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

I. OCCURRENCE OF LARVAE IN THE PLANKTON*

ABSTRACT: The occurrence was investigated of D. polymorpha larvae in the water of several lakes. The time of appearance, numbers, horizontal and vertical distribution in several growing seasons, and the body-size structure of planktonic larvae were analysed. A great variation was found of abundance dynamics of larvae in different lakes and in the same lake, but in different years. During peak occurrence periods several thous. to several hundred thous. ind. $\cdot m^{-3}$ were found. Larvae were found to usually occur in larger numbers in the littoral than in the pelagial.

KEY WORDS: Lakes, Dreissena polymorpha, mussels, planktonic larvae, distribution, numbers, size structure.

Contents

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1. INTRODUCTION

Dreissena polymorpha is a mussel species commonly occurring in the littoral and partially in the sublittoral of various water bodies, where it dominates in respect of biomass, and often also in respect of numbers, among the invertebrates of this zone.

Although at present D. polymorpha occurs in fresh and brackish waters, it has retained in its development certain features indicating its marine origin. These include the high fecundity and presence of a free-swimming veliger larva. Among Central-European mussels D. polymorpha is the only species which possesses a planktonic larva.

In lakes, sedentary D. polymorpha attain a density of up to several thousand individuals per 1 m^2 of lake bottom in the area of their occurrence (Stańczykowska 1964, Schalekamp 1971, Stańczykowska, Schenker and Fąfara 1975, Kornobis 1977 and others), in dammed reservoirs - over a dozen thousand up to several dozen thousand individuals per 1 m^2 (e.g., Kacănova 1963, Dyga and Lubjanov 1972, Dyga, Lubjanov and Zolotareva 1975), and, for instance, in the Lagoon of Szczecin its abundance at some stations in the zone of its occurrence exceeded 100 thousand individuals per 1 m^2 (Wiktor 1969).

Due to its mass occurrence, D. polymorpha plays an important role in aquatic ecosystems, because it represents a food supply

for different fish species (Pliszka 1953, Wiktor 1958, Grigoraš 1963, Nebolsina 1965, Micheev 1966, Olszewski 1978 and others) and birds (Leuzinger and Schuster 1970, Stempniewicz 1974, Borowiec 1975 and others) and functions as a filter which on the one hand removes suspensions from the water (Micheev 1967, Mattice, Stańczykowska and Ławacz 1972, Stańczykowska, Ławacz and Mattice 1975, Alimov 1981), with large populations this being very efficient (Stańczykowska 1968, Wiktor 1969, Spiridonov 1971, Stańczykowska et al. 1976, Kondratev 1977), and on the other hand - it makes these suspensions available, after gluing them together with slime (in form of faeces and pseudofaeces), to bacteria, and even to other benthonic invertebrates (e.g., Chironomidae) (Izvekova and Lvova-Katchanova 1972, Spiridonov 1976).

It is chiefly the negative role of D. polymorpha that is highlighted in the literature. This negative role is connected with the mass attachment of individuals to various hydrotechnical installations, which makes their functioning difficult, and sometimes impossible (e.g., Wilhelmi 1922, Clarke 1952, Ljachov 1964, Dzjuban and Kirpičenko 1965, Micheev, Dudnikov and Štern 1969, Dyga, Lubjanov and Zolotareva 1975). So far no efficacious methods have in fact been developed for the control of D. polymorpha, and the control of this species is difficult, because, among other things, of the occurrence in its development of the planktonic larva which can penetrate practically everywhere.

The high level of abundance attained by this mussel species and its economic importance account for the common interest of scientists in D. polymorpha and its biology. The bibliography of this species comes up to 2000 entries (Limanova 1964, 1978). The relevant literature contains relatively many data on sedentary

adult forms of D. polymorpha, whereas data on the occurrence of its larvae in the plankton of different lakes are far fever in number, most of them concerning dammed reservoirs of the European part of the Soviet Union.

In Poland, D. polymorpha larvae were analysed in a small number of water bodies: in the Lagoon of Szczecin (W i k t o r 1958, W i k t o r 1969), in heated lakes of the Konin complex of lakes (S t a ń c z y k o w s k a 1976, K o r n o b i s 1977) and in two Masurian lakes (H i l l b r i c h t - I l k o w s k a and S t a ń c z y k o w s k a 1969). Because of this scarcity of data on the occurrence of D. polymorpha larvae especially in Polish lakes, it was decided to extend the scope of the present research into the nature of the occurrence of planktonic larvae, to cover a larger number of lakes.

The aim of this part of the study concerned with the dynamics of numbers of D. polymorpha populations in lakes, with a particular consideration given to early developmental stages (planktonic larvae, settling postveligers), was to analyse the occurrence of D. polymorpha larvae in the water of different lakes. The period of appearance of larvae, their numbers, as well as the spatial and temporal variation were studied during several growing seasons.

2. STUDY AREA AND METHODS

Investigations into the nature of the occurrence of planktonic larvae of D. polymorpha were carried out with a variable frequency in the years 1976-1978 in 7 Masurian lakes, 5 of which (Majcz Wielki, Inulec, Głębokie, Zelwążek, Jorzec) are connected by a river, and in 1980 in Żarnowieckie Lake (Table I).

To study the horizontal distribution of larvae, in most of the lakes plankton samples were collected in the littoral - above sedentary D. polymorpha, and in the pelagial - far from adult individuals. In 1976, samples were collected every 2 weeks, and in the next years more often (every 5-8 days), in the littoral at

Table I. Description of the lakes studied

No.	Lake	Area (ha)	Depth (m)		Limnol. type	Years of studying D. polymorpha larvae			
			max.	av.		1976	1977	1978	1980
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	Zelwążek	11	7.4	3.7	eutrophic	+			
5	Jorzec	42	11.6	5.5	eutrophic	+	+		
6	Ołów	61	40.1	12.9	b-mesotrophic			+	
7	Kołowin	78	7.2	4.0	eutrophic			+	
8	Żarnowieckie	1432	19.4	8.4	b-mesotrophic				+

2-4 stations and in the pelagial at 1-2 stations in each lake throughout the period of the presence of larvae in the plankton.

