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LONG-TERM CHANGES IN THE MALACOFAUNA OF THE POND-TYPE EXPERIMENTAL LAKE WARNIAK (MAZURIAN LAKELAND, NORTH-EASTERN POLAND)

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Abstract: Warniak is a shallow eutrophic pond-type lake, part of the Mazurian Great Lakes. Since the late 1960s it has been subject to long-term experiments: introducing fish stocks of varied size and composition, resulting in massive physical, chemical and biotic changes in the lake's ecosystem. The aim of this study was an assessment of changes in the lake's mollusc assemblages 17 years after the first investigations (1998). The comparison of malacofauna in 1998 and 2015 showed changes in its composition, a significant decline in species richness and abundance, reduction in vertical distribution, increase in spatial variation of composition, richness and abundance. The proportion of rare species (i.e. found in one or two samples) increased from 17.4% to 64.7%. The dominance pattern became simplified and the frequencies of most species decreased. In 2015 *Anodonta cygnea* (L.) was still the most widespread unionid and one of the three most frequent species. The changes in the malacofauna occurred despite the lack of significant changes in the lake trophy. The deterioration of conditions for molluscs may result mainly from the impoverishment of macrophytes and the decrease in their abundance.

Key words: molluscs, species richness, abundance, long-term changes, shallow lake

INTRODUCTION

Lake Warniak was subject to long-term experiments which involved introduction of fish stocks of varied size and composition (Zawisza & Ciepielewski 1973, Węgleńska et al. 1979, Zdanowski et al. 1999). In 1967–1969 a large stock of benthophagous fishes – common carp (*Cyprinus carpio* L.) and bream (*Abramis brama* L.) – was introduced into the lake. After the winter-kill resulting from a long-lasting oxygen deficit in the winter 1969/1970, when nearly all the fish died, lake Warniak was stocked with benthophagous (common carp, bream), phytophagous (grass carp *Ctenopharyngodon idella* Val.) and planktivorous fishes (silver carp *Hypophthalmichthys molitris* Val. and bighead carp *Aristichthys nobilis* Rich.). The benthivorous species (mainly common carp) and the herbivorous grass carp reached their highest biomass in 1976, the seston-feeding silver and bighead carp stocks reached their peak in 1989–1994. Subsequently, the abundance of the species mentioned was reduced owing to the winter kills in 1985, 1987 and 1996, as well as to the intensive exploitation in 1995 and 1997. In 1976–1990 the biomass of autochthonous fishes (pike *Esox lucius* L., tench *Tinca tinca* (L.), bream, roach *Rutilus rutilus* (L.)) was reduced by half and then it increased as a result of favourable spawning conditions due to the renewed succession of submerged vegetation. Since 1994 the lake has been stocked with pike every year (Zdanowski et al. 1999). Since 2000 autochtonous fishes have become the main component of the ichthyofauna and their biomass was similar to or lower than that biomass before the experiments (B. Zdanowski, personal communication).

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The changes in the ichthyofauna strongly affected physical and chemical conditions of the lake ecosystem, as well as the structure and functioning of the biocoenosis (ZACHWIEJA 1973, KAJAK & ZAWISZA 1973, WĘGLEŃSKA et al. 1979, KRZYWOSZ 1999, ZDANOWSKI et al. 1999). The pressure of benthivorous fishes on macrobenthos and on macrophyte-associated macroinvertebrates caused a decrease in their biomass (KAJAK & DUSOGE 1973, PIECZYŃSKI 1973, WĘGLEŃSKA et al. 1979). The vegetation removal by grass carp was also the crucial factor in the macroinvertebrate decline. Molluscs were not included in the assessment of changes in benthic communities, except a short information concerning the total species richness and dominance pattern of Unionidae in 1998 (ZDANOWSKI et al. 1999).

The aim of the present study was an assessment of changes in the mollusc assemblages 17 years after the first investigations carried out in 1998. The number of species, abundance, dominance pattern of molluscs, as well as frequencies of individual species were analysed. Spatial distribution of mollusc species richness and abundance was compared.

STUDY AREA

Lake Warniak (54°07’17”N, 21°48’04”E) belongs to the System of Mazurian Great Lakes. It is a shallow pond-type lake 38.4 ha in area, maximum depth 3.3 m, mean depth 1.2 m and the volume of 460,800 m^3. Its direct basin is covered mostly by forests and swamps. A small tributary flows into the northern part of the lake. The lake water is of the calcium bicarbonate type, the bottom sediments are composed of calcareous gyttja; according to ZDANOWSKI et al. (1999) they contain 54% calcium carbonate and ca. 25% organic matter. The littoral zone constitutes 82% of the lake surface and till 1976 it was overgrown by macrophytes. As a result of the pressure of grass carp and common carp the vegetation completely disappeared and regenerated only in the 1990-ties after the removal of the large stocks of silver and bighead carp. The maximum biomass of macrophytes, recorded at the beginning of the 21st century, was followed by a considerable decrease (B. ZDANOWSKI, personal communication). In 2015 the macrophytes were far sparser than in 1998. In 1995–1998 Warniak was eutrophic, with an increased phosphorus concentration (maximum 0.13 mg/dm^3) and poor transparency (SD<0.5 m), especially in summer (e.g. KRZYWOSZ 1999). In August 2015 the visibility of Secchi disc (SD) was 0.6 m and the phosphorus concentration was still similar to that of 1995–1998 (Table 1). Changes in other environmental parameters in 2015 compared to 1995–1998 were also rather small (Table 1).

