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DEVELOPMENT OF THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA* (PALL.), POPULATION IN A HEATED LAKES ECOSYSTEM. II. LIFE STRATEGY

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ABSTRACT. The aim of the study was to describe the mechanisms by which the zebra mussel, *Dreissena polymorpha* (Pall.), populations form and settle in the thermally and hydrodynamically varied ecosystem of the Konin heated lakes. The stability of the populations inhabiting the lotic and lentic environments of the lakes stemmed from their exploitation of better habitat conditions for survival, which was manifested in the effective settling of larvae on substrata, an even sex ratio, higher survival, and better condition and growth rates (strategy *K*). In lotic and lentic habitats that were heated intensely, unstable populations were noted with a higher share of females, a shorter life span, and lower individual maximum weight. The survival of these populations in these habitats was possible thanks to increased reproductive potential, including a larger share of females and an increased spawning cycle (strategy *r*). Under stressful conditions, including long-term, elevated water temperatures (>28°C), mass mortality of these mussels could occur in these habitats and the area that they inhabit throughout the system could shrink.

Key words: ZEBRA MUSSELS, ABUNDANCE, BIOMASS, LIFE STRATEGY, HEATED WATER

INTRODUCTION

The waters of basins that receive post-cooling waters from power plants have altered thermal and hydrodynamic regimes and are classified as aquatic ecosystems at high ecological risk. Long-term information about their environments and biocenoses is significant for extrapolating these transformations to those that might occur in nature as a consequence of global climate change (Hillbricht-Ilkowska 1993, 1998).

The risk of ecological change in heated lakes is usually evaluated in terms of either positive or negative categories of consequences that, above all, refer to changes in water purity (eutrophication), or to the loss of natural or exploitable attributes (Patalas 1976,

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Protasov and Zdanowski 2003). It has been demonstrated that more intense decomposition of organic matter at higher temperatures can equalize the rise in primary production and limit the eutrophication of waters (Patalas 1970, Zdanowski 1988, Świątecki and Zdanowski 2007). However, water flow can limit dangerous blue-green algae blooms (Simm 1988, Socha 1997), and can also limit phosphorus precipitation on calcite and to the sediments, which significantly reduces increased phosphorus loading from the catchment in the lake (Hillbricht-Ilkowska and Zdanowski 1988a, b, Zdanowski et al. 1988, Pyka et al. 2007). Trophic niches relinquished by stenotrophic crustaceans and fish can be occupied in this system by commonly-occurring organisms (Leszczyński 1976, Hillbricht-Ilkowska et al. 1988, Tunowski 1988, Wilkońska 1994, Tereshchenko et al. 2007). These are only some examples of opposing processes that are mutually equalizing (Protasov and Zdanowski 2003). Thanks to these, drastic deterioration of the environment is avoided, and during some periods it even improves indicating the oligotrophization of the waters (Hillbricht-Ilkowska and Zdanowski 1988a, b, Hillbricht-Ilkowska et al. 1988, Simm 1988, Zdanowski 1994).

It would be unrealistic to anticipate such equilibrium in an environment that is suffering from progressing environmental pollution (Patalasa 1976, Zdanowski 1994), and is currently in the stage of being taken over by alien species of vegetation such as *Vallisneria spiralis* L., crustaceans, including the Chinese mussel, *Sinanodonta woodiana* (Lea), and the African snail, *Melanoides tuberculatus* (Müller), or fish, like the stone moroko, *Pseudorasbora parva* (Temminck and Schlegel), grass carp, *Ctenopharyngodon idella* (Val.), silver carp, *Hypophthalmichthys molitrix* (Val.), bighead carp, *Aristichthys nobilis* (Richardson), usually thermophilic species that were either accidentally or purposefully introduced to heated waters (Protasov et al. 1994, 1997, Piechocki et al. 2003, Kraszewski and Zdanowski 2007). The mass mortality of any of these organisms could provoke a drastic decline in water purity. Consequences such as these were noted in a large Ukrainian dam reservoir following the extinction in it of the zebra mussel (Protasov et al. 1991).