To determine the vertical distribution of larvae, in 1976, in the deep lakes sampling was done separately for each of the 3 layers (epi-, meta- and hypolimnion). A more detailed analysis of the vertical distribution has been carried out for two lakes (Majcz Wielki and Żarnowieckie) during periods of peak occurrence of larvae in the plankton. Samples were collected in the littoral and pelagial at one-metre intervals of depth, from the surface to the bottom.

In all the above-described investigations Bernatowicz's 5-litre sampler was used with which water was sampled at 1 m depth intervals and the samples were subsequently pooled by pouring them through a plankton net according to the 3 layers: epi-, meta- and hypolimnion. For the detailed analysis of the vertical distribution of larvae, at each depth 15-litre samples were collected by pooling the contents of three samplers passed through a net. For the preservation a 4% formalin solution was used. In the laboratory the samples were condensed and reduced to a specified volume (15-35 ml) and subsamples of a total volume of 1 ml were examined under the microscope.

The larvae were measured in the microscope by means of a measuremer ocular with an accuracy to the nearest 15 µm. From each sample 50-100 larvae were measured. A total of about 600 samples have been collected, and over 6.5 thous. individuals have been measured.

3. RESULTS

3.1. Abundance dynamics and horizontal distribution

In the lakes under investigation the first appearances of planktonic D. polymorpha larvae were usually found in the second half

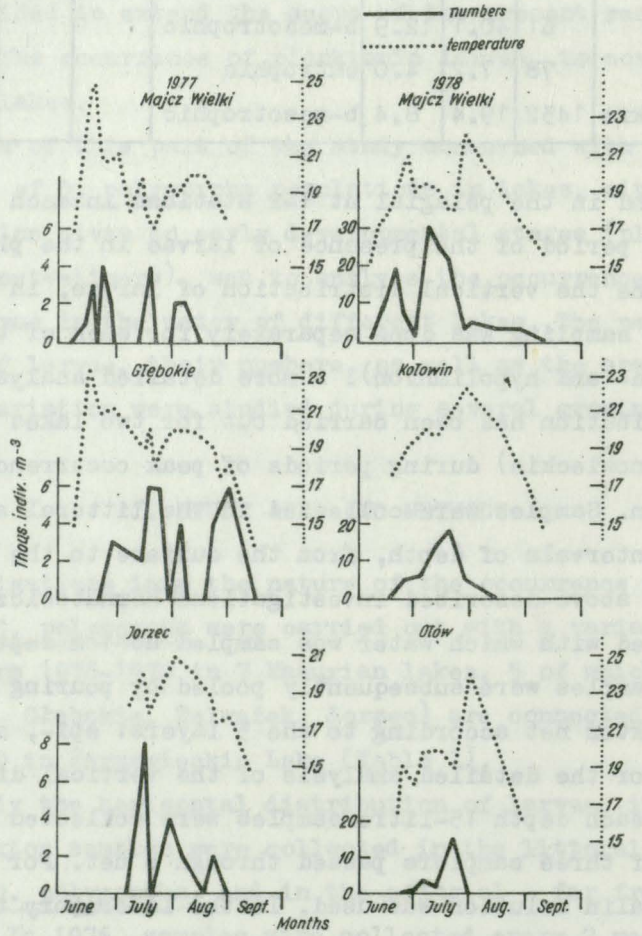

Fig. 1. Numbers of D. polymorpha larvae in the lake littoral in relation to surface water temperature changes

of June, or, sometimes, at the beginning of July. Sometimes larvae were noted at an earlier time, e.g., in Lake Majcz Wielki in the years 1977 and 1978, where they could be observed already in the first half of June.

At the time of the first occurrences of larvae the surface water temperature was usually 17-19°C. An exception was Lake Majcz Wielki in which in 1977 the first planktonic larvae were observed at a higher temperature (24°C), but it was only the beginning of June (Fig. 1). The course of the dynamics of larvae depends on changes in the water temperature - a rise of temperature is usually accompanied by an increase in numbers of the larvae in the plankton, whereas a fall of temperature is followed by their disappearance (Fig. 1). Disappearance of larvae from the plankton was as a rule

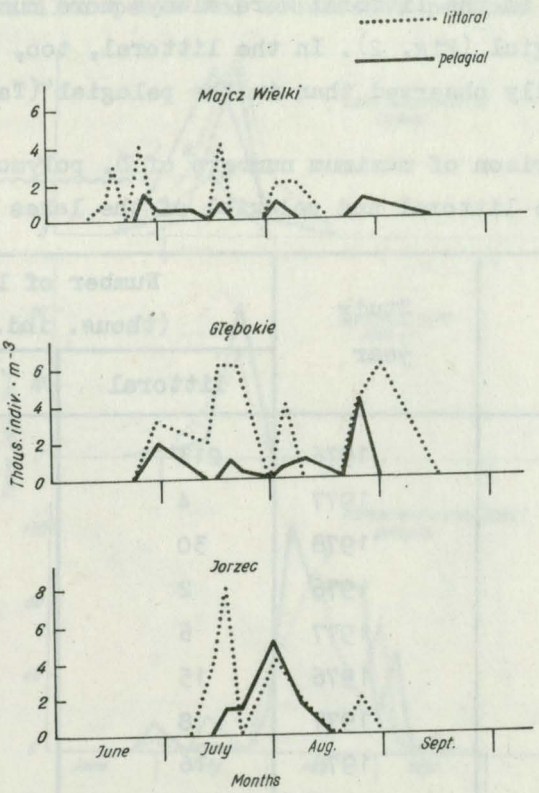

Fig. 2. Occurrence of D. polymorpha larvae in the littoral and pelagial of three lakes (1977)

seen in August, or September, often at a surface water temperature (16-18°C) still suitable for the reproduction of D. polymorpha.

