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LITTORAL AND SUBLITTORAL MALACOFAUNA OF THE EUTROPHIC LAKE MIKOŁAJSKIE (NORTH-EASTERN POLAND)

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Abstract: Studies on the occurrence of molluscs in Lake Mikołajskie (Masurian Lakeland, NE. Poland) were carried out in 2011–2015. Samples were taken yearly from 5–10 sites in the littoral and sublittoral. Twenty four mollusc species were recorded, including 12 snails and 12 bivalves. Moreover, empty shells of another eight species were found. The most common species in most sites were snails *Bithynia tentaculata* (Linnaeus), *Valvata piscinalis* (O. F. Müller) and *Potamopyrgus antipodarum* (Gray), and bivalves *Unio tumidus* Philipsson and *Dreissena polymorpha* (Pallas). Live molluscs were recorded to the depth of 5 m and their mean density in particular sites ranged from 100 to 300 individuals per m^2. Compared to earlier studies, the number of species was markedly smaller which may be partly associated with the increasing trophic status of the lake. On the other hand, alien species (*P. antipodarum*, *Lithoglyphus naticoides* (C. Pfeiffer)) appeared in the lake in various periods of time and some species (e.g. *Anodonta cygnea* (Linnaeus)), not recorded for many years, returned to their sites. *D. polymorpha* had been studied permanently (with short breaks) for 50 years in the lake. Its abundance at the beginning of the 21st century was markedly higher than in the last two decades of the 20th century but far smaller than the enormous densities noted before. The live malacofauna differed greatly from the collection of empty shells in its species composition, dominance structure as well as in the age and size structure of selected species.

Key words: molluscs, long-term changes, alien species, shells, Lake Mikołajskie

INTRODUCTION

Lake Mikołajskie – one of the lakes in the Great Masurian Lake system – has been an object of intensive hydrobiological studies for many decades (Pieczyński & Rybak 1990). Its hydrochemistry, processes at the water-bottom sediments interphase, plankton, benthic organisms, periphyton, macrophytes, ichthyofauna and catchment basin are all well known; many publications deal with Lake Mikołajskie (Kajak 1975, 1978, Pieczyńska 1976, Gliwicz et al. 1980 and others).

Lake Mikołajskie is much affected by eutrophication caused by such factors as communal waste or summer tourist activities. Numerous studies indicate various environmental and biocoenotic changes associated with its increasing trophic status. Long-term changes observed in the lake involve phytoplankton (Spodniewska 1976), filamentous algae (Pieczyńska et al. 1988), submerged and emergent vegetation (Ozimek & Kowalczewski 1984, Królikowska 1987, Kowalczewski & Ozimek 1993), as well as zooplankton (Spodniewska et al. 1973, Ejsmont-Karabin & Hillbricht-Ilkowska 1994).

Studies on the lake's aquatic molluscs are relatively numerous but they either date from rather remote past (Berger 1960) or refer to selected taxa and ecological groups, for example gastropods (Kołodziejczyk 1984, 2001), unionid bivalves (Lewandowski & Stańczykowska 1975, Lewandowski 1976, 1991, Lewandowski & Kołodziejczyk 2014), *Dreissena*

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polymorpha (STAŃCZYKOWSKA 1961, 1975, 1977, 1978, STAŃCZYKOWSKA et al. 1976, STAŃCZYKOWSKA & LEWANDOWSKI 1993a, 1993b, 1995) and periphytic molluscs (SOSZKA 1975). This study was aimed at analysing the status of mollusc community in Lake Mikołajskie at the beginning of the 21st century, considering live molluscs and empty shells in the lake's sublittoral and at comparing the results with historical data.

STUDY AREA AND METHODS

Lake Mikołajskie (53°46'38"N, 21°35'36"E), situated in the central part of the Great Masurian Lakes system, is directly connected with lakes Tałty, Śniardwy and Bełdany. It is a through-flow water body (fed from lakes Tałty and Bełdany and discharging into Lake Śniardwy), eutrophic, 460 ha in area and maximum and mean depth of 27.8 and 11.3 m, respectively. The littoral occupies 19% of its surface (KAJAK 1978). The town of Mikołajki, located at the north-eastern end of the lake, with permanent population of 4 thousand, is a popular yachting and tourism centre. The western shores are high and forested, the south-eastern ones are low and fringed by meadows and crop fields. The shores are overgrown by reed *Phragmites australis* (Cav.) Trin. ex Stend. (Fig. 1) which is, however, absent in the north-eastern part of the lake i.e. near the town and harbours (Fig. 2). The central and southern parts of the lake fall within the borders of the Masurian Landscape Park.

Since the 1970s Lake Mikołajskie has undergone a marked eutrophication, manifest as a decrease in water transparency (GLIWICZ et al. 1980), increase in biomass of phytoplankton and filamentous algae (SPODNIEWSKA 1976, PIECZYŃSKA et al. 1988) and decline of submerged macrophytes (OZIMEK & KOWALCZEWSKI 1984, KOWALCZEWSKI & OZIMEK 1993). A slight improvement in the water quality: increase in its transparency, noted after 2003, (LEWANDOWSKI & KOŁODZIEJCZYK 2014), may be a consequence of the 1977 installation of biological wastewater treatment plant with phosphorus removal in Mikołajki (CYDZIK et al. 2000).

