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DEVELOPMENT OF POPULATIONS OF *DREISSENA POLYMORPHA* (PALL.) IN LAKES

KRZYSZTOF LEWANDOWSKI

Department of Hydrobiology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, 05-092 Łomianki, Poland (e-mail: k.b.lewandowski@wp.pl)

ABSTRACT: The paper summarizes the results of a long-term study on the ecology of *Dreissena polymorpha* (Pall.) in several dozen lakes of different size, depth and trophy. The abundance of adults, planktonic larvae, and settled postveligers was found to vary widely between the lakes, localities within a lake, and years. The temperature influences the period of appearance and abundance dynamics of planktonic larvae; wind affects their vertical and horizontal distribution in the water column; winds and water currents displace settling postveligers. Settling postveligers display preferences for various natural substrates: most often they settle on submerged plants, especially perennials. The age structure of *D. polymorpha* settled on plants (dominance of young individuals, at most 3 years old) differs from that in colonies settled on the littoral bottom. The abundance of mussel populations in lakes is primarily determined by the mortality at the transition from planktonic to sedentary life, and by the mortality of individuals settled on submerged plants.

KEY WORDS: lakes, *Dreissena polymorpha*, population dynamics, age structure, planktonic larvae, postveligers, settling

CONTENTS

INTRODUCTION

The zebra mussel, *Dreissena polymorpha* (Pall.), is a commonly known small bivalve, occasionally occurring in large numbers in fresh and brackish waters (e.g. J. WIKTOR 1969, PIECHOCKI & DYDUCH-FALNIOWSKA 1993). Its ontogeny includes a free-swimming larva of the veliger type, a settled postplanktonic juvenile called postveliger, and a sedentary stage (adult). Settled mussels rarely occur singly. Typically, they form colonies of several dozen or even several thousand interconnected individuals, firmly attached to the substrate with their byssus threads.

In some habitats, the mussels can reach high numbers. Their densities in lakes may exceed ten thousand individuals per square metre of the littoral and partly also sublittoral zones. Similar densities were noted in rivers. In dam reservoirs, the mussel densities can be several times higher. In the Gulf of Szczecin, densities of up to 114 thousand mussels per m^2 were reported in the 1960s (J. WIKTOR 1969). At such high densities, the mussels form thick, multi-layered shoals, tightly encrusting the bottom. The total weight of individuals from 1 m^2 may reach several to several dozen kilograms.

Due to their occasionally very high numbers, the mussels can play an important part in various habitats. Their negative role is often emphasized, as they create serious technical problems when coating various kinds of hydrotechnical structures and precluding their functioning (e.g. WILHELMI 1922, CLARKE 1952, DYGA et al. 1975, KOVALAK et al. 1993).

In lakes and natural running waters, the mussels perform important and positive functions. They constitute a food resource for many fish species (e.g. DE NIE 1982, PREJS et al. 1990, RUTKOWSKI 1994, NAGELKERKE & SIBBING 1996, TUCKER et al. 1996) and water birds (LEUZINGER & SCHUSTER 1970, STEMPNIEWICZ 1974, BOROWIEC 1975, WORMINGTON & LEACH 1992), but most of all, being efficient and abundant filter feeders, the zebra mussels contribute to the reduction of threats resulting from water pollution and eutrophication (STAŃCZYKOWSKA 1968, LVOVA-KACHANOVA 1971, STAŃCZYKOWSKA et al. 1975, REEDERS et al. 1993, LEWANDOWSKI & STAŃCZYKOWSKA 1995, HORGAN & MILLS 1997).

Among the freshwater bivalves of Poland, the zebra mussel shows the highest fecundity (GILYAROV 1970, WALZ 1977, SPRUNG 1993). Its eggs are deposited in doses over the breeding period, typically extending from late spring to early autumn. The reproductive activity of the mussels depends on the water temperature, i.e. mainly on the geographic location of water bodies and their thermal conditions.

The eggs, fertilised in the water, hatch into free-swimming veliger larvae. The presence of planktonic larvae in the life cycle of *D. polymorpha* is indicative of a relatively recent marine origin of this bivalve (ACKERMAN et al. 1994).

The larvae usually remain in the plankton for 8–10 days (SHEVTSOVA 1968, HILLBRICHT-ILKOWSKA & STAŃCZYKOWSKA 1969, J. WIKTOR 1969). During that period they are exposed to predators, mainly fry, accounting for approximately 20% mortality (J. WIKTOR 1969, STAŃCZYKOWSKA 1977). When ca. 200 µm long, the larvae start falling slowly towards the bottom, and firmly attach themselves to the substratum. This stage is called postveliger (J. WIKTOR 1969, DYGA & LUBYANOV 1975, and others).

Postveligers are very sensitive to oxygen deficit in water. Below the 50% saturation they stop settling, migrate, and die after some time (KUZIN 1964, MIKHEYEV et al. 1969). On the bottom, they often encounter such conditions.

Availability of a suitable substrate to settle is a basic factor determining the survival of postveligers. The important traits of the substrate include its physical (e.g. hardness) and chemical properties, as well as its location in relation to the bottom, water current, etc. The studies carried out thus far clearly show that not all hard substrates are equally suitable for settling postveligers. According to WALZ (1973, 1975), plates of the same size made of copper and brass were colonised by a few postveligers, plates made of perspex, concrete, aluminium, and zinc by several hundred, and those of iron and PVC by over one thousand.

Studies focused on the protection of hydrotechnical installations against infestation by mussels are rather common. Few papers, however, are concerned with substrate selection under natural conditions, and this may be of crucial importance to the fates of the mussels in different habitats.

The transition from planktonic to sedentary life is critical to mussels, as described by KIRPICHENKO (1965), who suggested that this might be a period of the highest mortality; the same view was expressed by J. WIKTOR (1969) and STAŃCZYKOWSKA (1977). My own studies and calculations concerning this period (LEWANDOWSKI 1982b) indicate that the problem of abundance dynamics is complex and requires further investigations (LEWANDOWSKI 1982c).

The process of postveliger settling can follow different patterns, depending on the lake, site within a lake, and year. This may be a consequence of differences in habitat conditions or of year-to-year weather changes.

The postveliger stage persists for about ten days, then the mussels gradually become adult. Adults are attached to the substrate with their byssus threads, but under extreme conditions may detach the byssus and relocate passively or actively.

Typically, the life span of adult mussels is 4–5 years, occasionally extending even up to 7 years, and shells of such old animals are about 4 cm long (PIECHOCKI & DYDUCH-FALNIOWSKA 1993).

The species raises an enormous interest. The existing overviews (LIMANOVA 1964, 1978, SCHLOESSER et al. 1994) already comprise approximately 2,500 papers. After ten years of mussel invasion in the Great Lakes of North America (LEWANDOWSKI 1990, and others), a genuine explosion of papers on this species is observed in the USA and Canada.

These papers deal with the morphology, anatomy, physiology, and other aspects of the biology of the zebra mussel. In many publications, the mussels are considered as one of many components of biocoenoses. Numerous papers concentrate on damage caused by the mussels and on their control. Likewise, many publications discuss various aspects of the ecology of this species, its filtration capability or interactions with other organisms, especially fishes and birds.

Extensive field data, including those from the Masurian Lakeland, are used in models predicting changes in the zebra mussel abundance (RAMCHARAN et al. 1992a, b).

Mussel populations were thoroughly analysed in relatively few waters. These include the Gulf of Szczecin (J. WIKTOR 1969), Lake of Constance (WALZ 1973), Uchinskiy Dam Reservoir (LVOVA 1980), and the Rhine (JANTZ 1996). Various aspects of the ecology of adult mussels were extensively described by STAŃCZYKOWSKA (1964, 1977) and STAŃCZYKOWSKA & LEWANDOWSKI (1993b), based on long-term studies conducted in several dozen lakes in Poland and other European countries.

The materials collected mainly from the Masurian Lakeland in previous co-operative studies were also used (CZARNOŁĘSKI et al. 2000) to test predictions of the optimization model developed by KOZŁOWSKI & TERIOKHIN (1999). Tests of the optimization theory are now conducted under the project 6/P04C/050/15, State Comittee for Scientific Research: "Study on the life history traits of the zebra mussel *Dreissena polymorpha*".

Although extensive literature on the zebra mussel is available, some aspects of the ecology of this species still remain insufficiently explored. Most of the world literature concerns settled adult mussels. Data on planktonic larvae are much less abundant, and most of them concern mussel larvae as a component of the plankton in dam reservoirs of the European part of Russia. Still less information can be found on the specific period in the life of mussels – the transition from planktonic to sedentary life. No papers exist on relations between these three stages of the mussel life history.

The present paper is an attempt at a comprehensive description of the zebra mussel populations in lakes. It comprises all the three periods of its ontogenic development, i.e.:

- the stage of planktonic larvae, which takes several days and determines the expansion of this species,
- the critical period of transition from planktonic to sedentary life, which, although very short, counted even in hours, is decisive of the possibility of survival and population growth, and
- the period of sedentary and adult life, covering several years.

It seems that at various developmental stages, different environmental factors determine the abundance of the mussels: planktonic larvae are subject to factors different from those affecting postveligers, while adults are affected by still other factors.

This paper is an attempt at answering the question whether, and in which way, factors affecting juvenile stages influence the population of adult mussels and at analysing the effects of diversified mussel populations on the functioning of aquatic ecosystems. Some of these problems have been partly analysed in earlier papers (LEWANDOWSKI 1976, 1982a, b, 1983a, b, 1991, 1992, 1996a, b, 1999, STAŃCZYKOWSKA et al. 1976, 1983a, b, 1988, 1997, STAŃCZYKOWSKA & LEWANDOWSKI 1980, 1993a, b, 1995, LEWANDOWSKI & EJSMONT-KARABIN 1983, LEWANDOWSKI & STAŃCZYKOWSKA 1986, PREJS et al. 1990, LEWANDOWSKI et al. 1997, LEWANDOWSKI & OZIMEK 1997); this one is a comprehensive re-analysis, supplemented with new, previously unpublished data.

STUDY AREA

The main object of my study were zebra mussel populations in lakes of northern Poland. In total, 82 lakes were examined (Appendices 1 and 2). Most of them were located in the Masurian Lakeland. These were lakes of the Jorka basin, the river Krutynia, some lakes of the Great Masurian Lakes complex, and 42 scattered, mostly small lakes that do not belong to the Great Masurian Lakes complex. Moreover, the occurrence of mussels was analysed in three lakes of the Wigry National Park (Suwalskie Lakeland): Białe Wigierskie, Pierty, and Wigry, as well as in the Żarnowieckie Lake (Koszalińskie Coastland), and in heated lakes of the Gosławsko-Ślesińskie complex (Wielkopolskie Lakeland) forming a part of the cooling system of the Konin and Pątnów power plants.

The studied lakes varied considerably in their characteristics. Their surface area ranged from ca. 10 ha (Malinówko, Zelwążek) to several dozen or even over 100 km^2 (Mamry, Niegocin, Śniardwy, Wigry), the maximum depth varied from 2–3 m (Gosławickie, Iławskie, Jerzewko, Malinówko, Siercze) to over 50 m (Ełckie, Mokre, Piłakno, Wigry).

Most of the lakes were eutrophic, 12 were hypertophic, 15 mesotrophic, and one (Białe Wigierskie) can be regarded as oligotrophic (HILLBRICHT-ILKOWSKA & WIŚNIEWSKI 1996, KAJAK 1983, ZDANOWSKI 1992). It should be noted that the study on the occurrence of mussels in the mesotrophic lake Kołowin (Masurian Lakeland) was conducted before the ecological catastrophe in mid-1980s when, among others, all fishes were poisoned.

Six Gosławsko-Ślesińskie Lakes (Gosławickie, Licheńskie, Mikorzyńskie, Pątnowskie, Ślesińskie, Wąsoskie) form a complex connected by canals and included in the cooling system of the Konin and Pątnów power plants. Water temperature in these lakes varies but is always higher than in non-heated lakes. They are not covered with ice in winter, and the highest temperature in summer is usually about 30°C (ZDANOWSKI 1994).

The Żarnowieckie Lake was studied in the period when the project to construct a nuclear power plant, and a pumped-storage plant using lake waters for cooling was discussed (STAŃCZYKOWSKA & ZDANOWSKI 1986). The need to guarantee a trouble-free functioning of the cooling system was a starting point to study the mussel population in the lake and to predict its future development.

The lakes selected for the study of the mussel populations constituted a representative sample of lakes of Poland. They covered a large spectrum of environmental variation (size, depth, trophy, human impact, etc.) of the lakes colonised by the mussels. The lakes from which mussels are absent as a rule (e.g. distrophic lakes) were excluded.

In the 1970s, 1980s, and 1990s, the zebra mussel populations were investigated in these lakes with varying intensity. In some of them, all developmental stages, i.e. planktonic larvae, attached postveligers, and colonial adults, were examined, and in others only some stages. In some lakes, the studies were very intense, including many years, with samples taken several times over the growing season and at many sites. In other lakes, the study was less intense (Appendices 1 and 2, see: the end of the paper).

METHODS

The lack of comprehensive papers dealing with all the three developmental stages may arise from the fact that each stage requires different methods of research. In the case of free-swimming larvae, these are methods typically used in the studies on plankton, postveligers require methods used for studying periphyton, and adults require mainly benthological methods.

In this study, planktonic larvae were quantitatively sampled and processed with the standard technique described by HILLBRICHT-ILKOWSKA & PATALAS (1967). The occurrence of postveligers in the lakes, and especially their preferences for settling on different artificial and natural substrates were analysed with the author's own methods described in detail elsewhere (LEWANDOWSKI 1982b). For studying adults, the methods developed for large bivalves during long-term co-operative investigations, mainly in the Masurian Lakes (STAŃCZYKOWSKA 1964, LEWANDOWSKI & STAŃCZYKOWSKA 1975, STAŃCZYKOWSKA et al. 1983b, LEWANDOWSKI et al. 1997) were applied.

To study **planktonic larvae**, a 5-litre apparatus of Bernatowicz type and a planktonic mesh screen with 30 µm mesh were used. To analyse seasonal dynamics of abundance of larvae, plankton samples were taken at 5–8 day intervals over the period of their occurrence in the plankton. To analyse horizontal distribution of larvae, samples were taken from the littoral above shoals of attached mussels and from the pelagial, far from the adults, usually at several littoral and pelagic sites. To compare year-to-year variation, samples were taken at 17 sites in the lake Inulec during two consecutive seasons (1997, 1998).

To determine vertical distribution of larvae, samples were taken at one-metre intervals from the water surface. In the Gosławsko-Ślesińskie Lakes, samples were taken from three layers: epi-, meta-, and hypolimnion, separately.

Larvae were measured with a calibrated eyepiece, to the nearest 15 µm. From each sample, 50–100 larvae were measured. In total, about 950 samples were taken and over 8 thousand larvae measured.

Postveliger settling on artificial and natural substrates was experimentally examined in the Mikołajskie Lake in 1975, in Majcz Wielki in 1978, and in Inulec in 1998. Sets of artificial substrates were used to analyse the phenology of settling and growth of postveligers. Natural substrates were used to study site selection.

Microscope slides were used as artificial substrates. They were placed in an aquarium for two weeks prior to the experiments, to allow a development of a thin film of periphyton. Thus, settling postveligers were attached to periphyton algae, rather than to smooth glass surface. Sets of different numbers of settling slides were also used to determine the horizontal and vertical distribution of postveliger settling in the lake (Fig. 1).

In experiments on substrate selection by postveligers, live organic substrates (zebra mussel col-

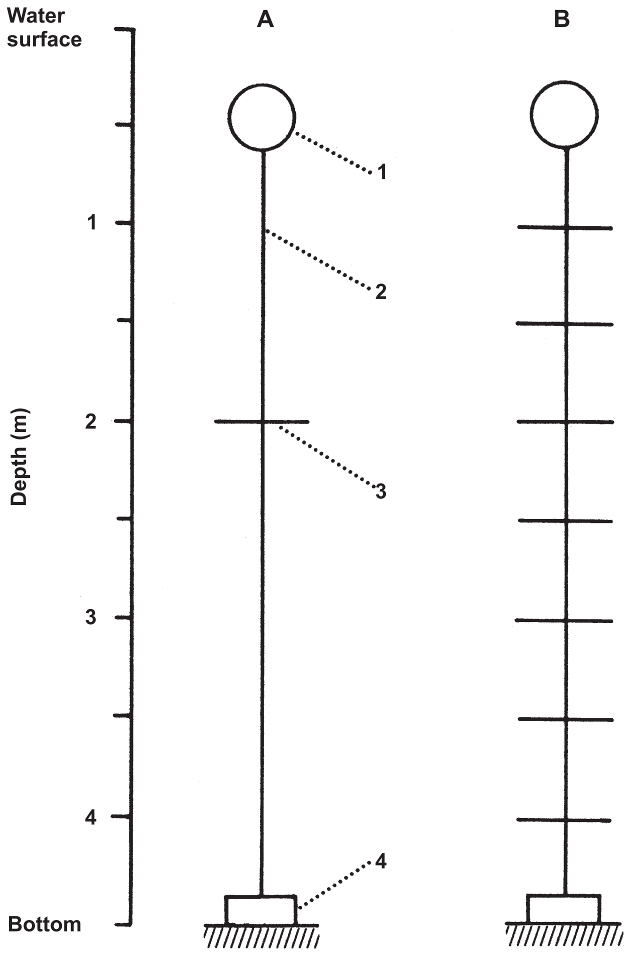


Fig. 1. Scheme of "glass" setups, A – basic setup, B – setup used for mussel settling at different depths, 1 – buoy, 2 – rope, 3 – setup (plastic netting + slide), 4 – brick

onies, plants), silt, and also inorganic substrates (sand, stones) were applied. The experimental setups were exposed in the lake littoral during the growing season (from May to September). The number of attached postveligers was determined by surveying the preserved material on a tray, and then under a stereomicroscope to record the smallest individuals (200–300 µm in length).

In these experiments and in "slide" experiments jointly about 5.5 thousand postveligers were measured.

The occurrence of postveligers in lakes was assessed by surveying under a stereomicroscope various kinds of substrates removed from lakes, such as stones, empty mollusc shells, unionid bivalves, mussel colonies, and plants. Various species of Unionidae were considered, as well as different species of plants grouped into annuals and perennials.

The occurrence of **adult zebra mussels** in the lakes was determined from different numbers of sites. In small lakes with little diversified littoral, mussels were collected from 2–3 sites. The number of sites was larger in larger lakes, reaching a maximum of 50 sites in the lake Inulec, with a very complex littoral.

The samples were taken along the slope, typically at 1-m intervals, across the whole zone of mussel occurrence that was 4–7 m deep during the study period.

In shallow places, samples were taken with a 0.5 × 0.5 m frame from which mussels were removed manually. In deeper places, Bernatowicz sampler with a catching surface of 0.16 m^2 was used, or a bottom dredge with a side of 40 cm, dragged along a bottom section, parallel to the shoreline. In several lakes, samples were taken with the help of a diver who collected shells from the area delimited by a frame thrown onto the bottom at random. The contents of the frame, dredge, or Bernatowicz sampler were placed in a benthos sieve, and live mussels, occurring mainly in colonies, were selected. Samples from shallower sites typically contained juvenile mussels attached to submerged plants. These were samples abounding in mussels and uniform, hence they were not divided into subsamples.

Based on the samples taken, densities of mussels per m^2 bottom were calculated, and for individuals settled on plants per m^2 of vegetation-covered bottom. Wet biomass (with shells) was determined by weighing mussels after draining water on a filter paper. The length of mussels was measured with a caliper slide to the nearest 0.1 mm.

The age of adult mussels was determined by counting rings of annual growth on the shell. This is a commonly used method of mussel ageing (NEGUS 1966, SPIRIDONOV 1975, STAŃCZYKOWSKA 1977), although subjective and not always reliable, especially in the case of old individuals. Age determination was facilitated by collecting mussels in different periods of the growing season, when the zone of the annual growth was differentially developed, as well as by detailed observations of young individuals of the year (LEWANDOWSKI 1983b), and field experiments on the growth of mussels of different age (STAŃCZYKOWSKA & LEWANDOWSKI 1995).

RESULTS

1. DISTRIBUTION OF SETTLED ZEBRA MUSSELS IN DIFFERENT HABITATS

In the lakes under study, the zone of occurrence of adult mussels covered the littoral and partly the upper sublittoral, so that the mussel colonies formed a ring around the lake, though sometimes interrupted and incomplete.

The abundance of mussels in these rings or zones of occurrence varied widely. In the lakes under study, the abundance of mussels occurring in colonies on the littoral bottom was usually of the order of several hundred individuals per m^2. Only in seven out of 83 lakes examined no mussels were found (Kraksy Duże, Sarż, Sędańskie, Siercze, Spychowskie, Szeląg Mały, and Zyzdrój Mały), and in nine other lakes (Białe Wigierskie, Burgale, Ełckie, Hartowiec, Juno, Uplik, Wobel, Zdrużno and Zyndackie) the densities were very low (below 10 individuals m^{-2}). In 16 lakes, the mean densities in the zone of occurrence in different periods exceeded 1,000 ind. m^{-2}, with a maximum of about 3,500 ind. m^{-2} (wet mass of about 1.7 kg m^{-2}) in Lampackie and Tałty.

1.1. Effect of lake trophy on the occurrence of the zebra mussel

The zebra mussel occurs in a rather wide range of lake trophic conditions, and its densities can vary widely between lakes of similar trophy.

One of the oligotrophic lakes (Białe Wigierskie) was almost devoid of the mussels, only one live individual being recorded. As no empty mussel shells were found, this might have been an accidental individual.

The mussels occurred in all the 15 mesotrophic lakes. In three of them (Gant, Kołowin, and Ołów) the mean densities in the zone of occurrence were of the order of 2 thousand individuals per m^2, and in only 2 lakes (Gim and Piłakno) they did not exceed 100 ind. m^{-2}. In the remaining mesotrophic lakes, the mean densities were of the order of several hundred individuals per m^2.

The mussels were found to disappear from heavily polluted hypertrophic lakes; in such conditions their densities were very low, below 100 ind. m^{-2} at most (such lakes as Hartowiec, Iławskie, Kraksy Duże, Tuchel, Wobel).

The occurrence of mussels was most variable in eutrophic lakes. In some of them there were no mussels at all (e.g. Sarż, Sędańskie, Siercze, Zyzdrój Mały), whereas in others the highest densities exceeded 2–3 thousand ind. m^{-2} (e.g. Lampackie, Lampasz). The latter group of lakes, which was situated on the river Krutynia, was characterised not only by a suitable substrate for settled mussels, but also by a moderate water flow favourable for these bivalves.

1.2. Differences in mussel densities in lakes connected by a river

Two river-lake systems were examined: the system of the river Jorka, connecting five lakes, and the system of the river Krutynia, connecting 19 lakes. The lakes of the Jorka system comprise Majcz Wielki, Inulec, Głębokie, Zelwążek and Jorzec. At the end of the 1970s, the mean mussel densities in consecutive lakes were found to decline downstream (Fig. 2). The mussels were the most abundant in the mesotrophic lake Majcz Wielki, situated the highest in the basin, where on the average 510 ind. m^{-2} were noted in the zone of occurrence. The decline in mussel densities in the lower situated lakes may have been due to the rainbow trout (*Salmo gairdneri*) culture in the Głębokie Lake, which was a source of nutrients and eutrophication of these lakes. In Jorzec, the lowermost lake of the system, the mean densities of mussels were merely 130 ind. m^{-2} (Fig. 2).