D. polymorpha larvae thus occurred in the plankton of the lakes as a rule for 1.5 to about 3 months. They were observed for the longest time in the plankton of Żarnowieckie Lake, for the shortest time - in Lake Jorzec (in 1977). An exception was Lake Zelwążek in which in 1976 larvae were found once only in August.

D. polymorpha larvae appeared at the earliest in the littoral of the lakes, i.e., in the area where there occur breeding adult individuals, and only several days later were they seen in the pelagial, where they were brought by water currents. Great differences in numbers were found between the larvae in the littoral and those in the pelagial of the lakes studied. In the first breeding period the larvae in the littoral were always more numerous than those in the pelagial (Fig. 2). In the littoral, too, higher peak numbers were usually observed than in the pelagial (Table II).

Table II. Comparison of maximum numbers of D. polymorpha larvae found in the littoral and pelagial of the lakes studied

Lake	Study year	Number of larvae (thous. ind. $\cdot m^{-3}$)	
		littoral	pelagial
Majcz Wielki	1976	213	146
Majcz Wielki	1977	4	2
Majcz Wielki	1978	30	42
Inulec	1976	2	14
Głębokie	1977	6	4
Jorzec	1976	15	2
Jorzec	1977	8	5
Ołów	1978	16	5
Kołowin	1978	18	56
Żarnowieckie	1980	354	124

Because of the presence of reproducing D. polymorpha individuals, the littoral zone was often characterized by a much greater variation of numbers of the larvae in the plankton than the pelagial zone. An increase or decrease in numbers of the larvae in the littoral were more rapid than in the pelagial, the course of abundance dynamics was usually gentler. This may have been caused on the one hand by the reproductive activity of the individuals in the littoral (a growth in number of the larvae), and on the other hand by the abundance in this zone of substrates suitable for the settling of larvae, this favouring the elimination of the latter from the plankton (decrease in numbers of the larvae).

Different stations within the same environments (littoral, pelagial) of the lakes showed a similar course of the larval abundance curves, and similar peaks and occurrence periods (Fig. 3).

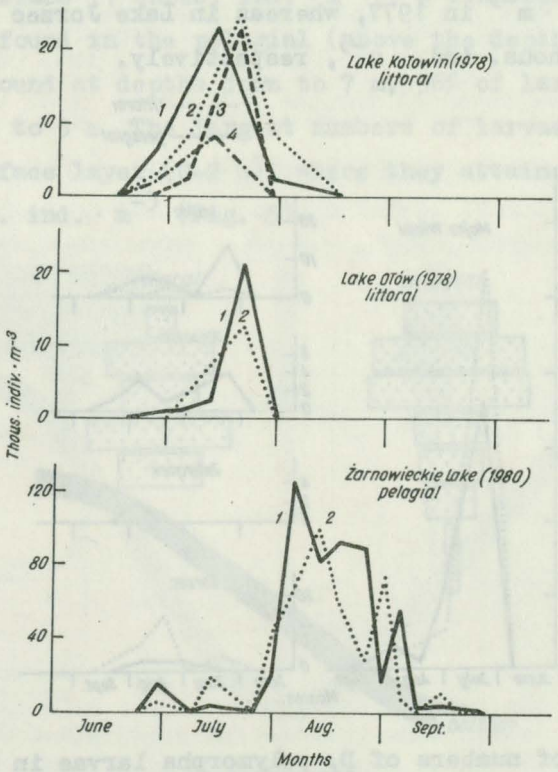

Fig. 3. Occurrence of D. polymorpha larvae at different stations within the same lake zones (littoral or pelagial)
1-4 - stations

The lakes under study were found to differ considerably in the abundance of larvae. In the group of 5 lakes interconnected by a river, studied the same year, Lake Majcz Wielki appeared to have the largest numbers of larvae (in July - over 200 thous. $\cdot m^{-3}$). In the remainder of the lakes much lower numbers were found (several thous. - over a dozen thous. $\cdot m^{-3}$) (Fig. 4).

The individual study years, too, were found to differ very considerably in the abundance of larvae. In Lake Majcz Wielki the highest numbers were recorded for 1976 (146-213 thous. $\cdot m^{-3}$), the lowest for 1977 (a maximum of 2-4 thous. $\cdot m^{-3}$). During the peak occurrence in 1978 30-42 thous. ind. $\cdot m^{-3}$ were found in this lake. Two other lakes did not show such great differences during two consecutive years in which the peak numbers of larvae were relatively low: in Głębokie Lake 4 thous. ind. $\cdot m^{-3}$ were found in 1976, and 6 thous. ind. $\cdot m^{-3}$ in 1977, whereas in Lake Jorzec - 15 thous. ind. $\cdot m^{-3}$ and 8 thous. ind. $\cdot m^{-3}$, respectively.

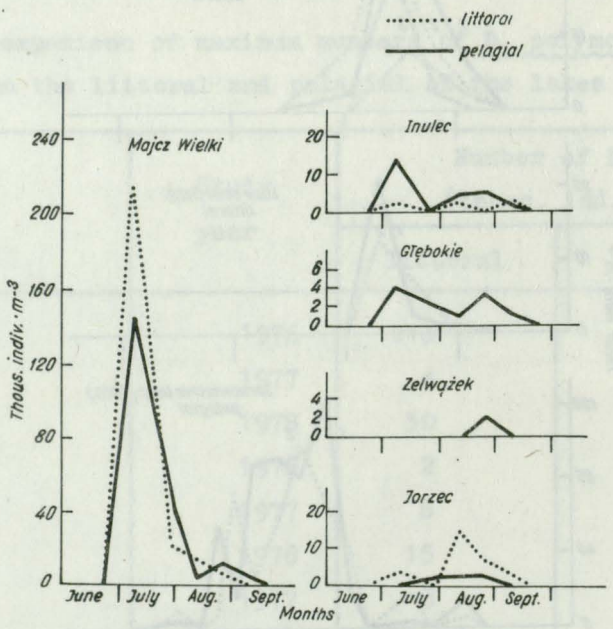

Fig. 4. Dynamics of numbers of D. polymorpha larvae in five lakes in the catchment area of the Jorka River in 1976
There are no data for the littoral of the lakes Głębokie and Zelwążek