Fig. 1. Lake Mikołajskie – eastern part. Photo: K. LEWANDOWSKI

Fig. 2. Lake Mikołajskie near town Mikołajki. Photo: K. LEWANDOWSKI

Studies on the occurrence of molluscs in the lake were carried out in the summers of 2011–2015. In 2011 and 2015 samples were collected from ten sites evenly distributed along the shore (Fig. 3) and in 2012–2014 in five sites (nos. 2, 3, 4, 6 and 7) only. In most sites samples were collected at depths of 0.5 m (except dense reed-beds), 1.0 m and then at every 1 m until the disappearance of molluscs, thus covering the littoral and sublittoral zones.

At the depth of 0.5 m molluscs were sampled by hand from a square frame of 0.25 m^2 placed randomly several times on the bottom. In deeper sites Günther's sampler of 276 cm^2 was used (three samples from each depth). The material was washed on a sieve of 0.5 mm mesh, to retrieve live molluscs and empty shells. The molluscs were preserved in 75% alcohol, except unionid bivalves which were released after determination of species, age and size. Species identification was based on keys by PIECHOCKI (1979), PIECHOCKI & DYDUCH-FALNIOWSKA (1993) and WELTER-SCHULTES (2012), the nomenclature updated according to PIECHOCKI & WAWRZYNIAK-WYDROWSKA (2016). Shells of selected species were measured with a calliper and the age was determined by counting rings of winter growth inhibition. Only left halves of shells were counted in case of empty shells of *D. polymorpha*. In total, 980 live individuals and 8,430 empty shells were collected.

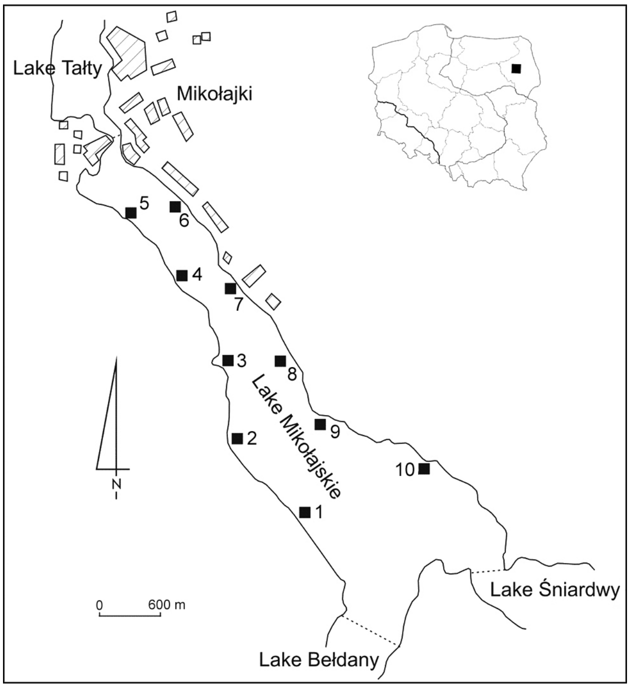

Fig. 3. Distribution of study sites in Lake Mikołajskie in 2011 and 2015

RESULTS

Twenty four mollusc species including 12 snails and 12 bivalves were found in Lake Mikołajskie during the five-year study. Apart from live individuals, empty shells of another eight species were collected (Table 1). The most common species found in most sites were snails *Bithynia tentaculata*, *Valvata piscinalis* and *Potamopyrgus antipodarum*, and bivalves *Unio tumidus* and *D. polymorpha*.

Live molluscs were found to occur to the depth of 5 m. Their highest densities (200–300 ind. m^{-2} on average) were noted at the depths of 1 to 4 m. The highest local densities reached 1,300 ind. m^{-2} (Fig. 4). The mean mollusc density in particular sites during the study period ranged from 100 to 300 ind. m^{-2}. Slightly higher densities (250–300 ind. m^{-2}) were recorded in sites remote from the town (sites 1, 2, 3, 10), compared to other sites under greater human influence, where 100 to 230 ind. m^{-2} were observed. In some years, however, densities deviated from such a spatial pattern. For example, in sites 1–3 densities

Table 1. Malacofauna of Lake Mikołajskie in 2011–2015

Species	Years					
	2011	2012	2013	2014	2015	2011–2015
Gastropoda						
Theodoxus fluviatilis (Linnaeus, 1758)	+	+	o	o	+	+
Viviparus contectus (Millet, 1813)	+	o	+	+	+	+
Viviparus viviparus (Linnaeus, 1758)	+	+	+	+	+	+
Bithynia leachii (Sheppard, 1823)			o	o	o	o
Bithynia tentaculata (Linnaeus, 1758)	+	+	+	+	+	+
Lithoglyphus naticoides (C. Pfeiffer, 1828)	+	+	+	+	+	+
Potamopyrgus antipodarum (Gray, 1843)	+	+	+	+	+	+
Valvata cristata O. F. Müller, 1774			o	o	o	o
Valvata piscinalis (O. F. Müller, 1774)	+	+	+	+	+	+
Acroloxus lacustris (Linnaeus, 1758)	+			o	o	+
Lymnaea stagnalis (Linnaeus, 1758)	o	o	o	o	o	o
Radix auricularia (Linnaeus, 1758)	+	o	+	o	+	+
Radix balthica (Linnaeus, 1758)	+	o	o	o	+	+
Bathyomphalus contortus (Linnaeus, 1758)		o		o	o	o
Gyraulus albus (O. F. Müller, 1774)	o			o	+	+
Planorbarius corneus (Linnaeus, 1758)	+	o	o	+	o	+
Planorbis carinatus O. F. Müller, 1774		o	o	o	o	o
Planorbis planorbis (Linnaeus, 1758)					o	o
Bivalvia						
Anodonta anatina (Linnaeus, 1758)	+	+	+	+	+	+
Anodonta cygnea (Linnaeus, 1758)	+			o	+	+
Pseudanodonta complanata (Rossmässler, 1835)	o					o
Unio pictorum (Linnaeus, 1758)	+	+	o	o	+	+
Unio tumidus Philipsson, 1788	+	+	+	+	+	+
Pisidium amnicum (O. F. Müller, 1774)			o	o	o	o
Pisidium casertanum (Poli, 1791)	o			+	+	+
Pisidium henslowanum (Sheppard, 1823)	o			+	+	+
Pisidium nitidum Jenyns, 1832	+			+	+	+
Pisidium subtruncatum Malm, 1855	+	+	+	+	+	+
Pisidium supinum A. Schmidt, 1851	o				+	+
Sphaerium corneum (Linnaeus, 1758)	+	o	o	+	+	+
Sphaerium rivicola (Lamarck, 1818)					+	+
Dreissena polymorpha (Pallas, 1771)	+	+	+	+	+	+
Number of species based on live individuals	19	11	11	16	22	24
Number of species based on empty shells	6	8	10	12	9	8
Total number of species	25	19	21	28	31	32