Zebra mussel, *Dreissena polymorpha* (Pall.) is an important element in the trophic structure of the heated Konin lakes (Protasov et al. 1994, 1997, Sinicina and Zdanowski 2007) as its participation in metabolizing organic matter determines water quality (Sinicyna et al. 2001). The retreat from habitats, the inhabitation of a limited

area, or the mass mortality of these mussels might have disadvantageous consequences. Learning about the life strategies of these mussels inhabiting thermally and hydrodynamically differentiated areas of this ecosystem is important. The aim of the study was to attempt to define the mechanisms that shape the structure of populations of zebra mussel in the ecosystem of the heated Konin lakes. Changes in the population structure of the mussels was evaluated based on density and biomass in the summers of the 1993-2006 period (Sinicyna and Zdanowski 2007). The paper used published data from mussel studies conducted from 1993 to 1998 (Protasov et al. 1994, 1997, Sinicyna et al. 2001).

MATERIALS AND METHODS

The zebra mussel population was studied at six permanent study stations from 1993 to 2006 (Sinicyna and Zdanowski 2007). Station 6, located in the northern part of Lake Ślesieński, presented conditions similar to those that are natural, while conditions at the others varied under the impact of the heated waters from the power plants. The mean annual water temperature ranged from 13.0 to 20.6°C, while the water flow rate in the lotic environments was from 0.05 to 0.32 m s⁻¹ (Table 1). The maximum thermal loading of the mussel population was 1.7 times higher in the heated zones.

TABLE 1

Habitats of *D. polymorpha* in the heated lakes ecosystem in the 1993-2006 period (according to Sinicyna and Zdanowski 2007)

Site	Biotope type	Depth (m)	Temperature (°C)	Water flow (m s ⁻¹)	Substrate
1 Initial cooling reservoir	dam	0.6-1.5	20.6±0.9	lotic	rock
	bottom beyond dam	2.0			mussels
2 Licheńsko-Pątnowski Canal	bottom	2.0-2.5	16.4±0.8	lotic	various*
3 Lake Licheńskie	bottom	3.0	16.0±0.8	lentic	rock
		1.2-3.0			various*
4 Piotrkowicki Canal	bottom	1.1-3.0	15.2±0.9	lotic	various*
5 Konin Power Plant intake canal	rock embankment reinforcement	2.1-2.8	14.3±0.7	lotic	rock
	bottom	3.0-3.3			various*
6 Lake Ślesieński	bottom	2.0	13.0±0,7	lentic	rock
		2.7-4.5			various*

*mussels, empty mussels, rocks

The mussels were collected with the free diving method. After a visual exploration to determine a typical zone for a given habitat, mussels were collected underwater by hand with all the substrates (mussels, empty mussels, single rocks, wood) using a 50 x 50 cm frame (in at least three replicates) and then recalculated for one m² of bottom area. Mussels that were attached to the rocks reinforcing canal embankments and from the cement dams and barriers were collected in three replicates from a surface area of 10 cm² and then recalculated to one m² of the given substrate. Length and weight measurements of the zebra mussels were performed to the nearest 0.1 mm and 0.001 g (shell wet weight), respectively. Juvenile mussels were measured with a binocular micrometr eyepiece, while adult specimens were measured with a slide caliper. Descriptions of the size, age, and sex structures of the mussel population can be found in Sinicyna and Zdanowski (2007).

RESULTS AND DISCUSSION

Dynamic changes in the abundance and biomass of zebra mussel populations can depend on the effectiveness of spawning, the settling of larvae on available substrata, the growth of adults depending on trophic conditions, and food availability, their survival depending on the thermal and oxygen conditions of the water (Stańczykowska 1977, 1997, Marvin and Howell 1997, Miller and Payner 1997, Rajagopal et al. 1997, Lewandowski 1999, 2001), and food competition from fish that feed on the same species (Morrison et al. 1997). Lower frequency (< 50%) of maximum density and biomass of mussels in the Konin heated lakes system was noted more often in the lentic habitats, while higher frequency was noted in the lotic ones (> 60%). Higher mussel density was usually noted in habitats that are moderately heated, but with a higher flow of water (Table 2).

