text{m}^{-3}$. So the total number of D. polymorpha larvae in the epilimnion of Lake Majcz Wielki (a volume of 6224.6 thous. m^3) in the growing season of 1978 may have amounted to $756.3 \cdot 10^9$ individuals.

Individuals that settled in 1978 represented 4.2% of the above value, so the mortality at the stage of transition from the planktonic to sedentary habits and during the first moments of the sedentary life amounted in Lake Majcz Wielki to 95.8%.

A similar calculation has been made for Lake Kołowin (the volume of the epilimnion - 2843.4 thous. m^3) in which the total number of planktonic larvae in 1978 was approximately $2 \cdot 10^{11}$. The smaller number of larvae than in Lake Majcz Wielki resulted from smaller average numbers of larvae found each day during the breeding season ($14000 \text{ ind.} \cdot \text{m}^{-3}$) and a shorter breeding season which lasted only 50 days (from 22 June to 10 August 1978). Due to this, on the termination of the breeding season of D. polymorpha the average number of current year's individuals in the zone of inhabitancy was only 7500 individuals per 1 m^2 of littoral bottom.

The total number of these individuals in the whole lake in September may thus have been $128 \cdot 10^7$. Such a high mortality, amounting to 99.4%, during the transition to the sedentary life may be accounted for by a low percentage in the lake of a surface suitable

for the colonization by D. polymorpha. In Lake Kołowin the zone suitable to D. polymorpha represents 21.8% of the lake surface area, while in Lake Majcz Wielki it represents as much as 56.4%, and it ends at a smaller depth in the former than in the latter lake. Consequently, there were far fewer planktonic larvae above this zone than in Lake Majcz Wielki.

A mortality higher than in Lake Kołowin was found in Lake Ożów. It was caused, as has been mentioned earlier on, by a very poor zone of submerged vegetation and thereby a smaller, than in Lake Majcz Wielki, and Lake Kołowin, surface suitable to settling postveligers. During 60 days of the breeding season in 1978 there were approximately $81 \cdot 10^9$ larvae in the plankton of Lake Ożów. In the littoral to the depth of 5 m, this representing 22.1% of the lake surface area, a total of about $35 \cdot 10^7$ postveligers settled (an average of $2600 \text{ ind.} \cdot \text{m}^{-2}$). Thus the mortality of D. polymorpha larvae before attaining the stage of postveliger amounted in this lake in 1978 to 99.6%.

4. DISCUSSION

In the relevant literature some data can be found on the settlement of D. polymorpha larvae on various artificial substrates. These data are difficult to compare, because of the different exposure times allowed, but all the investigators who carried out the experiments obtained lower numbers of settled larvae per 1 m^2 than those obtained in this series of experiments with glass substrates, which indicates that glass is a very good substrate for settling larvae. In Lake Majcz Wielki a maximum number of 480 thous. postveligers per 1 m^2 of glass substrate has been found. A similar maximum number - 400 thous. $\text{ind.} \cdot \text{m}^{-2}$ was obtained by L u f e r o v (1965) in Rybinskoe Dam Lake on wooden substrates exposed from May to October. Smaller numbers were recorded when wooden substrates were exposed for about 1 month in Gorkovskoe Dam Lake - a maximum

of 115500 individuals per 1 m^2 was recorded, in most cases less than $10000 \text{ ind.} \cdot \text{m}^{-2}$ (S k a l s k a j a 1976). In the Dnepr-Kri-voj Rog Canal glass substrates were used on which over $30000 \text{ ind.} \cdot \text{m}^{-2}$, at the most, settled during a 10 days' period in July (Š e v c o v a 1968).

On asbestos substrates, used in a dam lake near London, a maximum of less than $2000 \text{ ind.} \cdot \text{m}^{-2}$ settled (M o r t o n 1969). A comparative analysis, from the point of view of hydraulic engineering, of the vulnerability of substrates of different kind to the settlement of D. polymorpha larvae has been made by W a l z (1973) in Lake Constance. Iron and PVC have proved to be the best for D. polymorpha. On plates ($10 \times 10 \text{ cm}$) made of these materials over 1000 postveligers settled, that is, up to about $160000 \text{ ind.} \cdot \text{m}^{-2}$. On each plate of plexiglass, concrete, aluminium and zinc several hundred larvae settled, and the least suitable to the settling larvae proved to be copper and brass plates, on each of which as few as several individuals settled. D. polymorpha showed some selectivity also with regard to plates of different varieties of PVC (W a l z 1975).

Steelon nets have also been used as a substrate for settling D. polymorpha larvae (S z l a u e r 1974). Curtains made of such nets were placed in a water course to protect hydrotechnical installations. About 5 million individuals, that is, 200 thous. individuals per 1 m^2 of net settled on a 26 m^2 curtain.

A detailed analysis of the size of D. polymorpha larvae passing from the planktonic to sedentary habits in Lake Majcz Wielki has shown that most of the larvae settled at a body-length of over $200 \mu\text{m}$, but among larvae attached to a substrate individuals measuring $140 \mu\text{m}$ and even less could also be encountered (Fig. 3). Statements in the literature always say that settling D. polymorpha larvae are over $200 \mu\text{m}$ long (K i r p i č e n k o 1962, 1965, W i k t o r 1969, S z l a u e r 1974, D y g a and L u b j a n o v 1975 and others). In the Cimiljanskoe Dam Lake most individuals settled at body-lengths of 225-250 and even $255 \mu\text{m}$ (K i r-

p i ě e n k o 1971c). Only in the Kujbyševskoe Dam Lake were smaller individuals found among settled D. polymorpha, but they always measured over 175 μm (K i r p i ě e n k o 1964), that is to say, more than those in Lake Majcz Wielki.

The settling of larvae appears to be spread throughout the growing season, due to which late in the autumn, at the end of the growing season the body-size dispersion of current year's D. polymorpha is very big. In Lake Majcz Wielki it ranged from 0.5 to 12 mm. This has also been pointed by other authors. For instance, in a canal extending from the lower Odra river current year's D. polymorpha were from 1 to 14 mm long (S z l a u e r 1974), in the Cimiljanskoe Dam Lake - from 0.3 to 15 mm (K i r p i ě e n k o 1971c), and the Kujbyševskoe Dam Lake - from 0.2 to 16 mm (K i r p i ě e n k o 1971a).