(+ – represented by live individuals, o – represented by empty shells).

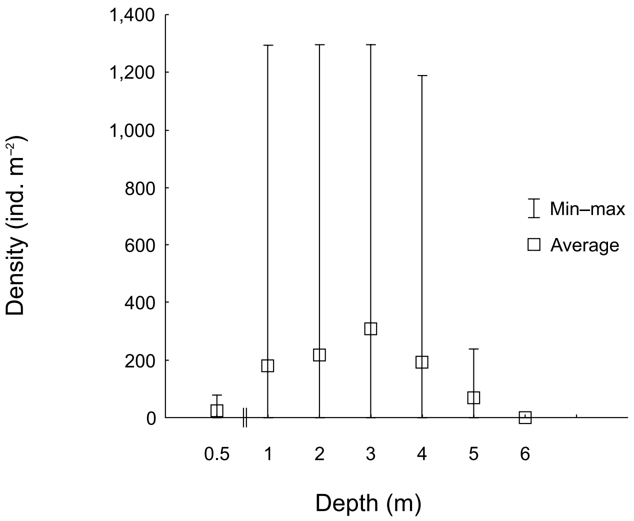

Fig. 4. Density of molluscs (ind. m^{-2}) at various depths of Lake Mikołajskie in 2011–2015

of less than 100 ind. m^{-2} were recorded in some years and in site 6 situated near the town the density in 2015 exceeded 400 ind. m^{-2}.

Apart from native gastropods, Lake Mikołajskie hosted two alien snail species: *P. antipodarum* and *Lithoglyphus naticoides*. In the study period *P. antipodarum* occurred to the depth of 4 m and usually reached densities of several dozen to several hundred individuals per square metre. The highest local density (site 2, depth 4 m) of this snail was 850 ind. m^{-2}. In the whole study period *L. naticoides* occurred in the south-western part of the lake (sites 2 and 3) and in 2014 and 2015 it was also present in the north-eastern part (site 7). The snail was noted at the depths of 1 to 4 m and its density was usually below 100 ind. m^{-2} with the maximum of 250 ind. m^{-2}.

Seven species of small bivalves of the family Sphaeriidae were recorded in 2011–2015, including two species of the genus *Sphaerium* and five of the genus *Pisidium*. The sixth species (*P. amnicum*) was found only in the form of empty shells. The Sphaeriidae attained relatively small densities of less than 100 ind. m^{-2} and the maximum of ca. 300 ind. m^{-2}.

Bivalves of the family Unionidae were dominated by *U. tumidus*, whose proportion varied from 56 to 94% in 2011–2015. The youngest (1-year-old) individuals, often less than 5 mm long, constituted most (36%) of the population. Subsequent age classes (2–5 years) formed a similar proportion of about fifteen percent. The oldest *U. tumidus* attained the age of 8–9 years and the largest individual was 58.3 mm long. The mean density of this species in its range of occurrence (to the depth of 4 m) was 22 ind. m^{-2} and the maximum density locally exceeded 150 ind. m^{-2}. *Anodonta anatina* was also recorded in all the study years but its proportion was much smaller (6–30%). The oldest individuals were four years old and these individuals dominated in the population although many one-year-olds were also observed. The largest *A. anatina* was 61.6 mm long. *Unio pictorum* was found less frequently and not every year. Its greatest proportion among the unionids (almost 11%) was recorded in 2011. The oldest *U. pictorum* were seven years old and their length ranged from 58 to 60 mm. One and two years old individuals dominated in the population. Only two individuals of *Anodonta cygnea* were found during the whole study period. In 2011 we found a four years old individual, length 73.2 mm (site 6, depth 3 m) and in 2015 – a one year old individual 10 mm long (site 7, depth 2 m). The fifth unionid species – *Pseudanodonta complanata*, was represented only by empty shells. Two shells, length 48.4 mm (4 years old) and 43.8 mm (3 years old), were collected in 2011 in site 2 at the depth of 5 m.

The population of *D. polymorpha* was stable in 2011–2015 but its density was relatively small – less than 100 ind. m^{-2} within the range of occurrence (to 5 m depth) with the local maximum of about 430 ind. m^{-2}.