The 19 lakes of the Krutynia system represented almost all trophic types, from clean mesotrophic to

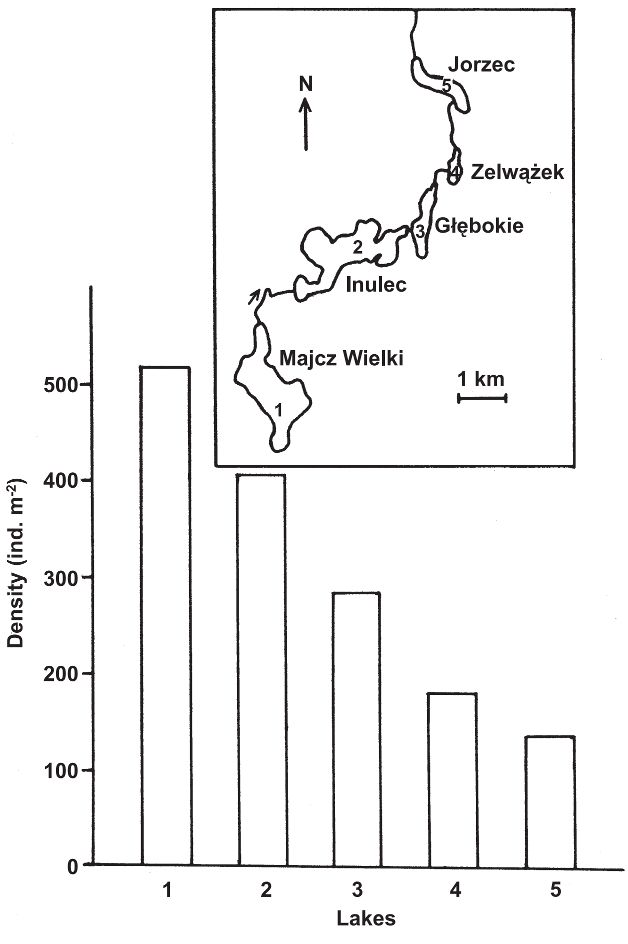


Fig. 2. Mean densities of *D. polymorpha* in lakes of the Jorka river-lake system in the 1970s (based on the data from STAŃCZYKOWSKA et al. 1983b)

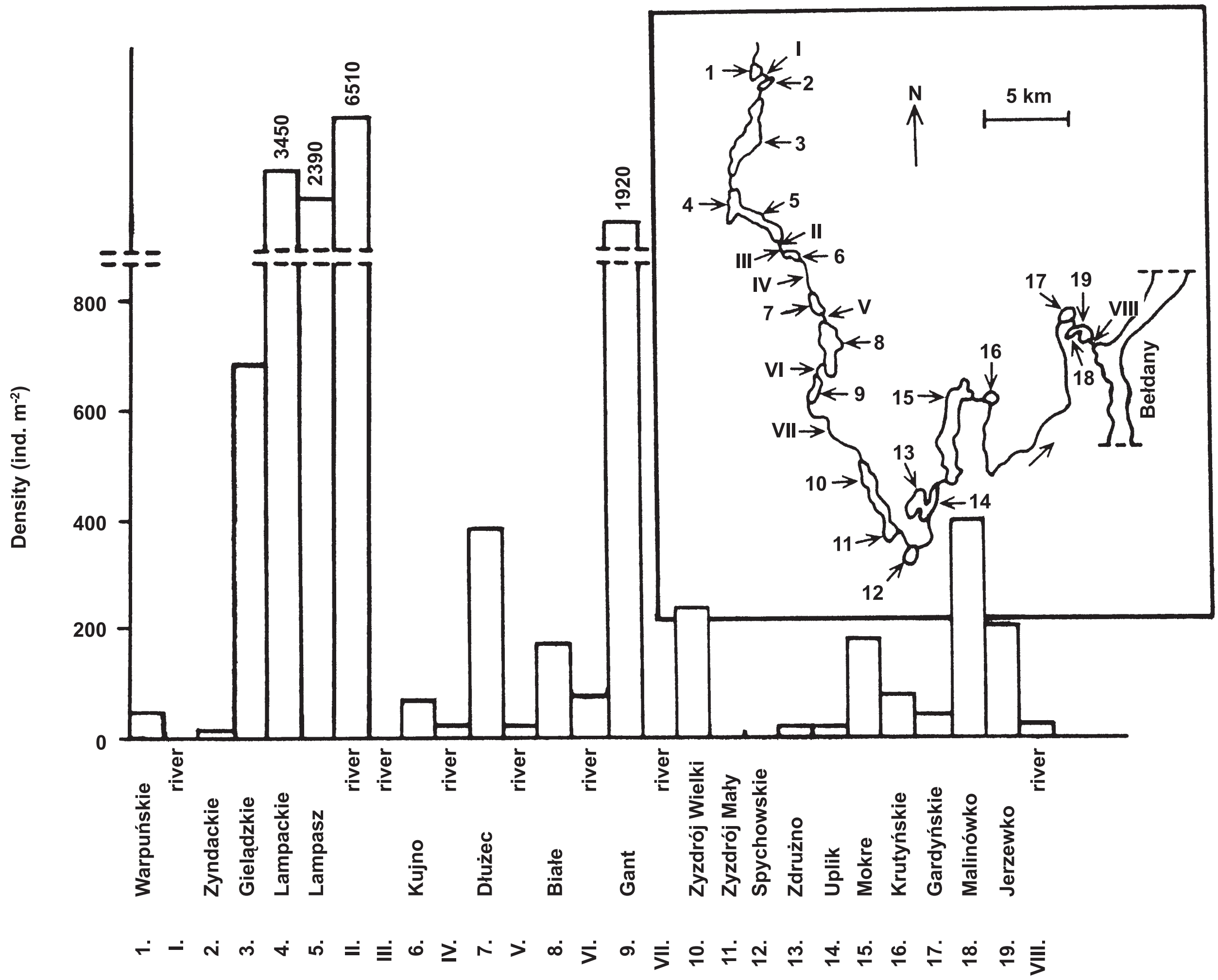


Fig. 3. Mean densities of *D. polymorpha* in lakes and river sections of the Krutynia river-lake system (after LEWANDOWSKI 1996a, modified)

heavily polluted lakes. Consequently, the mussel densities differed considerably. Even larger differences were noted in the mussel densities in river sections of the Krutynia system (Fig. 3). In several sections, the mussels were absent, and the highest mean density (below lake Lampasz) was 6,500 ind. m^{-2} (wet mass about 4.6 kg m^{-2}). In this place, a thick uniform mussel layer coated a large part of the river bed. A maximum of over 11 thousand ind. m^{-2} was noted (biomass of 7.9 kg m^{-2}).

A specific habitat where the mussels can settle is constituted by the transition zone between a river and a lake. In the Krutynia river-lake system such zones were analysed in detail in two lakes: a eutrophic Kujno and a mesotrophic Gant (LEWANDOWSKI 1996b). Very high densities of mussels were observed in the river part of the transition zone, at the river outflow from these lakes. The mussels were more abundant in the transition zones of the mesotrophic lake Gant (Table 1), in places reaching densities of 6,000–9,000 ind. m^{-2}, and biomass of the order of 4–5 kg m^{-2}.

Table 1. Mean densities of *Dreissena polymorpha* (ind. m^{-2}) in the river and lake transition zones of two lakes (after LEWANDOWSKI 1996b, modified)

Lake		Kujno	Gant
Zone of river inflow	river	0	20
	lake	0	1,600
Zone of river outflow	lake	950	1,200
	river	2,900	7,900

1.3. Vertical distribution of the zebra mussel

The depth of mussel occurrence varied between the lakes, the maximum observed depth being 13 m. To that depth, mussels occurred in the mesotrophic lake Mamry Płn. In other mesotrophic lakes (e.g. Kierzlińskie, Majcz Wielki, Ołów, Piłakno), they were noted to a depth of 6–7 m. Only in few eutrophic lakes, the maximum range was to 5–6 m (e.g. Głębokie, Inulec, Żarnowieckie). Most often, in eutrophic lakes, the mussels did not occur deeper than 4 m.

Typically, within their zone of occurrence in lakes, the mussels were the most abundant at a depth of 2–4

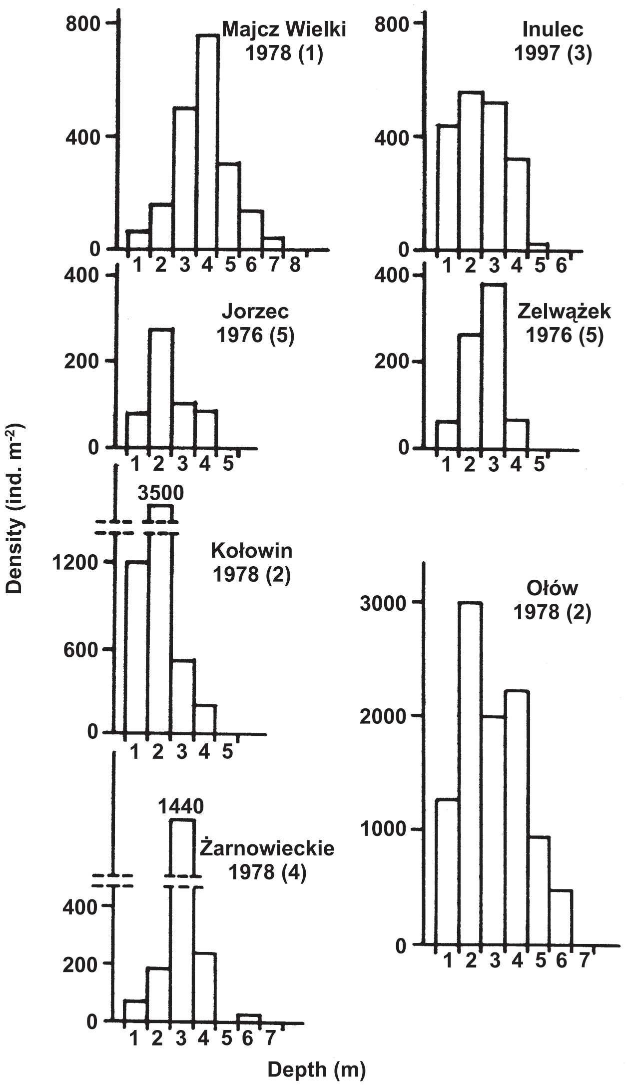


Fig. 4. Mean densities of *D. polymorpha* at different depths of selected lakes (based on: 1 – LEWANDOWSKI 1982b, modified, 2 – LEWANDOWSKI 1991, modified, 3 – LEWANDOWSKI 1999, modified, 4 – LEWANDOWSKI & STAŃCZYKOWSKA 1986, modified, 5 – STAŃCZYKOWSKA et al. 1983b, modified)

m. In general, above and below this depth their densities were lower (Fig. 4). In some situations, such as extremely suitable substrates, the mussels may locally reach very high densities at the shallowest sites (0.2–0.3 m). This was the case e.g. in the lake Inulec, where approximately 6,500 ind. m^{-2} were noted within a small area, or in the Żarnowieckie Lake, where, in the shallowest places, sites with no mussels bordered on sites supporting about 7,600 ind. m^{-2}.

1.4. Horizontal distribution of the zebra mussel in lakes

Usually, the "ring" of the lake littoral is not uniform; likewise, the mussels living in the littoral do not form uniform rings in lakes. A relatively even horizontal distribution of settled mussels can be found in rather small lakes, sheltered from winds, and of very slight flow. They were represented by a mesotrophic lake Kuc, where the littoral was uniformly covered with a carpet of *Chara* spp., and by the lake Ołów, almost totally devoid of submerged plants, thus with the littoral of a similar character in the entire lake (Fig. 5).

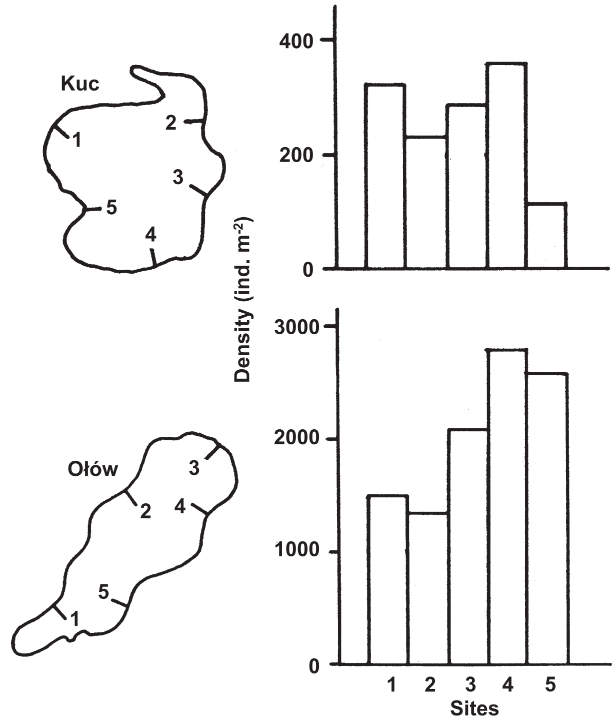


Fig. 5. Distribution of *D. polymorpha* in lakes with little diversified littoral (after LEWANDOWSKI 1991, modified)

Most often, the littoral is diversified, mosaic, and the abundance of mussels also varies under such conditions. In the lakes Jorzec and Głębokie (basin of Jorka), lower densities of these bivalves were observed, e.g. in heavily silted bays (Fig. 6). In the Mikołajskie Lake, there were no or few mussels e.g. in heavily polluted places (urban region) (Fig. 7).

Based on a very detailed two-year study conducted in the lake Inulec, basin of Jorka (50 sites in the lake, assistance of a diver), a map of the occurrence of mussels was prepared. The lake is characterised by a complicated shape, numerous bays, peninsulas, islands, and shallow reedbeds. The horizontal distribution of settled mussels was uneven. Their densities were the highest in the eastern part of the lake, where over 1,000 ind. m^{-2} were noted on a large part of the bottom (Fig. 8). Mussels were absent from small silted bays. The occurrence of mussels around islands varied widely, mussel-free places adjoining those with abundant adults. Especially high densities of mussels, up to 6,500 ind. m^{-2}, were noted at the south-eastern shore of an island situated in the central part of the lake. Places abundantly colonised by mussels were typically characterised by a stony bottom, suitable for settling young individuals.

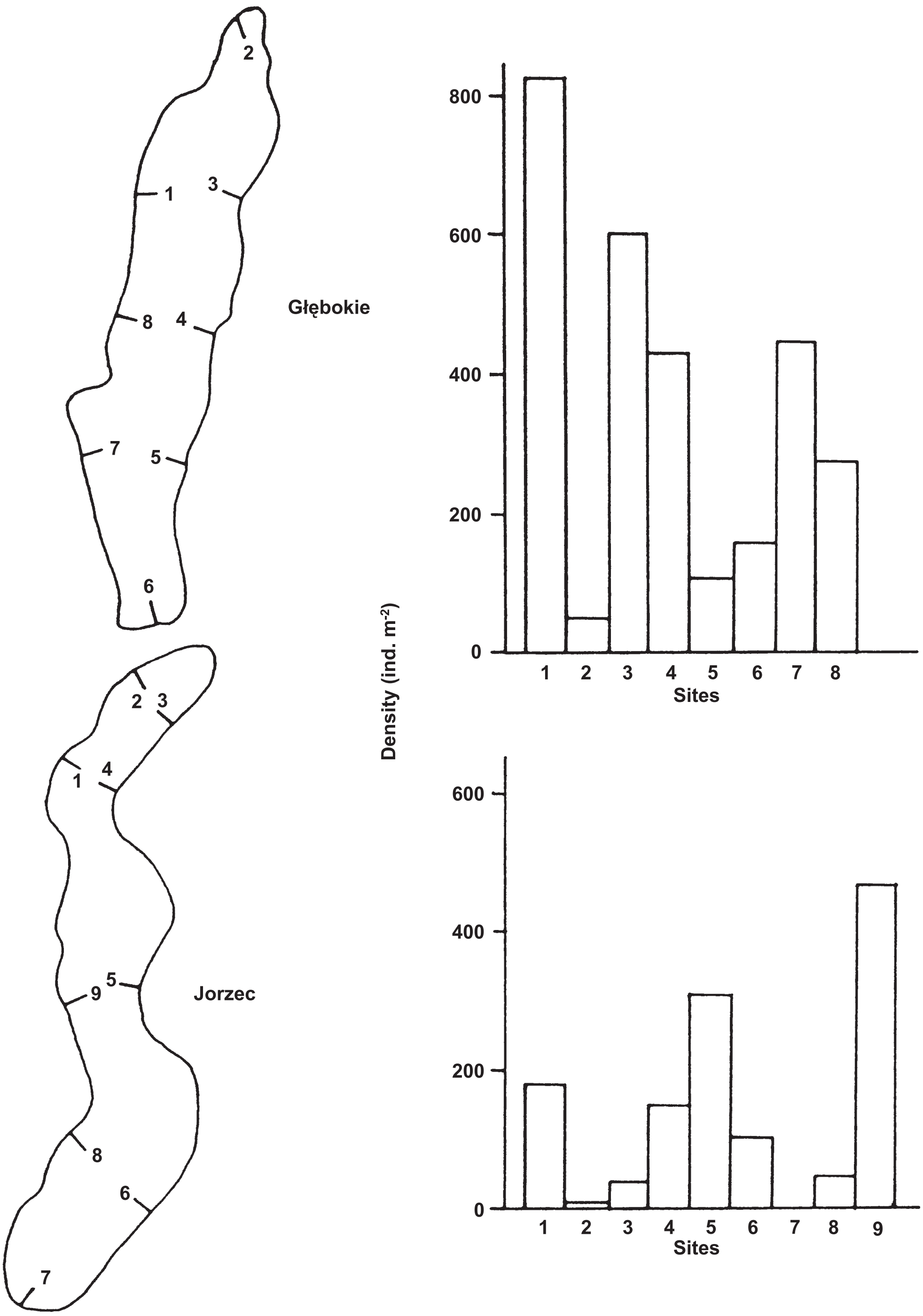


Fig. 6. Distribution of *D. polymorpha* in lakes Jorzec and Głębokie (after STAŃCZYKOWSKA et al. 1983b, modified)

1.5. Long-term changes in abundance of settled zebra mussels

Long-term studies, as well as repeated studies at several-year intervals, on the occurrence and density of settled mussels, showed that their populations were not stable. Occasionally, they were characterised by large variation (LEWANDOWSKI 1982c – literature review, STAŃCZYKOWSKA & LEWANDOWSKI 1993b, 1997).

During the last 20-year period, the mussels were investigated on three occasions in five lakes connected by the river Jorka. Their abundance at the end of the 1970s (as noted above, showing a steady decline downstream), differed markedly from that recorded in the early 1990s. The smallest changes were noted in the mesotrophic lake Majcz Wielki, where the mussel densities, though slightly declined, were maintained within the order of magnitude similar to that observed in the 1970s (several hundred mussels m^{-2}). In the lake Inulec, situated lower downstream, the mussel density increased. Most drastic changes occurred in the three lowermost lakes of the Jorka system. In these heavily eutrophicated lakes, the mussel abundance declined significantly as compared to earlier years, in places even to zero. This decline may have been due to the trout culture in the Głębokie Lake that largely increased the trophy of these lakes. The culture ceased to exist as late as in 1988. In the late 1990s, a steady restoration of the mussel population was observed in central lakes of the system, but not yet in the lowermost lake Jorzec (Table 2).

Large fluctuations of the mean mussel densities were observed in the Żarnowieckie Lake. Over the eight-year study period (in the 1970s and 1980s), the population increased from 65 ind. m^{-2} to almost 600 ind. m^{-2}, that is, by a factor of 9, then it decreased to one-fifth (not much more than 100 ind. m^{-2}) (LEWANDOWSKI & STAŃCZYKOWSKA 1986).

Long-term studies on the occurrence of mussels were conducted in the eutrophic Mikołajskie Lake. In the first period of the study (1960s and 1970s), large abundance fluctuations were observed, from nearly 0 to more than 2,000 settled individuals per m^2 of the bottom in the zone of occurrence (STAŃCZYKOWSKA 1961, 1977). In the later period (1980s and 1990s), after a dramatic decline to several or several dozen individuals, this low level was maintained for a long time with almost no fluctuations (STAŃCZYKOWSKA & LEWANDOWSKI 1993b) (Fig. 9). The first period, in which two violent population declines from a very high level were observed, did not seem to reflect the increasing trophy of the lake, as this factor would prevent the restoration of the population after crashes. These deep declines occurred from very high population levels in the whole lake, and might be related to population overdensity. However, after the last crash in mid-1970s, the population did not recover and its very low density might be a consequence of the heavy pollution of the lake. Perhaps, the urban sewage treatment plant established in the early 1990s will stop the degradation of this lake. A small increase in the mussel abundance at the end of the 1990s may signal this tendency.

In addition to changes in the density of mussels, pronounced changes were observed in the depth of mussel occurrence in the Mikołajskie Lake. In the initial period of the study, especially in the years of very high abundance of mussels, they occurred to a depth of 7.5 m. In the second half of the 1970s, the maximum depth was reduced by 2 m (STAŃCZYKOWSKA & LEWANDOWSKI 1993a). More recent studies, conducted in 1997, showed that the mussels were present only to a depth of 2 m. When considering the role of mussels in a lake ecosystem, also significant changes in the width of the zone of their occurrence should be observed in addition to changes in their abundance. It should be noted here that during the three years prior to the last observations (1997) no mussels were noted in the Mikołajskie Lake (Fig. 9).