3.2. Vertical distribution

In the lakes under study D. polymorpha larvae occurred principally in the epilimnion. In 1976, larvae from this layer, for example in Lake Majcz Wielki, represented 98%, and in Głębokie Lake - 95% of all the larvae present in the lake. On account of this pattern of occurrence of D. polymorpha larvae, the analysis carried out in the subsequent years was restricted to the epilimnion layer.

A detailed analysis of the vertical distribution of larvae, carried out in Lake Majcz Wielki in July 1978 at a wind force of 1-2 degrees on Beaufort's scale, showed that in the littoral (above the depth of 4.5 m) most larvae (95%) were distributed fairly uniformly in the 1-4 m layer, attaining there a level of numbers of 22-40 thous. ind. $\cdot m^{-3}$. The smallest number of larvae was found near the surface (7 thous. ind. $\cdot m^{-3}$). A different distribution of larvae was found in the pelagial (above the depth of 10 m). They were only found at depths down to 7 m, 96% of larvae occurring at depths down to 5 m. The largest numbers of larvae were recorded for the surface layer (0-2 m), where they attained the level of 27-44 thous. ind. $\cdot m^{-3}$ (Fig. 5).

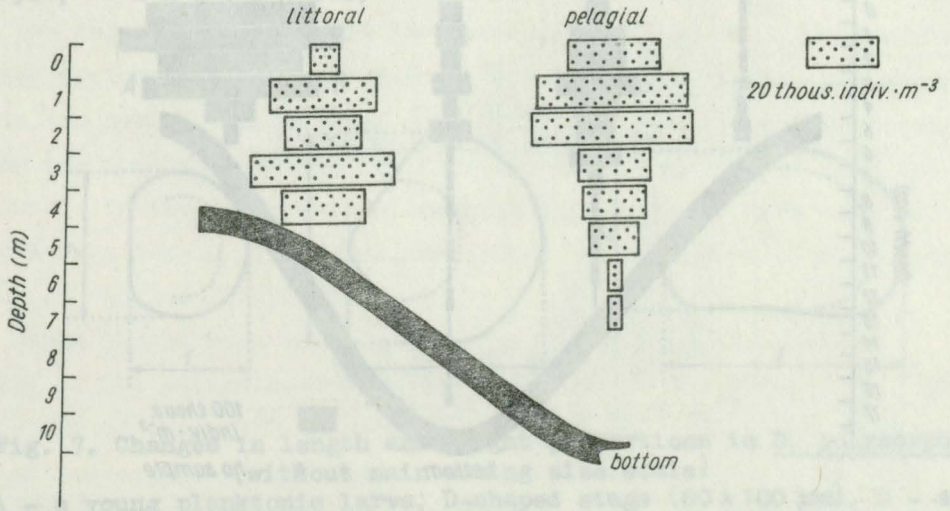

Fig. 5. Vertical distribution of D. polymorpha larvae in Lake Majcz Wielki (12 July 1978)

A similar analysis has been carried out in the Żarnowieckie Lake in August 1980, also at a wind force of 1-2°B. In spite of the relatively great depth of the lake, in its pelagial D. polymorpha larvae were found to be present down to the bottom (16 m), though their number at the bottom was small (4-13 thous. ind. · m^{-3}). The larvae occurred mainly in the 0-6 m deep zone (about 90%), where their number varied between several dozen thous. and over 100 thous. ind. · m^{-3}, the maximum being 277 thous. · m^{-3}.

Very great differences in the numbers of larvae were found between two littoral stations differently oriented in relation to the wind (a leeward station and a windward station). At the leeward station the average level of numbers was 18 thous. ind. · m^{-3}, being fairly uniform almost throughout a water column (7-17 thous. ind. · m^{-3}), and the highest level of numbers (39 thous. ind. · m^{-3}) was found near the bottom. At the windward station many times higher numbers were recorded (on the average 354 thous. ind. · m^{-3}). The highest numbers were recorded for the 0-3 m deep layer (the maximum

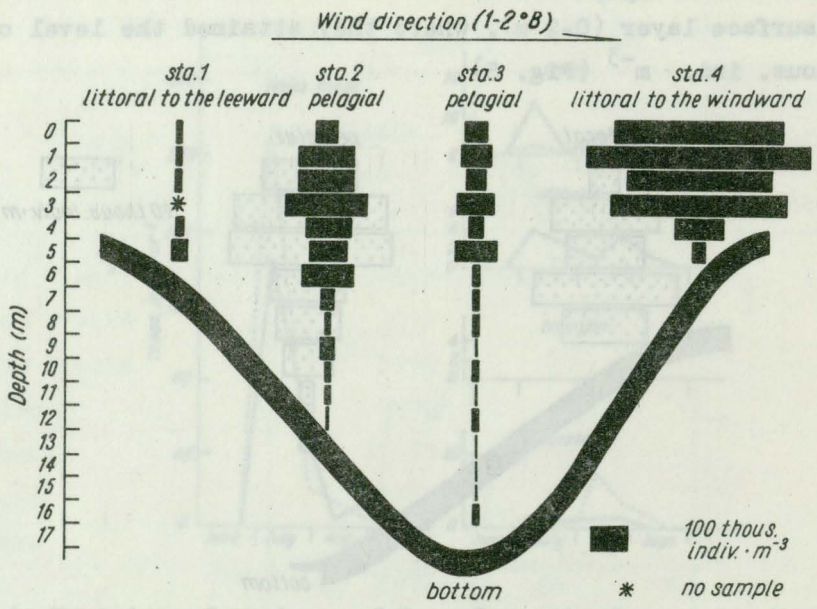

Fig. 6. Vertical distribution of D. polymorpha larvae in Żarnowieckie Lake (5 August 1980)

being 608 thous. ind. $\cdot m^{-3}$) and the lowest for the bottom (Fig. 6).