Table 1. Environmental characteristics of lake Warniak in summer 2015 and comparative data from 1995–1998 (after ZDANOWSKI et al. 1999); * – recalculated from original data

Parameter	2015	1995–1998
	Water	
pH	8.0 ± 0.4 (7.3–8.6)	8.4 (7.2–9.6)
Temperature (°C)	27.4 ± 5.1 (16.5–31.2)	–
Conductivity (μS/cm)	386 ± 48 (342–488)	274 (182–419)
N-NH_4^+ (mg/dm^3)	0.025 ± 0.017 (0.01–0.05)	–
N-NO_3^- (mg/dm^3)	0.082 ± 0.013 (0.07–0.10)	–
P-PO_4^{3-} (mg/dm^3)	0.0175 ± 0.0021 (0.015–0.02)	–
TP (mg/dm^3)	0.08 ± 0.02 (0.06–0.11)	0.07 (0.04–0.13)
TN (mg/dm^3)	1.357 ± 0.218 (1.17–1.58)	1.4 (1.0–2.2)
Ca^{+2} (mg/dm^3)	41.9 ± 4.99 (35,3–47.3)	44 (19–96)
Mg^{+2} (mg/dm^3)	10.4 ± 1.3 (9.1–12.0)	11.0 (5.8–17.5)
Cl^- (mg/dm^3)	15.3 ± 0.6 (14.5–16.0)	10.7 (6.1–15.7)
Alkalinity (mval/dm^3)	2.1 ± 0.5 (1.6–2.8)	2.5 (0.8–4.9)
COD_{Mn} (mg O_2/dm^3)	17.1 ± 1.051 (15.6–18.0)	9.9 (4.2–19.2)
	Bottom sediments	
Organic matter content (%)	15.8 ± 7.8 (6.4–26.5)	22.6 (18.9–24.1)*
TP (mg/g d.w.)	1.48 ± 0.39 (1.04–2.02)	1.54 (1.23–1.89)*
TN (mg/g d.w.)	5.07 ± 2.80 (2.20–9.71)	–
Ca^{+2} (mg/g d.w.)	119.32 ± 40.98 (67.6–174.8)	159.04 (136.32–186.73)*
Fe^{+3} (mg/g d.w.)	10.36 ± 11.26 (2.12–28.84)	18.2 (16.1–21.0)*

MATERIAL AND METHODS

Molluscs were sampled in the summer of 1998 (late July) and 2015 (early August) at 15 sites located around the lake (Fig. 1) using a 0.16 m^2 Bernatowicz rake, Günther's sampler (276 cm^2) and a hand net with a working side of 25 cm and mesh size of 0.5 mm. Samples were collected from ca. 1 m^2 of the bottom from the depths of 0.2–0.5 m, 1 m, 1.5 m, 2–2.5 m and 3 m (the last two only in 1998). They were washed on a sieve of 0.5 mm mesh and preserved in 75% ethyl alcohol. In the laboratory the molluscs were sorted, counted and identified using the key of Piechocki & Wawrzyniak-Wydrowska (2016).

The true total species richness in the lake was estimated with sample-based rarefaction curves (Gotelli & Colwell 2001, Colwell et al. 2004), which are the expected species accumulation curves based on a re-sampled total observed species (S_{obs}). Samples were randomized separately for 1998 and 2015. The non-parametric abundance-based estimator Chao2 was used to estimate predicted values of species richness based on its observed performance in other studies (e.g. Hortal et al. 2006, Soberón et al. 2007, Jurkiewicz-Karnkowska 2014). Datasets were considered complete if at least 90% of the number of species predicted with Chao2 were found, and representative when over 70% of the predicted number of species were recorded. Jaccard similarity

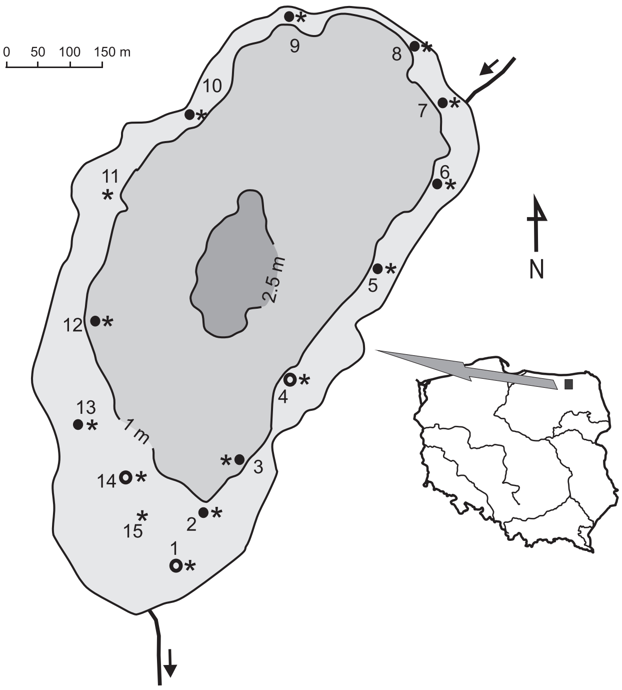

Fig. 1. Study area and location of sites; sites where living molluscs were found marked with asterisks for 1998 and with black circles for 2015: black rings – sites where in 2015 only empty shells were collected

coefficient (J) was calculated for all pair-wise comparisons of sites where molluscs were present, separately for 1998 and 2015. All the calculations were carried out with EstimateS, v. 9 software (Colwell 2013).

Frequency of occurrence of individual mollusc species was calculated based on living molluscs (only samples containing living molluscs were included). Molluscs were regarded as rare when they occurred in one or two samples and common when they were found in at least half of all samples.

Water samples for chemical analyses were collected in August 2015 from four sites distributed in different parts of the lake, and samples of bottom sediments were taken at nine sites evenly distributed within the lake. Temperature, pH and conductivity were measured in the field with a multiple sensor (Combo, Hanna Instruments, HI 98 128).

Organic matter content in the bottom sediments was determined as loss of weight on ignition (ashed in 530°C for 4 hours). Sub-samples of water and bottom sediments were digested with persulphate, enabling simultaneous determination of nitrogen and phosphorus. In the resulting solutions nitrogen was determined with indophenol blue method (Solórzano 1969) and phosphorus with molybdenum blue method with ascorbic acid as a reducing agent (Standard methods 1960), using a spectrophotometer (Shimadzu, UV-1800). Sub-samples of water were filtered through Whatmann GF/C filters prior to analyses of Ca, alkalinity, SRP (soluble reactive phosphorus), N-NO$_3$ and N-NH$_4$. SRP and N-NO$_3$ were determined with molybdenum blue method and phenyldisulphonic method, respectively (Standard methods 1960). N-NH$_4$ was determined with phenylhypochloride method (Solórzano 1969). Calcium, magnesium, chlorides, alkalinity and chemical oxygen demand (COD$_{Mn}$) were measured with titrimetric methods. Iron in the bottom sediments was determined with spectrophotometric (thiocyanate) method (Marczenko 1979).