Besides live molluscs, empty shells accumulated on the bottom, including large shell mounds in the sublittoral, were analysed both quantitatively and qualitatively. The percentage of empty shells in the littoral and sublittoral increased with depth. In shallow sites (0.5 to 1.0 m depth) they constituted 40–

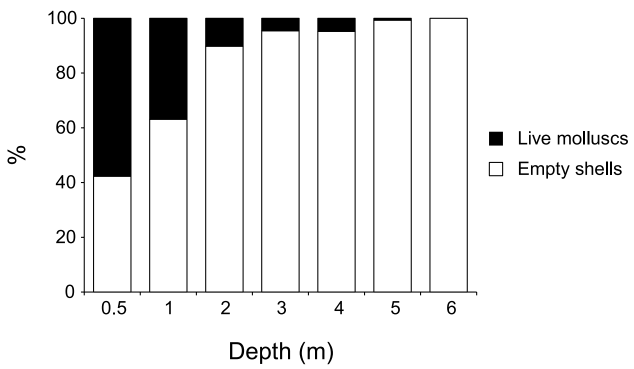

Fig. 5. Proportion of live molluscs and empty shells at various depths of Lake Mikołajskie in 2015

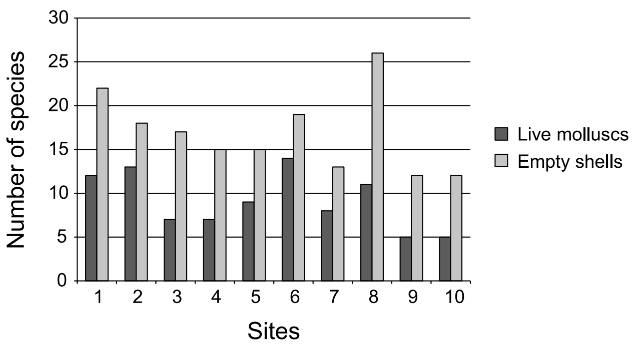

Fig. 6. Number of mollusc species represented by live individuals and shells in particular sites of Lake Mikołajskie in 2015

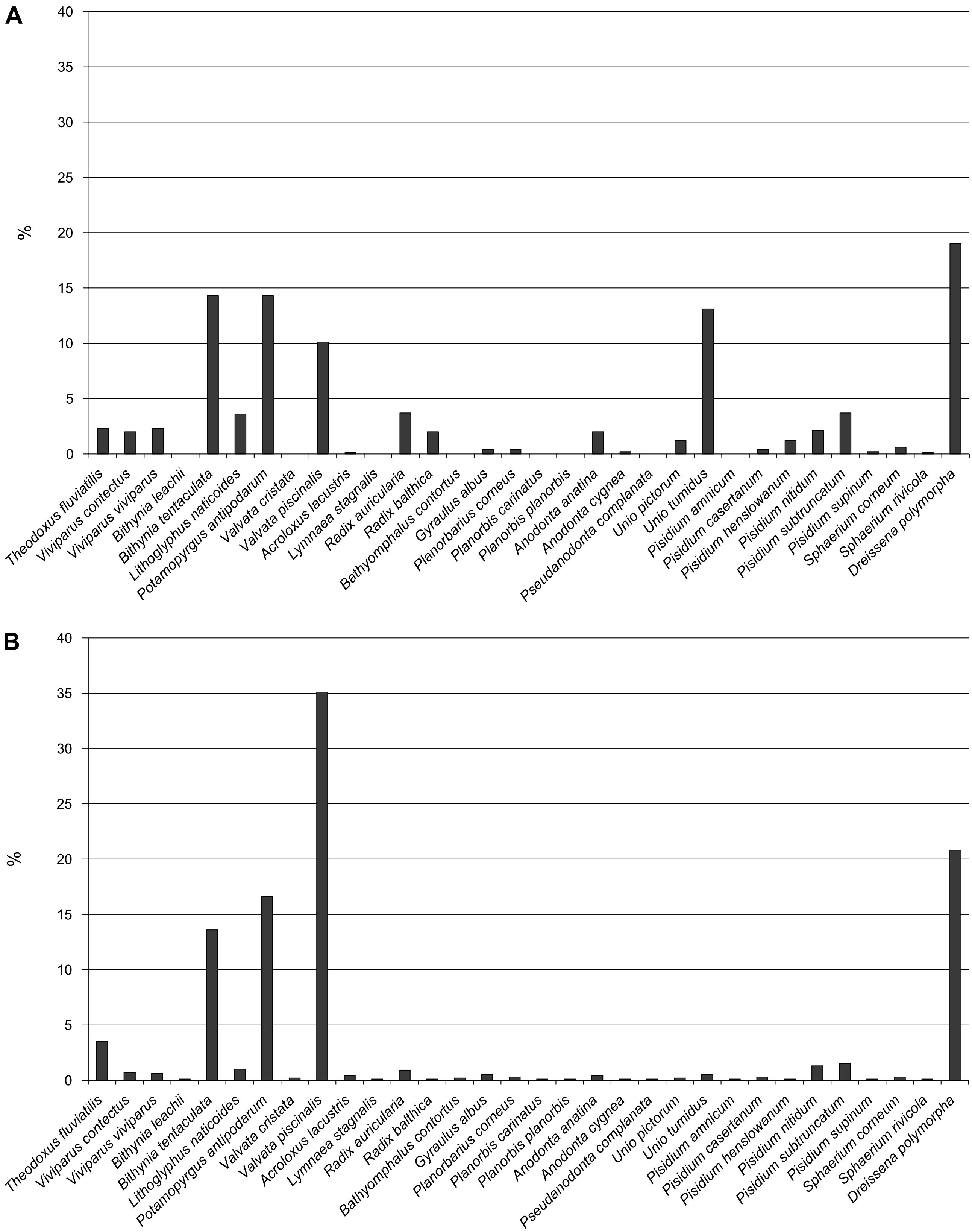

Fig. 7. A – dominance structure among live molluscs in Lake Mikołajskie in 2011–2015; B – dominance structure among empty shells in Lake Mikołajskie in 2011–2015

60% of the mollusc samples, deeper their proportion increased to 100% (Fig. 5). In the sublittoral empty shells outnumbered live molluscs up to 20 times. Sometimes the number of empty shells was 20,000 per square metre of sublittoral.