Mussel growth was usually higher in lotic environments, where water flow provided the mussels with a continual source of food. The height of abundance of mussels was usually the effect of the mass settling of larvae. The most important role was played by 1+ age individuals and those which had settled in the previous fall in November. Although the size structure of the mussels during the summer season in the more intensively heated environments could be dominated distinctly by one size group,

sometimes co-domination was noted among various groups that occurred in more or less even proportions (Sinicyna and Zdanowski 2007).

Gonad maturation in mussels is dependent on the effective temperature sum. This occurred in the ecosystems of the Konin lakes, similarly to other environments (Alimov 1974, Nichols 1996, Susan 1996, Gist et al. 1997, Rajagopal et al. 1997, Lewandowski 1999), after 2500 degree days. In the coldest zone located the farthest away from the impact of the post-cooling water discharge, the thermal conditions were only able to activate one spawning cycle (60% frequency) that happened during the period from June to August. In the warmer seasons, sometimes two reproduction cycles were noted (40% frequency) that occurred from May to September. The heated environments, however, ensured that there were two reproductive cycles (80% frequency). The mussels inhabiting the most intensely heated environments could reproduce from March to October; this was analogous to the results of histological examinations of the gonads of mussels inhabiting the heated water of the lower Oder (Domagała et al. 2002). These mussels could have been limited to one reproduction cycle if the summer water temperature remained elevated for long periods (> 28°C); but there could be three reproduction cycles in a season if the spring and fall periods are warm but the summer is cool. Despite the relatively short development period of mussel larvae, which is usually 8 to 10 days (Lewandowski 2001), it was confirmed to be a permanent component of the plankton and to move through the ecosystem (Stańczykowska 1976, Kornobis 1977, Stańczykowska et al. 1988). The occurrence of a subsequent cohort of larval *D. polymorpha* is associated with the high natural reproductive potential (Borcherding 1991), the varied reproductive period of mussels inhabiting different zones, and the constant recirculation of lake waters and of the waters between them.

Despite the increased abundance of larvae and the extended period during which they occurred in the plankton, the abundance and biomass of *D. polymorpha* in the Konin lakes ecosystem at the peak of their expansion was similar to populations noted in unheated lakes (Stańczykowska et al. 1988). Again, in spite of the high reproductive potential and the dispersal of larvae thanks to the intense circulation of water, the high mortality of larvae in the cooling systems of both power plants could have been one of the reasons that the effectiveness of settling on substrates declined as did the zebra mussel population on the whole throughout the heated ecosystem and also in the zone unaffected by the post-cooling warm waters.

TABLE 2

Variability of abundance and biomass of *D. polymorpha* in the heated Konin lakes system in the 1993-2006 period

Year	Site	Abundance (in thous. indiv. m ⁻²)		Biomass (in kg m ⁻²)	
		min	max	min	max
1993	5		9.3		2.59
	6	0.4		0.06	
1994	2		11.7		1.05
	5*		147.9*		2.38*
	4	8.7		1.02	
1995	No data				
1996	1*		9.9*		1.73*
	6	2.1			
1997	3			0.28	
	1*		108.2*		
	4		111.9		12.12
1998	3	11.3		1.07	
	1*		166.7*		
	5				18.16
1999	3	3.5		0.71	
	1*		140.2*		11.04*
	5		58.1		8.43
2000	4	3.2		0.26	
	2		30.8		3.00
2001	6	4.4		1.66	
	5		18.6		2.05
	5*		186.4*		
2002	6*				12.49*
	6	0.3		0.07	
	5		20.5		
2003	6				0.28
	1	0.5		0.04	
	2		8.4		0.84
2004	3	0.4		0.05	
	2		10.9		2.79
2005	6	1.1			
	3			0.17	
	2		20.5		2.28
2006	3	0.3		0.03	
	5		5.1		0.36
2006	6	0.1		0.02	