Physico-chemical data for the water and bottom sediments in 1995–1998 were obtained from Zdanowski et al. (1999).

Data on species richness and abundance at different depths were compared with nonparametric Kruskal-Wallis test. Nonparametric U Mann-Whitney test was used for comparisons between 1998 and 2015 and between the northern and southern parts of the lake. The mean species similarity (J) in 1998 and 2015 was compared with t-test. The calculations were carried out with STATISTICA 10.0 software (StatSoft).

RESULTS

Twenty three mollusc species (12 gastropods and 11 bivalves) were recorded; another 10 species were determined based on empty shells in 1998 (Table 2). In 2015, 17 living species were found, as well as empty shells of another 13 species. The mollusc species lists based on the 1998 data can be regarded as complete (>90% of species richness estimated with Chao2). The 2015 collection was only representative (>70% of Chao2 value) mainly due to the high value of Chao2 resulting from the large proportion of rare species, i.e. those found in one or two samples (64.7%, compared to only 17.4% in 1998).

Seven species present in 1998 (including four found only as empty shells) were not observed in 2015, whereas two new species and empty shells of another two were found (Table 2). The species similarity (J) between malacocoenoses of all pairs of sites indicated a high spatial variation of their composition. The values of Jaccard similarity coefficient ranged from 0 (17% of comparisons in 1998 and 20% in 2015) to more than 0.5 (4.8% of comparisons in 1998 and 11% in 2015). The mean J value was higher in 1998 than in 2015 (0.24 ± 0.16 and 0.19 ± 0.16 in

Table 2. Composition of malacofauna in lake Warniak in summer 1998 and 2015; o – empty shells

Species	1998	2015
Prosobranchia		
Viviparus contectus (Millet, 1813)	+	o
Bithynia tentaculata (Linnaeus, 1758)	+	+
B. leachii (Sheppard, 1823)	o	o
Marstoniopsis insubrica (Küster, 1853)	o	–
Potamopyrgus antipodarum (Gray, 1843)	o	–
Valvata cristata O. F. Müller, 1774	o	o
V. piscinalis (O. F. Müller, 1774)	+	+
Pulmonata		
Acroloxus lacustris (Linnaeus, 1758)	–	o
Galba truncatula (O. F. Müller, 1774)	o	–
Lymnaea stagnalis (Linnaeus, 1758)	+	o
Radix ampla (Hartmann, 1821)	+	+
R. auricularia (Linnaeus, 1758)	+	+
R. balthica (Linnaeus, 1758)	+	+
Stagnicola palustris (O. F. Müller, 1774)	+	o
Physa fontinalis (Linnaeus, 1758)	+	–
Anisus vortex (Linnaeus, 1758)	+	+
Bathyomphalus contortus (Linnaeus, 1758)	o	–
Gyraulus albus (O. F. Müller, 1774)	+	+
G. crista (Linnaeus, 1758)	o	o
G. laevis (Alder, 1838)	–	o
Hippeutis complanatus (Linnaeus, 1758)	o	o
Planorbarius corneus (Linnaeus, 1758)	o	o
Planorbis carinatus (O. F. Müller, 1774)	+	o
Segmentina nitida (O. F. Müller, 1774)	o	o
Bivalvia		
Anodonta anatina (Linnaeus, 1758)	+	+
A. cygnea (Linnaeus, 1758)	+	+
Unio pictorum (Linnaeus, 1758)	+	+
U. tumidus Philipsson, 1788	+	+
Musculium lacustre (O. F. Müller, 1774)	+	–
Pisidium casertanum (Poli, 1791)	+	+
P. henslowanum (Sheppard, 1823)	+	+
P. milium Held, 1836	–	+
P. moitessierianum (Paladilhe, 1866)	–	+
P. nitidum Jenyns, 1832	+	+
P. subtruncatum Malm, 1855	+	o
Sphaerium corneum (Linnaeus, 1758)	+	+
Dreissena polymorpha (Pallas, 1771)	+	–
Number of living species	23	17
Number of species based on empty shells	10	13
Total number of species	33	30

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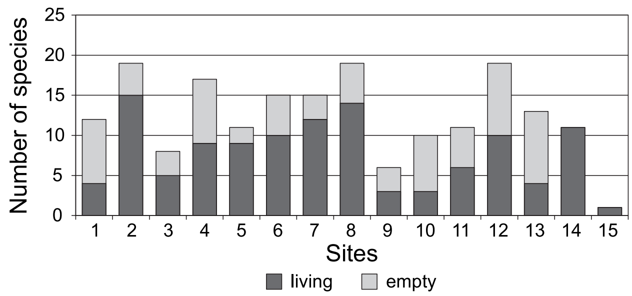

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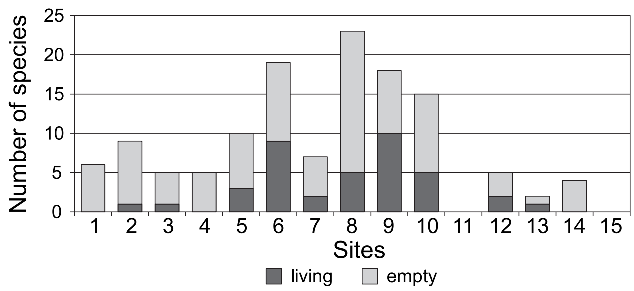

Figs 2–3. Numbers of mollusc species at sites investigated within lake Warniak: 2 – 1998, 3 – 2015

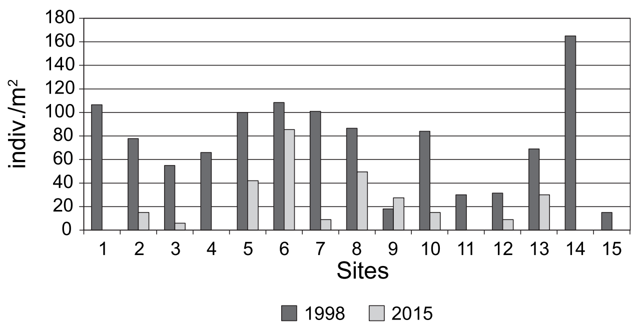

Fig. 4. Mollusc abundance at sites investigated within lake Warniak

1998 and 2015, respectively), but the difference was not significant ($t = -1.5224$, $df = 148$, $p = 0.1300$).