The species composition differed distinctly between live molluscs and empty shells collected in 2011–2015. Thirty two species were represented by empty shells whereas only 24 species were represented by live individuals (Table 1). The differences were visible in every site, covering the whole profile from littoral to sublittoral. For example, in site 8 visited in 2015 live individuals represented 11 species while 26 species were identified among empty shells (Fig. 6).

Likewise, the dominance structure differed greatly. In the whole collected material *D. polymorpha* dominated among all molluscs (19%), the next most abundant species were *B. tentaculata* (14.3%) and *Potamopyrgus antipodarum* (14.3%) (Fig. 7A). Most (35.1%) of all the empty shells, however, belonged to *V. piscinalis*. Shells of *D. polymorpha* were the second most abundant and constituted 20.8% of the whole collection (Fig. 7B). *U. tumidus* was relatively frequent among live molluscs (13.1%). The proportion of its empty shells was very small – only 0.5% of all collected shells.

Empty shells found in the sublittoral were often larger than those of their live conspecifics. The largest live *D. polymorpha* collected during the study period was 29–31 mm long at the maximum age of six years and the largest empty shells were 33–34 mm long (maximum age of 7 years). A similar regularity was noted for *A. anatina* and *U. pictorum* – the largest empty shells were longer by several millimetres than the largest live individuals. The age of the oldest empty shells of *A. anatina* was estimated at six years and that of *U. pictorum* – at seven years. An opposite tendency was observed for *U. tumidus*. The largest empty shells of this species were slightly smaller (maximum 6 years of age) than the shells of the largest live individuals.

Table 2. Gastropoda of Lake Mikołajskie in various periods

Species	Years of studies and source			
	1953 (Berger 1960)	1969 (Soszka 1975)	1978–1982 (Kołodziejczyk 1984)	2011–2015 (This study)
Theodoxus fluviatilis (Linnaeus, 1758)	+	+	+	+
Viviparus contectus (Millet, 1813)	+	–	+	+
Viviparus viviparus (Linnaeus, 1758)	+	+	+	+
Bithynia leachii (Sheppard, 1823)	–	–	+	–
Bithynia tentaculata (Linnaeus, 1758)	+	+	+	+
Marstoniopsis insubrica (Küster, 1853)	+	–	+	–
Lithoglyphus naticoides (C. Pfeiffer, 1828)	–	–	–	+
Potamopyrgus antipodarum (Gray, 1843)	–	–	+	+
Valvata cristata O. F. Müller, 1774	–	+	+	–
Valvata macrostoma Mörch, 1864	–	–	+	–
Valvata piscinalis (O. F. Müller, 1774)	+	+	+	+
Acroloxus lacustris (Linnaeus, 1758)	–	+	+	+
Galba truncatula (O. F. Müller, 1774)	–	–	+	–
Lymnaea stagnalis (Linnaeus, 1758)	+	+	+	–
Myxas glutinosa (O. F. Müller, 1774)	–	+	+	–
Radix auricularia (Linnaeus, 1758)	+	–	+	+
Radix balthica (Linnaeus, 1758)	+	+		+
Stagnicola corvus (Gmelin, 1778)	+	+	–	–
Physa acuta (Draparnaud, 1805)	–	+	–	–
Physa fontinalis (Linnaeus, 1758)	+	–	+	–
Anisus vortex (Linnaeus, 1758)	–	+	+	–
Bathyomphalus contortus (Linnaeus, 1758)	–	+	+	–
Gyraulus albus (O. F. Müller, 1774)	–	+	+	+
Gyraulus crista (Linnaeus, 1758)	–	+	+	–
Planorbarius corneus (Linnaeus, 1758)	+	+	+	+
Planorbis carinatus O. F. Müller, 1774	+	–	+	–
Planorbis planorbis (Linnaeus, 1758)	–	+	–	–
Segmentina nitida (O. F. Müller, 1774)	–	–	+	–
Number of species	13	17	23	12

(+ – present, – – absent)

DISCUSSION

Eutrophication of Lake Mikołajskie as an effect of wastewater discharge and seasonally intensive tourist activity has been described in detail by many authors (e.g. KAJAK 1978, GLIWICZ et al. 1980, PIECZYŃSKA et al. 1988). The lake waters, particularly deoxygenated near the bottom in summer, are phosphorus- and nitrogen-rich. The high degree of eutrophication is reflected by the composition of phytoplankton: it is dominated by chrysophytes and cyanobacteria in spring and cyanobacteria alone in summer (SPODNIEWSKA 1976, CYDZIK et al. 2000). The advancement of eutrophication has resulted in an increase of biomass of filamentous algae on the one hand (PIECZYŃSKA et al. 1988) and in a limited range and impoverished species composition of macrophytes on the other (OZIMEK & KOWALCZEWSKI 1984, KRÓLIKOWSKA 1987, KOWALCZEWSKI & OZIMEK 1993). The high trophic status has resulted in changes in the fish fauna – mainly decline of coregonid abundance and decreased efficiency of fishery (KOZIKOWSKA 1970, CYDZIK et al. 2000).