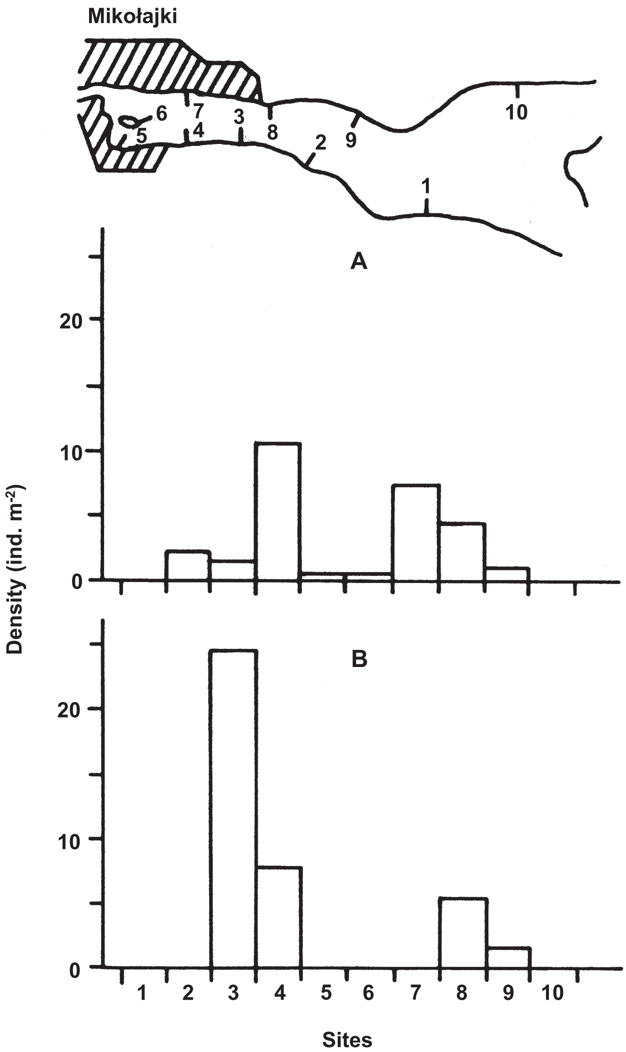


Fig. 7. Distribution of *D. polymorpha* in the Mikołajskie Lake in 1987 (A – after STAŃCZYKOWSKA & LEWANDOWSKI 1993a, modified) and in 1997 (B)

Table 2. Mean densities (ind. m^{-2}) of *Dreissena polymorpha* in the lake zone of the Jorka river basin in three periods

Lake	1970s (STAŃCZYKOWSKA et al. 1983b)	Early 1990s (LEWANDOWSKI et al. 1997)	Late 1990s (LEWANDOWSKI, unpublished)
Majcz Wielki	510	360	180
Inulec	400	1,300	860
Głębokie	280	20	80
Zelwążek	175	0	5
Jorzec	130	0	0

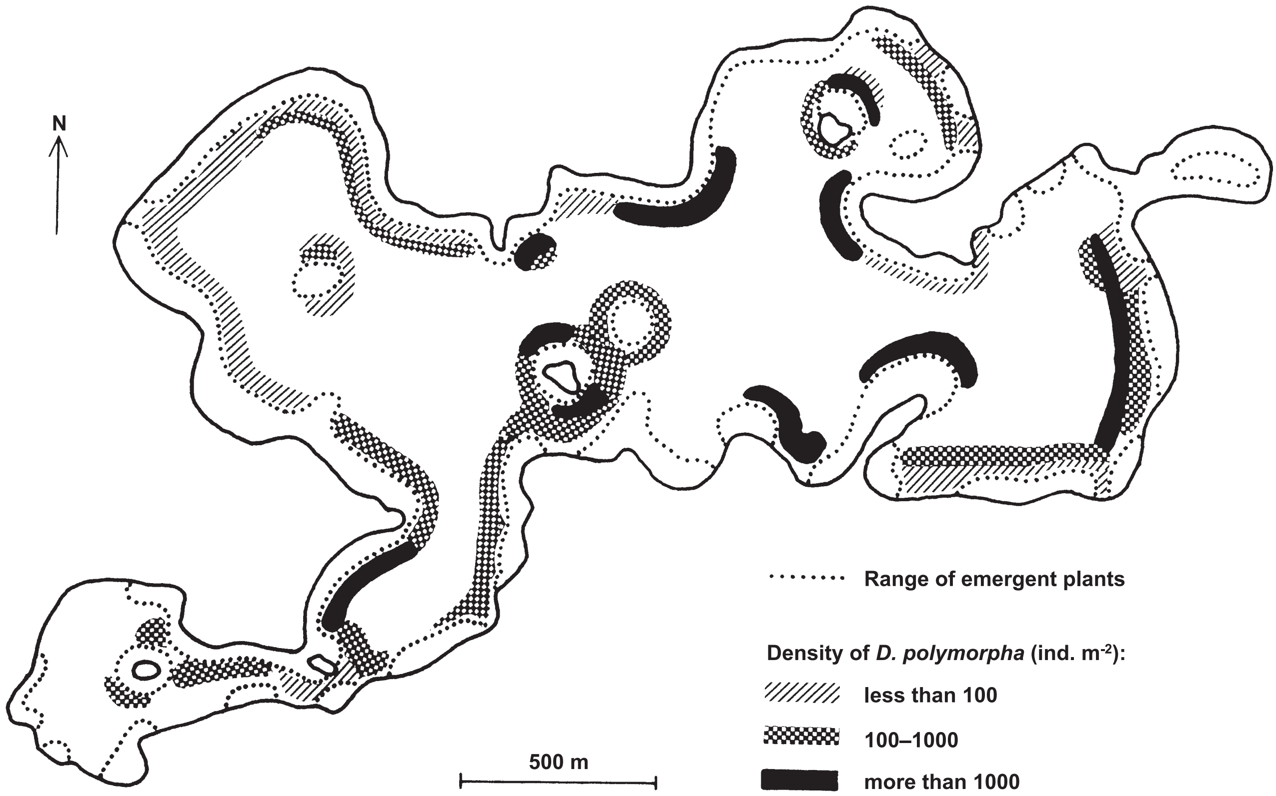


Fig. 8. Distribution of settled *D. polymorpha* on the bottom of the lake Inulec in 1997 (after LEWANDOWSKI 1999, modified)

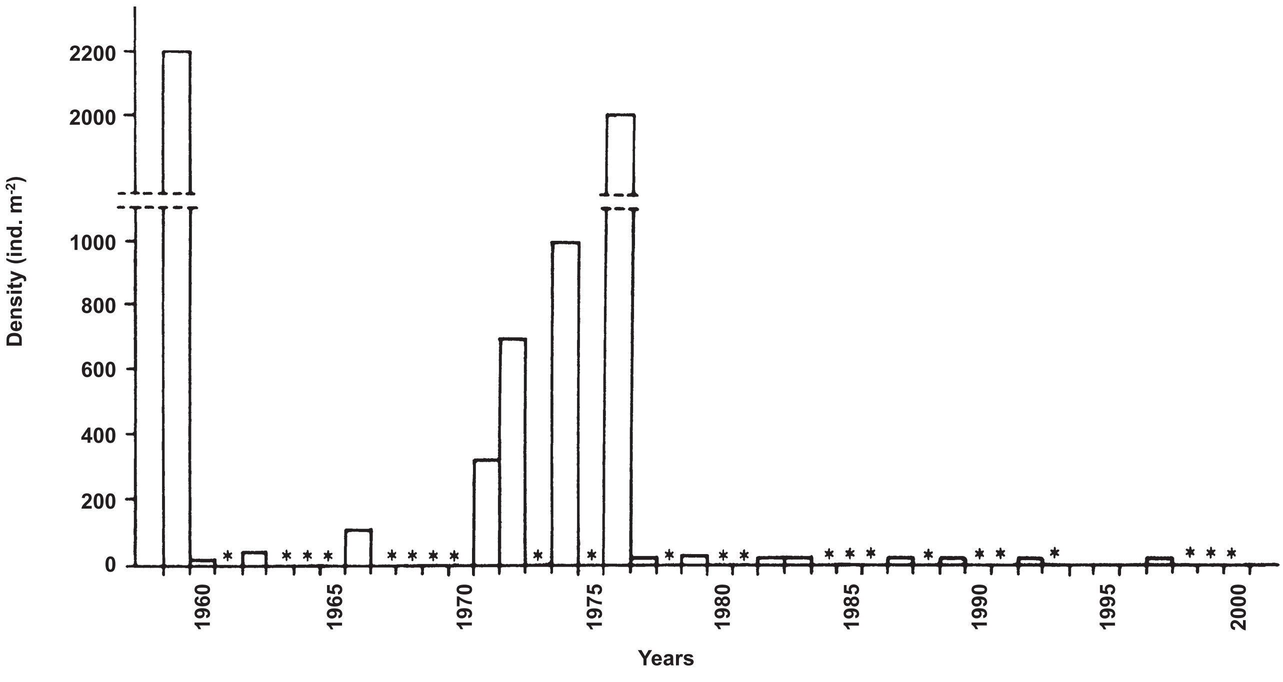


Fig. 9. Population dynamics of settled *D. polymorpha* in the Mikołajskie Lake (asterisk denotes lack of data) (based on STAŃCZYKOWSKA 1975, LEWANDOWSKI 1982c, supplemented)

Long-term observations on mussel populations were conducted also in other lakes of the Great Masurian Lakes complex. In most of them, populations were observed to vary from year to year. For example, in the lakes Śniardwy and Nidzkie, at population densities of the order of several hundred individuals per m^2, the abundance varied by factor of 2–4. In many lakes of the central part of the system of the Great Masurian Lakes, which were most eutrophicated, deep declines in the abundance of mussels were noted often from a very high level (e.g. in the 1970s: 3,600 ind. m^{-2} in Tałty, 1,300 ind. m^{-2} in

Niegocin), even to their total disappearance. In the 1950s and 1960s, the mean densities of mussels in lakes of the central part of the Great Masurian Lakes system (e.g. Boczne, Jagodne, Ryńskie, Szymon) examined by STAŃCZYKOWSKA (1964) exceeded 1,000 ind. m^{-2}. Throughout the study period, the most stable and abundant populations of mussels were noted in the northern part of the Great Masurian Lakes system, i.e. in the lakes of relatively low trophy (complex of the lake Mamry) (STAŃCZYKOWSKA & LEWANDOWSKI 1993b, STAŃCZYKOWSKA et al. 1997).

2. DISTRIBUTION AND ABUNDANCE DYNAMICS OF PLANKTONIC LARVAE IN LAKES

Colonisation of new habitats by the zebra mussel, so characteristic of this invasive species in spite of the sedentary life of adults, is possible due to their free-swimming planktonic larvae.

During the several-day period of planktonic life (typically 8–10 days), larval mussels grow from the length of several dozen micrometers to over 200 µm. In the lakes that I studied, the smallest planktonic larvae were 65 µm in length and the longest were 275 µm.

As the fecundity of the mussels is high, planktonic larvae can be very abundant. From several thousand to several hundred thousand larvae per 1 m^3 of water were noted in peaks, the number of which can vary from one to several. Also the duration of the reproductive period in the studied lakes may vary from one to three months.

2.1. Effect of temperature on abundance dynamics

According to the literature data, the reproductive activity of mussels begins at temperatures of about 12–17°C, and the maximum reproduction occurs at 20–22°C (J. WIKTOR 1969, WALZ 1973, LVOVA 1980, SPRUNG 1989).

In the Masurian lakes under study, first larvae were noted most often in June (sometimes later), at surface water temperatures of 17–20°C. The disappearance of planktonic larvae was generally observed in September, at water temperatures of 14–18°C. Changes in the abundance of larvae corresponded to changes in the water temperature: the abundance increased with temperature, and declining temperatures were associated with reduction in the number of larvae or their disappearance from the plankton (Fig. 10). In the initial period of the occurrence of planktonic larvae, their numbers were low. Peaks were noted in the warmest periods (end of June, July). In the final, coolest period of the season (September), densities of larvae were low, and they disappeared when temperatures continued to drop.

A clear effect of temperature on the occurrence of larval mussels was observed in heated lakes of the Gosławsko-Ślesiński complex (for thermal conditions

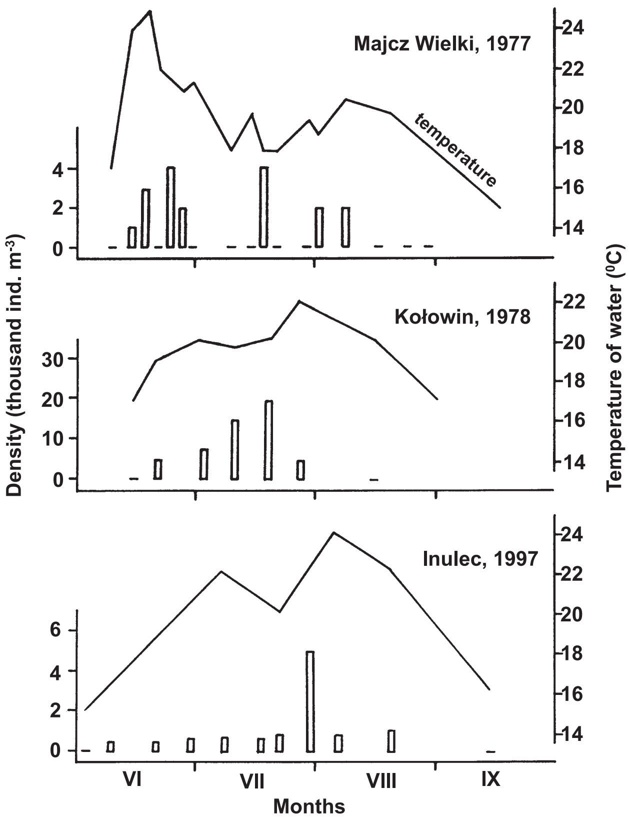


Fig. 10. Density of *D. polymorpha* larvae in the plankton of different lakes in relation to changes in the temperature of surface waters (based on LEWANDOWSKI 1982a, LEWANDOWSKI 1999)

see "Study area"); the waters of these lakes reach the temperature suitable for mussel reproduction by about two months earlier than e.g. Masurian lakes. In some of them, planktonic larvae were present already in March–April (Fig. 11). In these lakes, larvae disappeared from the plankton in September, thus like in the Masurian lakes, but water temperatures in the heated lakes at that time were often higher than 20°C. Even in November they exceeded 12°C, thus being suitable for mussel reproduction.

Thus, the water temperature clearly influenced the timing of the appearance of larval mussels in the plankton and their abundance dynamics, whereas the termination of reproductive activity and disappearance of larvae from the plankton should rather be related with the seasonal exhaustion of gametes in adults.

2.2. Differences in densities of larvae between connected lakes

The complex of the six heated Gosławsko-Ślesińskie Lakes described above represents a closed system of lakes connected by canals. Although the water flow is forced, the lakes differ markedly with respect to the abundance of mussel larvae. The peak densities ranged from 140 thousand per m^3 (Wąsoskie Lake) to

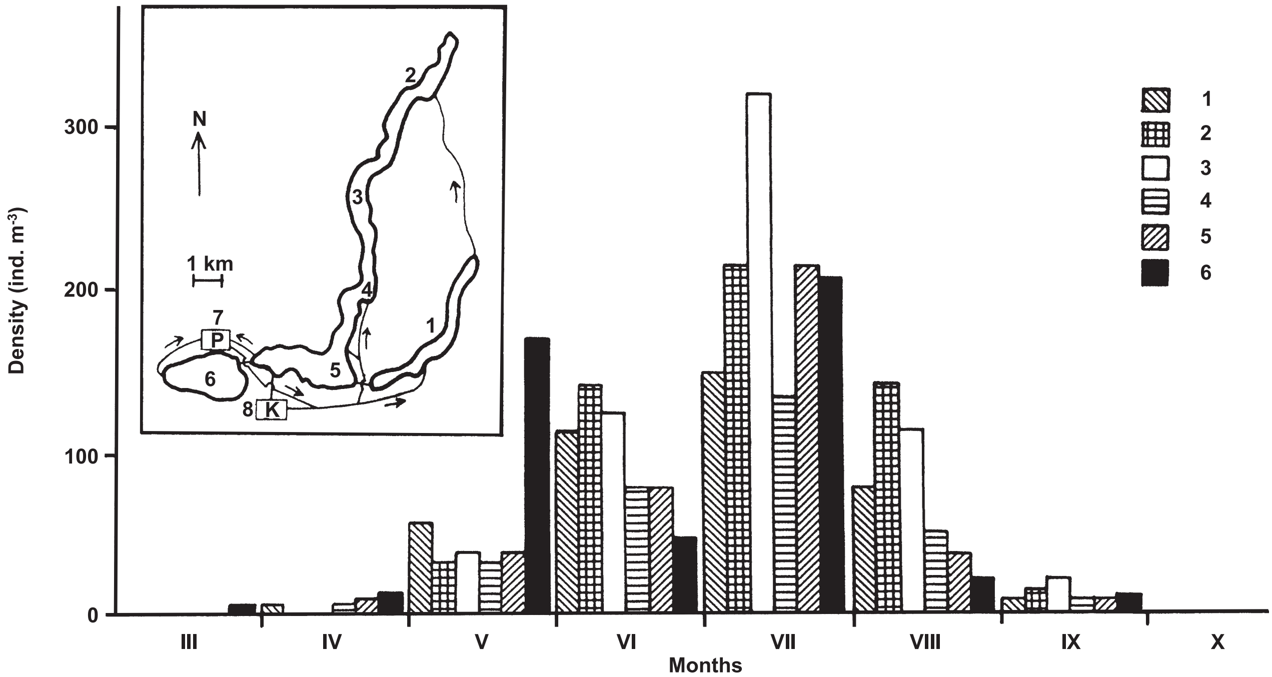


Fig. 11. Density of *D. polymorpha* larvae in the plankton of heated lakes: 1 – Licheńskie Lake, 2 – Ślesińskie Lake, 3 – Mikorzyńskie Lake, 4 – Wąsoskie Lake, 5 – Pątnowskie Lake, 6 – Gosławickie Lake; 7 – Pątnów power plant, 8 – Konin power plant (after LEWANDOWSKI & EJSMONT-KARABIN 1983, modified)

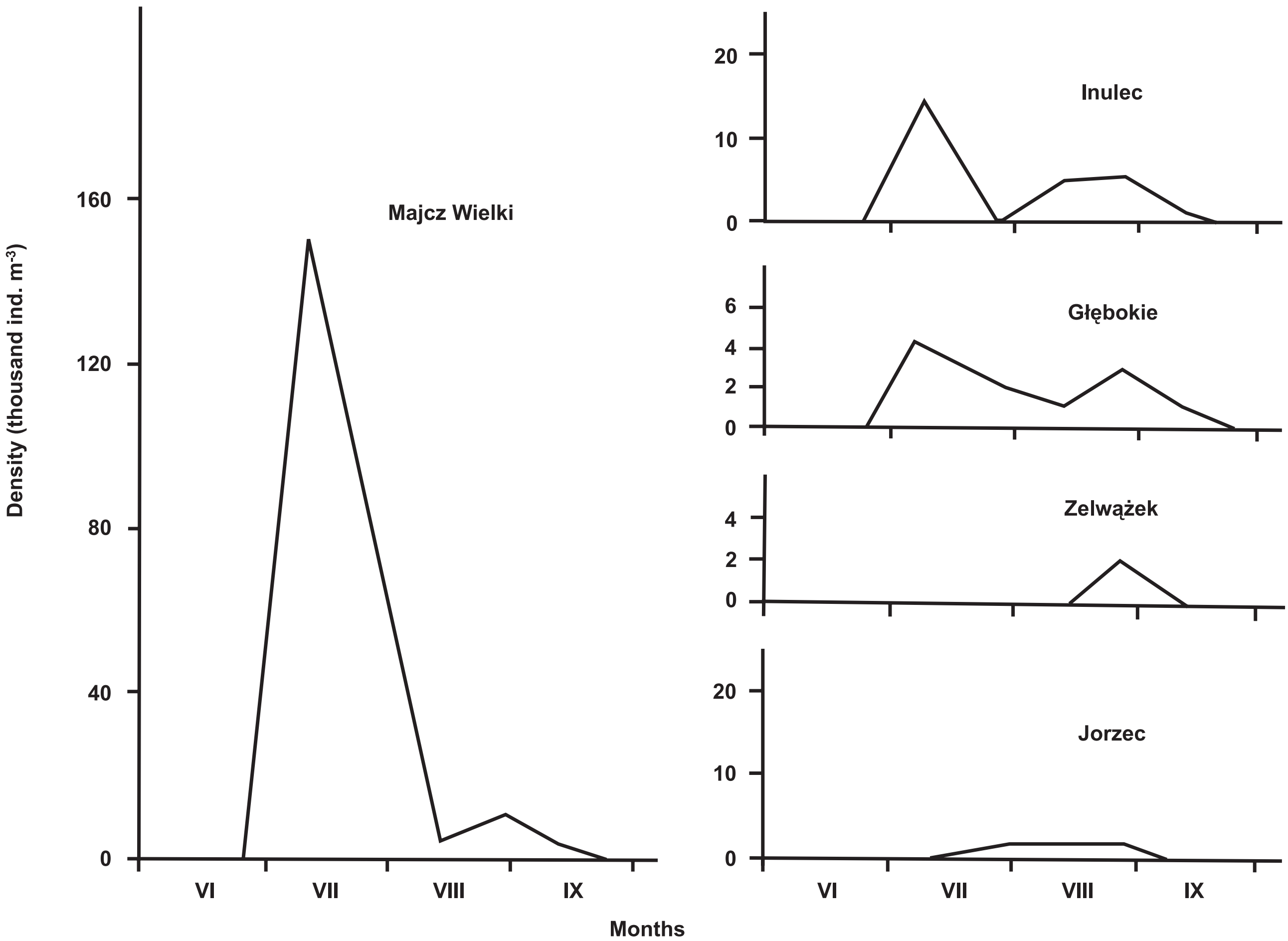


Fig. 12. Population dynamics of *D. polymorpha* larvae in the pelagial of five lakes in the Jorka basin in 1976 (after LEWANDOWSKI 1982a, modified)

320 thousand per m^3 (Mikorzyńskie Lake). No differences, however, were observed in the abundance of larvae between less heated and more heated lakes. In more heated lakes (Licheńskie, Ślesińskie), the maximum densities did not depart markedly from those observed in the remaining lakes of this complex (Fig. 11).

Five lakes on the Jorka river are situated close to each other. At the same time, their densities of planktonic larvae differed markedly, and also their abundance dynamics differed. The highest densities were observed in the mesotrophic lake Majcz Wielki, situated in the upper part of the system (146 thousand m^{-3}), and the lowest densities in the eutrophic lake Zelwążek, located in the lower part of the Jorka basin (2 thousand m^{-3}) (Fig. 12).

2.3. Year-to-year fluctuations in abundance of larvae

The population dynamics of planktonic larvae was examined in the lake Inulec (Jorka basin) during two consecutive years. In both these years, larvae appeared in the plankton in the first half of June and disappeared in September, but changes in their densities showed differences. In the first year (1997), a peak of 4,800 larvae per m^3 was noted at the end of July and the beginning of September. In the second year, two peaks were observed: in the first half of June and in the second half of July. Densities in both peaks (10,800 and 11,300 ind. m^3) were over two times higher than the maximum in the preceding year (Fig. 13).