The occurrence of D. polymorpha on plants is a problem that has hardly ever been dealt with in the literature. Investigations carried out during the present research have shown unequivocally that the occurrence is of a mass nature. On the one hand in most of the lakes under study plant-dwelling D. polymorpha represented over 85% of a whole population (Fig. 6), and on the other hand - the number of individuals settled on the vegetation covering 1 m² of the littoral was often higher than the number of D. polymorpha settled directly on the bottom (in form of colonies), and many a time they exceeded 100 thous. individuals (Table IV). Considerable differences have been revealed when comparing the colonization by D. polymorpha of different plant species, and of annuals and perennials in particular. D. polymorpha that settled on submerged vegetation were characterized by a specific age-structure which consisted only of the youngest individuals. This pattern of distribution of D. polymorpha on plants appears to be typical of most of the lakes investigated during the present study.

Some investigators restrict their reports to the statement that D. polymorpha do occur on plants (e.g., W i k t o r 1969, K o n s t a n t i n o v and S p i r i d o n o v 1977), and some-

times also that the number of young D. polymorpha on plants is very large (K a č a n o v a 1961, 1963, 1965, D y g a and L u b j a n o v 1975), but there have been hardly any more specific numerical data, and the possible mechanisms and factors affecting plant-dwelling D. polymorpha have been ignored completely. This is probably connected with the fact that the settlement on plants concerns mainly the current year's D. polymorpha, that is, the smallest ones, already from a body-length of about 200 μm . According to K o r n o b i s (1977), a precise determination of the numbers of this class by the methods used frequently is practically impossible. M o r t o n (1969) observed current year's individuals only in September when they were already about 6 mm long.

Certain numerical data, though not considering the smallest postveligers and thereby difficult to interpret, have been reported in papers on plant-associated fauna. In Lake Druzno, for example, the highest density of D. polymorpha has been found on Myriophyllum spicatum (L.) - about 800 individuals per 1 m^3 of space filled with vegetation. In this lake D. polymorpha occurred also on Ceratophyllum demersum (L.) (about 600 ind. $\cdot \text{m}^{-3}$), Stratiotes aloides (L.) (about 400 ind. $\cdot \text{m}^{-3}$) and on Potamogeton crispus (L.) (several ind. $\cdot \text{m}^{-3}$) (K a r a s s o w s k a and M i k u l s k i 1960). Of similar nature are the data on the occurrence of Bivalvia (mainly D. polymorpha, but also Pisidium sp.) on submerged macrophytes of the Mikołajskie Lake (S o s z k a 1975) where an average of 78 individuals (up to about 1700) were found on 1 m^2 of littoral surface, and an average of 11 individuals (up to about 200) per 100 g of plant weight.

The only more detailed data on this subject have been reported by M i c h e e v (1969) for the Pljalovskoe Dam Lake. He found the largest number of settled plant-dwelling D. polymorpha in September-October. D. polymorpha abundantly colonized plants directed towards open parts of the water body: for example he found about 28000 individuals per 1 kg of Myriophyllum spicatum and about 11000 D. polymorpha per 1 kg of reed.

Of other substrates accessible to settling D. polymorpha larvae in the littoral it is the formed adult D. polymorpha colonies that are readily colonized, as indicated by the results of the present investigations and by numerous data in the literature (Walz 1973, Kirpičenko and Antonov 1977, Kornobis 1977 and others). Earlier studies (Lewandowski 1976) indicate that young D. polymorpha settle more readily on formed colonies of their species than on empty shells and stones of a similar size. D. polymorpha find a very convenient substrate for settling on submerged bushes and trees which are particularly abundant in dam lakes found in the European part of the Soviet Union. Mass occurrence of D. polymorpha on such substrates has been found, for instance, in the Kamskoe Dam Lake (Gromov 1965), in the Stalingradskoe Dam Lake (later on named Volgogradskoe) (Ljachov 1961, Beljavskaja 1965, Konstantinov and Spiridonov 1977) and in many others (Lufarov 1966, Kirpičenko and Antonov 1977). Substrates of this kind can be found, if on a much smaller scale, also in lakes, where they are represented primarily by fallen tree trunks, broken branches, e.g., in the Szymbarskie Lake (Orzechowski 1966).

It seems that the size of a postveliger population settled on a substrate depends to a very large extent on the degree of substrate complexity, that is, the real surface accessible to settling postveligers. Larger numbers were found, for instance, on plants such as Ceratophyllum demersum and Fontinalis antipyretica, and lower on Elodea canadensis and on reed stalks. A similar interpretation can be given to the results of the experiments concerned with the settling of larvae on different natural substrates. The density of postveligers increased with the growing complexity of substrates: from sand and mud through stones and D. polymorpha colonies to plants. Similar observations have been made also with regard to other invertebrates. Fischer (1964), for example, found considerable differences in the number of Odonata (Lestes),

depending on the architectonics of the plants on which they occurred, whereas D u s o g e (1966) observed higher densities of Hirudinea, Asellus aquaticus (L.) and Ephemeroptera larvae on D. polymorpha colonies than on stones.

The age-structure of sedentary D. polymorpha in various bodies of water is very rarely analysed. The age-structures reported by different authors very much resemble the results of the present study if they relate only to colonial individuals (Figs. 7, 10 - Lake Jorzec and Głębokie Lake). It seems that such a picture of the age-structure of D. polymorpha populations in different lakes in most cases results on the one hand from the fact that the youngest current year's individuals are ignored, and on the other hand from the fact that plant-dwelling individuals are ignored, the latter cause being related to the former one. In the Lagoon of Szczecin, for instance, current year's individuals represented on an average 2.2% of close communities of D. polymorpha, outside the zone of submerged vegetation, while one year old individuals represented 39%, current year's individuals being taken into account only from a body-length of 2 mm on (W i k t o r 1969). In Lake Crapina (flood plain of the Danube) individuals aged 2-3 years dominated among sedentary D. polymorpha (F l o r e s c u 1970). This author relates the low density of the youngest age classes to the feeding of fish. Likewise, 2-3 year old D. polymorpha dominated in the Volgogradskoe Lake (S p i r i d o n o v 1975).