In 1998, 1–15 living species and 0–9 species represented by shells only were collected at individual sites (Fig. 2), whereas in 2015 the respective numbers were 0–10 and 0–18 (Fig. 3). In 2015 the proportion of species found only as empty shells considerably increased (43.3% of the total number of species) compared to 1998 (30.3%). Overall, most of living molluscs were not observed at depths exceeding 1 m, except unionids in 1998 and *Pisidium nitidum* in 2015 (only at site 12, at 1.5 m). The mean mollusc density at individual sites ranged from 15 to 165 indiv./m^2 in 1998 and from 0 to 85 indiv./m^2 in 2015 (Fig. 4).

The decrease in the number of species at individual sites and the absence of live molluscs at five out of the 15 sites in 2015 resulted in a significant decline in species richness per site compared to 1998 (Fig. 5, $Z = 2.6416$, $p = 0.0083$). The density per site was also significantly smaller in 2015 (Fig. 6, $Z = 3.4222$, $p = 0.0006$).

In 1998 the species richness and abundance were rather evenly distributed between the northern and southern parts of the lake (Figs 7–8, $Z = -1.2075$, $p = 0.2272$ and $Z = -0.4211$, $p = 0.6737$ for species richness and abundance, respectively). In 2015 a spatial variation in species richness and abundance was observed: considerably higher values were recorded in the northern part of the lake compared to the southern side (Figs 9–10, $Z = -3.1953$, $p = 0.0014$ and $Z = -2.3276$, $p = 0.0199$ for species richness and abundance, respectively).

Some vertical variation of species richness and abundance was observed (Table 3). In 1998 the values of both were distinctly smaller at depths exceeding 1 m than within the shallower zone ($H(2, N = 29) = 9.3120$, $p = 0.0095$ and $H(2, N = 29) = 10.1194$, $p = 0.0063$ for species richness and abundance, respectively). In 2015 comparison was possible only for depths up to 0.5 m and 1 m (only one mollusc-containing sample was collected at the depth >1 m). There was no significant difference

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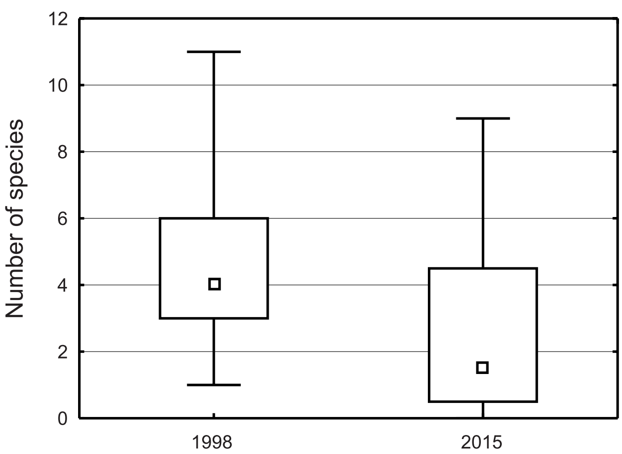

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Figs 5–6. Comparison of mollusc species richness and abundance in lake Warniak in 1998 and 2015: 5 – species richness, 6 – abundance; tickmark – median, box – interquartiles, whiskers – extreme values

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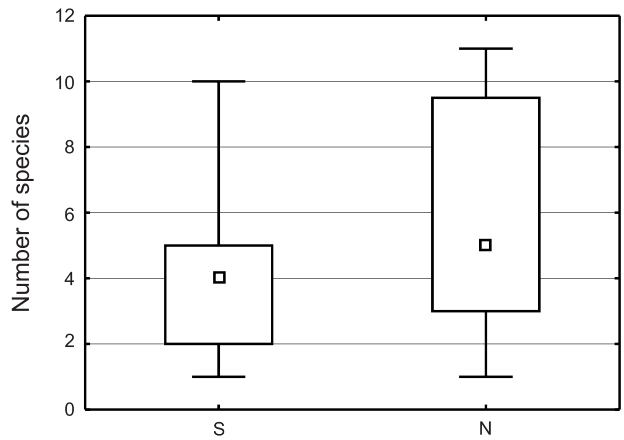

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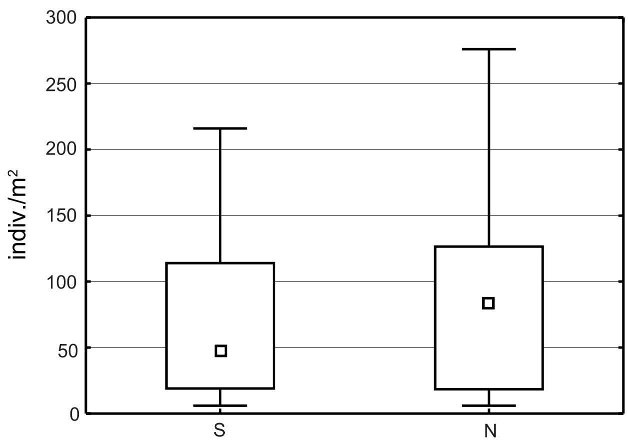