*On rocky substrate calculated for 1 m⁻² of rock surface

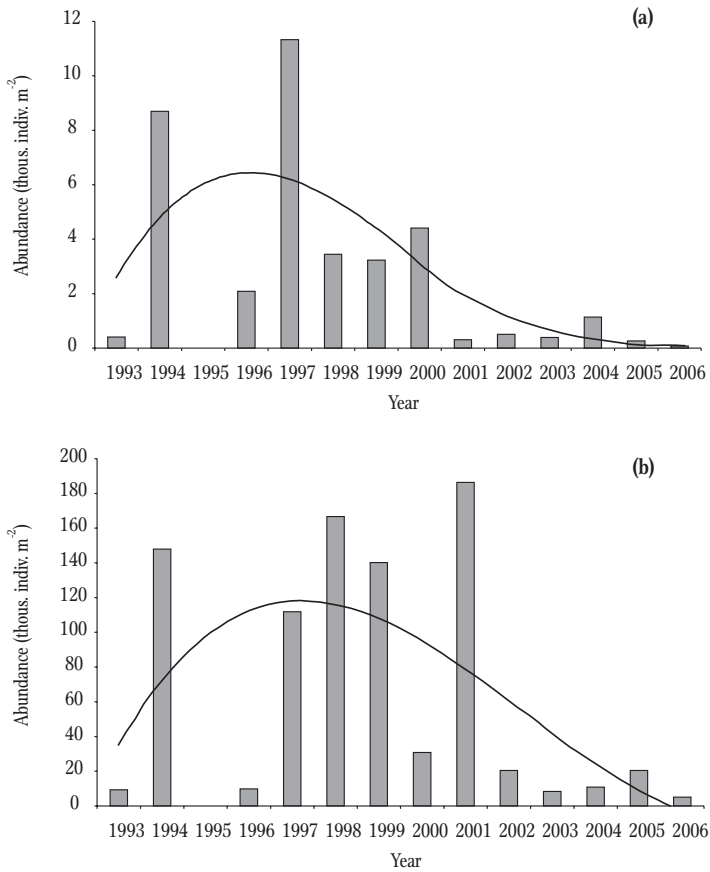


Fig. 1. Tendencies of minimum (a) and maximum (b) changes in the abundance of *D. polymorpha* in the heated lakes system in the 1993-2006 period.

Changes in abundance (Fig. 1) and biomass (Fig. 2) in the 1993-2006 period might indicate that the mussel population develops in cycles in the heated lakes ecosystem. The decrease in mussel frequency noted in recent years, which probably occurs at decade intervals, could have happened previously in this ecosystem after it was included in the power plant cooling system in 1958. The amplitude of fluctuation in abundance and biomass, which is significantly greater than in unheated basins (Stańczykowska 1977, 1997, Lewandowski et al. 1997, Lewandowski 2001), is considered to be a symptom of the adaptation of *D. polymorpha* during vegetation seasons and in the long-term to the heavily altered thermal and hydrological regimes of environments with progressive eutrophication or pollution. The genetically determined