3.3. Size structure

A characteristic feature of D. polymorpha is changes in shell proportions with the growth of an individual. At the initial stage of its planktonic life the larva has a D-shaped body, while at the terminal stage it takes a nearly round shape. It is only the settling larvae that grow like adults in their ever-elongating body shape. Consequently, the expression "individual body length" is not always unequivocal. The length of a larva adopted in the present study is a length corresponding to attached individuals, but not being the greatest dimension in the youngest larvae (Fig. 7). W a l z (1973) determined the larval body length in a similar way. In the literature a different length is sometimes adopted as the length of larval body (segment 2 in Fig. 7) (e.g., H i l l b r i c h t - - I l k o w s k a and S t a ń c z y k o w s k a 1969, G a l p e r i n a 1974). Most often, however, authors do not specify what they adopt as the length of a larva (K i r p i č e n k o 1964, W i k t o r 1969, K o r n o b i s 1977 and others).

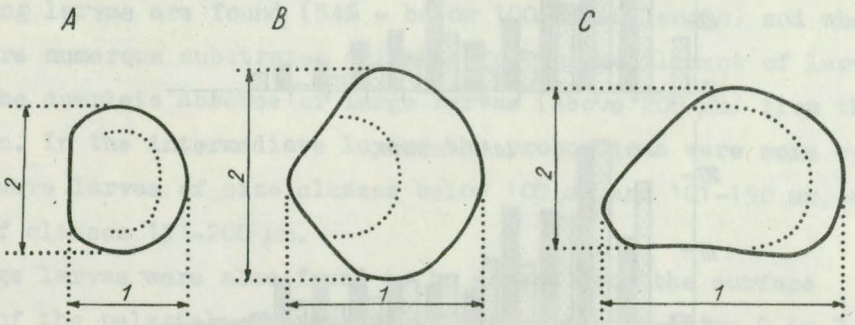

Fig. 7. Changes in length and height proportions in D. polymorpha (without maintaining size scale)
A - a young planktonic larva, D-shaped stage (80 x 100 µm), B - an older planktonic larva (200 x 200 µm), C - a young sedentary individual (900 x 600 µm), 1 - length, 2 - height

In the lakes under the present study larvae were found with body lengths from 65 µm (height 80 µm) to 245 µm (height 270 µm). The smallest larvae, 65 µm long, were found only in the littoral zone, that is, in the breeding area of D. polymorpha (Fig. 8).

An analysis of the size structure of D. polymorpha larvae present in the plankton throughout the breeding season has shown that the smallest (youngest) larvae were very numerous at the beginning of this period; the largest larvae were not present at that time. As the time passed the percentage of small larvae decreased while that of large larvae increased. Towards the end of the breeding season there were only large larvae in the plankton (Fig. 9).

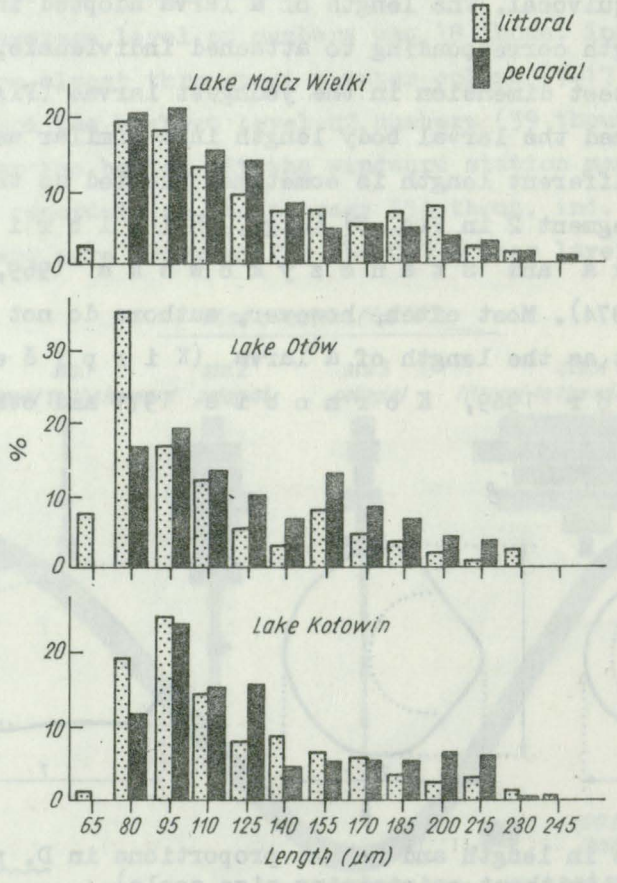

Fig. 8. Proportion of D. polymorpha larvae of specified length in the littoral and pelagial of three lakes (1978)