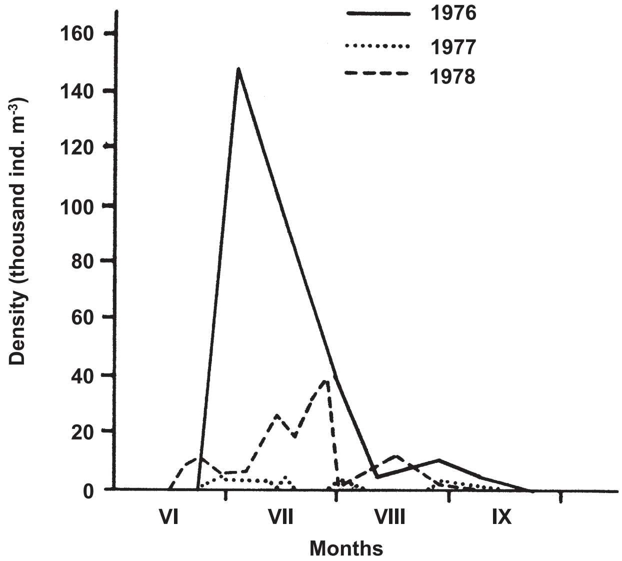


Fig. 14. Population dynamics of *D. polymorpha* larvae in the pelagial of the lake Majcz Wielki during three successive years (after LEWANDOWSKI 1982a, supplemented)

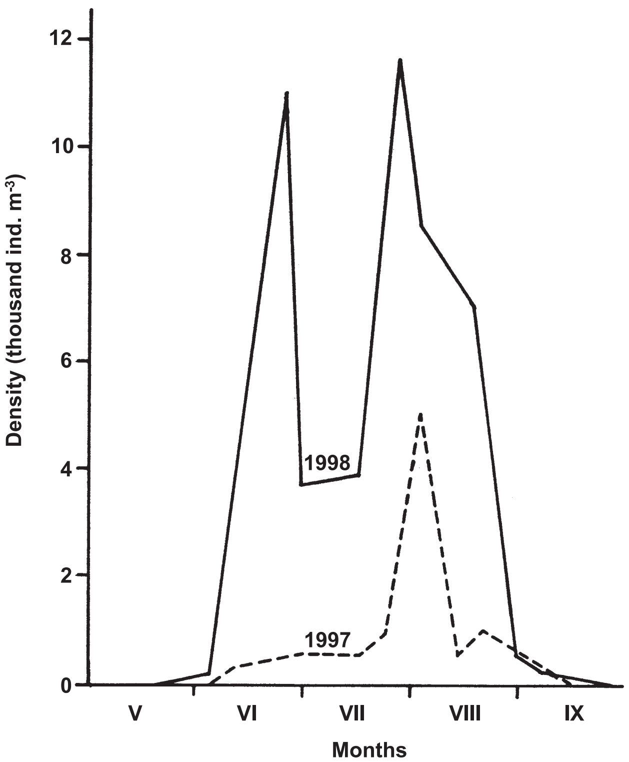


Fig. 13. Population dynamics of *D. polymorpha* planktonic larvae in the lake Inulec in 1997 and 1998 (after LEWANDOWSKI 1999, modified)

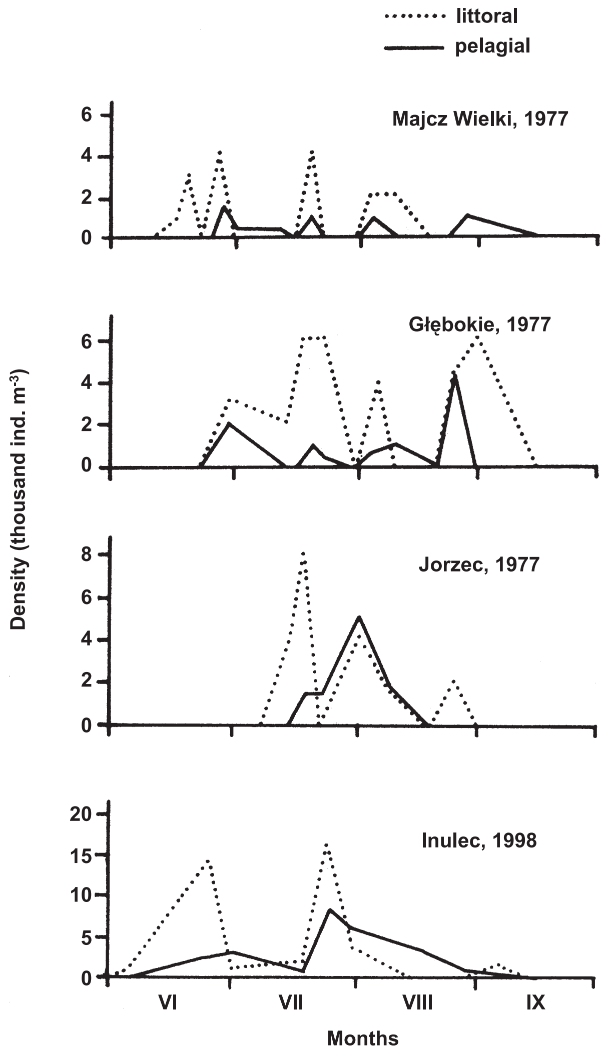


Fig. 15. Occurrence of *D. polymorpha* larvae in the littoral and pelagial of different lakes (after LEWANDOWSKI 1982a, supplemented)

Even larger differences in the number of larvae were found in the lake Majcz Wielki (Jorka basin) during three successive seasons. Peak densities in various years differed by several dozen times (Fig. 14).

2.4. Horizontal distribution of larvae within a lake

Although adult mussels occur mainly in the near-shore zone (littoral, partly sublittoral), their planktonic larvae are distributed throughout the lake, but their distribution is not uniform. In a detailed study on lakes of the Jorka basin, the densities were compared between the littoral and the pelagial. The results showed that larvae appeared first in the littoral – the place where adult reproducing mussels occurred, and were noted in the pelagial several days later, carried by water masses (currents caused by winds or water flow). Large differences were found in the abundance of larvae between the littoral and the pelagial. In the first period of reproductive activity, larvae were more abundant in the littoral than in the pelagial (Fig. 15).

The abundance of planktonic larvae in the littoral was more variable than in the pelagial (Fig. 15). This could have been due to the presence of reproducing adults in the littoral (increase in the density of larvae), which is also indicated by the fact that the smallest larvae, 65 μm in length, were noted only in the littoral, i.e. in the zone of mussel reproduction (Fig. 16). On the other hand, substrates suitable for settling were plentiful in this zone, enhancing the disappearance of larvae from the plankton (decrease in the abundance of larvae). Differences in the pattern of changes in densities, great in the littoral and small in the pelagial, may also be related to the fact that in most lakes the surface area of the zone of open water, i.e. epilimnion of the pelagial, is larger than the water surface in the littoral.

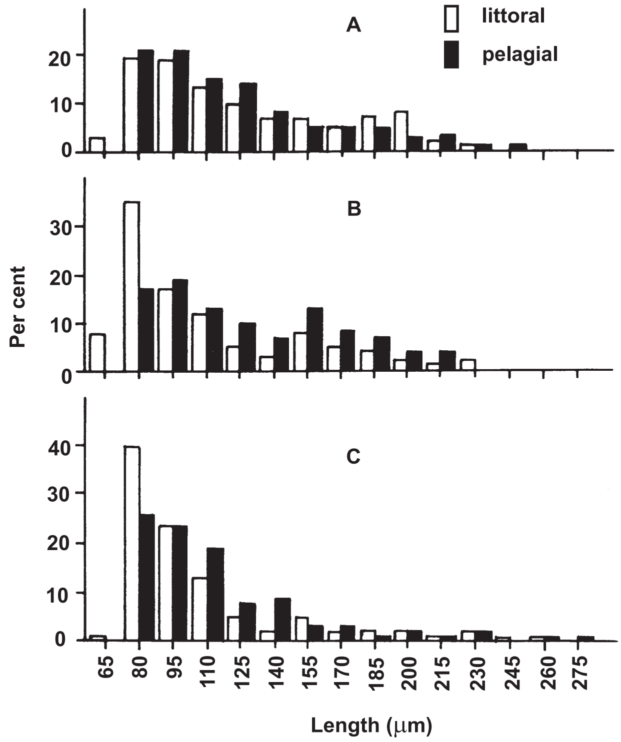


Fig. 16. Proportion of *D. polymorpha* larvae of specified lengths in the littoral and pelagial of selected lakes, A – Majcz Wielki (1978), B – Ołów (1978), C – Inulec (1998) (after LEWANDOWSKI 1982a (A, B) and LEWANDOWSKI 1999 (C))

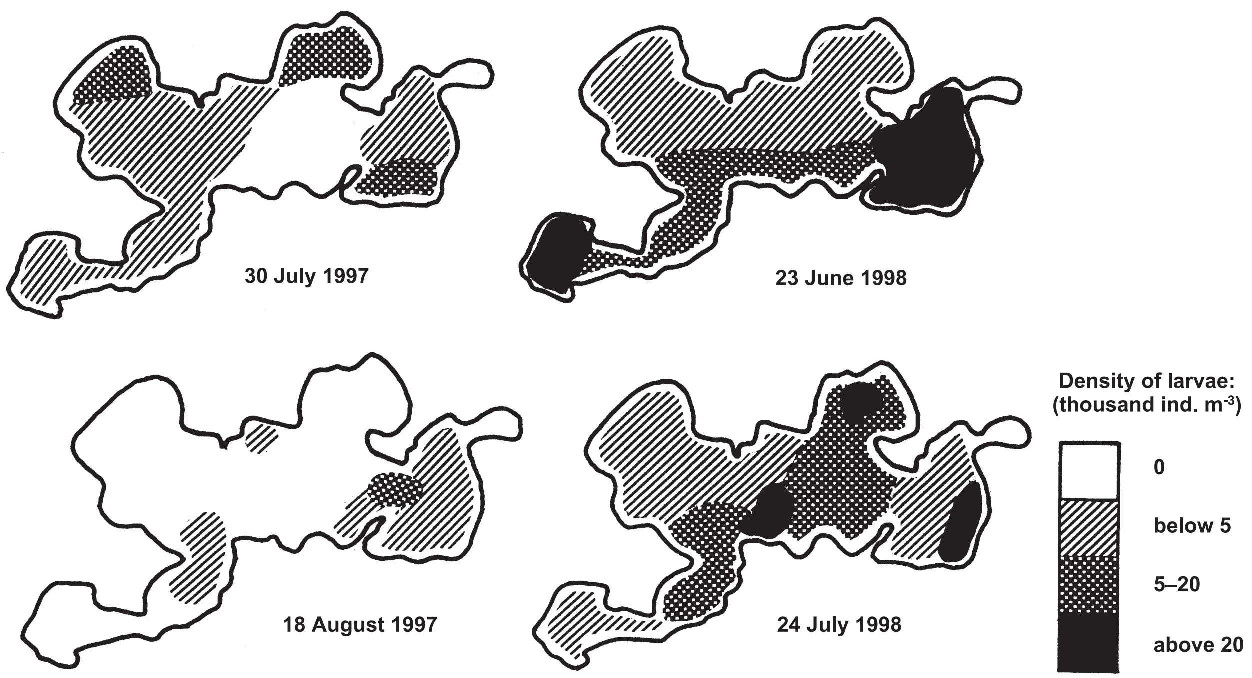


Fig. 17. Examples of the horizontal distribution of *D. polymorpha* larvae in the lake Inulec (after LEWANDOWSKI 1999, modified)

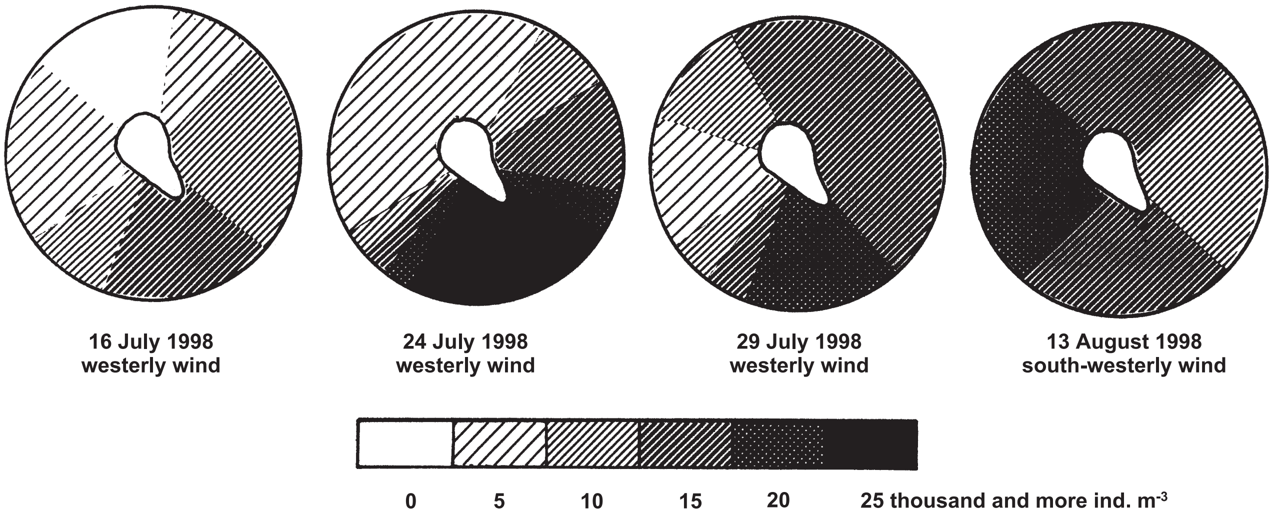


Fig. 18. Variation in the distribution of *D. polymorpha* larvae in the plankton surrounding islands on the lake Inulec

A detailed study of the horizontal distribution of larval mussels was conducted in the lake Inulec during two reproductive seasons. The densities of larvae showed great differences between various sites in this lake. On a single sampling date at several sites, densities of larvae ranged from zero to several dozen thousand per m^3 (Fig. 17). The pattern of horizontal distribution of larvae in the plankton varied widely, depending on the direction and velocity of the wind, obstacles in the lake (islands, peninsulas, emergent plants), intensity of spawning by adults, settling of growing larvae, etc. This variation in time and space can be exemplified by the distribution of larvae around one of the islands on the lake Inulec (Fig. 18).

2.5. Vertical distribution of larvae within a lake

Planktonic larvae of the zebra mussel occur mainly in the epilimnion, where in general 90–100% of all larvae are noted.

In the littoral, larvae occur throughout the water column, i.e. from the surface to the bottom, although their distribution may not be uniform, depending e.g. on the wind (Fig. 19). In addition, the distribution of larvae can be influenced by a variable recruitment of the youngest larvae, depending on the variation in the intensity of reproduction by adults.

An especially interesting example of the distribution of larvae in the plankton is the vast, wind-exposed, Żarnowieckie Lake, with a relatively poorly developed littoral. In the littoral of this lake, large differences were observed in the distribution of larvae between the leeward and windward sites (Fig. 20).

The effect of wind on the vertical distribution of larvae is evident when samples taken from the pelagial above a deeper place are analysed. In the lake Majcz Wielki at a slow wind (1–2 B) larvae occurred only to a depth of 7 m, and 96% of all larvae occurred to a depth of 5 m. The highest densities of larvae were noted in the surface layer (0–2 m deep) (Fig. 21). A similar distribution of larvae on windless days was noted in the lake Inulec in 1998 (Fig. 22).

A stronger wind (3–4 B) either caused the densities throughout the water column to be equal, or even increased the densities of larvae in deeper layers (Fig. 23).

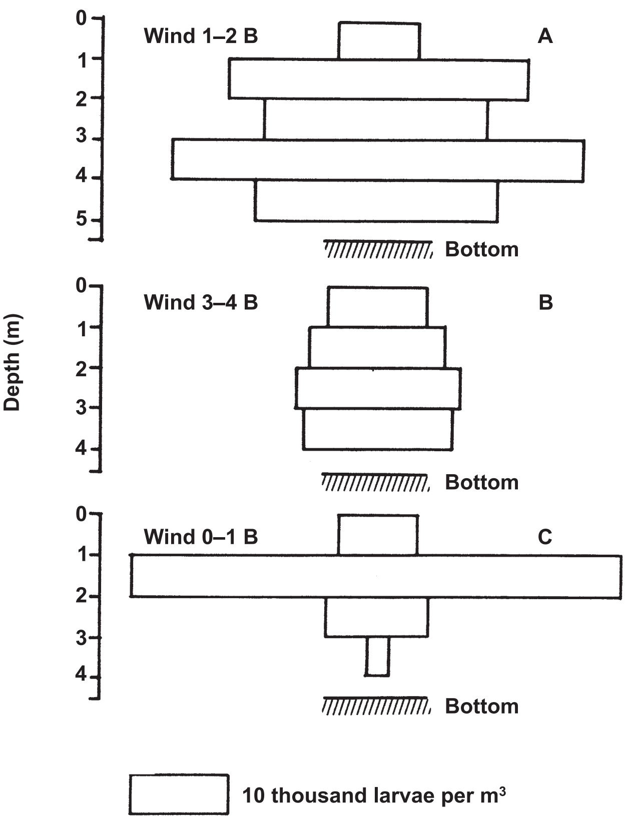


Fig. 19. Examples of vertical distribution of planktonic *D. polymorpha* larvae in the littoral of lakes in the Jorka basin at different wind velocities, A – Majcz Wielki, 12 July 1978, B – Inulec, 23 June 1998, C – Inulec, 24 July 1998 (after LEWANDOWSKI 1982a, 1999, modified)

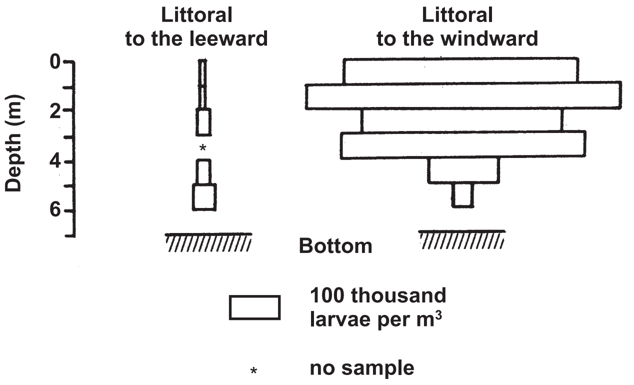


Fig. 20. Vertical distribution of *D. polymorpha* larvae in the littoral to the leeward and windward of the Żarnowieckie Lake (after LEWANDOWSKI & STAŃCZYKOWSKA 1986, modified)

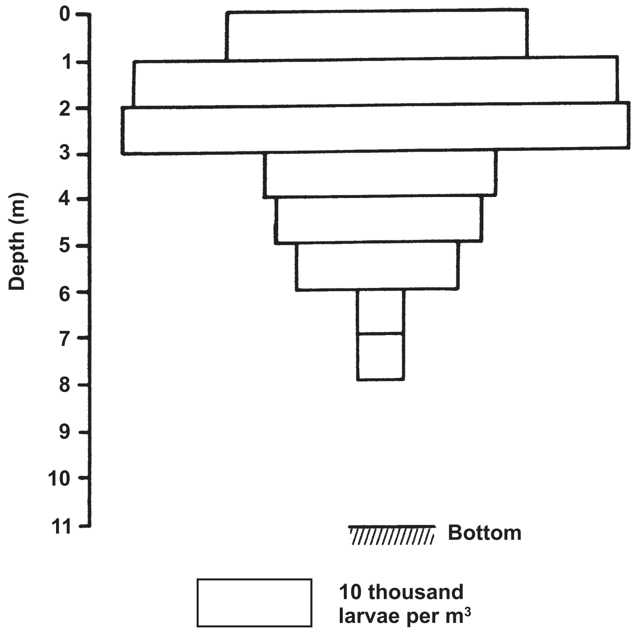


Fig. 21. Vertical distribution of *D. polymorpha* larvae in the pelagial of the lake Majcz Wielki, 12 July 1978 (after LEWANDOWSKI 1982a, modified)

An unusually strong effect of wind on the distribution of planktonic larvae was observed in the pelagial of the Żarnowieckie Lake. Already at 1–2 B, larvae were present in deep layers of the hypolimnion (Fig. 24).

Specific effects of environmental conditions on the vertical distribution of planktonic larvae were observed in the heated Ślesińskie Lake. In the place of the waterfall discharge of heated water to the lake, larval mussels were uniformly distributed throughout the water column, although this was a deep place (20 m), and sometimes their densities were higher in deeper layers than in the epilimnion. In this place, no summer thermal stratification was developed because of mechanical mixing. Another site in this lake, located far from the water discharge, was characterised by a typical thermal stratification and occurrence of larvae mainly in the epilimnion (Fig. 25).

3. TRANSITION OF PLANKTONIC LARVAE TO SETTLED LIFE

When planktonic larvae of the zebra mussel are about 200 μm long, they start settling, i.e. attach themselves to various submerged objects. Settling is a passive process in which older larvae fall down mechanically as the weight of the shell increases, but it also involves an active search for a suitable substrate to attach.

My research shows that the dynamics of postveliger settling corresponds to the abundance dynamics of planktonic larvae, shifted in time. In the lake Majcz

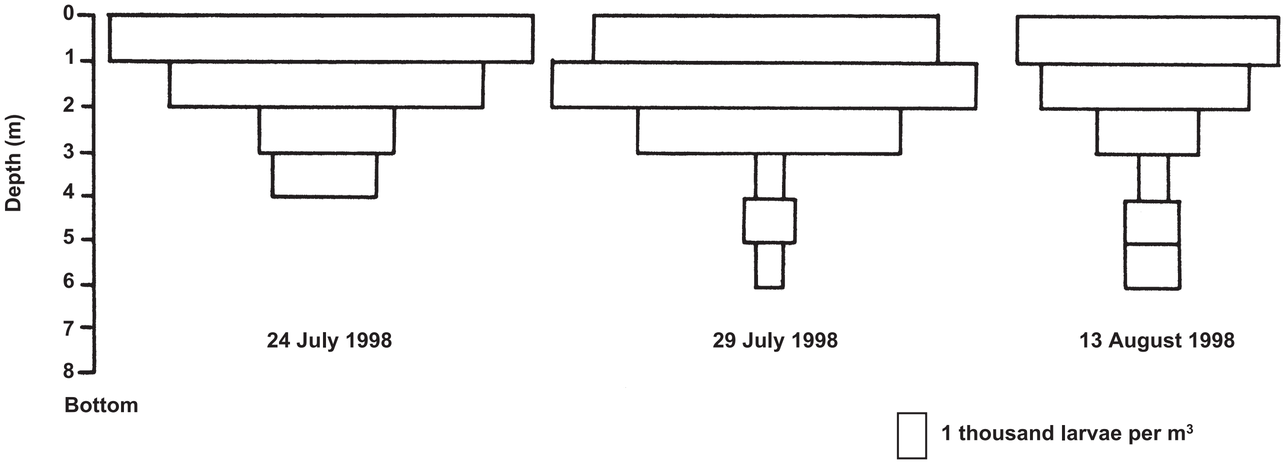


Fig. 22. Vertical distribution of *D. polymorpha* larvae in the pelagial of the lake Inulec on a windless day (after LEWANDOWSKI 1999, modified)

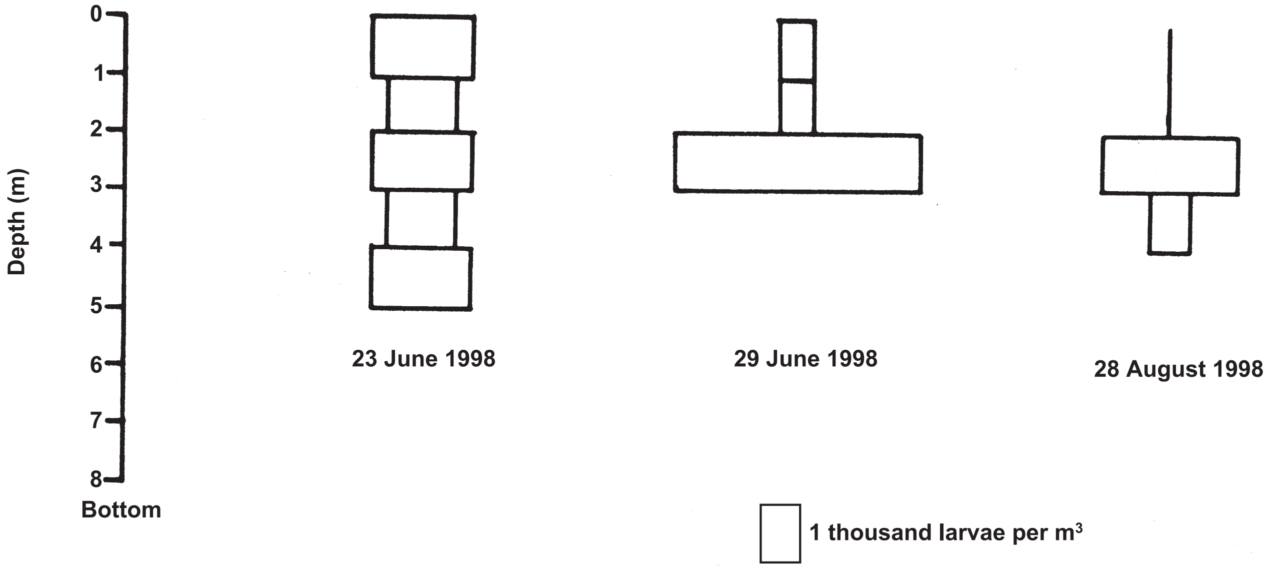


Fig. 23. Vertical distribution of *D. polymorpha* larvae in the pelagial of the lake Inulec at a wind velocity of 3–4 B (after LEWANDOWSKI 1999, modified)

Wielki, the curve of changes in the abundance of planktonic larvae had two peaks in 1978. The curve of changes in the abundance of postveligers had also two peaks: the first, small, in June, and the second, considerably higher, in July (Fig. 26).