The Secchi disc visibility is a clear indicator of environmental changes in Lake Mikołajskie. In the 1950s the visibility in summer was 3 m (SZCZEPAŃSKI 1968) but dropped to 1 m in the 1970s and remained at the same level during the next three decades (PIECZYŃSKA 1976, GLIWICZ et al. 1980, CYDZIK et al. 1995, 2000). The 1997 installation of wastewater treatment plant in Mikołajki, and the directing of the effluents outside the lake were probably the reasons why water transparency slightly increased to 1.4–1.8 m in 2005–2008 (LEWANDOWSKI & KOŁODZIEJCZYK 2014). Similar signs of lake oligotrophication were also observed in a nearby Lake Niegocin after installation of a modern wastewater treatment plant in Giżycko (KAUPPINEN 2013).

The abatement of wastewater discharge to Lake Mikołajskie alone will not guarantee a fast improvement of the water quality. The phosphorus load in the lake is still substantial. The internal input of phosphorus is a result of accumulation of the long-term supply of substances contained in poorly treated wastewater in the bottom sediments (CYDZIK et al. 2000).

All the snails recorded in Lake Mikołajskie are common, often euryoecious species associated with stones, muddy bottom and less frequently with sandy bottom or plants. The earliest, though only qualitative, data on the lake's snails can be found in BERGER's (1960) paper, with the list of 13 species collected in 1953. For 1969 SOSZKA (1975) reported 17 snail species several of which were found as empty shells in the present study (*Lymnaea stagnalis*, *Valvata cristata*, *Bithynia leachii*, *Planorbis planorbis*, *P. carinatus*).

As many as 23 snail taxa were recorded by KOŁODZIEJCZYK (1984) in 1978–1982. He reported some species not found in 2011–2015: *Valvata macrostoma*, *Marstoniopsis insubrica*, *Physa fontinalis*, *Myxas glutinosa*, *Anisus vortex*, *Segmentina nitida*. Ten years later studies by the same author (KOŁODZIEJCZYK 1995) on periphytic snails indicated a distinct qualitative impoverishment – some species, both rare and common earlier, had disappeared (*Valvata piscinalis, Marstoniopsis insubrica, Physa fontinalis*).

The studies of 2011–2015 showed a remarkable decline of the number of snails compared to the literature data (Table 2). A similar impoverishment in the malacofauna of lakes of the Jorka River basin (a river near Lake Mikołajskie but discharging to Lake Tałty) was observed by KOŁODZIEJCZYK et al. (2009), who compared 2006 data with those from 1976 and 1997. The same trends were noted by JURKIEWICZ-KARNKOWSKA (1998) in her long-term studies of a lowland dam reservoir (Zegrzyński Reservoir, central Poland). Many authors pointed out an unfavourable effect of increasing eutrophication on the malacofauna (e.g. NALEPA et al. 1991, 2007, PIECZYŃSKA et al. 1999, PATZNER & MÜLLER 2001, PIP 2006).

Besides the disappearance of some mollusc species caused by eutrophication, new species invade lakes. *Potamopyrgus antipodarum*, an invasive species from New Zealand, was first found in Lake Mikołajskie in the late 1970s/early 1980s by KOŁODZIEJCZYK (1984). Later studies indicate an already stable population of this species in the lake. Another alien snail species – *L. naticoides*, was also found in Lake Mikołajskie by KOŁODZIEJCZYK (2001) in 1997, in only one site near the south-western shore and it was observed only there in subsequent years. In our studies the species was found there (sites 2 and 3) every year from 2011 to 2015. However, in 2014 and 2015 its presence was also recorded in another site (site 7) near the north-eastern shore, just opposite to the earlier sites. The question is how the snail got across to the new site. It is unlikely that it did it by itself since the new and the old sites are separated by the deep profundal zone, and the spread along the shore, many kilometres long, is improbable because the snail was not found in any place in-between. The only option is passive, human- or bird-mediated transport but it is still unclear from where the snail was transferred – a site on the other side of the lake or from another region of Poland as it happened in 1997. It is noteworthy that the nearest sites of *L. naticoides* are in the Narew River (far south of Lake Mikołajskie) and in the Vistula Lagoon (far north of the lake) (KOŁODZIEJCZYK 2004). It should, however, be borne in mind that, despite its low mobility, the snail invaded an area of about 1 million km^2 during its 100-year-long expansion in Europe from the Ponto-Caspian region (NOWAK 1971). Another alien snail species – *Physa acuta* – was found only once in Lake Mikołajskie, in 1969 (Soszka 1975). Even its empty shells were never found subsequently.

The only literature data on the bivalves of the family Sphaeriidae in Lake Mikołajskie date from 60 years ago. Berger (1960) recorded five species of *Pisidium* (*P. amnicum*, *P. henslowanum*, *P. nitidum*, *P. subtruncatum*, *P. supinum*) and *Sphaerium corneum*. All these species were observed in Lake Mikołajskie in 2011–2015, although *P. amnicum* was found only in the form of empty shells. Two more sphaeriid species – *P. casertanum* and *S. rivicola* – were found during the study period. Most of these bivalves are common euryoecious species tolerant to water pollution. Only *P. amnicum* and *P. supinum* require clean and well aerated waters for their development. The environmental conditions in Lake Mikołajskie in the 1950s met these criteria. According to Piechocki & Dyduch-Falniowska (1993) the sensitivity of *P. supinum* to water pollution makes this species threatened by extinction. Finding *P. supinum* in Lake Mikołajskie in 2015 may indicate a water quality improvement in the lake.