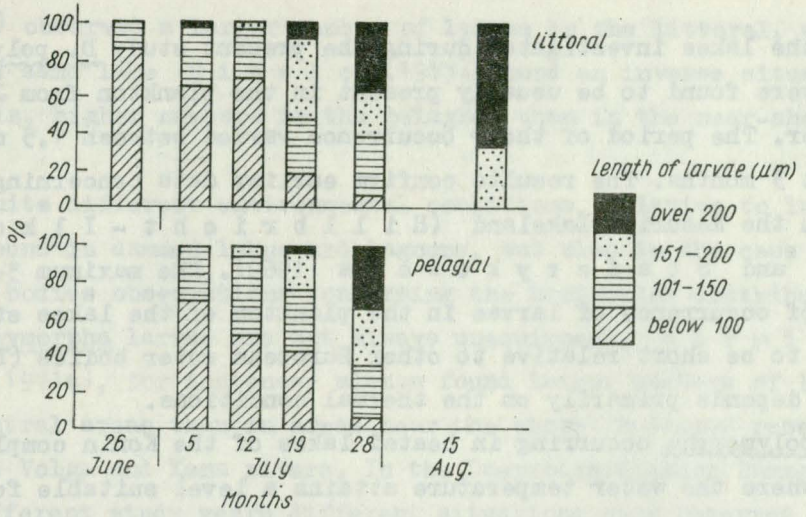

Fig. 9. An example of size structure of D. polymorpha larvae in the littoral and pelagial (Lake Kołowin, 1978)

In July 1978, with an almost wind-less weather, large larvae of over 150 µm in body length were completely absent from the surface water layer of the littoral of Lake Majcz Wielki, while at the same time the smallest individuals dominated there (71% - below 100 µm). A similar situation was found immediately above the bottom (at the depth of 4 m) - this is where aggregations of D. polymorpha producing larvae are found (54% - below 100 µm in length) and where there are numerous substrates suitable for the settlement of larvae, hence the complete absence of large larvae (above 200 µm) from the plankton. In the intermediate layers the proportions were more even: 40-45% were larvae of size classes below 100 µm and 101-150 µm, and 5-10% of classes 151-200 µm.

Large larvae were also found to be absent from the surface layers of the pelagial, whereas at different depths (from 0 to 7 m) 28 to 64% of the smallest larvae (below 100 µm) were found, 28 to 55% of larvae 101-150 µm long, 4 to 33% of larvae 151-200 µm long and up to 6% of the largest larvae.

4. DISCUSSION

In the lakes investigated during the present study D. polymorpha larvae were found to be usually present in the plankton from June to September. The period of their occurrence varied between 1.5 months to about 3 months. The results confirm earlier data concerning two lekes in the Masurian Lakeland (H i l l b r i c h t - I l k o w s k a and S t a ń c z y k o w s k a 1969). The maximum 3-month period of occurrence of larvae in the plankton of the lakes studied appears to be short relative to other European water bodies (Fig. 10). It depends primarily on the thermal conditions.

D. polymorpha occurring in heated lakes of the Konin complex of lakes, where the water temperature attains a level suitable for breeding already in April, begin their reproductive activity two months earlier than those living in the Masurian lakes (S t a ń c z y k o w s k a 1976, K o r n o b i s 1977, K. Lewandowski, J. Ejsmont-Karabin - unpublished data). Noteworthy is the earlier, than indicated by the water temperature, disappearance of larvae from the plankton in autumn, in both the Masurian and the heated lakes, which seems to be particularly surprising in the latter case, as the time of disappearance of planktonic larvae is similar to that found for the Masurian lakes (S t a ń c z y k o w s k a 1976). The period of the presence of larvae in the plankton elongates as we move to the south of Europe, to warmer and warmer zones, and in Lake Ochryda in Yugoslavia D. polymorpha larvae occur in the plankton throughout the year (S e r a f i m o v a - H a d i š č e 1957).

The results of the present study indicate that in the first period of reproductive activity of D. polymorpha the larvae are always more abundant in the littoral, that is, in the area of occurrence of reproducing individuals, than in the pelagial, and it is usually in the littoral that higher peak numbers are found than in the pelagial.

However, most of the data in the literature concern only the numbers of larvae in the pelagial, and in only a few papers is the

littoral taken into account. For example, in Lake Constance W a l z (1973) observed a larger number of larvae in the littoral, while in the same lake E i n s l e (1973) found an inverse situation, that is, higher numbers in the pelagial than in the near-shore zone.

Quite different environmental conditions, relative to lakes, are found in dammed lakes and lagoons, but also in the case of these water bodies observations concerning the horizontal distribution of D. polymorpha larvae are not always unequivocal. K i r p i č e n k o (1971a), for instance, always found larger numbers of larvae in central areas than in areas near the shore in dammed reservoirs on the Volga and Kama rivers. In the Dneprodzeržynskoe Dammed Lake in different study years different situations were observed (D y g a 1971), and larger numbers of larvae near the shore than in the pelagial have also been mentioned by: W i k t o r (1958) (the Lagoon of Szczecin), K a č a l o v a and S l o k a (1964) (the Kegums Reservoir) and D y g a and L u b j a n o v (1975) (the Zaporožskoe Reservoir).

As has been found in the Żarnowieckie Lake, winds and currents have a strong influence on the horizontal distribution of larvae in the lake water. In areas exposed to wind action much larger numbers of D. polymorpha were found than in other areas. The influence of these factors on the spreading of D. polymorpha larvae in the initial developmental period when it proceeded only in warmer areas was observed by K i r p i č e n k o (1964) and K o r n o b i s (1977). From those areas the larvae were subsequently carried to zones where adult D. polymorpha did not occur, or where reproduction had not started yet, for this reason, K i r p i č e n k o (1965a, 1971b) calls them "allochthonous" larvae.