Some authors analyse D. polymorpha populations for body-size and not for age. With some approximation made, body-size can be referred to the age of individuals, and then also low numbers of the youngest individuals are found. In the Szymbarskie Lake individuals representing size classes of 10-20 mm and 20-30 mm positively dominated (O r z e c h o w s k i 1966). This author relates the very low proportion of smaller individuals to the mortality and variation of numbers of D. polymorpha in the different years.

It was probably due to the ignoring of the smallest settled individuals of D. polymorpha in the dam lake near London that the

proportion of current year's individuals in the population on the termination of breeding in the autumn of 1967 was very small, and increased only the next year, but already as the proportion of one year old individuals (Morton 1969); this resembles the situation found in the present series connected with an increase in numbers of one year old individuals in colonies due to the migration of plant-dwelling D. polymorpha, but in his studies Morton (1969) did not take into account individuals less than 4 mm in body-length.

On the basis of an age-structure determined once only some authors determine the mortality of D. polymorpha from year to year at the transition from one age class to another. Wiktor (1969), for instance, analysed this problem in the Lagoon of Szczecin by assuming that the yearly recruitment of the D. polymorpha population in this water body is a constant quantity and that the population is in a biological equilibrium. In his considerations the last-cited author does not take into account current year's individuals, because at the time of investigations the process of settling was not yet terminated. The initial value is the number of one year old individuals. Wiktor's data (1969) on mortality very much resemble the situation found during the present series in Lake Ołóż (Table XI), where the littoral vegetation is very poor and D. polymorpha virtually occur only in colonies. In the Lagoon of Szczecin, where only colonial individuals were analysed, it has been found that mortality is at its lowest between 1st and 2nd year of life (10.9%), being higher between 2nd and 3rd (55.8%) and 3rd and 4th (50.1%) years of life, and the highest between 4th and 5th (83.7%) and 5th and 6th years of life when all the remaining individuals die (100%).

The mortality of the youngest D. polymorpha that settled on experimental plates in Lake Constance was determined by Walz (1975). Between 10 October 1973 (the largest number of current year's individuals) and 10 April 1974 the mortality on the under side of plates placed at a depth of 5 m was, according to the above-

-quoted author, 95%, and on the upper side - 43%. As it is difficult in this case to speak only of mortality, because there may have taken place some migration (sets of plates were arranged on large base-plates), and some individuals may have come off the plates, which has been mentioned earlier on. It is for this reason, that such calculations have not been made in this study. It may be stated, merely for the purpose of comparison with W a l z ' s (1975) data, that in Lake Majcz Wielki the loss of young D. polymorpha on experimental plates between 20 July 1978 and 29 May 1979 (Table II) on the upper side was similar to that on the under side and amounted to 94-95%.

On the basis of the results from the present investigations and data in the literature it is possible to trace the particular life stages of D. polymorpha, considering them from the point of view of the formation of populations of this mussel species in lakes.

D. polymorpha is characterized by a very high fecundity - 30-40 thous. eggs were found in mature females (K a r p e v i č 1955, G i l j a r o v 1970, and others).

Nothing is known about the mortality of eggs, that is, at the earliest stage of ontogenic life. We do not know what percentage of eggs in the water are not fertilized, what biocoenotic or other factors may cause death at this stage, etc.

The next stage at which part of the individuals are eliminated is the planktonic stage. Planktonic larvae may become a food item for some fish species and some invertebrates. W i k t o r (1958) found D. polymorpha larvae in the alimentary tracts of the European smelts (Osmerus eperlanus L.), perch-pike (Lucioperca lucioperca L.), ruff (Acerina cernua L.) and the roach (Rutilus rutilus L.), up to 65 individuals in one alimentary tract. G r i g o r a š (1963) found up to 125 larvae in the alimentary tracts of the roach. The use of this food item by the fry may vary considerably, depending on the density of the larvae in the plankton, on the season and on the intensity of fish reproduction, and in most cases it lasts for a relatively short time (in the Lagoon of Szczecin, e.g., - 2-4 weeks) and concerns only a specific size class of fry, mostly those above a

dozen mm long (W i k t o r 1958). Among invertebrates some species of Cyclopidae may feed on planktonic larvae of D. polymorpha (K a r a b i n 1978) and so may some filtering organisms such as adult D. polymorpha (M i c h e e v 1967).

The occurrence in the bottom sediments of Lake Majcz Wielki of empty shells of typically planktonic larvae indicates that at this stage there also occurs natural mortality not caused by biocoenotic factors. Environmental factors that may cause a reduction in numbers of the larvae include water pollution (this applying to all age classes of D. polymorpha) (D y g a and L u b j a n o v 1972), mechanical destruction of larvae, e.g., during their passage through technical installations (J a r o š e n k o and N a b e r e ž n y j 1971), or the carrying away of larvae by tidal waves (W i k t o r 1969, K i r p i č e n k o 1971b and others). It seems, however, that the mortality of D. polymorpha at this developmental stage is relatively low. When determining the reproductive potential of D. polymorpha populations on the basis of literature data on the average number of eggs in females from which the actual numbers of planktonic larvae were subtracted, W i k t o r (1969) and S t a n c z y k o w s k a (1977) have established that in two completely different types of environment (a coastal lagoon and a lake) the reduction at this stage amounted to about 20% and was caused primarily by biocoenotic conditions.

A critical moment in the life of D. polymorpha is the transition from the planktonic to the sedentary habits. The very high mortality at this stage is caused mainly by environmental conditions the most important of which is the lack of a suitable substrate for settling. As indicated by the present investigations, only a per cent fraction (0.4% - Lake Ożów, 0.6% - Lake Kołowin), and in the case of a large littoral rich in suitable substrates only several per cent (4.2% - Lake Majcz Wielki) of settling larvae find a suitable substrate and thus the possibility to undergo further development. Those of them which happen to settle on a bad substrate (mud, sand) or fall into the profundal where there are in addition bad

oxygen conditions need not die at once. This is indicated by the results of an experiment during which postveligers vegetated for several months on sand and mud (Tables III, X), and by the range of body size of dead individuals found in the profundal, showing clearly that growth in length had continued for some time. This finding is confirmed by data found in the literature. K i r p i ě e n k o (1971c), for example, analysed the growth of settled postveligers lowered to various depths in the Cimiljanskoe Lake. To the depth of 18 m he observed at first a clear growth in size of the individuals and only after 14 days did their dying begin. Likewise, in Lake Constance to the depth of 60 m W a l z (1975) observed a decrease in numbers, progressing with time, of postveligers settled earlier, and only after several months did mortality on experimental plates attain the level of 100%.