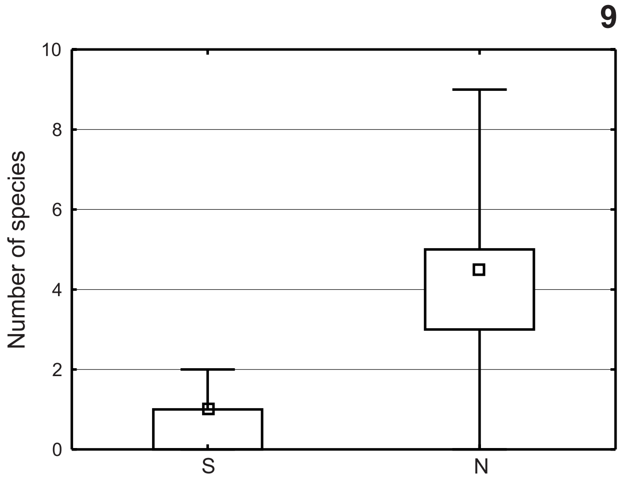
Figs 7–8. Comparison of mollusc species richness and abundance in the southern (S) and northern (N) parts of Warniak in 1998: 7 – species richness, 8 – abundance; tickmark – median, box – interquartiles, whiskers – extreme values

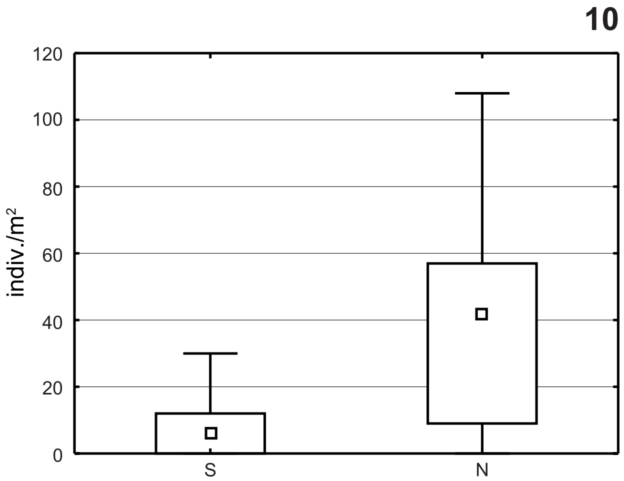
Table 3. Comparison of vertical distribution of mollusc species richness and abundance in lake Warniak in 1998 and 2015: mean values ± SD, median (Me) and ranges (in parentheses)

Depth (m)	1998	2015
	Number of species	
≤0.5	4.8 ± 2.9; Me = 4.0 (1–10)	3.9 ± 2.6; Me = 3.0 (1–9)
1	6.5 ± 2.8; Me = 5.0 (4–11)	2.7 ± 2.1; Me = 2.5 (1–5)
>1	1.2 ± 0.5; Me = 1.0 (1–2)	1
	Abundance (indiv./m²)	
≤0.5	81.0 ± 68.5; Me = 55.0 (15–216)	29.2 ± 19.8; Me = 27.0 (4–63)
1	105.5 ± 79.7; Me = 84.0 (24–276)	44.2 ± 48.8; Me = 31.5 (6–108)
>1	10.5 ± 5.7; Me = 9.0 (6–18)	6

in the respective values at depths up to 0.5 m and 1 m between 1998 and 2015.

In 1998 only *Anodonta cygnea* could be regarded as common (F = 50%) and the frequencies of another 11 species exceeded 20% (Fig. 11), whereas in 2015 only three species had frequencies exceeding 20%. The frequencies of all species, except *Pisidium nitidum*, *Radix ampla*, *Anisus vortex* and *Unio tumidus*, decreased in 2015 compared to 1998. Although the frequen-





Figs 9–10. Comparison of mollusc species richness and abundance in the southern (S) and northern (N) parts of Warniak in 2015: 9 – species richness, 10 – abundance; tickmark – median, box – interquartiles, whiskers – extreme values

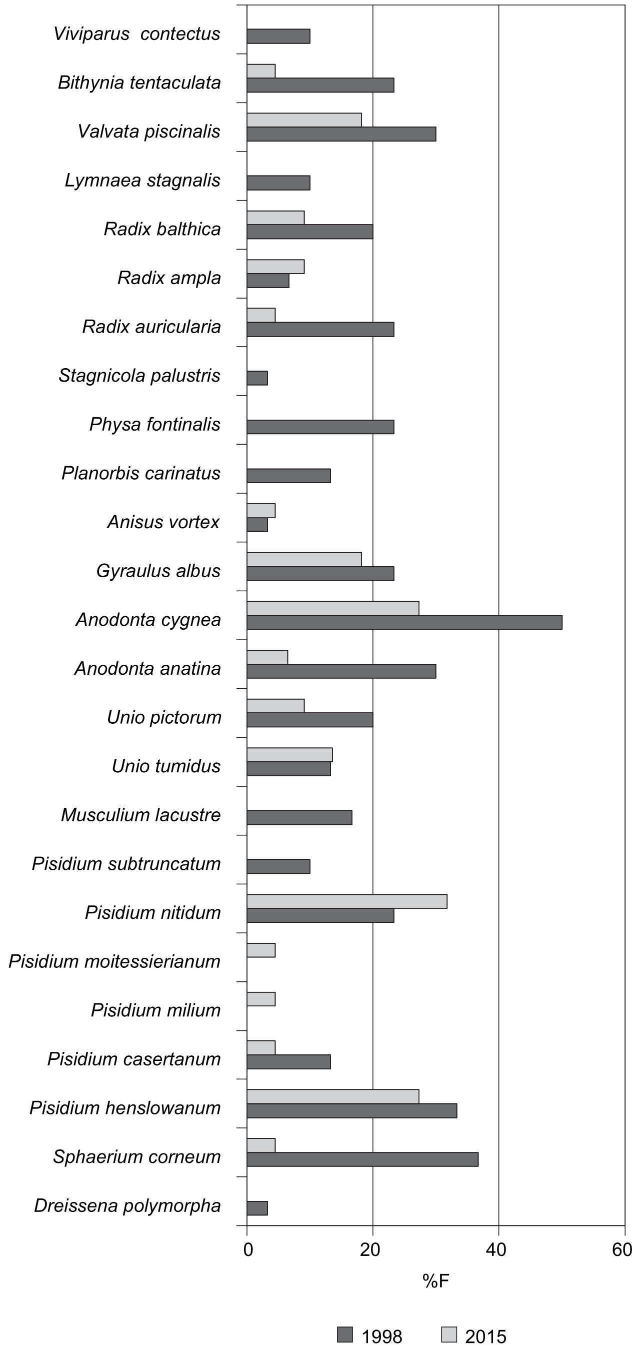


Fig. 11. Comparison of frequencies (%F) of individual mollusc species in 1998 and 2015

cy of *A. cygnea* decreased in 2015, this bivalve was still the most common among the representatives of Unionidae. Moreover, the mean density of *A. cygnea* at sites where it occurred was by 65% higher than in 1998 (16 ± 11.6 and 9.7 ± 4.7 indiv./m^2 in 2015 and 1998, respectively).