The transition from planktonic to sedentary life encounters many problems, and this may be a critical period to individuals and the population. First of all, at the appropriate time, larvae must be in the vicinity of substrates suitable for settling. Such substrates are

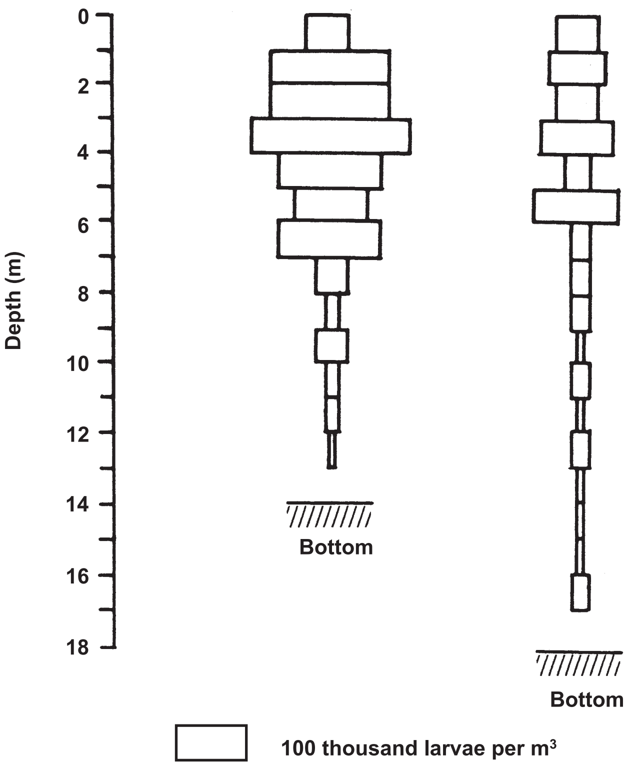


Fig. 24. Vertical distribution of *D. polymorpha* larvae in the pelagial of the Żarnowieckie Lake (after LEWANDOWSKI 1982a, modified)

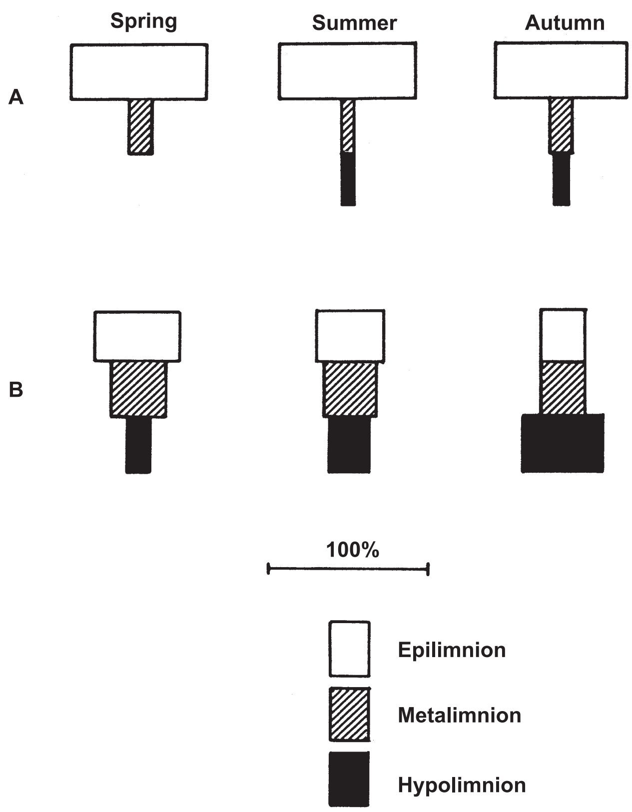


Fig. 25. Vertical distribution of *D. polymorpha* larvae in the Ślesińskie Lake, A – site far from the cascade water discharge, B – site at the water discharge (after LEWANDOWSKI & EJSMONT-KARABIN 1983, modified)

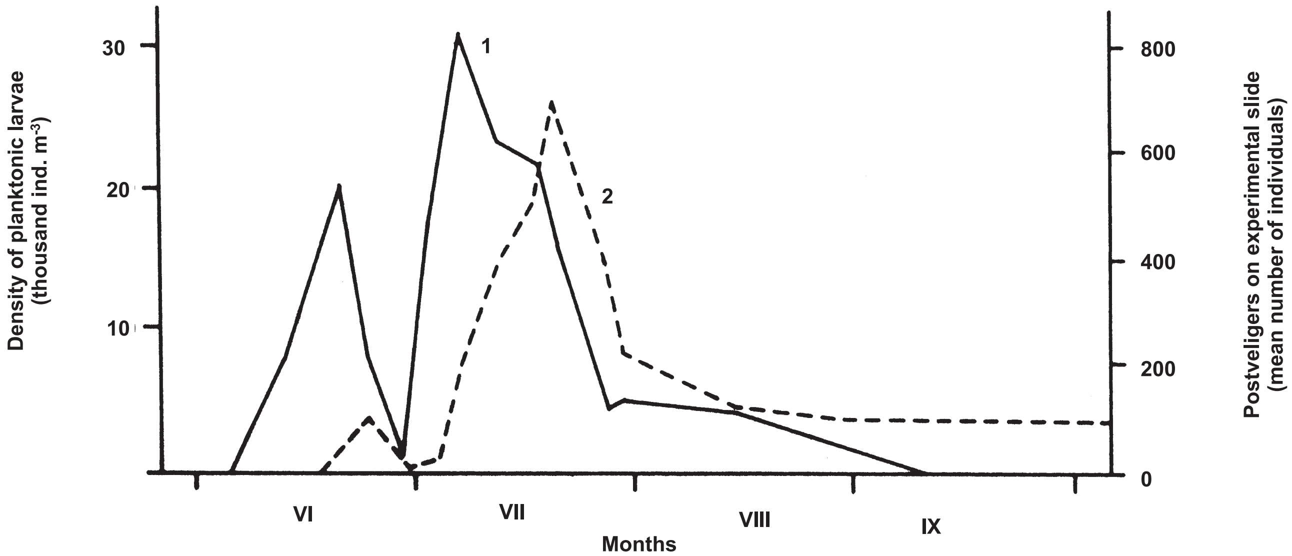


Fig. 26. Population dynamics of planktonic larvae (1) and settling postveligers (2) of *D. polymorpha* in the lake Majcz Wielki (after LEWANDOWSKI 1982b, modified)

absent from the pelagial or profundal, where also oxygen is often deficient. In the littoral and partly in sublittoral, various objects and substrates are plentiful (stones, poles, branches, mollusc shells, plants, etc.), but they are not equally attractive to the mussels. Important factors are substrate hardness, surface characteristics (smooth, rough), chemical properties, location, surface of a live organism or dead surface, etc.

Detailed studies conducted in the Masurian Lakeland showed that substrates suitable for larval settling could be even very smooth but they should be coated with a film of periphyton. For example, larvae would not settle on growing plant parts, nor on smooth, newly submerged glass surfaces. Glass surfaces, such as microscope slides, become suitable after about two weeks, i.e. after a film of periphyton has developed on them.

To assess the intensity of larval settling on different substrates, a number of field experiments were conducted in which artificial substrates were exposed (microscope slides covered with periphyton) under different environmental conditions, and also natural substrates. The occurrence of postveligers on natural substrates was also observed in various lakes.

3.1. Settling of postveligers

A detailed analysis of microscope slides exposed in the lake Majcz Wielki in the reproductive season of the zebra mussel showed that postveligers could settle abundantly on substrates of this kind.

In the period of peak settling (20 July), 673 postveligers were attached to a slide, on the average, i.e. over 200 thousand per m^2. A maximum in that period was 875 postveligers per slide, or 270 thousand per m^2.

In the “slide” experiments, more veligers were attached to the lower than to the upper side of the slides. On the average, it was 2–6 times more, with a maximum of 17 times more. The highest density noted on the lower side was 776 postveligers, or 480 thousand per m^2.

A detailed analysis of the sizes of planktonic larvae and the youngest, newly settled postveligers showed that the transition from planktonic to attached life could occur in a rather broad range of body sizes. Most larvae settle when over 200 µm long. However, also considerably smaller individuals were attached. The smallest postveligers attached to the substrate with their byssal threads were 140 µm long (Fig. 27). An analysis of live material showed that a large part of settling larvae did not attach to the substrate immediately, but moved actively using the foot. Among such individuals there were typical planktonic larvae, even merely 80 µm in length, as well as quite big individuals several mm long.

A monthly exposure of glass substrates at different depths of the Mikołajskie Lake showed that substrates placed close to the bottom of the littoral were most densely colonised (Fig. 28).

Winds and water currents that carry settling postveligers in suitable or unsuitable directions may act as important factors to the new generation of mussels.

In the lake Inulec, where settling plates for postveligers were exposed at eight uniformly distributed sites, the most intense settling occurred in the eastern part of the lake (37% of all attached postveligers), while it was less intense in the western part (31% of all postveligers). The fewest postveligers (12%) settled in the northern part of the lake. This pattern of postveliger distribution is consistent with the prevalence

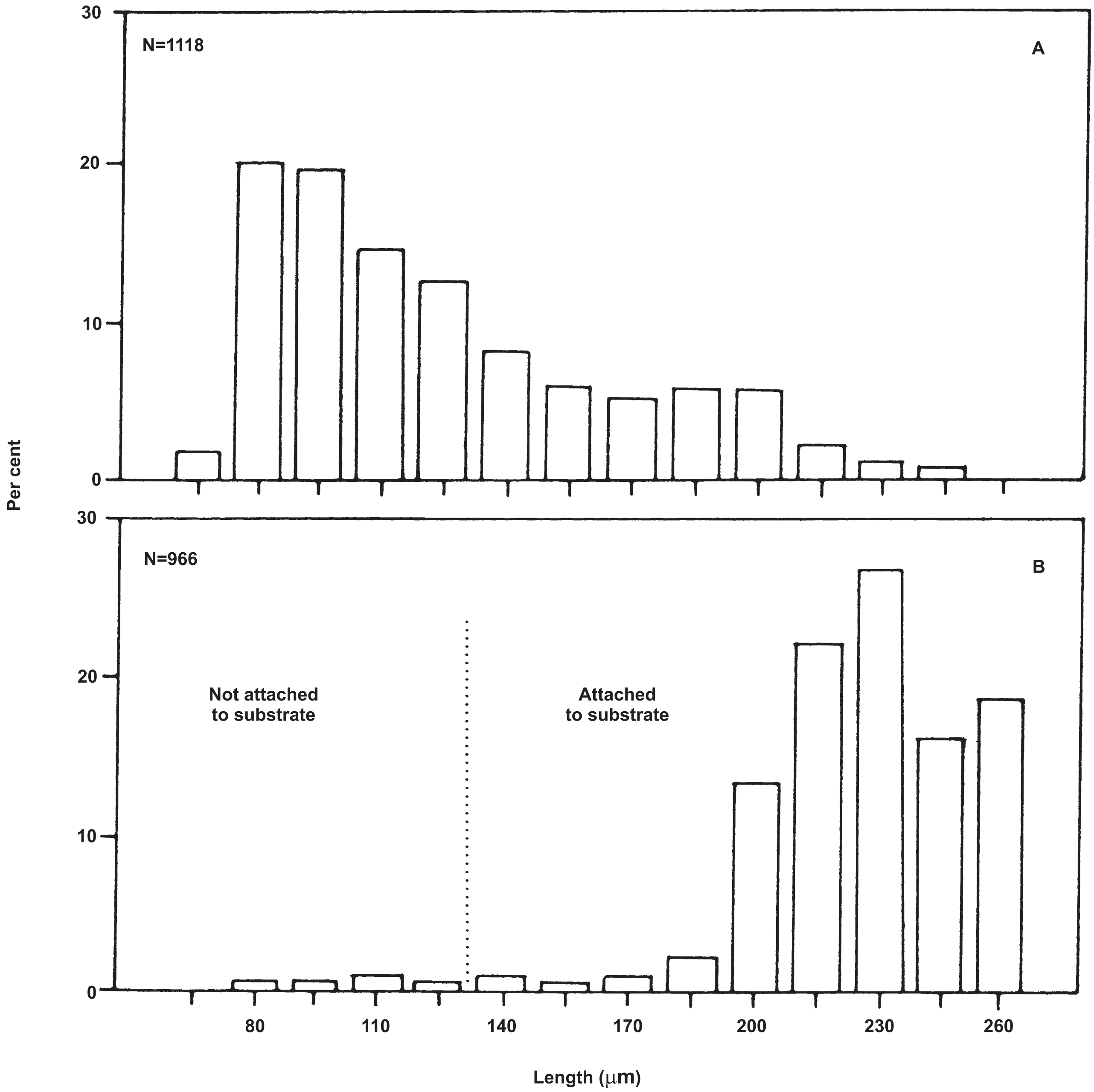


Fig. 27. Sizes of planktonic larvae (A) and settled postveligers (B) of *D. polymorpha* in the lake Majcz Wielki (after LEWANDOWSKI 1982b, modified)

of westerly winds that relocate larvae eastwards, and with the Jorka flow through this lake.

A similar situation was found in a small flow lake Zelwążek (the Jorka basin), where the eastern and western parts of the littoral were alike. Prevailing westerly winds and the current of the Jorka, flowing into the lake in the western part and flowing out from the northern part of the lake, directed postveligers towards the eastern shore, and this could account for their greater densities in the eastern part (Fig. 29).

A very important feature of the new generation of mussels, which renders the estimation of age structure difficult, is a prolonged settling of postveligers, and, consequently, a wide scatter of the sizes of young-of-the-year mussels. For this reason, age structure of the population has been determined on rare occasions, whereas the size structure of the population has often been described.

In the lake Majcz Wielki, settling postveligers appeared at the end of June. Already after one month, individuals growing at the highest rate were 2 mm long. After two months, they were 4 mm long, and 7 mm after three months. However, as late as in September, larvae of 0.2 mm continued settling (Fig. 30). In December, the length of young-of-the-year mussels ranged between 0.5 mm and 12.0 mm, and in May of

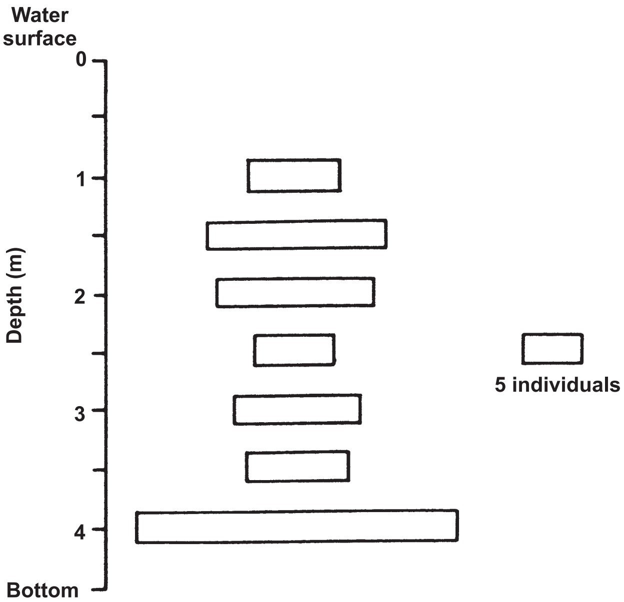
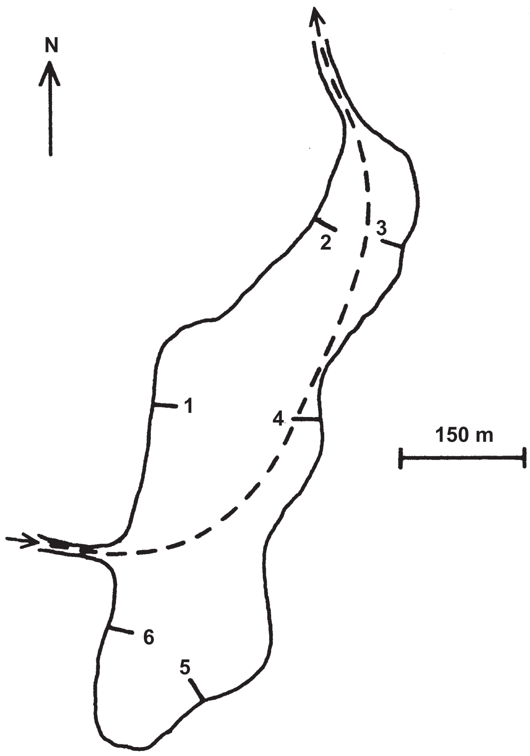


Fig. 28. Settlement of *D. polymorpha* postveligers (mean number per slide) at different depths of the Mikołajskie Lake (August 1975)



the following year, i.e. before the appearance of the next generation, the length of the youngest mussels that survived one winter varied from 0.7 to 15.0 mm.

3.2. Occurrence of postveligers on plants

Submerged plants represent one of the potential substrates available for larvae shifting from planktonic to sedentary life, and searching for a suitable substrate. Literature data on the occurrence of mussels on plants are extremely scarce, and my numerous studies show that the occurrence of mussels on aquatic plants is a common and mass phenomenon.

An experiment conducted in the lake Majcz Wielki to analyse substrate selection by postveligers, including natural substrates available in lakes (small stones, colonies of adult mussels, submerged plants such as *Chara* sp., silt, sand) showed that plants were the most abundantly colonised substrate (Table 3).

In most Masurian lakes, almost the whole littoral is overgrown with vegetation. Submerged plants often cover very large areas of lakes. For example, according to OZIMEK (1983), the area covered with submerged vegetation ranged from 7.9% (lake Jorzec) to 35.6% (lake Zelwążek) of the lake surface area. These may be dense, single-species carpets, or mosaics in the case of a high plant species diversity. Due to their

Table 3. Settling of *Dreissena polymorpha* veligers on various natural substrates (Lake Majcz Wielki, 30 experimental containers 7×10 cm, exposure from May through September) (after LEWANDOWSKI 1982b, modified)

Substrate	Number of postveligers per container (mean and range)
Chara spp.	1,727 (604–2,720)
D. polymorpha colonies	455 (167–697)
Stones	61 (25–109)
Sand	13 (7–23)
Silt	13 (3–38)

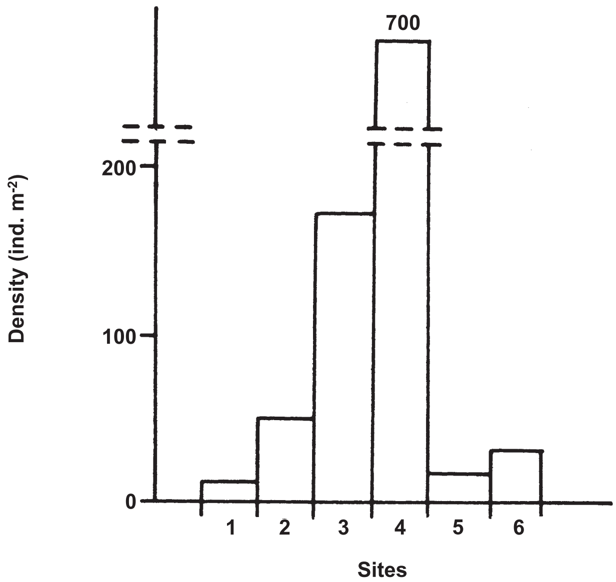


Fig. 29. Distribution of *D. polymorpha* in the flow lake Zelwążek (after STAŃCZYKOWSKA et al. 1983b, modified)

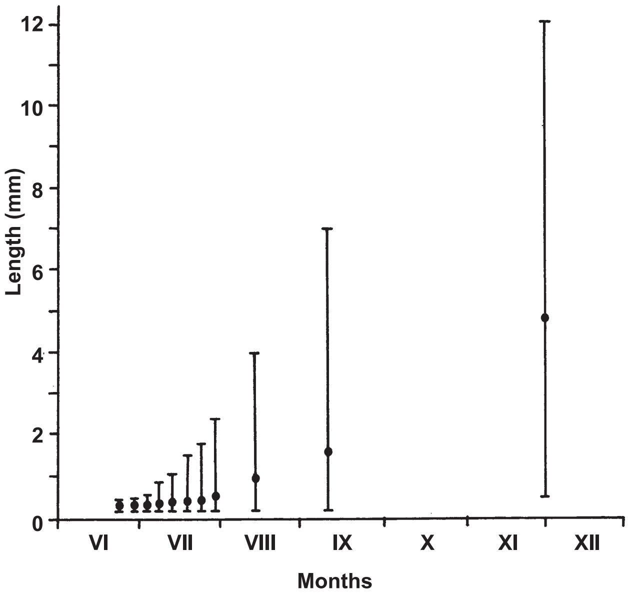


Fig. 30. Variation of the size (range and mean) of young-of-the-year *D. polymorpha* (lake Majcz Wielki, 1978) (after LEWANDOWSKI 1982 b, modified)

structural diversification, individual plant species offer various possibilities to postveligers.

The studies conducted in several dozen Masurian lakes showed that the highest postveliger densities were noted on perennial plants (*Ceratophyllum demersum, Fontinalis antipyretica, Chara* spp., *Elodea canadensis)*, compared to annuals (*Myriophyllum spicatum, Potamogeton perfoliatus, P. pectinatus, P. lucens, P. mucronatus).* In the former case, the maximum densities approached 500,000–800,000 ind. per m^2 plant-covered bottom, whereas in the latter situation they did not exceed 5,000 ind. per m^2.

Perennial plants were occupied by mussels throughout the year (also in winter under ice), whereas annuals were occupied only by postveligers that settled in mid-summer.

The distribution of mussels on plants was analysed in detail in the lake Majcz Wielki (Jorka basin) where submerged vegetation accounted for more than 30% of the lake surface (OZIMEK 1983, 1997). The most common plants were *Chara* spp. Also *Elodea canadensis* and *Ceratophyllum demersum* were abundant. In autumn, when the settling of larval mussels at a depth of 1.0–2.5 m where submerged plants were most abundant, was completed, the mean postveliger density was 145,000 ind. per m^2 of the littoral covered with submerged vegetation. In the zone 2.5–5.0 m deep, where plants were less abundant, densities of postveligers were lower, averaging 10,000 ind. per m^2. The mean density of mussels settled on plants in the zone of the submerged vegetation in this lake was about 60,000 ind. per m^2 of the littoral.

In many Masurian lakes, postveliger densities exceeding 100 thousand per m^2 of the vegetation-covered bottom were not rare. For example, in the lake Czos in mid-August, i.e. after the period of most intense settling, the mean density of zebra mussels settled on plants was 280,000 per m^2 of the littoral bottom covered with submerged vegetation, and in some places the densities reached up to 700,000 ind. m^{-2}. The highest abundance of mussels on plants was noted in the lake Rumian, where over 1.7 million individuals per m^2 of the bottom covered with plants were recorded.

Submerged plants were occupied only by the youngest mussels. These were mostly young of the year (in autumn) and one-year old (in spring). The oldest mussels noted on plants were three years old. This age structure of zebra mussels settled on plants is common in various lakes (Fig. 31).