It is thus only the small proportion of larvae which have found themselves on suitable substrates that have the chance to survive. The subsequent fate of settled postveligers depends to a large extent on the kind of the substrate. Two basic types can be distinguished among substrates suitable for the settling larvae. One of the types is a positively good substrate on which individuals that have settled can occur throughout their life. It is represented primarily by formed colonies of D. polymorpha and to a lesser extent by stones, living mussels of the Unionidae family (L e w a n d o w s k i 1976), empty shells of molluscs, etc. The other type represents substrates which are also very good for settling, but by contrast to the former type they are short-lived, i.e., their duration is shorter than the life span of D. polymorpha. This type includes aquatic vegetation. However, even on the best substrates (D. polymorpha colonies, plants, glass plates) a certain relatively small percentage of postveligers can be found to have died within a short time after settling (Tables IX, X). According to K i r p i ě e n k o (1971a), it is at this stage of ontogenic life that the weak and poorly developed individuals die. For the transition from the planktonic to the sedentary habits is connected with metamorphosis, that is, with a consid-

erable reconstruction of many organs and body systems of the individuals. It is at the first moments of life that any developmental anomalies may become conspicuous (K i r p i ě e n k o 1971a).

In the Masurian lakes most D. polymorpha larvae settle on submerged plants. The initial conditions which are very good for settling postveligers are followed by a high rate mortality of these individuals. This is caused primarily by environmental conditions - dying of the existing substrate and the necessity to look for a new one. Mass mortality of D. polymorpha affects first of all individuals settled on annuals, because these plants decompose in the autumn. Less rapid, but also intense is the dying of D. polymorpha on perennials on which individuals older than 3 years are not found. Apart from the breaking-off and dying of the macrophytes themselves, there may be a strong mortality-causing effect on D. polymorpha of periphytic filamentous algae attached to macrophytes. Such a situation was found in Lake Czoz, for instance, where submerged plants were covered with a thick layer of algae to which settling postveligers attached. The death of the algae between August and September caused a very rapid death of plant-dwelling D. polymorpha (Fig. 11). The possibility, mentioned by K a ě a n o v a (1961), that sedentary individuals may return to the plankton when the original substrate decomposes seems to be debatable. Such a return would only be possible in the case of the smallest settled postveligers (Fig. 3), which are, however, very few in number when the vegetable substrate disintegrates; most of the postveligers will have exceeded 250 μm by then, that is, a body size that makes their return to the planktonic habits impossible (Fig. 4).

Apart from environmental conditions, mortality of D. polymorpha settled on plants may to some extent result also from biocoenotic factors. In this case an important role may be played by fish species feeding directly on D. polymorpha (mainly the roach). According to M i c h e e v (1969), young D. polymorpha which live on plants are more accessible to fish than are individuals strongly connected with colonies. Small postveligers can by chance be eaten by organisms

feeding on periphyton (e.g., Gastropoda) and plants (e.g., of fishes - the rudd, Scardinius erythrophthalmus L., of birds - the swan, Cygnus olor Gm. and others). Not only the eating, but also a mechanical knocking of young D. polymorpha off plants on to a sandy or muddy substrate can reduce their numbers. During its feeding the snail, Radix ovata (Draparnaud), for instance, destroys about half the available periphyton which when separated from the substrate falls on to the bottom (P i e c z y ń s k a 1970). Some of the young D. polymorpha that fall off plants and on to the bottom do not die, as has already been mentioned, but principally join already formed D. polymorpha colonies. In general, however, young (up to 3 years) D. polymorpha settled on plants die in large numbers. At that stage the mortality from year to year usually exceeds 90%.

Responsible for mortality within formed colonies can be mainly biocoenotic factors. D. polymorpha is the food item of some fish (roach, Rutilus rutilus L., bream, Abramis brama L. and others) (P l i s z k a 1953, K o n d r a t e v 1958, N e b o l s i n a 1962, 1965, M e j s n e r and M i c h e e v 1965, M e j s n e r 1966, M i c h e e v 1966, 1974, O l s z e w s k i 1978 and others) and birds (chiefly the coot, Fulica atra L.) (L e u z i n g e r and S c h u s t e r 1970, S t e m p n i e w i c z 1974, W i ś n i e w s k i 1974, B o r o w i e c 1975 and others), as well as of crayfishes (Orconectes limosus Raf.) (P i e s i k 1974, S z l a u e r 1974). The mortality of the youngest classes (0-2 years), to some extent blurred by the recruitment of individuals that leave plants, is comparatively small as is that of the middle-aged classes (2-4 years) (Table XI, W i k t o r 1969). It is only in older age classes that the death rate clearly increases. In the latter case the cause, in addition to the ageing of individuals, may also be, especially in large colonies, a limited supply of food and oxygen to older individuals which are in the deepest layers of the colonies (M i c h e e v 1969).

Numerous data found in the literature and the author's own findings indicate that D. polymorpha colonies are very variable. Dif-

ferences were found in numbers, age-structure, etc. between water bodies that often were interconnected and formed one complex, between years in the same water body, and even between sites of the same water body, that is differences in time and space. This variable picture of D. polymorpha populations in different ecological situations results from the effect of a whole complex of factors affecting mainly the early developmental stages of this mussel. A significant role is played by the initial density of a population and its age-structure, due to which the production of planktonic larvae may vary. Planktonic larvae present in the epilimnion will be subject to the action primarily of water currents and atmospheric conditions: temperature and directions and force of winds. Water movement caused by winds, for instance, may have a decisive effect on the survival rate of larvae passing to the sedentary habits, as a result of finding themselves over an area that is suitable or unsuitable for their settlement. This will depend also on the lake morphometry, and especially on the surface area and nature of the littoral, on the presence of vegetation in it, on the species-composition of the vegetation, on the presence or absence of other substrates and on other factors.