The dominance pattern clearly changed in 2015 compared to 1998 (Fig. 12). The number of species with proportion exceeding 5% decreased from eight to four and the dominance structure changed. In 1998 *Sphaerium corneum*, *Radix balthica* and *Pisidium henslowanum* constituted the greatest proportion in the total mollusc abundance. In 2015 the highest percentages were distributed evenly among *P. nitidum*, *A. cygnea* and *Valvata piscinalis*, the proportion of *P. henslowanum* was smaller, but remained similar to that of 1998.

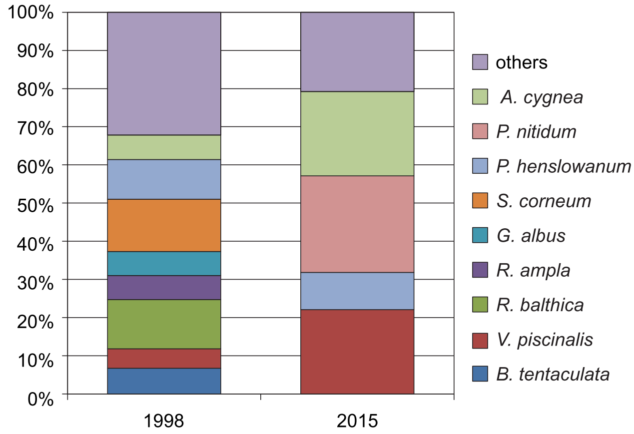


Fig. 12. Dominance patterns of molluscs in lake Warniak in 1998 and 2015

DISCUSSION

The total number of living mollusc species (γ diversity) in lake Warniak was relatively high despite the rather low mean number of species per site (α diversity) in both 1998 and 2015. It decreased in 2015, but it still remained quite high considering the lake's ecological conditions. Similar values were reported from a number of polymictic lakes of moderate trophy (up to 100 μg P/dm^3) within the Mazurian Lakeland (e.g. Stańczykowska et al. 1983), but considerably smaller species richness was found in small flow-through lakes of the Jorka River system (Kołodziejczyk et al. 2009). Lake Warniak harboured a similar or higher number of species compared to large permanent floodplain water bodies representing younger succession stages within the lower Bug River valley (Jurkiewicz-Karnkowska 2006, 2009, Jakubik & Lewandowski 2013), some oxbow lakes of the Wkra River (Lewin 2014) and some ponds in the nature reserve Stawy Siedleckie (Jurkiewicz-Karnkowska & Zontek 2014).

The mollusc abundance in lake Warniak was relatively low, but higher than, for example, in a shallow lake Oświn (Lewandowski 2005). In 1998 it was comparable to that reported from a number of polymictic lakes of moderate trophy and in 2015 to the values recorded in some eutrophic polymictic lakes (Stańczykowska et al. 1983). A similar abundance was also found in a number of floodplain water bodies of the lower Bug River (Jurkiewicz-Karnkowska 2006, 2009, Jakubik & Lewandowski 2013), some oxbow lakes of the Wkra River (Lewin 2014) and ponds in the nature reserve Stawy Siedleckie (Jurkiewicz-Karnkowska & Zontek 2014).

Valvata piscinalis was the most abundant gastropod in Warniak, similarly as in a shallow Dutch lake Veluwemeer (Van den Berg et al. 1997), but its density in Warniak was at least a hundred times smaller. The density of Unionidae in lake Warniak, especially that of *A. cygnea*, was comparable to the values reported from some oxbow lakes of the Bug, Pilica and Wkra rivers (Abraszewska-Kowalczyk 2002, Lewandowski 2006, Lewin 2014). The proportion of unionids in the abundance of mollusc assemblages in Warniak was high (14.4% and 27.2% in 1998 and 2015, respectively). It was considerably higher than that reported from ponds in the nature reserve Stawy Siedleckie (Jurkiewicz-Karnkowska & Zontek 2014) and similar to the values recorded for two oxbow lakes of the Wkra River (Lewin 2014). According to Lewin (2014) *A. cygnea* was dominant in two oxbow lakes of the Wkra River, but its proportion (6.0% and 8.8% of mollusc density) was considerably lower than in lake Warniak (22.1%). The bivalve was also dominant in the shallow lake Oświn (Lewandowski 2005).

The trophic state, oxygen conditions, composition and abundance of macrophytes (especially submerged ones), as well as the pressure of benthophagous fishes, considered as important factors influencing the development of mollusc assemblages (e.g. Lodge 1985, Pip 1987, Hanson 1990, Costil & Clement 1996, Mouthon 1996, Batzer et al. 2000, Jurkiewicz-Karnkowska 2011, Lewin 2014), seem to limit the mollusc species richness and abundance in Warniak. The trophic state has not changed significantly during the 17 years, whereas the macrophytes were considerably sparser in 2015 than in 1998. The abundance of benthophagous fishes decreased in 1998 compared to the earlier period, to reach a level similar to that from before the beginning of experiments; this state is currently retained. However, the poor macrophyte cover provided fewer refuges from fish pressure in 2015.