In 1953 Berger (1960) recorded four unionid species in Lake Mikołajskie: *Anodonta anatina*, *A. cygnea*, *Unio pictorum* and *U. tumidus*. Another species of the family – *Pseudanodonta complanata* – was found there in 1972 (Lewandowski & Stańczykowska 1975). *A. cygnea* and *P. complanata* disappeared completely from the lake in subsequent years (Lewandowski 1991, Lewandowski & Kołodziejczyk 2014). The dominance structure of the Unionidae markedly changed during 40 years (Fig. 8). In the 1970s and 1990s *A. anatina* prevailed among the unionids; after 2000 *U. tumidus* became the dominant. *U. pictorum* formed a small proportion of the community during that period. It seems that the population of *U. tumidus* in Lake Mikołajskie was in very good condition in 2011–2015, as indicated by the high densities, dominance of young individuals and by the attained age of at least 8–9 years, which was not recorded in 1980s and 1990s (Lewandowski 1991, Lewandowski & Kołodziejczyk 2014). An indirect evidence of the population status my be the fact that the live individuals were sometimes larger than the empty shells of individuals which had died in the previous years. Noteworthy is the finding of protected *Anodonta cygnea* after its 40-year-long absence in Lake Mikołajskie. Live individuals were observed in 2011 and 2015. *P. complanata* was found in the lake only once, in 1972, although its empty shells were found in 2011.

The population of *D. polymorpha* in Lake Mikołajskie, stabilised in 2011–2015 at a relatively low density, was far from the densities of several thousand individuals observed in the 1950s and 1970s (Stańczykowska 1975, Lewandowski &

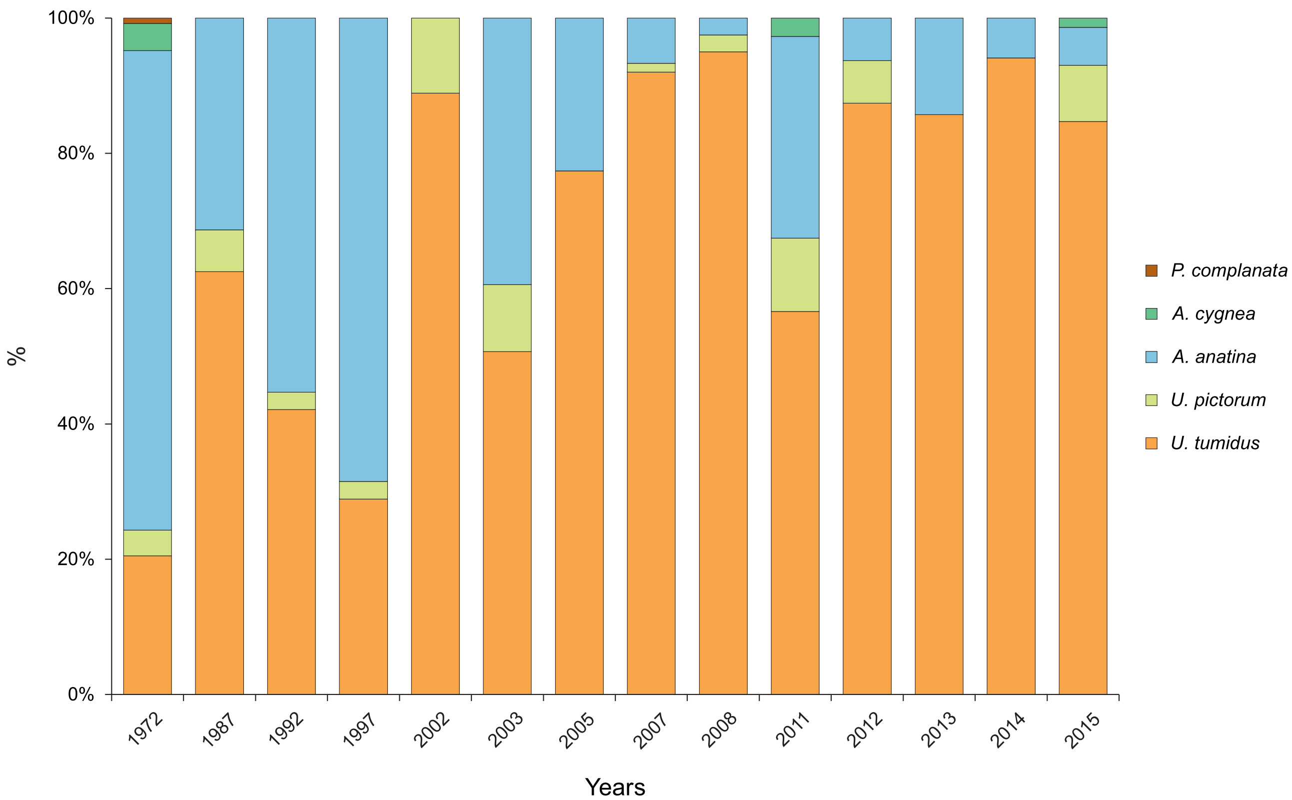

Fig. 8. Dominance structure of Unionidae in Lake Mikołajskie in various periods (1972 – after Lewandowski & Stańczykowska 1975; 1987 – after Lewandowski 1991; 1992–2008 – after Lewandowski & Kołodziejczyk 2014; 2011–2015 – this study)