An analysis, made during this study, of the death rate of D. polymorpha at different stages of life has shown that in most Masurian lakes two moments critical for the formation of a population can be distinguished. The first moment is the transition of planktonic larvae to the sedentary habits when the survival rate is often equal to a per cent fraction and at its maximum to several per cent. The picture of this process seems to be similar in all bodies of water. The second critical moment is the high mortality of postveligers settled on plants. Only several per cent of settled postveligers in a lake survive the first year of life. This applies to those lakes the littoral zone of which is covered with submerged vegetation, this being typical of most Masurian lakes. This factor, affecting the formation of a D. polymorpha population in lakes, does not occur in dam lakes where there are more permanent than

vegetable substrates, and it is most probable that owing to the absence of the second critical moment in the life of D. polymorpha in dam lakes, the abundance of this species in them is much greater than in ordinary lakes.

ACKNOWLEDGMENTS: I wish to express my cordial thanks to Ass. Prof. A. Stańczykowska for guidance during the investigations. My thanks are extended also to J. Ejsmont-Karabin, M.Sc., for help with the collecting and preparation of the planktonic material. I am indebted to my colleagues in the Department of Hydrobiology, Institute of Ecology, Polish Academy of Sciences, for critical comments during the preparation of the manuscript.

5. SUMMARY

In the years 1976-1979 investigations of sedentary Dreissena polymorpha were carried out in 26 Masurian lakes. The intensity of the investigations varied. To determine changes against time, in several lakes samples were collected at the same station for 2-4 consecutive years, and in Lake Czoz - every month throughout the growing season (1978). To determine the numbers in a new D. polymorpha generation, a detailed analysis of the occurrence of sedentary individuals was made twice during the year: before the beginning and after the termination of the breeding season in 3 lakes (Majcz Wielki, Kołowin and Ożów). Apart from this, in Lake Majcz Wielki in the years 1977, 1978 field experiments were carried out to study the settlement of D. polymorpha larvae on natural and artificial substrates.

The generalized results are as follows:

1. Larvae passing from the planktonic to the sedentary habits settle most readily on submerged vegetation (Table III). Larvae settle on annuals at a different rate than on perennials, the rate of their settling on plants varies also from species to species,

depending among other things on the structure (architectonics) of plants (Tables V, VI). Settlement on formed D. polymorpha colonies and on stones is less intense, sand and mud being entirely unsuitable as substrates (Table III).

2. In the majority of the lakes under study plant-dwelling D. polymorpha represented over 85% of the population (Fig. 6), and the densities of individuals settled on the vegetation covering 1 m² of the littoral were many times higher than the density of those that settled directly on the bottom (in colonies), and many a time they exceeded 100 thous. individuals (Table IV).

3. Due to the spreading of the breeding of D. polymorpha in time and the settling of larvae in the growing season, the range of body-lengths of current year's individuals is very wide and may amount to over a dozen millimetres (Fig. 4).

4. D. polymorpha settled on plants and colonial D. polymorpha differ completely in their age-structure. On plants, only the youngest - mainly current year's and one year old individuals are found, and at the most (sporadically) - 3 year old ones. In colonies, all age classes, that is, until 5th-6th year of life, occur, middle-aged individuals usually dominating (Figs. 7, 9, 12, Table VII).

5. After the death of plants the young D. polymorpha that settled on them eventually join, due to a passive and active translocation, colonies of this species formed on the lake bottom of the littoral zone (Fig. 14).

6. Two moments critical to the formation of a population and connected with mortality are distinguished in most lakes. The first moment is the transition from the planktonic to the sedentary habits when over 99% of individuals may die. Only a per cent fraction and at the most several per cent of settling individuals find a suitable substrate. The second critical moment is connected with the mortality of postveligers settled on submerged vegetation - only several per cent of settled postveligers in a lake survive till the end of the first year of their life. Due to the effect of ecological conditions which are different in each lake and year, and

act on the early developmental stages of D. polymorpha at the two critical moments, the picture of the different populations of this mussel species shows a great variation.

6. POLISH SUMMARY

W latach 1976-1979 w 26 jeziorach mazurskich prowadzono badania nad występowaniem osiadłych Dreissena polymorpha. Badania prowadzono z różną intensywnością. Dla uchwycenia zmian w czasie w kilku jeziorach próby pobierano na tych samych stanowiskach przez 2-4 kolejne lata, a w jeziorze Czoz - co miesiąc w okresie sezonu wegetacyjnego (1978 r.). W celu określenia liczebności nowego pokolenia D. polymorpha szczegółową analizę występowania osiadłych osobników przeprowadzono dwukrotnie w ciągu roku: przed rozpoczęciem i po zakończeniu sezonu rozrodczego w 3 jeziorach (Majcz Wielki, Kołowin, Oźów). Ponadto w jeziorze Majcz Wielki w latach 1977-1978 w eksperymentach terenowych (rys. 1, 2) badano osiedlanie się larw D. polymorpha na podłożach naturalnych i sztucznych.

Ogólne wyniki przedstawiają się następująco:

1. Larwy przechodzące z planktonowego do osiadłego trybu życia najintensywniej osiedlają się na roślinności zanurzonej (tab. III). Intensywność tego procesu jest różna w przypadku roślin jednorocznych i wieloletnich, w przypadku różnych gatunków roślin i zależy m.in. od struktury (architektoniki) roślin (tab. V, VI). W mniejszym stopniu larwy osiedlają się na ukształtowanych koloniach D. polymorpha i na kamieniach, a podłożem zupełnie nieodpowiednim jest piasek i muł (tab. III).

2. W większości badanych jezior naroślinne D. polymorpha stanowiły ponad 85% liczebności całej populacji (rys. 6), a liczebności osobników osiadłych na roślinności porastającej 1 m² litoralu były wielokrotnie wyższe od liczebności D. polymorpha osiadłych bezpośrednio na dnie (w formie kolonii) i niejednokrotnie przekraczały 100 tys. osobników (tab. IV).

3. Rozciągnięcie w czasie rozrodu D. polymorpha i procesów osiadania larw w sezonie sprawia, że pod koniec okresu wegetacyjnego rozpiętość długości tegorocznych osobników jest bardzo duża i wynosić może kilkanaście milimetrów (rys. 4).