Zebra mussels settled on plants did not form colonies so characteristic of benthic individuals. On some plant species, such as *Ceratophyllum demersum* and especially *Stratiotes aloides,* young mussels were more

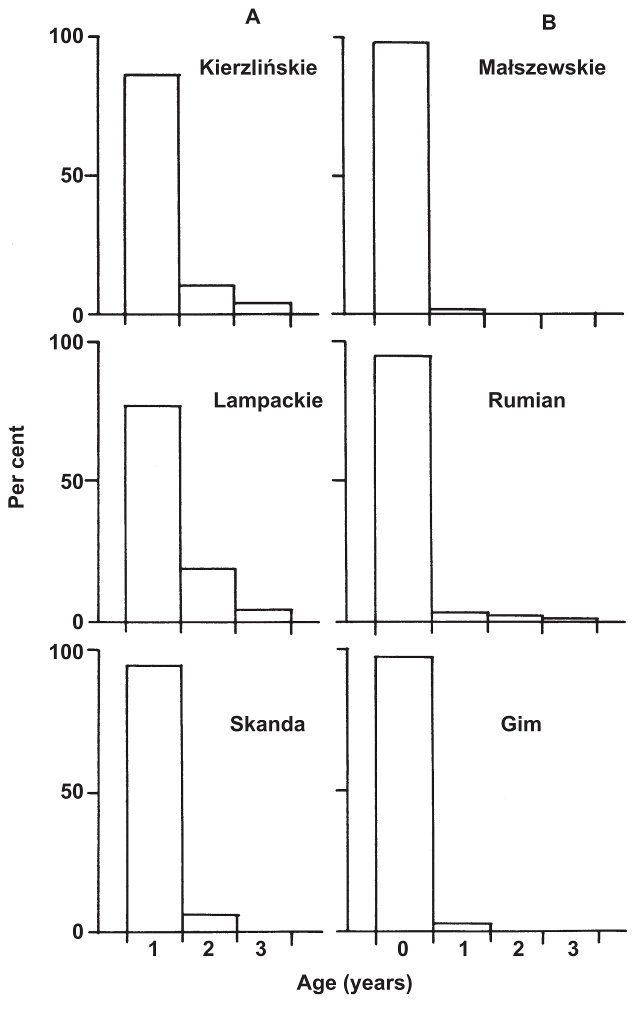


Fig. 31. Age-structure of *D. polymorpha* settled on plants in selected Masurian lakes in spring prior to reproduction (A) and in autumn after reproduction (B) (after LEWANDOWSKI 1982b, modified)

abundant at bases of leaves than on their exposed parts. This may be an effective way of avoiding predation by fish.

Mussels settled on plants are typically dominant in the population. In most lakes under study they accounted for over 85% of the total population.

4. AGE STRUCTURE IN RELATION TO ABUNDANCE DYNAMICS OF SETTLED ZEBRA MUSSELS

Even-aged settled zebra mussels display a wide variation in size, since settling of each new generation takes about 3 months. Individuals shifting from the planktonic to sedentary life at the beginning of the reproductive season (June), when they are 0.2 mm long, can be more than 10 mm long at the end of the growing season. Individuals that settle e.g. in late August, i.e. at the end of the reproductive season, can be less than 1 mm long when wintering. Often, rapidly growing young settled mussels are longer than slowly growing individuals from the previous year. As a result, the size ranges of mussels of different age classes may overlap. Examples of the body-size structures in uneven-aged zebra mussel colonies collected early and late in the growing season are shown in Figures 32 and 33.

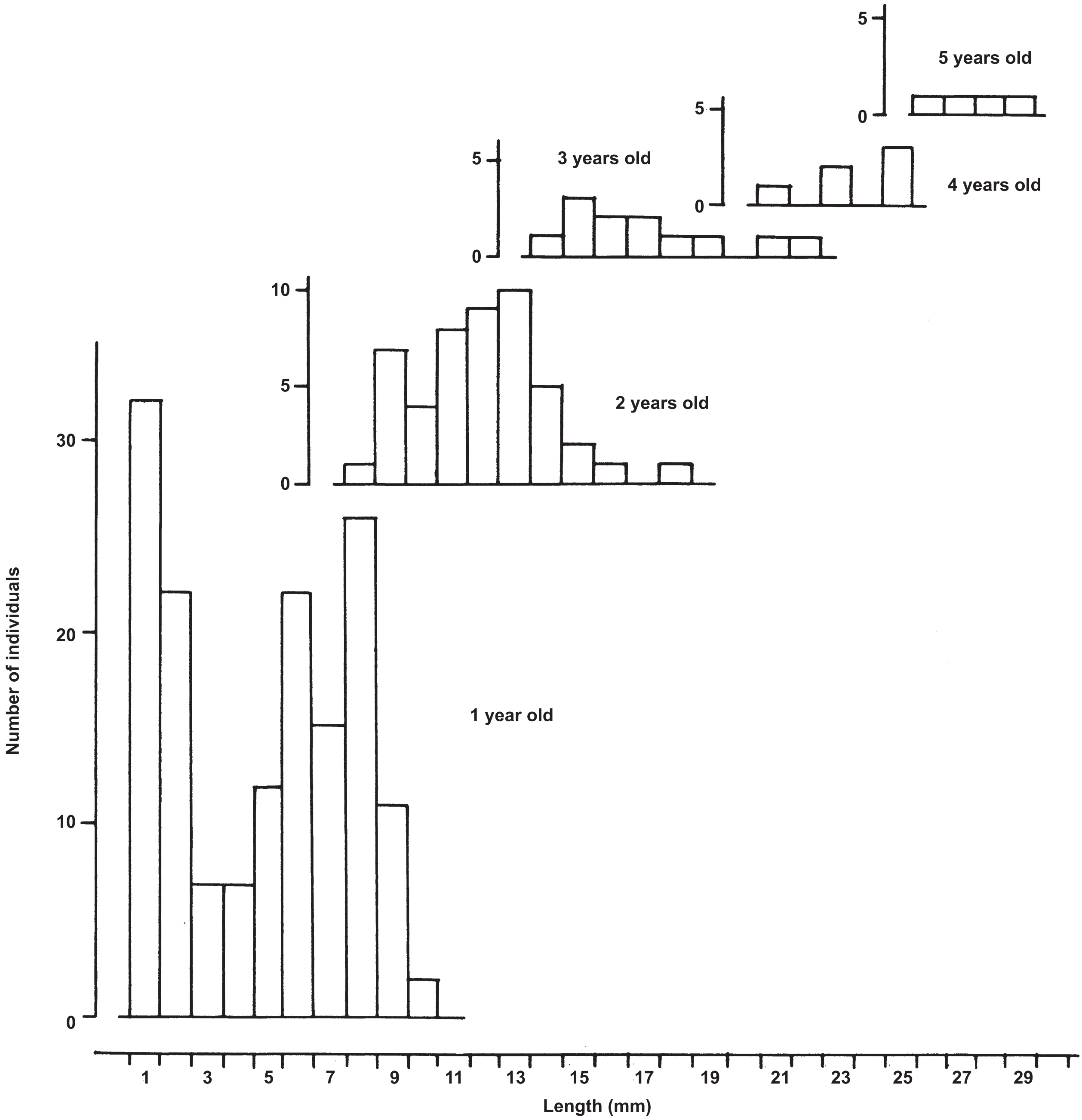


Fig. 32. Age-structure of *D. polymorpha* colonies collected early in the growing season in the lake Ołów (June 1978, 3 colonies, total 229 individuals) (after LEWANDOWSKI 1991, modified)

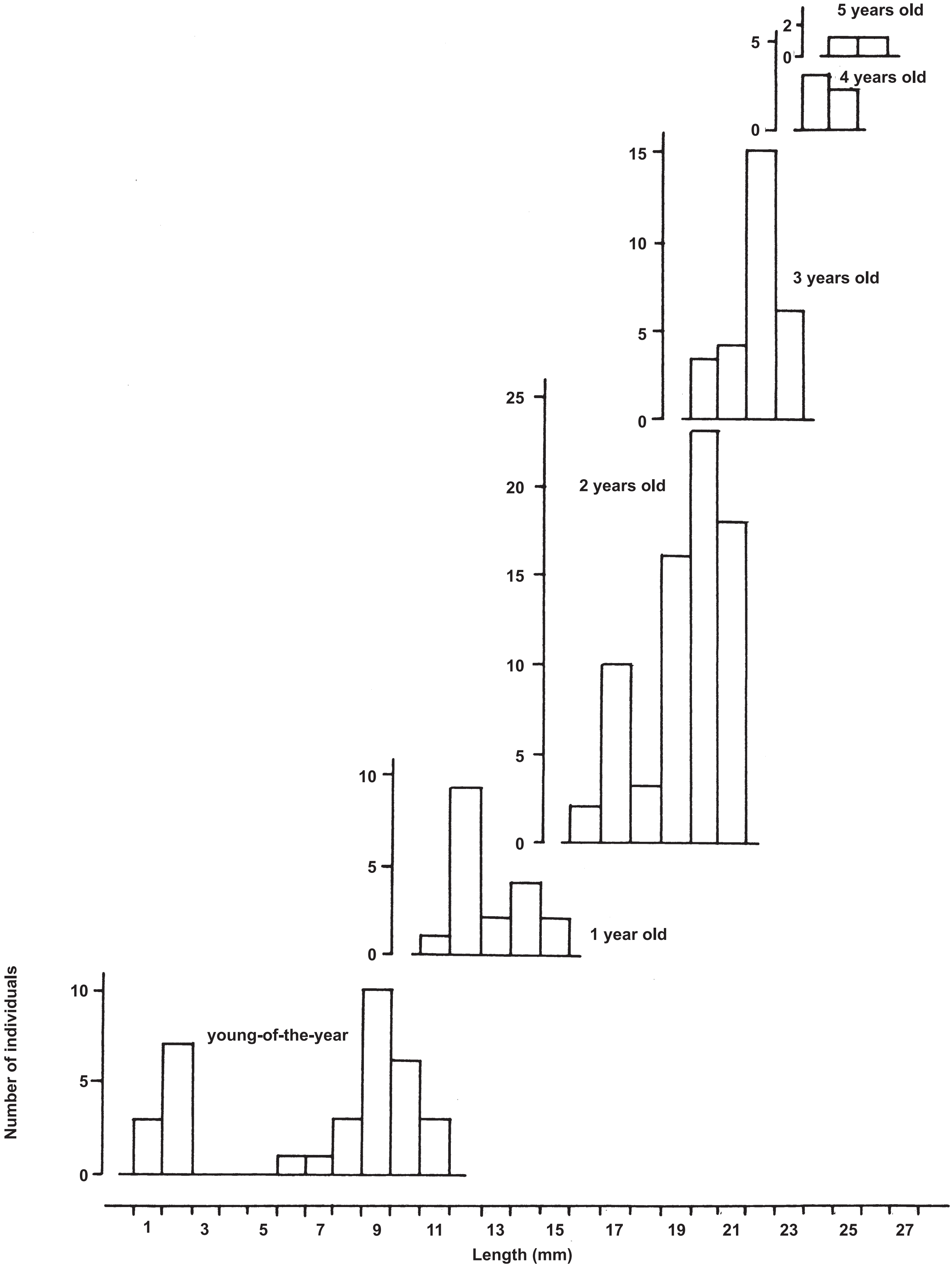


Fig. 33. Size structure of *D. polymorpha* colonies collected late in the growing season in the lake Inulec (October 1998, 5 colonies, total of 159 individuals)

Extensive data on the age, length, and growth of zebra mussels collected from several dozen lakes sampled during many years were used to construct curves showing the possible range of size and growth rate (Fig. 34). They illustrate the range of sizes of even-aged individuals, and they also show that individuals of the same size can markedly differ in age.

The age and size structures of mussel populations may vary widely from lake to lake. Differences in age structure may, for example, be responsible for the biomass of these bivalves. In two neighbouring lakes connected by the river Krutynia the following relationships were found. In the Lampackie Lake the mean density of mussels was over 3,400 ind. m^{-2} and the biomass was ca. 1.7 kg m^{-2}, whereas in the lake Lampasz there were ca. 2,400 ind. per m^2 and their biomass was over 2 kg. The higher biomass at the lower density of mussels in the Lampackie Lake as compared to Lampasz was a result of marked differences in the age and size structure of the mussel populations in these lakes. In the Lampackie Lake, the proportion of young individuals in the population was much higher than in Lampasz where the proportion of older and larger individuals was high (Fig. 35).

The appearance of a new generation of mussels was reflected in the age structure of settled shoals and colonies. This was evident in the studies conducted in the lake Inulec. Relatively low densities of planktonic larvae in 1997, as noted above, accounted for a low recruitment of this generation to the mussels settled on the bottom of the lake. After the termination of the reproductive period and disappearance of larvae from the plankton, the proportion of young-of-the--year mussels (generation 0) averaged merely 2.5% of the settled zebra mussels (Fig. 36), ranging from 0 to

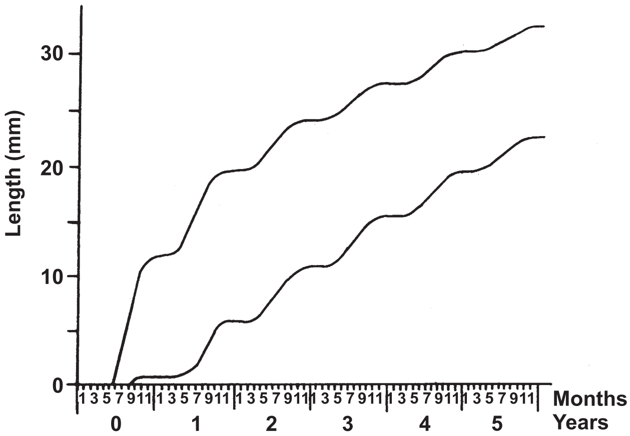


Fig. 34. Minimum and maximum sizes of *D. polymorpha* in Masurian lakes (after LEWANDOWSKI 1982c, modified)

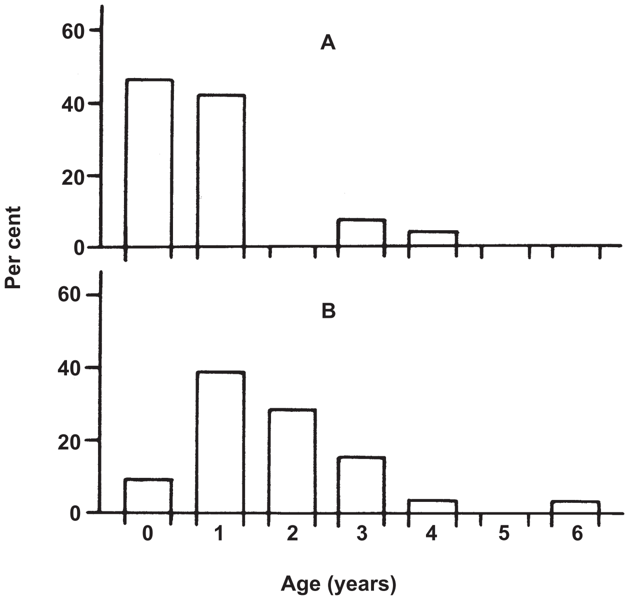


Fig. 35. Age-structure of *D. polymorpha* population in lakes Lampackie (A) and Lampasz (B) (after LEWANDOWSKI 1996a)

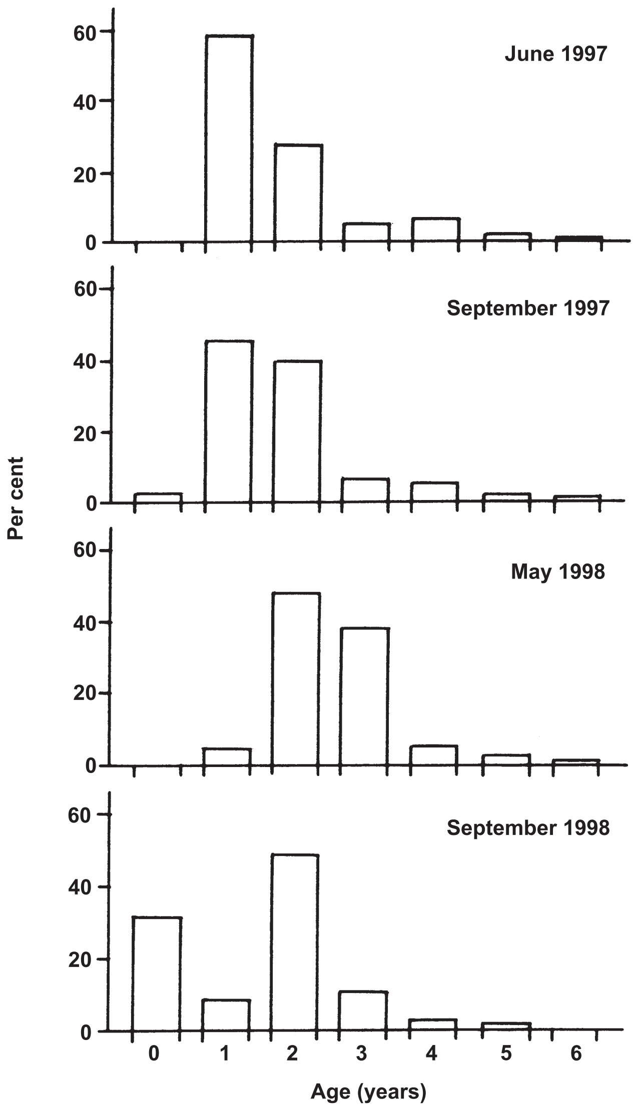


Fig. 36. Age structure of settled *D. polymorpha* before and after the reproductive seasons of 1997–1998 in the lake Inulec (after LEWANDOWSKI 1999)

4% from site to site. This was about one-twentieth of their proportion in the preceding year.

Much higher densities of planktonic larvae in 1998 gave rise to a higher proportion of the new generation among the settled mussels. On an average, individuals of the year at the end of September 1998 accounted for 25.7% of the settled mussels. This was a much higher proportion compared to the preceding generation, but lower compared to the generation of two years ago (Fig. 36)

The patterns of the age structure of settled mussels varied from site to site, the deviation from the mean being the largest at the eastern shore of the lake, where the youngest generation was dominant (Fig. 37).

The lake Inulec is an example of a water body with relatively poor submerged vegetation, where zebra mussels live mostly in colonies on the bottom. However, as already noted, in most lakes under study mussels settled on plants, and they were the dominant part of the population with respect to their numbers (though not biomass). Thus, when analysing changes in the age structure of zebra mussels in lakes of this kind, the total population of these bivalves should be considered. A good example of this situation is the lake Majcz Wielki, where the mussels settled on plants constituted, on an average, 96% of the total population. An analysis of changes in the age structure of the two fractions of mussels (settled on plants and on the bottom) during several seasons showed that the proportions of successive generations depended on the abundance of planktonic larvae from year to year (Fig. 38).

Thus, the age structure of the total zebra mussel population in the lake depended on reproduction in different years and also on the mortality of different developmental stages, with a possible role of migration.

Owing to abundant data collected from different lakes, it is possible to follow in detail the fates of successive generations of settled zebra mussels. In the case of individuals settled on plants, their rapid disappearance from year to year was observed. From the time of settlement, 89–98% of individuals disappeared by the first year of life. For example, in the lake Czos, the proportion of the young-of-the-year mussels settled on plants declined by 78% during one month (from August to September). Also a very high decline, often of 100%, was noted for older age classes settled on plants, for example, at ages of 1 to 2 or 2 to 3 years. No individuals older than 3 years were noted on plants.

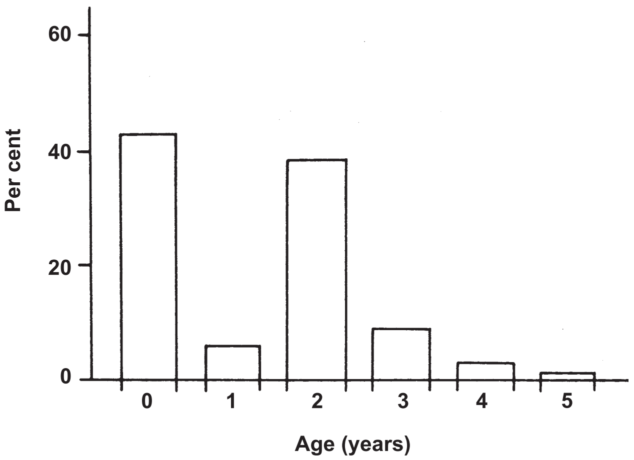


Fig. 37. Example of the age structure of settled *D. polymorpha* on a windward site (eastern shore, prevalence of westerly winds), (26 September 1998, lake Inulec) (after LEWANDOWSKI 1999)

Declines in the abundance of mussels settled on plants were mainly due to a mass mortality of postveligers and the youngest individuals, but also to migrations. Migrations, more often passive than active, typically occurred in autumn, when plants, especially annuals, were dying and breaking, and when young mussels had to search for a new substrate after falling to the bottom. In such situations, already established colonies of mussels on the bottom of the littoral were the most frequently used substrates. As a result, in the spring, e.g. an increase could be observed in the abundance of one-year-old mussels as compared with the abundance of individuals of class 0 in the autumn of the preceding year. In the lake Czos, once a threefold and once a fourfold increase was observed in the abundance of a mussel generation. Migrations of young mussels from plants to colonies settled on the bottom of the littoral may also occur between the first and the second year of life, as implied by the fact that the abundance of this generation in colonies increased in June as compared with that in September of the preceding year.

5. INTERACTIONS OF ZEBRA MUSSELS WITH OTHER ORGANISMS

Zebra mussels are involved in a wide variety of interactions with many organisms, when forming extensive shoals and colonies on the bottom of a mosaic lake littoral.

One of the most important kinds of interactions is associated with trophic webs, in which settled zebra mussels are prey of various predators. A good example is predation by one of the most common freshwater fish species, the roach (*Rutilus rutilus*). A detailed study showed that roach only 16 cm in length could feed on mussels, and when 20 cm long, they could specialise in "mussel" diet. This study showed also that not the whole spectrum of zebra mussel sizes could be used by the fish. Neither too small nor too large mussels are eaten. Only remains of medium-sized mussels were found in the roach gut. Selection of mussels by the roach was found to depend on the size of the food portion, not too much force needed to break byssal threads interconnecting the colony members, and moderate hardness of shells crushed with pharyngeal teeth (PREJS et al. 1990).