The Secchi disc transparency, total phosphorus (TP) and total nitrogen (TN) concentrations in the water in the summer of 2015 remained unchanged compared to the 1998 values, despite the restriction of fish abundance and consequently limiting of its negative effect on the lake's trophic conditions. A similar case from a very shallow eutrophic lake was reported, for example, by PHILLIPS et al. (2005) who observed recovery process during 20 years after the control of effluent-derived phosphorus. The phenomenon results from a high internal P loading from the sediments of shallow lakes (MARSDEN 1989, SØNDERGAARD et al. 1999). SØNDERGAARD et al. (1999) found that in less enriched shallow lakes (TP < 0.1 mg P/dm^3) in Denmark the phosphorus release from the sediments was restricted to July and August. Also JEPPESEN et al. (1997) found a marked TP increase during summer in nutrient-rich shallow lakes.

Considerable and sometimes long-lasting oxygen deficits in winter in lake Warniak (e.g. ZDANOWSKI et al. 1999) may be an important factor responsible for the unfavourable conditions for molluscs. Besides, in this shallow eutrophic lake anaerobic conditions, especially close to the bottom, are likely to occur during high temperatures in summer due to intensive decomposition of organic matter contained in the sediments.

Although the chemical parameters in lake Warniak did not deteriorate since 1995–1998, the conditions for molluscs seemed to be less favourable in 2015. It was reflected by the decrease in the total species richness and abundance, changes in the composition of mollusc assemblages, simplification of the dominance pattern, decrease in the frequencies of most species, as well as reduction of the vertical distribution of Unionidae. The increase in spatial heterogeneity in the species richness and abundance of molluscs after 17 years, especially the difference between the northern and southern parts of the lake, was probably associated with a positive (flushing) influence of the small stream flowing into the northern part and a long-term negative effect of the village located near the southern part.

The sparse macrophyte cover in 2015 might be the most important negative factor affecting the mollusc assemblages. In 1998 relatively abundant macrophytes provided important habitats for molluscs, especially since the bottom sediments were not favourable (sandy bottom in the shallowest zone and thick layer of dark mud farther from the shore). The depletion of macrophytes observed in 2015 might be one of the main reasons for the smaller mollusc species richness and abundance. HANSON (1990) found that the species composition of aquatic macrophyte beds could greatly influence the abundance, taxonomic composition, and size-structure of the littoral zone macroinvertebrate community. He also reported a considerably higher proportion of gastropods and bivalves of the family Sphaeriidae in the macroinvertebrate biomass on *Chara* beds compared to the respective values for rooted plants. In 2015 the occurrence of *Chara* spp. in lake Warniak was very limited (own observations), which might negatively affect its malacofauna.

Fresh but damaged mollusc shells, especially those of *V. piscinalis*, found in some samples could be a result of feeding of benthophagous fishes. PREJS (1973) reported a high frequency of molluscs in the food of autochtonous non-predatory fishes in lake Warniak (58–65% in the case of carp, tench and bream), but their weight proportion in the food was low. PIECZYŃSKI (1973) found smaller numbers of macrophyte-associated invertebrates (including molluscs) as a result of fish grazing. The shallowest zone (eulittoral) of Warniak is only periodically accessible to fishes because of drying and oxygen deficits (PIECZYŃSKA 1973). However, oxygen deficits are among the most important limiting factors for the occurrence of molluscs (e.g. MOUTHON 1996).

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REFERENCES

ABRASZEWSKA-KOWALCZYK A. 2002. Unionid bivalves of the Pilica River catchment area. Folia Malacol. 10: 99–173. https://doi.org/10.12657/folmal.010.011

BATZER D. P., PUSATERI C. R., VETTER R. 2000. Impacts of fish predation on marsh invertebrates: direct and indirect effects. Wetlands 20: 307–312. https://doi.org/10.1672/0277-5212(2000)020[0307:IOFPOM]2.0.CO;2

COLWELL R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Persistent URL <purl.oclc.org/estimates>

COLWELL R. K., MAO C. X., CHANG J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85: 2717–2727. https://doi.org/10.1890/03-0557

Costil K., Clement B. 1996. Relationship between freshwater gastropods and plant communities reflecting various trophic levels. Hydrobiologia 321: 7–16. https://doi.org/10.1007/BF00018672

Gotelli N., Colwell R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Hanson J. M. 1990. Macroinvertebrate size-distributions of two contrasting freshwater macrophyte communities. Freshwater Biol. 24: 481–491. https://doi.org/10.1111/j.1365-2427.1990.tb00726.x

Hortal J., Borges P. A. V., Gaspar C. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. J. Anim. Ecol. 75: 274–287. https://doi.org/10.1111/j.1365-2656.2006.01048.x

Jakubik B., Lewandowski K. 2013. Malacofauna in oxbow lakes of the Bug River within the Nadbużański Landscape Park. Teka Kom. Ochr. Kszt. Środ. Przyr. 10: 132–142.

Jeppesen E., Jensen J. P., Søndergaard M., Lauritzen T., Pedersen L. J., Jensen L. 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342/343: 151–164. https://doi.org/10.1023/A:1017046130329

Jurkiewicz-Karnkowska E. 2006. Communities of aquatic molluscs in floodplain water bodies of lowland river (Bug River, East Poland). Pol. J. Ecol. 54: 253–266.

Jurkiewicz-Karnkowska E. 2009. Diversity of aquatic malacofauna within a floodplain of a large lowland river (Lower Bug River, Eastern Poland). J. Mollus. Stud. 75: 223–234. https://doi.org/10.1093/mollus/eyp017

Jurkiewicz-Karnkowska E. 2011. Effect of habitat conditions on the diversity and abundance of molluscs in floodplain water bodies of different permanence and flooding. Pol. J. Ecol. 59: 165–178.

Jurkiewicz-Karnkowska E. 2014. Sampling intensity in biodiversity assessment: malacofauna of selected floodplain water bodies. Folia Malacol. 22: 21–30. https://doi.org/10.12657/folmal.022.002

Jurkiewicz-Karnkowska E., Zontek M. A. 2014. Malakofauna denna rezerwatu Stawy Siedleckie. In: Falkowski M., Nowicka-Falkowska K., Omelaniuk M. (eds). Bogactwo przyrodnicze rezerwatu Stawy Siedleckie. Kozak Druk, Siedlce, pp. 117–131.

Kajak Z., Dusoge K. 1973. Experimentally increased fish stock in the pond type Lake Warniak. 9. Numbers and biomass of bottom fauna. Ekol. Pol. 21: 563–573.