4. D. polymorpha osiadłe na roślinach i D. polymorpha kolonijne charakteryzują się zupełnie różną strukturą wiekową. Na roślinach występują tylko najmłodsze osobniki - głównie tegoroczne i jedno-roczone, a najwyżej (sporadycznie) - 3-letnie. W koloniach natomiast występują wszystkie klasy wiekowe, czyli do 5-6 roku życia, a dominują zwykle osobniki w średnim wieku (rys. 7, 9, 12, tab. VII).

5. Młode D. polymorpha osiadłe na roślinach, po ich obumarciu na skutek biernego i czynnego przemieszczania się zasilają z czasem ukształtowane kolonie występujące na dnie strefy litoralnej (rys. 14).

6. W większości jezior można wyróżnić dwa momenty krytyczne dla kształtowania się populacji, związane ze śmiertelnością. Moment pierwszy to przechodzenie z planktonowego do osiadłego trybu życia, kiedy może ginąć do ponad 99% osobników. Tylko ułamek procenta, a maksymalnie kilka procent osiadających osobników znajduje odpowiednie podłoże. Drugi moment krytyczny jest związany ze śmiertelnością postveligerów osiadłych na roślinności zanurzonej - do pierwszego roku życia przeżywa zaledwie kilka procent w stosunku do postveligerów osiadłych w jeziorze. Różnorodność warunków ekologicznych w różnych jeziorach i w różnych latach wpływająca na wczesne stadia rozwojowe D. polymorpha w obu momentach krytycznych powoduje bardzo zmienny obraz różnych populacji tego małża.

7. REFERENCES

1. B e l j a v s k a j a L. I. 1965 - Donnaja fauna Volgogradskogo vodochranilišča v 1959-1964 gg - Trudy saratov. Otd. gos. nauč.-isled. Inst. reč. ozer. ryb. Choz. 8: 62-76.
2. B ø h l e B. 1971 - Settlement of mussel larvae Mytilus edulis on suspended collectors in Norwegian waters (In: Fourth European

- Marine Biology Symposium, Ed. D. J. Crisp) - University Press, Cambridge, 63-69.
3. B o r o w i e c E. 1975 - Food of the coot (Fulica atra L.) in different phenological periods - Pol. Arch. Hydrobiol. 22: 157-166.
 4. C r o w l e y T. E. 1957 - Age determination in Anodonta - J. Conch. 24: 201-207.
 5. D u s o g e K. 1966 - Composition and interrelations between macrofauna living on stones in the littoral of Mikołajskie Lake - Ekol. pol. A, 14: 755-762.
 6. D y g a A. K., L u b j a n o v I. P. 1972 - Drejsseny i ich ličinki - indikatory zagraznenija vodoemov (In: Teoria i praktika biologičeskogo samoočišćenija zagraznennyh vod) - Izd. Nauka, Moskva, 164-166.
 7. D y g a A. K., L u b j a n o v I. P. 1975 - Biologičeskie osobennosti drejsseny Zaporožskogo vodochranilišča - Techn. Hidrobiol. 16: 40-52.
 8. F i s c h e r Z. 1964 - Cycle vital de certaines espèces de libellules du genre Lestes dans les petits bassins astatiques - Pol. Arch. Hydrobiol. 12: 349-382.
 9. F l o r e s c u M. 1970 - Aspecte ale donamicii populatiei de Dreissena polymorpha Pall. din Balta Crapina (zona inundabila a Dunari) - Comunicari Hidrobiol. 67-73.
 10. G i l j a r o v M. S. 1970 - Sposoby rasslenija i tipy razvitija presnovodnyh dvustvorčatych molljuskov (Bivalvia) - Zool. Ž. 49: 621-634.
 11. G r i g o r a š V. A. 1963 - Sutočnoj ritm pitaniya ličinek plotvy na rannich etapach razvitija (In: Učinskoe i Možajskoe vodochranilišča, Ed. N. J. Sokolova) - Izd. Moskovskogo Univ., Moskva, 235-261.
 12. G r o m o v V. V. 1965 - Rasprastranenie Dreissena polymorpha Pall. v Sylvenskom zalive Kamskogo vodochranilišča v 1963 godu - Zool. Ž. 44: 1084-1086.

13. J a r o š e n k o M. F., N a b e r e ž n y j A. I. 1971 - K biologii Dreissena polymorpha Pallas v Kučurganskom limane-ochladitele MGRES - Biol. Res. Vodoem. Moldavii, 8: 31-41.
14. K a č a n o v a A. A. 1961 - Nekotorye dannye o razmnoženii Dreissena polymorpha Pallas v Učinskem vodochranilišče - Trudy vses. gidrobiol. Obšč. 11: 117-121.
15. K a č a n o v a A. A. 1963 - O roste Dreissena polymorpha Pallas v Učinskem vodochranilišče i kanalach Mosvodoprovoda (In: Učinskoe i Možajskoe vodochranilišča, Ed. N. J. Sokolova) - Izd. Moskovskogo Univ., Moskva, 226-234.
16. K a č a n o v a A. A. 1965 - Drejssena Učinskogo vodochranilišča i vodoemov vostočnoj očiščnoj stancii Mosvodoprovoda (In: Soveščanie po biologii drejsseny i zaščite gidrotehničeskich sooruzenij ot ee obrastanij, Ed. N. A. Dzjuban) - Akademia Nauk SSSR, Inst. Biol. vnutr. Vod, Volžskaja GES im. V. I. Lenina, Toljatti, 16-17.
17. K a r a b i n A. 1978 - The pressure of pelagic predators of the genus Mesocyclops (Copepoda, Crustacea) on small zooplankton - Ekol. pol. 26: 241-257.
18. K a r a s s o w s k a K., M i k u l s k i J. S. 1960 - Studia nad zbiorowiskami zwierzęcymi roślinności zanurzonej i pływającej jeziora Druzno [Studies on animal communities associated with submerged and pleustonic vegetation in Lake Druzno] - Ekol. pol. A, 8: 335-353.
19. K a r p e v i č A. F. 1955 - Nekotorye dannye o formoobrazovanii u dvustvorčatych molljuskov - Zool. Ž. 34: 46-67.
20. K i r p i č e n k o M. J. 1962 - Izučenie biologii molljuska Dreissena polymorpha Pallas v Kujbyševskom vodochranilišče - Trudy zonalnogo soveščanija po tipologii i biologičeskomu obosnovaniju rybochozjajstvennogo ispolzovanija vnutrennych (presnovodnych) vodoemov južnoj zony SSSR, Izd. Štiinca, Kišinev, 139-143.
21. K i r p i č e n k o M. J. 1964 - Fenologija, dinamika čislenosti i rost ličinek drejsseny v Kujbyševskom vodochranilišče