Wind and currents also affect the vertical distribution of D. polymorpha larvae in the lake water. With a typical thermal and oxygen stratification in lakes almost all larvae occur in the epilimnion, as has been found, for instance, in the Głębokie Lake and in Lake Majcz Wielki. A slightly different situation is found

No.	Water bodies		Year	Months J	F	M	A	M	J	J	A	S	O	N	D
1	Masurian lakes	Majcz Wielki	1976												
2		"	1977												
3		"	1978												
4		Inulec	1976												
5		Głębokie	1976												
6		"	1977												
7		Jorzec	1976												
8		"	1977												
9		Ołów	1978												
10		Kołowin	1978												
11		Tałtowisko	1963												
12		"	1964												
13		Śniardwy	1966												
14		Żarnowieckie	1980												
15	Konin lakes complex (heated)	Ślesińskie	1971												
16		"	1972												
17		"	1974-75												
18		Pątnowskie	1971												
19		"	1972												
20		"	1974-75												
21		Mikorzyńskie	1971												
22		"	1972												
23		Wąsoskie	1971												
24		"	1972												
25		Mikorzyńsko-Wąsoskie	1974-75												
26		Licheńskie	1971												
27		Gosławickie	1972												
28	Lagoon of Szczecin		1955-56												
29	"		1961												
30	"		1962												
31	"		1963												
32	"		1964												
33	Gnadensee		1971												
34	Überlinger See		1971												
35	Lake Constance		1971												
36	"		1973												
37	"		1974												
38	Lake Pohlitzer		1956												
39	"		1957												
40	"		1958												
41	"		1959												
42	"		1960												
43	"		1961												
44	"		1962												
45	"		1963												
46	"		1964												
47	Lake Skadarskie		1952												
48	"		1953												
49	"		1954												
50	Lake Ochryda		1952-54												
51	dam reservoirs	Ucinskoe	1956-57												
52		"	1958												
53		"	1959												
54		Kujbyševskoe	1959												
55		"	1960												
56		"	1961												
57		"	1963												
58		Kamskoe	1964												
59		Cimljanskoe	1962												
60		Zaporožskoe	1961-63												
61		"	1964-70												
62		Kegums	1961												
63		Kuĭburganskoe	1965												
64		"	1967												
65	Canal Dniepr-Krivoj Rog		1965												
66	"		1966												
67	Babinsk Bay of the Oka		1961												
68	Oka		1961												

in the Żarnowieckie Lake, where due to the large surface area and proneness to mixing, the summer thermal and oxygen stratification is very poor and lasts only a short time (J. Zawisza, Z. Kajak, E. Pieczyńska - unpublished data). For this reason, in the deepest parts of this lake larvae were found to be present down to the very bottom.

A clear effect of mechanical water movements and currents on the vertical distribution of larvae was found in the Ślesińskie Lake, a heated water body (Stańczykowska 1976, K. Lewandowski, J. Ejsmont-Karabin - unpublished data). In the area of warm water-fall effluence larvae appeared to be evenly distributed throughout the water column, in spite of the considerable depth (20 m) of the lake, the density of larvae being sometimes higher in deeper layers than in the epilimnion. In the same area the summer thermal stratification was absent, too. At another station far from the water effluence the lake had a thermal stratification typical of lakes, and larvae occurred in it mainly in the epilimnion.

A relationship between the vertical distribution and winds has also been found in the Zaporožskoe Dammed Reservoir (Dyga and Galinskij 1975). During a windless weather the larvae were

Fig. 10. Different periods of occurrence of D. polymorpha larvae in the plankton

The data presented in the figure come from the following papers: Nos: 1-10 and 14 - the author's own investigations, 11-13 - Hillbricht-Ilkowska and Stańczykowska (1969), 15, 18, 23 - Stańczykowska (1976), 16, 19, 21, 22, 24, 26, 27 - K. Lewandowski, J. Ejsmont-Karabin (unpublished data), 17, 20, 25 - Kornobis (1977), 28 - Wiktor (1958), 29-32 - Wiktor (1969), 33, 34 - Walz (1973), 35 - Einsle (1973), 36 - Walz (1975), 37 - Walz (1978), 38-46 - Breitig (1965), 47-49 - Nedeljkovic (1959), 50 - Serafimova-Hadiščе (1957), 51-53 - Kačanova (1961), 54 - Kirpičenko (1962), 55, 56 - Kirpičenko (1964), 57 - Kirpičenko (1965b), 58 - Kirpičenko (1971b), 59 - Kirpičenko (1971c), 60, 61 - Dyga and Lubjanov (1975), 62 - Kačalova and Sloka (1964), 63, 64 - Jarošenko and Nabereżnyj (1971), 65, 66 - Ševcova (1968), 67, 68 - Birjukov et al. (1964)

most abundant at the depth of 5 m and did not occur in the near--bottom layer, while at a wind force of 2-3°B they appeared to be evenly distributed in the 0-20 m layer, and were also found at the bottom itself at the depth of 35 m.

The number of D. polymorpha larvae found in the Masurian lakes under study appeared to be comparatively low, relative to the data in the literature. The highest density of about 200 thous. larvae in a m^3 found in Lake Majcz Wielki in 1976 often represents an average for other lakes. In other Masurian lakes: Śniardwy and Tałtowisko, the abundance during the peak occurrence amounted to 200 thous. and 400 thous. ind. m^{-3}, respectively (H i l l b r i c h t - I l k o w s k a and S t a ń c z y k o w s k a 1969). A high level of numbers, almost 1000000 ind. $\cdot m^{-3}$ was found in 1961 by B r e i t i g (1965) in Lake Pohlitzer; in other years he usually found there from 100 thous. to 400 thous. larvae in 1 m^3. In an eutrophic part of Lake Constance (Gnadensee) W a l z (1973) found a density of almost 700 thous. larvae per 1 m^3.

Densities of similar order have also been found in dammed reservoirs and lagoons. In the Lagoon of Szczecin over 700 thous. ind. $\cdot m^{-3}$ were found in 1961; in other years - 200 thous. - 300 thous. ind. $\cdot m^{-3}$ (W i k t o r 1969). In dammed reservoirs in the Soviet Union (Kujbyševskoe, Učinskoe, Zaporožskoe) densities above 400 thous. ind. $\cdot m^{-3}$ have not been found (K a č a n o v a 1961, K i r p i č e n k o 1962, 1964, 1965b, D y g a and L u b j a n o v 1975).