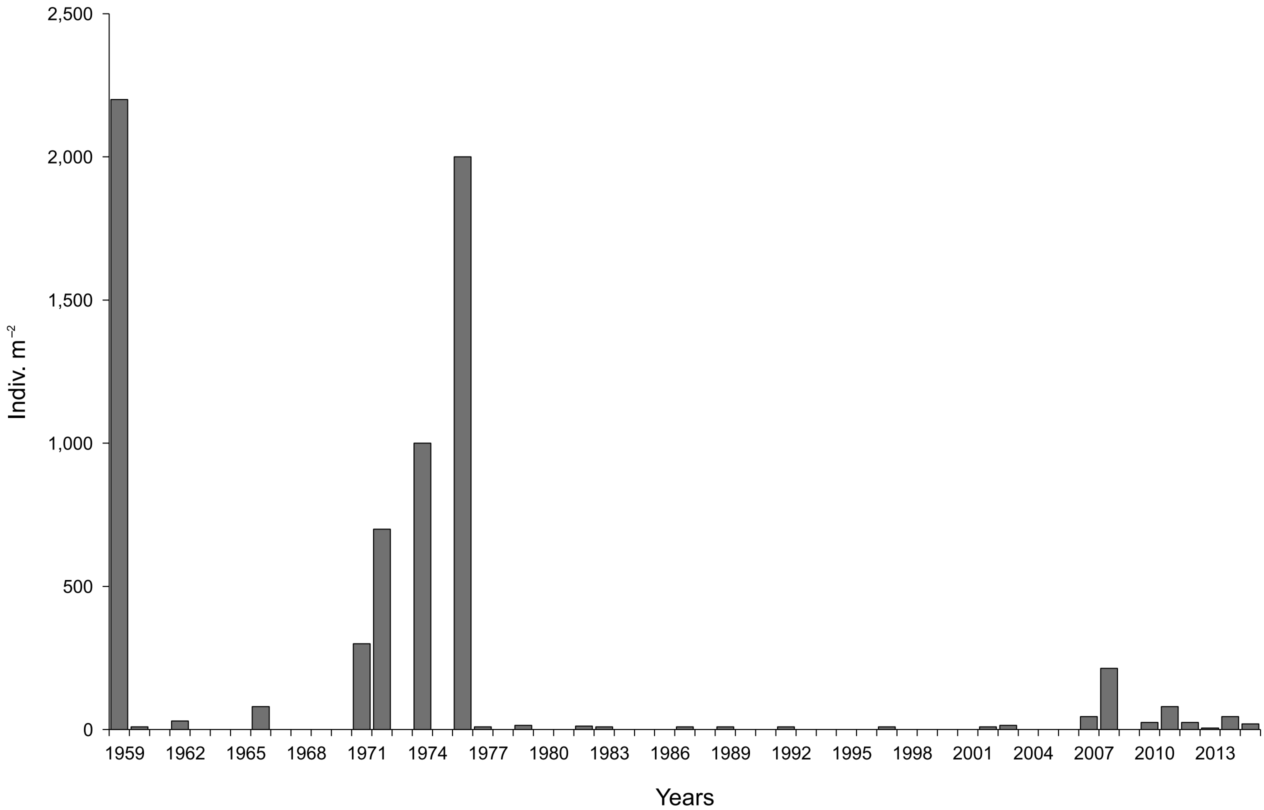

Fig. 9. Changes in mean density of *Dreissena polymorpha* in Lake Mikołajskie in 1959–2015 (1959–1976 after Stańczykowska 1978; 1977–2008 after Lewandowski & Stańczykowska 2014; 2010 – own unpublished results; 2011–2015 – this study)

Stańczykowska 2014). The fifty-year studies (with short breaks) on this Ponto-Caspian species in Lake Mikołajskie are, for their longevity, unique worldwide. Very high densities exceeding 2000 ind. m^{-2} in the zone of occurrence followed by a rapid decline to almost zero in the next year were observed twice during that period (Fig. 9). The declines followed by stable environmental conditions might be associated with density-dependent phenomena which accompanied overcrowding. The first reduction of population density was followed by a reconstruction which lasted about fifteen years. Only the second collapse of density in the mid-1970s and the resulting low density of *D. polymorpha* in the 1980s and 1990s might be associated with the intense eutrophication of the lake. In some years of that period (e.g. 1994–1996) despite intensive search no live individuals of *D. polymorpha* could be found in the lake (Lewandowski 2001). At the end of the 1990s a modern sewage treatment plant was set up in Mikołajki and probably the improved water quality brought about a slight increase in the density of this bivalve after several years. The huge number of empty shells of *D. polymorpha* in the sublittoral of Lake Mikołajskie reflects its high densities in the past. Their appearance (white and crushed) suggests a very long time of deposition in the lake.

Finding larger shells than those of live individuals in the lake's sublittoral is understandable since live molluscs were collected during their life and growth and it is unknown how long they would grow and when they would attain their maximum size. Shells accumulate in lakes' littoral for decades and undergo slow decomposition. The decomposition rate is much faster for small and thin shells of young individuals compared to larger and thicker shells of older snails and bivalves (Alexandrowicz & Alexandrowicz 2011). Mounds of empty shells do not reflect either species composition of living malacofauna in a lake (which may change with time), or age and size structure of living populations. All these population parameters might be affected by many factors, such as age-dependent mortality, predation on specific prey size and of course different rate of decomposition of shells of young and old individuals.

Lake Mikołajskie is a typical lowland and eutrophic lake of medium size, as many other in Masurian Lakeland. The long-term studies of its malacofauna show how variable the community is and how its species composition can change over time. Not only extinction of some species and appearance of other (alien) species can be observed, but also return of species not recorded for decades. The reasons for these changes might be different and mounds of empty shells in lake sublittoral may provide a historical record of the lake's malacofauna.

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