- (In: Biologia drejsseny i borba s nej, Ed. B. S. Kuzin) - Izd. Nauka, Moskva-Leningrad, 19-30.
22. K i r p i č e n k o M. J. 1965 - Ékologija rannich stadij ontogeneza Dreissena polymorpha Pallas - Avtoreferat, Dnepropetrovsk, 22 pp.
 23. K i r p i č e n k o M. J. 1971a - Ékologija ontogenetičeskich stadij drejsseny v Volge i Kame (In: Volga-1, Ed. N. A. Dzuban) - Kujbyševskoe Knižnoe Izd., Kujbyšev, 175-180.
 24. K i r p i č e n k o M. J. 1971b - Rečnaja drejssena na severo-vostočnoj okraine ee areala - Trudy Inst. Biol. vnutr. Vod, 21: 130-141.
 25. K i r p i č e n k o M. J. 1971c - K ékologii Dreissena polymorpha Pallas v Cimiljanskom vodochranilišče - Trudy Inst. Biol. vnutr. Vod, 21: 142-154.
 26. K i r p i č e n k o M. J., A n t o n o v P. I. 1977 - Intensivnost' zaselenija drejssenoj vodochranilišča (In: Krugovorot veščestva i energii v vodoemach. Ed. G. I. Galazij) - Akademia Nauk SSSR, Sibirskoe Otdelenie, Listveničnoe na Bajkale, 302-305.
 27. K o n d r a t e v T. M. 1958 - Massovoe pojavlenie drejsseny v Ugličskom i Rybinskom vodochranilišče - Ryb. Choz. 7: 25.
 28. K o n s t a n t i n o v A. S. S p i r i d o n o v J. J. 1977 - Zooperifiton (In: Volgogradskoe vodochranilišče, Ed. A. S. Konstantinov) - Izd. Saratovskogo Univ., Saratov, 120-132.
 29. K o r n o b i s S. 1977 - Ecology of Dreissena polymorpha (Pall.) (Dreissenidae, Bivalvia) in lakes receiving heated water discharges - Pol. Arch. Hydrobiol. 24: 531-545.
 30. L e u z i n g e r H., S c h u s t e r S. 1970 - Auswirkungen der Massenvermehrung der Wandermuschel Dreissena polymorpha auf die Wasser Vögel des Bodensees - Orn. Beob. 67: 269-274.
 31. L e w a n d o w s k i K. 1976 - Unionidae as a substratum for Dreissena polymorpha Pall. - Pol. Arch. Hydrobiol. 23: 409-420.
 32. L e w a n d o w s k i K. 1982 - The role of early developmental stages in the dynamics of Dreissena polymorpha (Pall.) popula-

- tion in lakes. I. Occurrence of larvae in the plankton - Ekol. pol. 30: 81-109.
33. L e w a n d o w s k i K., S t a n i c z y k o w s k a A. 1975 - The occurrence and role of bivalves of the family Unionidae in Mikołajskie Lake - Ekol. pol. 23: 317-334.
34. L j a c h o v S. M. 1961 - O massovom razvitii drejsseny v Stalingradskom vodochranilišče - Bjul. Inst. Biol. Vodochr. 10: 18-21.
35. L u f e r o v V. P. 1965 - Zaselenie drevesnogo substrata iz tolšči vody - Trudy Inst. Biol. vnutr. Vod Akad. Nauk SSSR, 8: 140-143.
36. L u f e r o v V. P. 1966 - Kratkaja sravnitel'naja charakteristika épifauny zatoplennykh lesov volžskikh vodochranilišč - Trudy Inst. Biol. vnutr. Vod. 12: 16-20.
37. M e j s n e r E. V. 1966 - Ispolzovanie zaroslevykh organizmov vodochranilišč dlja kormlenija ryby v plavučich sadkach - Trudy vses. naučn.-issled. Inst. prud. ryb. Choz. 14: 179-183.
38. M e j s n e r E. V., M i c h e e v V. P. 1965 - Ispolzovanie drejsseny dlja kormlenija ryby (In: Soveščanie po biologii drejsseny i zaščite gidrotehničeskikh sooruzenij ot ee obrastanij, Ed. N. A. Dzuban) - Akad. Nauk SSSR, Inst. Biol. vnutr. Vod, Volžskaja GES im. V. I. Lenina, Toljatti, 13-14.
39. M i c h e e v V. P. 1966 - Ispolzovanie drejsseny dlja kormlenija ryby v plavučich sadkach - Trudy vses. naučno-issled. Inst. prud. ryb. Choz. 14: 157-167.
40. M i c h e e v V. P. 1967 - Pitanie drejsseny (Dreissena polymorpha Pallas) - Avtoreferat, Leningrad, 22 pp.
41. M i c h e e v V. P. 1969 - O nekotorych osobennostjach dinamiki populacii drejsseny v Pjalovskom vodochranilišče - Sb. naučno-issled. Rabot vsesojuzn. naučn.-issled. Inst. prud. ryb. Choz. 2: 229-245.
42. M i c h e e v V. P. 1974 - Životnye korma vodochranilišč v sadkovykh rybovodnykh chozajstvach - Ministerstvo ryb. choz. SSSR,