Kajak Z., Zawisza J. 1973. Experimentally increased fish stock in the pond type Lake Warniak. 14. The relations between fish and other biocenotic components (summing up the studies). Ekol. Pol. 21: 631–643.

Kołodziejczyk A., Lewandowski K., Stańczykowska A. 2009. Long-term changes of mollusc assemblages in bottom sediments of small semi-isolated lakes of different trophic state. Pol. J. Ecol. 57: 331–339.

Krzywosz W. 1999. Relationships between trophic indicators and phytoplankton composition, biomass and photosynthetic activity in small eutrophic lakes. Pol. J. Ecol. 47: 15–27.

Lewandowski K. 2005. Mięczaki (Mollusca) jeziora Oświn. In: Gromadzki M., Wiśniewski R. J. (eds). Jezioro Oświn i okolice. Monografia przyrodniczo-kulturowa. Bogucki Wydawnictwo Naukowe, Poznań, pp. 157–163.

Lewandowski K. 2006. Bivalves of the family Unionidae in ox-bow lakes of the Bug River. Fragm. Faun. 49: 69–74. https://doi.org/10.3161/00159301FF2006.49.1.069

Lewin I. 2014. Mollusc communities of lowland rivers and oxbow lakes in agricultural areas with anthropogenically elevated nutrient concentration. Folia Malacol. 22: 87–159. https://doi.org/10.12657/folmal.022.012

Lodge D. M. 1985. Macrophyte-gastropod associations: observations and experiments on macrophyte choice by gastropods. Freshwater Biol. 15: 695–708. https://doi.org/10.1111/j.1365-2427.1985.tb00243.x

Marczenko Z. 1979. Spektrofotometryczne oznaczanie pierwiastków. PWN, Warszawa.

Marsden S. 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshwater Biol. 21: 139–162. https://doi.org/10.1111/j.1365-2427.1989.tb01355.x

Mouthon J. 1996. Molluscs and biodegradable pollution in rivers: studies into the limiting values of 11 physico-chemical variables. Hydrobiologia 319: 57–63. https://doi.org/10.1007/BF00020971

Phillips G., Kelly A., Pitt J., Sanderson R., Taylor A. 2005. The recovery of a very shallow eutrophic lake, 20 years after the control of effluent derived phosphorus. Freshwater Biol. 50: 1628–1638. https://doi.org/10.1111/j.1365-2427.2005.01434.x

Piechocki A., Wawrzyniak-Wydrowska B. 2016. Guide to freshwater and marine Mollusca of Poland. Bogucki Wydawnictwo Naukowe, Poznań.

Pieczyńska E. 1973. Experimentally increased fish stock in the pond type Lake Warniak. 11. Food resources and availability of the eulittoral zone for fish. Ekol. Pol. 21: 583–593.

Pieczyński E. 1973. Experimentally increased fish stock in the pond type Lake Warniak. 12. Numbers and biomass of the fauna associated with macrophytes. Ekol. Pol. 21: 595–610.

Pip E. 1987. Species richness of freshwater gastropod communities in central North America. J. Mollus. Stud. 53: 163–170. https://doi.org/10.1093/mollus/53.2.163

Prejs A. 1973. Experimentally increased fish stock in the pond type Lake Warniak. 4. Feeding of introduced and autochtonous non-predatory fish. Ekol. Pol. 21: 465–505.

Soberón J., Jiménez R., Golubov J., Koleff P. 2007. Assessing completeness of biodiversity databases at different spatial scales. Ecography 30: 152–160. https://doi.org/10.1111/j.0906-7590.2007.04627.x

Solórzano L. 1969. Determination of ammonia in natural waters by the phenylhypochlorite method. Limnol.

Oceanogr. 14: 799–800. https://doi.org/10.4319/lo.1969.14.5.0799

Søndergaard M., Jensen J. P., Jeppesen E. 1999. Internal phosphorus loading in shallow Danish lakes. Hydrobiologia 408/409: 145–152. https://doi.org/10.1023/A:1017063431437

Standard methods 1960. Standard methods for the examination of water and waste-water. Am. Publ. Health Assoc. Inc., New York.

Stańczykowska A., Jurkiewicz-Karnkowska E., Lewandowski K. 1983. Ecological characteristics of lakes in North-Eastern Poland versus their trophic gradient. X. Occurrence of molluscs in 42 lakes. Ekol. Pol. 31: 459–475.

Van den Berg M. S., Coops H., Noordhuis R., Van Schie J., Jan Simons J. 1997. Macroinvertebrate communities in relation to submerged vegetation in two *Chara*-dominated lakes. Hydrobiologia 342/343: 143–150. https://doi.org/10.1023/A:1017094013491

Węgleńska T., Dusoge K., Ejsmont-Karabin J., Spodniewska I., Zachwieja J. 1979. Effect of winter-kill and changing fish stock on the biocenose of the pond-type Lake Warniak. Ekol. Pol. 27: 39–70.

Zachwieja J. 1973. Experimentally increased fish stock in the pond type Lake Warniak.1. Physical and chemical conditions in lake water. Ekol. Pol. 21: 405–422.

Zawisza J., Ciepielewski W. 1973. Experimentally increased fish stock in the pond type Lake Warniak. 2. Changes of the autochtonous ichthyofauna due to introduction of carp (*Cyprinus carpio* L.) and bream (*Abramis brama* (L.)). Ekol. Pol. 21: 423–444.

Zdanowski B., Hutorowicz A., Tunowski J., Świątecki A., Olejnik G., Krzywosz T., Białokoz W., Chybowski Ł., Krzywosz W., Błocka B., Hutorowicz J., Robak A., Prusik S., Koprowska L., Ciemiński J., Węgleńska T., Lewandowski K., Jurkiewicz-Karnkowska E. 1999. Ecological effects of long-term pressure of phytophagous and seston-feeding fish on the structure and functioning of the shallow Lake Warniak (Mazurian Lakeland, Poland). Acta Hydrobiol. 41, Suppl. 6: 29–47.

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