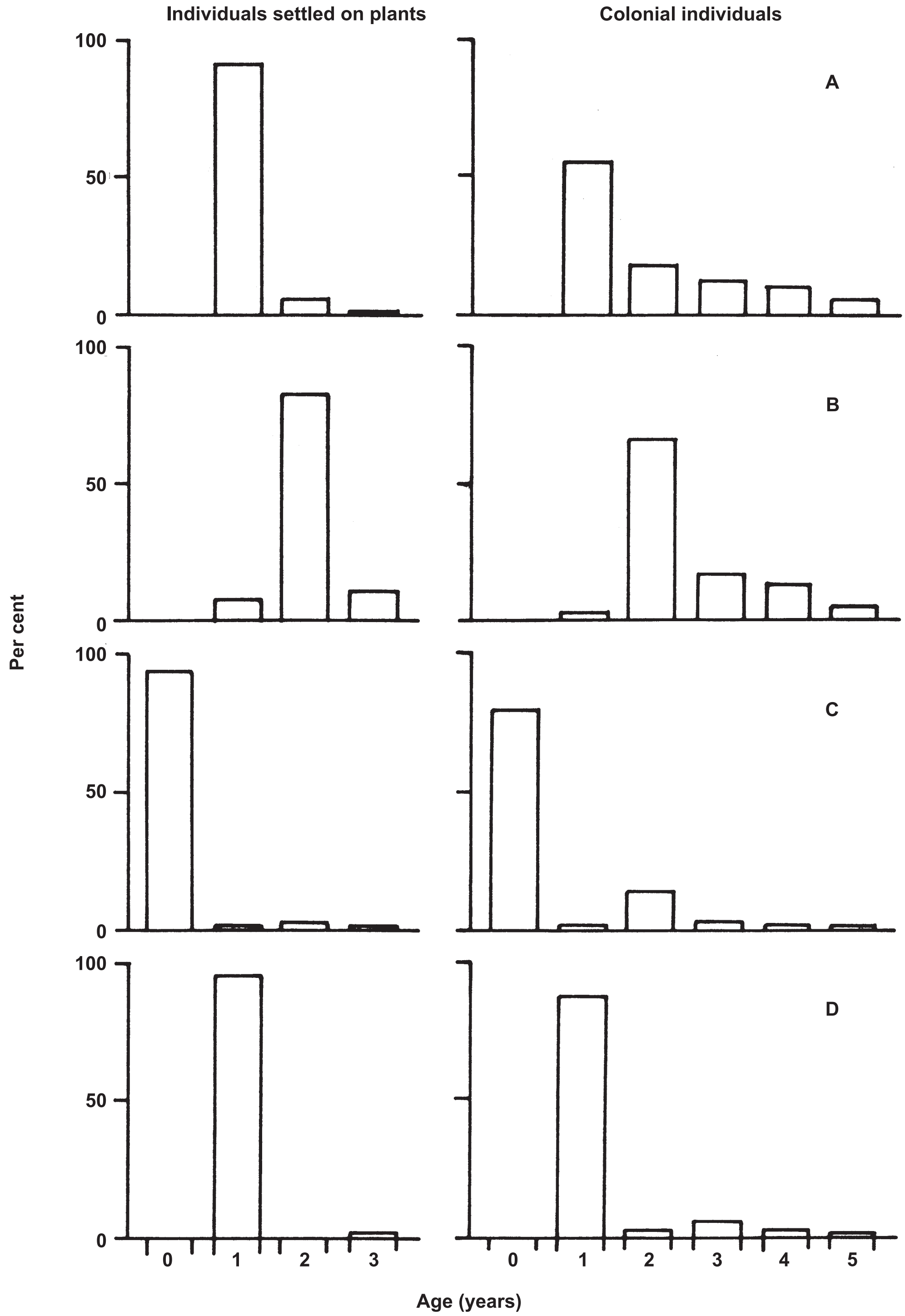


Fig. 38. Age structure of *D. polymorpha* settled on submerged plants and on the bottom (in colonies) in the lake Majcz Wielki during different periods: A – June 1977, B – June 1978, C – September 1978, D – June 1979 (A, C, D – after high density of planktonic larvae, B – after very low density of planktonic larvae (after LEWANDOWSKI 1982b, modified)

Relatively little known are interactions between settled zebra mussels and bivalves of the family Unionidae that occasionally serve as substrates for mussels, which can settle on them in large numbers. The scale of this phenomenon can be illustrated by observations in the Mikołajskie Lake (LEWANDOWSKI 1976). In the 1970s, i.e. the period when the zebra mussel population in this lake was abundant, these bivalves were attached to as many as 85% of the unionids sampled, a maximum infestation being up to 95% at a depth of 1.5 m (Fig. 39). On an average, 52 zebra mussels were noted on a single *Unio* or *Anodonta*, with a maximum of 132 (even higher densities were found in other Masurian lakes, e.g., 186 in Niegocin).

Table 4. Comparison of the mean shell weight and dry body mass in *Anodonta anatina* heavily infested by *D. polymorpha* (A) and not or slightly infested (B) in the Mikołajskie Lake (after LEWANDOWSKI 1976, modified)

Range of *A. anatina* length (mm)	Number of individuals analysed		Mean body length (mm)		Mean shell weight (g)		Mean dry body mass (g)	
	A	B	A	B	A	B	A	B
45–49	10	11	46.7	46.5	2.57	2.26	0.36	0.32
50–54	20	11	51.9	52.1	4.04	3.42	0.52	0.43
55–59	22	12	57.0	57.1	4.91	4.59	0.56	0.64
60–64	20	11	61.6	62.0	6.79	6.21	0.71	0.69
65–70	24	13	67.4	67.3	8.35	7.81	0.93	0.91

This phenomenon is even better illustrated by comparing the biomass of a single *Unio* or *Anodonta* with the biomass of zebra mussels attached to them. In as many as 35% of the Unionidae, the biomass of mussels was higher than the biomass of their host individual. In an extreme case, the mussel biomass was 17 times greater than that of *Anodonta anatina*.

However, heavy infestation with zebra mussels does not seem to affect their hosts negatively. For example, a mean dry weight of *Anodonta anatina* heavily infested by zebra mussels was often higher than that of similar individuals that were weakly infested or not infested at all. Instead, the weight of shells of heavily infested individuals tended to be higher, which may be a sign of their increased thickness (Table 4).

A comparison of the mean shell lengths of *A. anatina* showed that zebra mussels delayed length increments in young age classes of *Anodonta* (by an age of 4 years). Even a large number of settled mussels did not affect the growth of older individuals (Table 5).

An obvious consequence of the presence of a large number of mussels settled on unionids is sometimes a strong deformation of the posterior part (siphon) of their shell. In the Mikołajskie Lake, such deformations were noted only in *Anodonta anatina*, whose shell is thinner and more delicate than in members of the genus *Unio*. These deformations primarily involved hollows and bulges on the shell, bent shell margins, and a general change in the shape of the shell, as compared with typical shells. Individuals with deformed shells supported particularly large numbers of mussels. However, the comparison of their body weights with the weights of individuals of the same length but less infested by mussels showed again that settled mussels had no clear impact on the body weight of *A. anatina*, except for a slight positive effect on their shell weight.

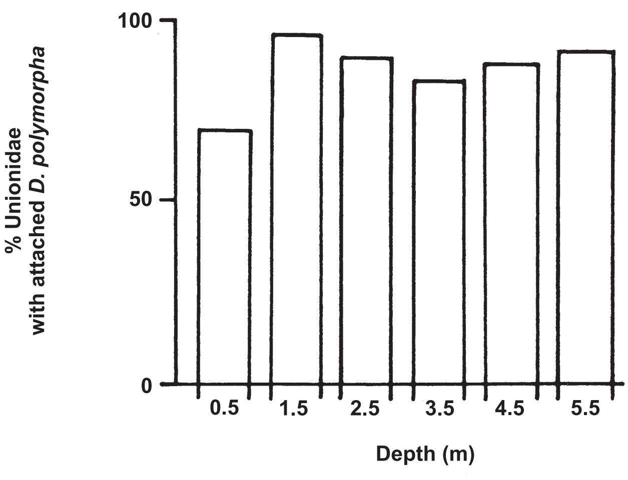


Fig. 39. Infestation of Unionidae by *D. polymorpha* at different depths of the Mikołajskie Lake (based on data from LEWANDOWSKI 1976)

The environment-forming role of the zebra mussel is still poorly known. Shoals and colonies of these bivalves, connected by byssal threads, form complex structures providing specific microhabitats for various organisms, especially invertebrates. During the study and field observations in lakes of the Masurian Lakeland, recesses of zebra mussel colonies were found to host abundant Hydrozoa, Turbellaria, Bryozoa, *Asellus aquaticus*, larval Chironomidae and Ephemeroptera, Gastropoda, occasionally bivalves of the family Sphaeriidae, and others (own, unpublished data). They used this habitat as foraging sites, shelters, and spawning sites.

The immense environment-forming role of the zebra mussel, especially when the bivalves occur in masses, can be seen in the lake-specific sublittoral zone

Table 5. Comparison of the mean length of *Anodonta anatina* heavily infested by *D. polymorpha* (A) and not infested (B) (after LEWANDOWSKI 1976, modified)

Age of *A. anatina* (years)	Number of individuals analysed		Shell length (mm)	
	A	B	A	B
3	10	17	39.0*	44.3*
4	30	18	49.9**	56.0**
5	34	23	59.0	60.0
6	39	12	64.5	65.0
7	11	10	73.8	74.1

* Statistically significant differences at $p<0.05$ (t-test)
** Statistically significant differences at $p<0.01$ (t-test)

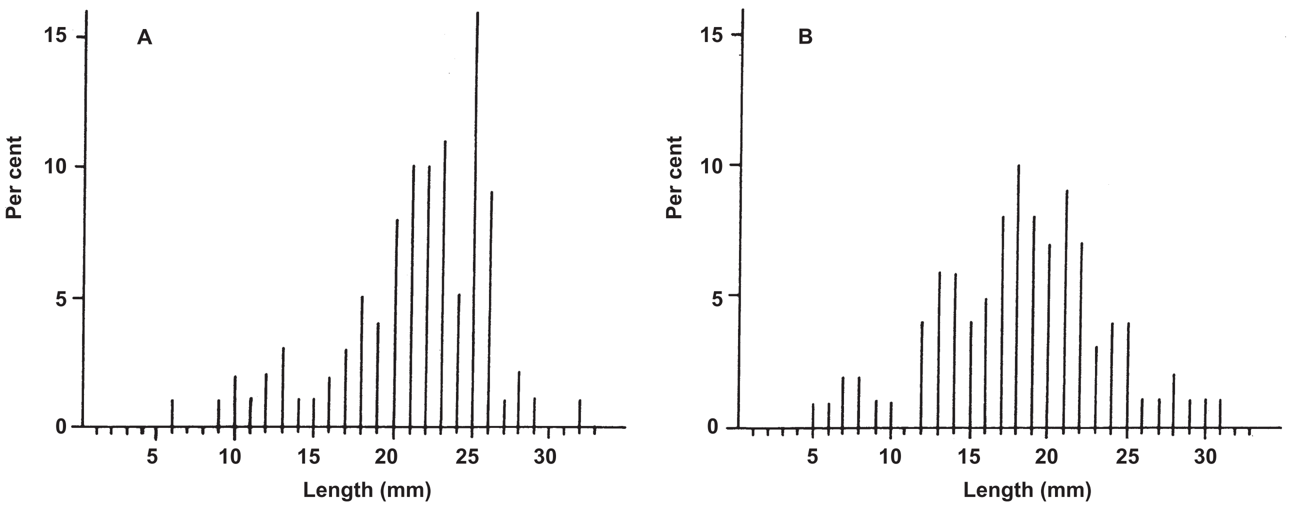


Fig. 40. Size structure of empty shells of *D. polymorpha* in the sublittoral of lakes Inulec (A) and Mikołajskie (B) (September 1997)

which is a shellbank. The empty shells of different species of molluscs occurring in the sublittoral are clearly dominated by mussel shells. For example, at high densities of zebra mussels in the lake Inulec, their empty shells in the sublittoral accounted for 95.3% on the average, and in the Mikołajskie Lake at low densities of the mussel population for 74.2% of all shells.

Despite the mass mortality of zebra mussels at early developmental stages, medium and large shells dominate quantitatively in the sublittoral shellbanks (Fig. 40) because of a rapid decomposition of small individuals (LEWANDOWSKI 1982b). The character of the sublittoral is primarily determined by medium-sized and large shells.

DISCUSSION

1. FACTORS DETERMINING DEVELOPMENT OF ZEBRA MUSSEL POPULATIONS

Zebra mussels tolerate a rather wide spectrum of environmental conditions (SMIT et al. 1992, CLAUDI & MACKIE 1994, MELLINA & RASMUSSEN 1994, HICKS & MACKIE 1997). They occur in lakes ranging from mesotrophic to heavily eutrophic. Typically, they are more abundant in mesotrophic lakes (LEWANDOWSKI 1991), but exceptions will always be found when a large number of lakes is surveyed. In some mesotrophic lakes, densities of mussels are low, and in some eutrophic lakes they are high. They tend to decline in heavily polluted polytrophic lakes (at a total phosphorus concentration in water of 300 μg l^{-1} in spring) (STAŃCZYKOWSKA et al. 1983a). These observations support the conclusion of MELLINA & RASMUSSEN (1994) that the water chemical composition is the most important factor for the presence or absence of zebra mussels in a lake, but it has no influence on their abundance, hence, no correlation exists between the abundance of mussels and such factors as pH, calcium concentration in water, and visibility of Secchi disk (STAŃCZYKOWSKA 1964).

My own numerous studies and literature data show that mussel populations are variable in space and time. Differences were found in the range of their occurrence, abundance (of larvae, postveligers, and adults), biomass, age structure, size structure, etc. between different water bodies, often interconnected and forming one complex, as well as between years and sites in the same water body. This variation in the populations of zebra mussels in various ecological situations results from an array of factors influencing different developmental stages of this bivalve.

The zebra mussel is characterised by a very high fecundity. In adult females as many as 30–40 thousand eggs (GILYAROV 1970, LVOVA 1980), and even higher numbers were recorded (WALZ 1978, SPRUNG 1993). Eggs fertilised in water produce free-swimming larvae 40–70 μm in length.

The maximum three-month period of the occurrence of larvae in the plankton (from June to September) in the Masurian lakes (HILLBRICHT-ILKOWSKA & STAŃCZYKOWSKA 1969, LEWANDOWSKI 1982a, 1999) is relatively short compared to other European water bodies. It primarily depends on thermal conditions.

The period of occurrence of larvae in the plankton in Europe becomes longer southwards, in increasingly warm zones. For example, in the Lake of Constance, planktonic larvae were noted from June to November (WALZ 1978), in a reservoir Modrac (the Balkan Peninsula) from May to October (ERBEN et al. 1995), and in the Skadarskie Lake from April to December (NEDELJKOVIC 1959). The example of the Lake Ochrida, the Balkan Peninsula, where planktonic larvae occur throughout the year (SERAFIMOVA-HADIŠČE 1957), is no longer valid, as the mussels from that lake were found to represent quite a different species, and even subgenus, described as *D.* (*Carinodreissena*) *stankovici* (LVOVA & STAROBOGATOV 1982). Zebra mussels occurring in heated waters of the Gosławsko-Ślesiński complex, where water temperature is suitable for reproduction already in April (STAŃCZYKOWSKA 1976, LEWANDOWSKI & EJSMONT-KARABIN 1983, STAŃCZYKOWSKA et al. 1988) start spawning two months earlier than in the Masurian lakes. It is worth noting that in autumn larvae disappear from the plankton of heated lakes earlier than indicated by the water temperature. The period of disappearance of planktonic larvae in these lakes is similar to that in the Masurian lakes.

The stage of planktonic larva is relatively short-lasting (8–10 days) but this is the most mobile, though passive, stage largely ensuring the dispersal of the species. At this stage a part of the mussel population is eliminated. Planktonic larvae are food of fry of some fish species and of some invertebrates. K. WIKTOR (1958) found larval mussels in guts of smelt sparling (*Osmerus eperlanus),* pike-perch (*Lucioperca lucioperca*), ruff (*Acerina cernua*), and roach (*Rutilus rutilus*), a maximum of 65 larvae per gut. GRIGORASH (1963) noted up to 125 larvae in the guts of the roach. The use of this food by fry can largely vary, depending on the density of larvae in the plankton or on the reproduction of fish, and typically lasts for a short time, for example, 2–4 weeks in the Gulf of Szczecin (K. WIKTOR 1958).

Among invertebrates, planktonic larvae can be eaten by Hydrozoa (J. WIKTOR 1969, MOLLOY et al. 1997), some species of Copepoda (KARABIN 1978, LIEBIG & VANDERPLOEG 1995) and by filtering organisms such as adult zebra mussels (MIKHEYEV 1967, MACISAAC et al. 1991).

Other factors reducing the abundance of planktonic larvae include water pollution (DYGA & LUBYANOV 1972), or transportation of larvae with outflow (HORVATH & LAMBERTI 1999a, b), which is of special importance in dam reservoirs (KIRPICHENKO 1971) or in the Gulf of Szczecin (J. WIKTOR 1969).

It appears, however, that the mortality of planktonic larvae is relatively low. J. WIKTOR (1969) and STAŃCZYKOWSKA (1977), who estimated the reproductive potential of zebra mussel populations and subtracted from it the observed number of larvae in the plankton, found that the reduction in that period, in two different habitat types (a gulf and a lake), was about 20%.

A critical moment in the life of zebra mussels is the transition from planktonic to settled life. This very short period in individual life can be of crucial importance to population survival, and this period was the prime subject of the studies described here. The factors involved are winds and water currents relocating larvae, the size of the littoral zone, cover of submerged vegetation, plant species, and other possible kinds of substrates. Only larvae settled on a suitable substrate can survive. Larvae that settle on unsuitable substrates, such as sand or silt, or those that fall into the profundal where also oxygen is deficient, will die.

The results of the studies and calculations show that a very low proportion of settling larvae can find a suitable substrate. This may be a fraction of a percent (0.4% in the lake Ołów, 0.6% in the lake Kołowin), or merely a few percent (4.2% in the lake Majcz Wielki) where the littoral is unusually developed and abounding with suitable substrates.

My studies demonstrate that further fates of settled postveligers largely depend on the kind of substrate. Substrates suitable to settling larvae can be classified into two basic types. The first type represents most suitable substrates where settled individuals can remain over their life span. They primarily comprise developed colonies of zebra mussels, stones, live unionids, empty mollusc shells, etc. Substrates of the second type are also suitable for settling but, unlike those of the first type, they are temporary and persist for a shorter time than the maximum life span of the mussel. This type is represented by aquatic plants.

The results presented above indicate that most larval mussels in the Masurian lakes settle on submerged plants. Although initial conditions are very good for the settled postveligers, these individuals rapidly die, mainly because the plant substrate dies and they have to search for a new substrate. Mass mortality of zebra mussels firstly concerns individuals settled on annual plants, totally dying in autumn. Less violent but also intense is extermination of mussels settled on perennials, where no individuals older than three years were noted. In addition to breaking and dying of vascular plants (and *Chara* spp.), also periphyton algae covering vascular plants, to which settling postveligers were attached, could largely influence the mortality of postveligers (AFANASYEV & PROTASOV 1987). The dying of periphyton algae in autumn was followed by a mass mortality of postveligers (LEWANDOWSKI 1982b).

Some reduction in the numbers of zebra mussels settled on plants can also be due to fishes directly feeding on them (mainly the roach). According to MIKHEYEV (1969), young mussels settled on plants are more available to fish than individuals strongly interconnected in colonies. Occasionally, postveligers can also be consumed by organisms feeding on periphyton (e.g. Gastropoda) and plants (e.g., among fish, the rudd *Scardinius erythrophthalmus,* among birds, the mute swan *Cygnus olor,* and others). Not only consumption but also mechanical removal of young mussels down from plants onto sandy or silty substrate by these animals may reduce their abundance. For example, a foraging snail *Radix ovata* destroys about half of the available periphyton which falls to the bottom after being detached from the substrate (PIECZYŃSKA 1970).

A part of the young mussels falling from plants onto the bottom do not die but settle on already established mussel colonies. In general, however, young (up to 3 years old) mussels settled on plants die in masses because they cannot find a new suitable substrate. Their mortality in this period typically exceeds 90% each year (LEWANDOWSKI 1982b).

The mortality of individuals in established colonies can primarily result from biocoenotic factors. The zebra mussel is predated by some fishes, birds, and crayfish. The mortality of the youngest age class (0–2 years old) is to some extent compensated for by new individuals that originally settled on plants, but it is relatively low, like the mortality of medium-age classes (3–4 years old) (J. WIKTOR 1969, LEWANDOWSKI 1982b). Only among older individuals, mortality increases markedly not only because of the old age but also, especially in large colonies, as a consequence of a restricted access to food and oxygen for older individuals that are located in the deepest layers of the colony (MIKHEYEV 1969, CZARNOŁĘSKI et al. 2000).

2. THE ROLE OF ZEBRA MUSSELS IN AQUATIC ECOSYSTEMS

The zebra mussel is a typical invasive species (NOWAK 1974, STAŃCZYKOWSKA 1983), whose range has been expanding in Europe for about 200 years. It originates from estuaries of rivers flowing to the Caspian, Black, and Azov Seas. Its northward and southward expansion started at the end of the 18th and beginning of the 19th century.

The zebra mussel colonises new freshwater habitats relatively fast. It appears in masses in dam reservoirs already in the first years after their establishment (DYGA & LUBYANOV 1975, KIRPICHENKO & ANTONOV 1977). Similarly, it colonises in masses newly-constructed canals, hydrotechnical devices, and water systems.

Under European conditions, the spread of the zebra mussel which is an invasive species, has continued for a relatively long time. In the 20th century, its appearance in various water bodies in Hungary (Lake Balaton), Scandinavian Peninsula, Switzerland, southern Germany, northern Italy, and Russia (dam reservoirs) took place under the eyes of researches who could trace further fates of the zebra mussel populations. Shortly after the appearance of the first mussels, an explosion of their abundance is observed. In later years, co-adaptation processes occur, predators switch to the new kind of prey, and as a result the mussel abundance decreases. A model example of these processes was observed in the Lake Balaton, where already first announcements of the mussel appearance in the 1930s documented huge numbers (SEBESTYÉN 1938). Later studies showed a much lower abundance (PONYI et al. 1974, PONYI, STAŃCZYKOWSKA, and own, unpublished).

In the 1980s, the zebra mussel appeared in the Great Lakes of North America (HEBERT et al. 1989, LEWANDOWSKI 1990). The species was first discovered in the Lake St. Clair on June 1st, 1988, and later in the western part of the Lake Erie. Based on the size and estimated age of the collected individuals, it is supposed that the initial colonisation of these waters by mussels took place in 1985. Planktonic larvae and postveligers were probably introduced to American lakes with ballast water discharged from European ships (HEBERT et al. 1989). In the 1990s, zebra mussels had already colonised all the Great Lakes and many large rivers in America (GRIFFITHS et al. 1991, DERMOTT & MUNAWAR 1993, FRENCH 1993, NALEPA & SCHLOESSER 1993, and others). It should be noted here that, in addition to *D. polymorpha*, another species of the genus, *D. bugensis* (Andr.), originally occurring mainly in Ukraine (ZHURAVEL 1951, SHEVTSOVA 1996) but absent from Poland, was introduced in North America at the same time. *D. bugensis*, like *D. polymorpha*, is spreading under American conditions, but its ecological niche differs slightly from that of *D. polymorpha* (MACISAAC 1994, SPIDLE et al. 1994, and others).

The zebra mussel is an important food source for many species. Among fishes, these are the roach (*Rutilus rutilus*), bream (*Abramis brama*), white bream (*Blicca bjoerkna*), carp (*Cyprinus carpio*), perch (*Perca flavescens*), and eel (*Anguilla anguilla*) (PLISZKA 1953, PREJS 1976, OLSZEWSKI 1978, DE NIE 1982, MARTYNIAK et al. 1991, NAGELKERKE & SIBBING 1996, TUCKER et al. 1996, MAYER et al. 2000, and others), among birds, mainly the coot (*Fulica atra*), tufted duck (*Aythya fuligula*), pochard (*A. ferina*), and goldeneye (*Bucephala clangula*) (LEUZINGER & SCHUSTER 1970, STEMPNIEWICZ 1974, WIŚNIEWSKI 1974, BOROWIEC 1975, STAŃCZYKOWSKA et al. 1990, SMIT et al. 1993).