In several cases, e.g., Lake Pohlitzer (B r e i t i g 1965), the Kujbyševskoe Reservoir (K i r p i č e n k o 1965b), the Učinskoe Reservoir (K a č a n o v a 1961) and the Zaporožskoe Reservoir (D y g a and L u b j a n o v 1975) data on the occurrence of larvae cover several (4-10) consecutive years. In these water bodies characteristic cycles are seen manifested by a very low level of numbers of larvae every 3-4 years. These cycles are not always noticeable, but the belief that they exist is very strong. For instance, in the Zaporožskoe Reservoir, investigated in the years

1961-1970 (D y g a and L u b j a n o v 1975), the great abundance of larvae in 1967, a year which according to these authors ought to be "infertile" in larvae, is attributed to their being imported from the neighbouring Dneprodzeržynskoe Dammed Lake which is located higher up.

Also in Lake Majcz Wielki, studied during the present research within which it would be hard to speak about cycles, as it only lasted three years, a rapid decrease in numbers was recorded in 1977 (up to 4 thous. ind. $\cdot m^{-3}$). A year before the numbers of larvae were 50 times, and a year later - 10 times as large. Some authors relate low densities of planktonic larvae in a particular study year, for example, to water pollution (e.g. D y g a and L u b j a n o v 1972), or to decreased numbers of adult individuals that are reproducing (M i c h e e v 1969). On the basis of a 3 years' study carried out in the Pjalovskoe Lake M i c h e e v (1969) has stated that individuals of a new generation which abundantly settle on D. polymorpha assemblages cause within a 2-3 year period such a deterioration of the oxygen and food conditions for older individuals present in deeper layers of an assemblage that they die, which in turn may reduce the production of planktonic larvae.

The value of the production of larvae is to a large extent connected with the age structure of the sedentary individuals, and with the proportion of sexually mature individuals in a population, as has been pointed by L v o v a (1977). In fact the relationship between the occurrence of D. polymorpha larvae and the age structure of the sedentary individuals has not hitherto been dealt with in the literature. This problem, as well as problems connected with the settling of larvae and the fate of individuals of the new generation will be the subject of the second part of the present series (L e w a n d o w s k i 1982).

5. SUMMARY

The dynamics of numbers of the planktonic larvae of D. polymorpha was investigated at a variable frequency in 7 Masurian lakes and in the Żarnowieckie Lake in the years 1976-1978 and 1980 (Table I).

D. polymorpha larvae were found to occur in the plankton of the study lakes usually from mid-June to September (Fig. 10). The course of the dynamics of numbers of the larvae varied from lake to lake and from year to year within the same lake. In the peak occurrence period in the different years and lakes densities of several thous. ind. $\cdot m^{-3}$ to several hundred thous. ind. $\cdot m^{-3}$ were found (Table II).

At the beginning of the breeding period the larvae were found to be present only in the littoral, that is, where there occurred adult individuals that were reproducing, and only after some time did they spread throughout the pelagial, owing to the action of currents and winds. The dynamics of numbers of the larvae in the plankton showed greater variations in the littoral than in the pelagial (Fig. 2); also the level of numbers was as a rule higher in the littoral.

Only in the littoral were larvae of the smallest body size found (Fig. 8); they were very numerous in the first period of the reproductive process of D. polymorpha. Towards the end of the breeding season (August-September) the smallest larvae disappeared from the plankton, where at that time larvae of larger body size dominated (Fig. 9).

In the lakes under study D. polymorpha larvae were found mainly in the epilimnion, where they represented over 90% of all the larvae present in the lake. Only in the Żarnowieckie Lake, a large water body prone to mixing, did larvae occur to the very bottom, where their numbers were, however, small relative to the epilimnion.

In that lake considerable differences in the number of larvae were found between sites differing in their orientation in relation to the wind. At a windward site the larvae were twenty times as numerous as at a leeward site (Fig. 6).

6. POLISH SUMMARY

Badania nad dynamiką liczebności planktonowych larw D. polymorpha prowadzono w 7 jeziorach mazurskich i w Jeziorze Żarnowieckim z różną intensywnością w latach 1976-1978 i 1980 (tab. I).

Stwierdzono, że występowanie larw D. polymorpha w planktonie

badanych jezior trwało przeważnie od połowy czerwca do września (rys. 10). Dynamika liczebności larw miała różny przebieg w różnych jeziorach i w różnych latach w obrębie tego samego jeziora. W okresie szczytów występowania w różnych latach i jeziorach stwierdzono liczebności od kilku tysięcy osobn. $\cdot m^{-3}$ do kilkuset tysięcy osobn. $\cdot m^{-3}$ (tab. II).

Na początku okresu rozrodczego larwy występowały tylko w litoralu, czyli w miejscu występowania rozradzających się osobników i dopiero po pewnym czasie pod wpływem prądów i wiatru rozprzestrzeniały się w całym pelagialu. Dynamika liczebności larw w planktonie wykazywała większe wahania w litoralu niż w pelagialu (rys. 2), przeważnie też liczebności w litoralu były większe.

Tylko w litoralu występowały larwy o najmniejszych rozmiarach (rys. 8); bardzo liczne były one w pierwszym okresie procesu rozrodczego D. polymorpha. Pod koniec okresu rozrodczego (sierpień-wrzesień) larwy najmniejsze znikały z planktonu, a dominowały w tym czasie larwy większych rozmiarów (rys. 9).

W badanych jeziorach larwy D. polymorpha występowały głównie w epilimnionie, gdzie stanowiły ponad 90% wszystkich larw występujących w jeziorze. Tylko w dużym i podatnym na mieszanie Jeziorze Żarnowieckim larwy występowały do samego dna, gdzie jednak liczebności były niewielkie w porównaniu z epilimnionem.

W jeziorze tym stwierdzono duże różnice w liczebnościach larw na stanowiskach różnie usytuowanych w stosunku do wiatru. W miejscu narażonym na wpływ wiatru liczebności były 20-krotnie wyższe od stanowiska zawietrznego (rys. 6).

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