- Vsesojuzn. naučno-issled. Inst. prud. ryb. Choz., Moskva, 72 pp.
43. M o r t o n B. S. 1969 - Studies on the biology of Dreissena polymorpha Pall. III. Population dynamics - Proc. Malac. Soc. London, 38: 471-482.
 44. N e b o l s i n a T. K. 1962 - Pitanie lešča, plotvy, gustery i sinca v pervye gody obrazovaniya Volgogradskogo vodochranilišča - Trudy Saratov. Otd. gos. naučno-issled. Inst. reč. ozer. ryb. Choz. 7: 148-174.
 45. N e b o l s i n a T. K. 1965 - Kačestvennaja i količestvennaja ocenka pitaniya lešča, gustery i plotvy Volgogradskogo vodochranilišča v 1962-1964 gg - Trudy Saratov. Otd. gos. naučno-issled. Inst. reč. ozer. ryb. Choz. 8: 108-127.
 46. N e g u s C. L. 1966 - A quantitative study of growth and production of unionid mussels in the river Thames at Reading - J. anim. Ecol. 35: 513-532.
 47. Ö k l a n d J. 1963 - Notes on population density, age distribution, growth and habitat of Anodonta piscinalis Nils. (Moll., Lamellibr.) in a eutrophic lake - Nytt. Mag. Zool. 11: 19-43.
 48. O l s z e w s k i Z. 1978 - Reconstruction of the size of mollusc shells in studies on the food of fish - Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 26: 87-91.
 49. O r z e c h o w s k i B. 1966 - Studies on the appearance and ecology of Dreissena polymorpha Pall. in the Szymbark Lake - Zesz. nauk. Uniw. M. Kopernika, Toruń, 16: 89-100.
 50. P i e c h o c k i A. 1969 - Obserwacje biologiczne nad małżami z rodziny Unionidae w rzece Grabi [Biological observations on the bivalve of the family Unionidae in river Grabia] - Acta hydrobiol., Kraków, 11: 56-67.
 51. P i e c z y Ń s k a E. 1970 - Perifiton jako pokarm zwierząt wodnych [Periphyton as food of aquatic animals] - Wiad. ekol. 16: 133-144.
 52. P i e s i k Z. 1974 - The role of the crayfish Orconectes limosus (Raf.) in extinction of Dreissena polymorpha (Pall.) subsisting on steelon-net - Pol. Arch. Hydrobiol. 21: 401-410.

53. P l i s z k a F. 1953 - Dynamika stosunków pokarmowych ryb jeziora Harsz [Dynamics of feeding relations in fish of the Lake Harsz] - Pol. Arch. Hydrobiol. 1 (14): 271-300.
54. Š e v c o v a L. V. 1968 - Razmnoženie i razvitie drejsseny v kanale Dnepr-Krivoj Rog - Gidrobiol. Ž. 5: 70-72.
55. S k a l s k a j a I. A. 1976 - Zaselenie drejssenoj (Dreissena polymorpha Pallas) novych substratov Gorkovskogo vodochranilišča - Biol. vnutr. Vod, 31: 30-34.
56. S o s z k a G. J. 1975 - The invertebrates on submerged macrophytes in three Masurian lakes - Ekol. pol. 23: 371-391.
57. S p i r i d o n o v J. I. 1975 - Vozrastnaja struktura populacij i prodolžitelnost' žizni drejsseny v Volgogradskom vodochranilišče - Trudy kompleksnoj ekspedicii Saratovskogo Univ. po izučeniu Volgogradskogo i Saratovskogo vodochranilišča, 5: 84-86.
58. S t ań c z y k o w s k a A. 1964 - On the relationship between abundance aggregations and "condition" of Dreissena polymorpha Pall. in 36 Mazurian lakes - Ekol. pol. A, 12: 653-690.
59. S t ań c z y k o w s k a A. 1977 - Ecology of Dreissena polymorpha (Pall.) (Bivalvia) in lakes - Pol. Arch. Hydrobiol. 24: 461-530.
60. S t ań c z y k o w s k a A., L e w a n d o w s k i K. 1980 - Studies on the ecology of Dreissena polymorpha (Pall.) in some lakes (In: Atti IV Congresso S. M. J., Siena, 6-9 Ottobre 1978, Ed. F. Giusti) - Atti Accademia Fisiocritici, Siena, 369-374.
61. S t e m p n i e w i c z L. 1974 - The effect of feeding of coot (Fulica atra L.) on the character of the shoals of Dreissena polymorpha Pall. in Lake Gopżo - Acta Univ. N. Copernici, Ser. mat.-przyr. 34: 84-103.
62. S z c z e p ań s k i A. 1978 - Ecology of macrophytes in wetlands - Pol. ecol. Stud. 4: 45-94.
63. S z l a u e r L. 1974 - Use of steelon-net veils for protection of the hydroengineering works against Dreissena polymorpha Pall. - Pol. Arch. Hydrobiol. 21: 391-400.

64. W a l z N. 1973 - Untersuchungen zur Biologie von Dreissena polymorpha Pallas in Bodensee - Arch. Hydrobiol. (Suppl.), 42: 452-482.
65. W a l z N. 1975 - Die Besiedlung von künstlichen Substraten durch Larven von Dreissena polymorpha - Arch. Hydrobiol. (Suppl.) 47: 423-431.
66. W a l z N. 1978 - Die Produktion der Dreissena-Population und deren Bedeutung im Stoffkreislauf des Bodenses - Arch. Hydrobiol. 82: 482-499.
67. W i d u t o J., K o m p o w s k i A. 1968 - Badania nad ekologią małżów z rodziny Unionidae w Jeziorze Kortowskim [Investigations into the ecology of mussels of the Unionidae family in the Kortowskie Lake] - Zesz. nauk. wyższ. Szk. roln. Olsztyn, 24: 479-497.
68. W i k t o r J. 1969 - Biologia Dreissena polymorpha (Pall.) i jej ekologiczne znaczenie w Zalewie Szczecińskim [The biology of Dreissena polymorpha (Pall.) and its ecological importance in the Firth of Szczecin] - Stud. Mat. Morsk. Inst. Ryb. Gdynia, A, 5: 1-88.
69. W i k t o r K. 1958 - Larwy Dreissensia polymorpha Pall. jako pokarm narybku [Larvae of Dreissensia polymorpha Pall. as a food for fish spawn] - Przegl. zool. 2: 182-184.
70. W i ś n i e w s k i R. 1974 - Distribution and character of shoals of Dreissena polymorpha Pall. in the bay part of Gopło lake - Acta Univ. N. Copernici, Ser. mat.-przyr. 34: 73-81.