The zebra mussel constitutes an especially important food source for birds in winter. Large flocks of water birds gather in places of abundant occurrence of mussels in winter (STEMPNIEWICZ 1974, MIKULSKI et al. 1975, BIJ DE VAATE 1991, WORMINGTON & LEACH 1992, CLEVEN & FRENZEL 1993). Long-term observations in the region of the Lake of Geneva and the Lake of Constance showed that after the appearance of mussels in these lakes in the 1960s, wintering populations of water birds increased considerably as they found there a new food source in the form of zebra mussel colonies (GEROUDET 1966, LEUZINGER & SCHUSTER 1970, JACOBY & LEUZINGER 1972, LEUZINGER 1972).

The mussel can also be eaten by small mammals (BEDULLI & FRANCHINI 1978, WOŁK 1979), various species of crayfish (PIESIK 1974, LOVE & SAVINO 1993, SCHREIBER et al. 1998), and other predatory invertebrates such as leeches *Glossiphonia complanata* (SMIT et al. 1993, MOLLOY et al. 1997).

An extremely important trait of the zebra mussels is their filter-feeding; huge amounts of water can be filtered in different ecosystems by this natural biofilter when colonies are large. Calculations made by different authors show that the mussels play an important part in water clearing. Occasionally, natural mussel populations can filter the whole volume of some lakes and such large water bodies as the Gulf of Szczecin or some dam reservoirs within a relatively short time, e.g. one month, (STAŃCZYKOWSKA 1968, J. WIKTOR 1969, SPIRIDONOV 1971, KONDRATEV 1977). These estimates concern individuals settled on the bottom in colonies and shoals. It has been found, however, that also the youngest, tiny postveligers settled primarily on submerged plants in lakes have a filtering capacity comparable to that of adults, since their densities are manifold higher (LEWANDOWSKI 1983a, MACISAAC et al. 1992, BUNT et al. 1993). Young mussels attached to artificial substrates introduced to water for protection of hydrotechnical installations against coating them by these mussels, unexpectedly became an efficient biofilter clearing the water from suspended matter (SZLAUER 1974, 1979, PIESIK 1983).

The zebra mussel feeds primarily on detritus or small organic particles, and in part on phyto- and zooplankton. The proportion of different components in their diet varies with age. In young individuals, detritus is dominant, whereas older individuals consume, in addition to detritus, various species of small algae, such as blue-green algae, diatoms, green algae and brown algae. The diet of the largest mussels comprises not only detritus and algae but also larger zooplankton such as rotifers, larval mussels, etc. The size of food items filtered by the zebra mussel ranges from 1–3 µm to 0.08–0.45 mm (MIKHEYEV 1967, SPRUNG & ROSE 1988, BASTVIKEN et al. 1998).

Filter feeding of the zebra mussel consists in catching edible items and directing them to the gut, and also in catching non-edible items, gluing them with mucus, and voiding in the form of so called pseudofaeces. In dense mussel populations, the total production of excreta (faeces and pseudofaeces) adds up to many tons of organic matter deposited in sediments of various water bodies over the season (STAŃCZYKOWSKA et al. 1975, NOORDHUIS et al. 1992, STAŃCZYKOWSKA & LEWANDOWSKI 1993a, CHARCHENKO 1995, RODITI et al. 1997). The filtration activity of the zebra mussel using seston suspended in the water column, i.e. food practically inaccessible to benthos, makes this organic matter accessible to bacteria and other benthic organisms, such as Chironomidae or Oligochaeta (IZVEKOVA & LVOVA-KATCHANOVA 1972, SPIRIDONOV 1976, SMIT et al. 1993, RICCIARDI 1994). The presence and activity of zebra mussels account for significant changes in planktonic and benthic communities (KARATAYEV & BURLAKOVA 1992, SLEPNEV et al. 1993, ŚWIERCZYŃSKI 1996, KURBATOVA 1998).

A quite new quality in terms of colonisation of new habitats was the appearance of the zebra mussel in the Great Lakes of North America in the 1980s, as a result of casual transportation (HEBERT et al. 1989). This species found excellent environmental conditions in America: a suitable quality of water, rich in oxygen and food, ideal stony substrates to attach, developed hydrotechnical systems, canals, and ship traffic promoting further expansion. The observed invasion of mussels in North America is a startling event, however, because of its unusual success and explosion on an extraordinary scale. The picture of this expansion involves the size of the invaded area (all the Great Lakes and many large rivers, thus, an area almost equal to that of Europe), secondly, the speed of this process (merely about a dozen years), and thirdly, a huge abundance, up to 700 thousand adults per m^2 in places, thus densities manifold higher than those observed in Europe (DERMOTT & MUNAWAR 1993, FRENCH 1993, NALEPA & SCHLOESSER 1993, CHASE & BAILEY 1999, and others).

Field experiments on the transition of mussel larvae from planktonic to settled life in American lakes (MARTEL 1993, MARTEL et al. 1994) support the results of earlier European experiments concerning mass mortality at this stage (LEWANDOWSKI 1982b, SPRUNG 1989). However, one important difference was observed, referring to the maximum size of planktonic larvae. In European water bodies, the largest planktonic larvae were typically 200–260 µm long, and occasionally up to 300 µm (WALZ 1973, LEWANDOWSKI 1982a, b, SPRUNG 1989). Such large larvae (300 µm) were recorded, for example, from the Ślesińskie Lake (heated lake of the Gosławsko-Ślesiński complex), where thermal-oxygen stratification was disturbed mechanically because of a cascade water discharge. Water turbulence in this place impeded settling of planktonic larvae (STAŃCZYKOWSKA et al. 1988). In the Great Lakes of North America, juvenile mussels 300–800 µm long, and even of 1–2 mm were frequently observed in the water column. These typically settled stages were particularly abundant in the water column during stormy periods. Thus also in this case mechanical effects of turbulence were involved, which impeded settling, or detached from the substrate already settled postveligers. According to MARTEL (1993), these processes are of great importance to the dispersal of zebra mussels over these large water bodies. Another mechanism promoting the spread of mussels may be the drift of macrophytes with attached young mussels (HORVATH & LAMBERTI 1997).

Although the zebra mussel has been present in American lakes for a relatively short time, ecological consequences of its expansion are already apparent. The number of species feeding on the mussels is already almost the same as in Europe (MOLLOY et al. 1997): the bivalves are eaten not only by invertebrates, fishes, including plankton-feeders (MILLS et al. 1995), birds, and mammals, but also by e.g. turtles (SERROUYA et al. 1995).

An example of a heavy impact of mussels on other aquatic organisms is their settling, often in masses, on live crayfish, snails, and bivalves of the family Unionidae (GILLIS & MACKIE 1994, TUCKER 1994, BAKER & HORNBACH 1997, BRAZNER & JENSEN 2000, and others).

The Great American Lakes are an area of comprehensive ecological studies conducted for dozens of years in many cases. The results of these studies and voluminous publications provide a rich and unique background against which the effects of zebra mussels, a new component of these ecosystems, are well pronounced.

Remarkable and rapid changes were noted in chemical composition of lake waters (LEACH 1993, FAHNENSTIEL et al. 1995a, b, HOLLAND et al. 1996, and others). The effects of mussels are often direct, as e.g. those on the plankton or benthos. Intense filter-feeding removes tiny planktonic organisms, and this promotes changes in the dominance structure of the bacterio-, phyto-, and zooplankton (CULVER 1991, NICHOLLS & HOPKINS 1993, BEETON & HAGEMAN 1994, COTNER et al. 1995, LAVRENTYEV et al. 1995, MACISAAC et al. 1995, MAKAREWICZ et al. 1999, FRISHER et al. 2000, and others). In many lakes the zebra mussel became the dominant component of the benthos which as a result underwent profound changes. Some species disappeared, whereas others found better microhabitat conditions because of the enrichment of sediments with faeces and pseudofaeces of the mussels (DERMOTT et al. 1993, GRIFFITHS 1993, BRUNER et al. 1994, STEWART & HAYNES 1994, WISENDEN & BAILEY 1995, DERMOTT & KEREC 1997, RICCIARDI et al. 1997, STEWART et al. 1998, 1999, HAYNES et al. 1999, HORVATH et al. 1999, and others).

Occasionally, the zebra mussel may have an indirect impact. A surprising effect, for example, was the influence of the mussel on fish catches. This effect can take two forms. On one hand, the filtration activity of these bivalves influences water quality and feeding conditions for planktivorous fishes, and on the other, it accounts for changes in the benthic zone that limit and hinders spawning (FRENCH & BUR 1993, LEACH 1993).

The presence of the zebra mussel in the benthic zone also creates additional shelters for potential prey of some planktivorous fishes (GONZÁLES & DOWNING 1999).

After a mass colonisation of a small (59 ha) lake by mussels, changes were found in its thermal and oxygen stratification, which will affect the whole ecosystem (YU & CULVER 2000).

A model example of the effects of the zebra mussel on a whole large ecosystem is the study conducted in the Saginaw Bay, Lake Huron, where the functioning of the entire ecosystem was changed after its mass colonisation by the bivalve (changes in chlorophyll and phosphorus concentrations, water transparency, transformations of different links in the trophic chain) (NALEPA & FAHNENSTIEL 1995).

The problem of fitting of the zebra mussel in trophic chains of aquatic ecosystems in North America was considered in many publications (MELLINA et al. 1995, RICCIARDI et al. 1997, NICHOLLS 1999). One of the examples of such a food chain developed after the invasion by the zebra mussel is seston – faeces and pseudofaeces of the mussels – *Gammarus* – fish – birds (BRUNER et al. 1994).

The effects of zebra mussel populations on various components of ecosystems discussed above, such as water quality and the composition of phyto- and zooplankton in the water column, or enrichment of bottom sediments with organic matter (faeces and pseudofaeces), creation of new microhabitats in the form of complex structures of shoals and colonies, and the influence on benthos composition are generally similar under North-American and European conditions. However, clear differences can be seen in interactions between the zebra mussel and unionid bivalves.

Under European conditions, mass coating of Unionidae by zebra mussels was not often described, but occasionally the scale of this process can be very large, e.g. 1,000 mussels settled on *Anodonta cygnea*, or the biomass of mussels 17 times exceeding that of their host *Anodonta anatina* (SEBESTYÉN 1935, WAGNER 1936, WIDUTO & KOMPOWSKI 1968, LEWANDOWSKI 1976). However, the effects of the zebra mussel on unionid bivalves are rather small. Among individuals heavily infested by mussels, distorted shells were only occasionally observed in *Anodonta anatina,* a thin-shelled species, and the effect on the growth of the young *A. anatina* was negligible. It seems that when settled *D. polymorpha* mechanically reduces the access of its host to food, the unionid would filter longer and more intensely. A more intense filtration at reduced food concentrations was already observed in other bivalves (e.g. MIKHEYEV 1967). The food rations of infested and uninfested unionids may thus be similar and, as a result, no clear effect on their growth was observed. It cannot be excluded that the infestation by zebra mussels confers some advantage on their unionid host, e.g. due to directing the current of seston-containing water towards mussel colonies, thus making food more available to *Unio* or *Anodonta.* It is possible, therefore, that the relationships between Unionidae and the zebra mussel are not competitive, or not only competitive. Other kinds of relationships may also be involved (e.g. neutrality, commensalism, and protocooperation).

In Europe, large unionid bivalves are represented only by a few species of the genus *Unio*, with thick shells, and of the genus *Anodonta*, with slightly thinner shells (NAGEL & BADINO 2001).

In American conditions, the situation of Unionidae is quite different from that in Europe. In America, they are represented by several dozen species (WILLIAMS et al. 1993, NEVES 1999, HORNBACH 2001) of various sizes and shell thickness, ranging from small bivalves, several cm in length, with delicate, thin shells, to species with heavy, thick shells, larger than the largest European unionids.

The mass invasion of Great Lakes of North America by the zebra mussel and its enormous densities in these ecosystems gave rise to dramatic changes in environmental conditions for unionid bivalves. Often several hundred mussels were attached to a single unionid, and maximum densities even exceeded 10,000 per host individual (HEBERT et al. 1991, GRIFFITHS 1993). Already several years after the appearance of the mussels, their negative effects on Unionidae were noticeable (HEBERT et al. 1991, MACKIE 1991, 1993, HAAG et al. 1993, HALLAC & MARSDEN 2000). Their densities started declining, many species, especially thin-shelled, started disappearing (GILLIS & MACKIE 1994, NALEPA 1994, RICCIARDI et al. 1995, 1998, and others). For example, several hundred Unionidae collected from the Lake St. Clair represented 18 species in 1986, 12 species in 1992, and only 5 species in 1994, only 6 individuals being alive among those collected in 1994 (NALEPA et al. 1996). In the western part of the Lake Erie, not a single live unionid was found several years after the mussel invasion, whereas in earlier years 5–8 species were found there (SCHLOESSER & NALEPA 1994). A similarly dramatic situation is observed in water courses of this region (TUCKER et al. 1993, TUCKER 1994, RICCIARDI et al. 1996, STRAYER & SMITH 1996, SCHLOESSER et al. 1998, and others).

The disappearance of Unionidae is a common and mass process. Clearly, they are losers in competition with the zebra mussel. However, this process has not come to an end as yet. Too little time has elapsed since the expansion of the mussel, and further fates of this species under American conditions are open to discussion – whether it will continue to expand (STRAYER 1991), or the initial explosion will be followed by a decline, and how American freshwater ecosystems will evolve.

The studies on the zebra mussel described in the present paper, and also results of many European and North American authors unequivocally show that this relatively small bivalve is an important component of freshwater ecosystems. Its role in nature can be considered on both global and local scales.

The global importance of mussels concerns their great capability of colonising habitats on new continents, and such barriers as the Atlantic are not an obstacle. It also involves their capability to spread rapidly over such vast water bodies as the Great Lakes of North America, that are the largest lakes of the world. Finally, their influence on changes in migration routes of water birds is a part of their global importance.

Within a lake ecosystem, the zebra mussel is a component with multiple effects. As larva it occurs in a part of plankton and explores mainly pelagic zone. Planktonic larvae occur also in the littoral, occasionally in greater densities than in the pelagial, but the littoral is primarily the place of occurrence of settled individuals, i.e. postveligers and adults. Settled mussels are often the dominant component of the benthos. Postveligers and young individuals can reach enormous densities within the periphyton and fauna associated with plants, and their role is often undervalued. The effects of the zebra mussel on communities, zones, or whole ecosystems can be direct and indirect. Direct effects concern the development of communities, creation of food resources for various organisms, clearing water from suspended matter. Indirect effects include environmental changes caused by the presence and activity of the mussels. An example can be changes in spawning sites of some fishes after the appearance of the zebra mussel in new habitats. Considering the fact that benthivorous fishes can consume mussels, planktivorous fishes and their fry feed on planktonic larvae, and bearing in mind that through their filtering activity, mussels influence food supply for planktivorous fishes, it is easy to understand that the zebra mussel interactions with necton, seemingly an independent system, are diverse and complex.

Moreover, the zebra mussel apparently contributes to the shape of the specific zone of the lake sublittoral, where the bank of empty shells mostly consists of mussel shells.

Local importance of the zebra mussel can be considered even on a micro-scale. For example, the environment-forming role of zebra mussels is important, especially the creation of microhabitats in recesses of shoals and colonies that serve as shelters for zoobenthos. Associated with this is the enrichment of bottom sediments with mussel faeces and pseudofaeces rich in organic matter. On the microscale, local differences in densities of settled mussels are frequent, especially in densities of planktonic larvae, susceptible to winds, water currents, and local barriers such as islands, peninsulas, and shoals.

Zebra mussel populations, involved in many interactions at the ecosystem level, are dynamic and variable in time. This is partly shown in the present paper which, on one hand, analyses the results of long-term studies and, on the other, the results of local studies conducted with a high frequency at a large number of sites.

Many new aspects of the zebra mussel ecology will hopefully be revealed by the comprehensive, though still not long-term, studies conducted in the region of the Great Lakes in North America, where this species appeared not much less than 20 years ago.

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Appendix 1. Characteristics of the lakes where planktonic larvae of *D. polymorpha* were studied (after: HILLBRICHT-ILKOWSKA 1983, KAJAK 1983, STAŃCZYKOWSKA & ZDANOWSKI 1986, ZDANOWSKI 1994)

No.	Lake	Surface area (ha)	Maximum depth (m)	Limnological type	Study year
1	Głębokie	47	34.3	eutrophy	1976, 77
2	Gosławickie	379	3.0	eutrophy (heated)	1974, 78
3	Inulec	178	10.1	eutrophy	1976, 97, 98
4	Jorzec	42	11.6	eutrophy	1976, 77
5	Kołowin	78	7.2	mesotrophy	1978
6	Licheńskie	154	13.3	eutrophy (heated)	1974, 78
7	Majcz Wielki	163	16.4	mesotrophy	1976–78
8	Mikorzyńskie	245 (with Wąsoskie)	38.0	eutrophy (heated)	1974, 78
9	Ołów	61	40.1	mesotrophy	1978
10	Pątnowskie	307	5.4	eutrophy (heated)	1974
11	Ślesińskie	148	25.7	eutrophy (heated)	1974, 78
12	Wąsoskie	245 (with Mikorzyńskie)	35.7	eutrophy (heated)	1974
13	Zelwążek	11	7.4	eutrophy	1976
14	Żarnowieckie	1,432	19.4	mesotrophy	1980

Appendix 2. Characteristics of the lakes where settled *D. polymorpha* were studied (after: Hillbricht-Ilkowska 1983, Kajak 1983, Stańczykowska & Zdanowski 1986, Zdanowski 1992, Hillbricht-Ilkowska & Wiśniewski 1996)

No.	Lake	Surface area (ha)	Maximum depth (m)	Limnological type	Study year	*D. polymorpha* density in occurrence zone (ind. m^{-2})
1	Barlewickie	64	8.5	hypertrophy	1987	20
2	Battąg	72	15.2	eutrophy	1977, 78	160–580
3	Bełdany	780	31.0	eutrophy	1972, 82, 85, 88, 94	0–400
4	Białe	341	31.0	eutrophy	1989	180
5	Białe Wigierskie	100	34.0	oligotrophy	1986	<1
6	Boczne	190	15.0	eutrophy	1972, 82, 85, 88, 93, 94	0–1,200
7	Brajnickie	186	5.2	hypertrophy	1977, 78	10
8	Burgale	79	7.4	eutrophy	1977, 78	5
9	Czos	279	42.6	eutrophy	1977–79	350–1,260
10	Długie	62	5.4	hypertrophy	1978	35
11	Dłużec	123	19.8	eutrophy	1989	380
12	Ełckie	382	55.8	hypertrophy	1978	5
13	Gant	75	28.3	mesotrophy	1987, 89	1,400–1,920
14	Gardyńskie	83	11.5	eutrophy	1989	30
15	Gielądzkie	475	27.0	eutrophy	1989	690
16	Gim	176	25.8	mesotrophy	1977	20
17	Głębokie	47	34.3	eutrophy	1976, 77, 93, 97	20–280
18	Gromskie	240	15.8	eutrophy	1977	300
19	Hartowiec	69	5.2	hypertrophy	1978	5
20	Inulec	178	10.1	eutrophy	1976, 93–98	400–1,300
21	Iławskie	154	2.6	hypertrophy	1978	65
22	Jagodne	936	34.0	eutrophy	1972, 82, 88, 94	0–50
23	Jaśkowskie	152	16.5	eutrophy	1977	200
24	Jerzewko	23	2.7	eutrophy	1989	200
25	Jorzec	42	11.6	eutrophy	1976, 77, 93, 97	0–130
26	Juno	381	33.0	eutrophy	1977	5
27	Kierzlińskie	93	44.5	mesotrophy	1977	600
28	Kisajno	2,536	24.0	eutrophy	1972, 85, 88, 94	500–1,200
29	Kołowin	78	7.2	mesotrophy	1978	2,340
30	Kraksy Duże	44	4.0	hypertrophy	1877, 78	0
31	Krutyńskie	55	3.2	eutrophy	1989	70
32	Kuc	98	28.0	mesotrophy	1977, 78	260–840
33	Kujno	24	6.0	eutrophy	1987, 89	70–480
34	Lampackie	198	38.5	eutrophy	1977, 89	500–3,400
35	Lampasz	88	21.7	eutrophy	1989	2,390
36	Lidzbarskie	122	25.5	eutrophy	1977	1,700
37	Majcz Wielki	163	16.4	mesotrophy	1976–79, 93, 94, 97	360–510
38	Mamry Północne	2,478	40.0	mesotrophy	1982, 88, 93, 94	1,000–1,600
39	Milanówko	16	2.7	eutrophy	1989	400
40	Małszewskie	202	16.9	eutrophy	1977	180

No.	Lake	Surface area (ha)	Maximum depth (m)	Limnological type	Study year	*D. polymorpha* density in occurrence zone (ind. m^{-2})
41	Maróz	332	41.0	mesotrophy	1977	230
42	Mikołajskie	460	27.8	eutrophy	1972, 74, 76, 77, 79, 82, 83, 87, 89, 92, 97	5–2,200
43	Mokre	841	51.0	mesotrophy	1989	160
44	Mój	116	4.1	eutrophy	1978	25
45	Nidzkie	1,724	25.0	eutrophy	1980, 94	300–700
46	Niegocin	2,499	40.0	eutrophy	1972, 82, 85, 88, 94	20–1,300
47	Ołów	61	40.1	mesotrophy	1977, 78	1,500–1,830
48	Pierty	228	38.0	eutrophy	1986	110
49	Piłakno	259	56.6	mesotrophy	1977	20
50	Probarskie	201	31.0	mesotrophy	1977	120
51	Rańskie	291	7.8	eutrophy	1978	15
52	Rumian	306	14.4	eutrophy	1977	530
53	Ryńskie	620	47.0	eutrophy	1982, 85, 88, 94	0–50
54	Rzeckie	56	29.0	eutrophy	1977	330
55	Sambród	128	4.3	hypertrophy	1978	20
56	Sarż	77	15.0	eutrophy	1977	0
57	Sędańskie	168	6.1	eutrophy	1977, 78	0
58	Siercze	55	2.0	eutrophy	1977, 78	0
59	Skanda	51	12.0	mesotrophy	1977	180
60	Spychowskie	49	7.7	eutrophy	1989	0
61	Szeląg Mały	84	15.2	eutrophy	1977	0
62	Szymon	204	34.0	eutrophy	1972, 82, 88, 94	0–1,500
63	Śniardwy	10,598	25.0	eutrophy	1972, 82, 85, 88, 93, 94	200–800
64	Święcajty	814	28.0	eutrophy	1982, 85, 88, 93, 94	1,000–1,800
65	Tałty	1,162	37.5	eutrophy	1972, 82, 85, 88, 94	0–3,600
66	Tuchel	43	5.1	hypertrophy	1978	10
67	Uplik	61	9.2	eutrophy	1989	5
68	Warpuńskie	49	6.9	hypertrophy	1989	45
69	Wigry	2,118	73.0	mesotrophy	1986	130
70	Wobel	24	15.0	hypertrophy	1978	5
71	Zdrużno	250	25.9	eutrophy	1989	5
72	Zelwążek	11	7.4	eutrophy	1976, 93, 97	0–175
73	Zyndackie	39	10.3	hypertrophy	1989	5
74	Zyzdrój Mały	51	12.8	eutrophy	1989	0
75	Zyzdrój Wielki	210	14.5	eutrophy	1989	240
76	Żarnowieckie	1,432	19.4	mesotrophy	1974, 78, 80, 81	65–590