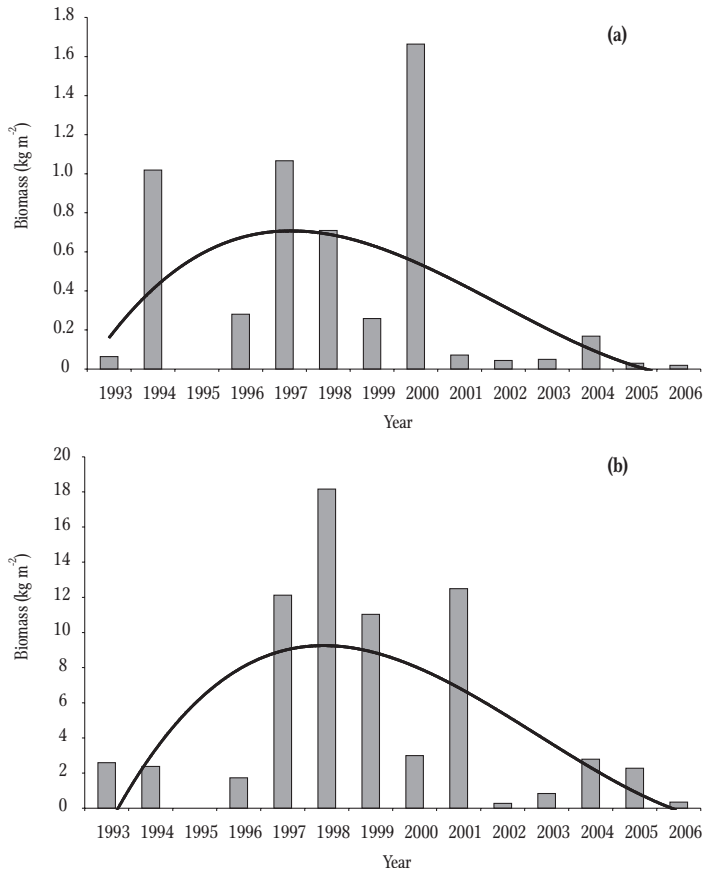


Fig. 2. Tendencies of minimum (a) and maximum (b) changes in the biomass of *D. polymorpha* in the heated lakes system in the 1993-2006 period.

plasticity of this species permits individual populations of *D. polymorpha* within an ecosystem to activate certain population mechanisms that aid in survival under conditions of stress; these include increasing reproductive potential, including an increased domination of females and an extended reproductive cycle.

The development of the mussel population in the heated lakes, as in other ecosystems (Stańczykowska 1977, 1997, Gist et al. 1997, Lewandowski 1999, 2001), could have depended not only on temperature, but also on the availability of appropriate substrates for larval settling. In the Konin lakes ecosystem, these included the sublittoral zone that was not overgrown with algae or hydrophytes, and the rock-reinforced sides of the initial cooling zone and the canals and other concrete

engineered structures. The zebra mussels on rocky substrates were dominated by juveniles measuring 5 mm in length, and could achieve an abundance as high as 186 thou. indiv. m⁻², and a biomass as high as 18.2 kg m⁻² (Protasov et al. 1994, 1997, Sinicyna et al. 2001, Sinicyna and Zdanowski 2007).

The mussels that attempted to colonize the warmest zone of the ecosystem had a lesser chance of success. Here they died in mass numbers during periods with increased water temperature (> 28°C) and as a result of increasing silting of the substrates. The mussel cohorts that settled lotic habitats rich in substrates that were moderately heated with substantial water turbulence and flow, which ensured continuous food delivery, had a greater chance of survival. In the opinion of many researchers (Stańczykowska 1977, 1997, Gist et al. 1997, Marvin and Howell 1997, Lewandowski 2001), this set of trophic conditions can be as important as water temperature in the settlement of mussels in certain locations. Conditions such as these in the Konin system were provided by some canals: including the one that delivers water to the Konin Power Plant (station 1) and the one that links Lake Licheńskie with Lake Pątnowskie (station 2). These habitats are the key zones



Photo. 1. *D. polymorpha* assemblages on rock reinforcements in Piotrkowicki Canal beyond the Piotrkowice pumping station (Fig.1) in March 1996. 1 – boundary of larval settlement after the canal became part of the water circulation system in May 2005. 2 – water level in the canal during the summer 2005 period.



Photo. 2. *D. polymorpha* assemblages on the rock reinforcement in Piotrkowicki Canal.

supporting the occurrence of the zebra mussel throughout the ecosystem. Similar habitats are provided by the Piotrkowicki Canal (after the pump station above station 4); however, this canal only carries Lake Licheńskie water to Lake Ślesińskie in the vegetation season from May to September. Mussels that settled in spring on the sides of this canal usually died after it was drained in the fall-winter period (Photo. 1 and 2).

CONCLUSIONS

Changes in the population structure of *D. polymorpha* in the Konin heated lakes ecosystem probably result from the combined effect of adaptation processes. The life strategy implemented by the mussels (K or r), in accordance with MacArthur and Wilson (1967) at the species level, or with Kasjanov (1989) at the population level, might provide then with the chance of surviving and maintaining the genotype in an anthropogenically altered environment.

The conditions in the lentic and lotic biotopes with moderate heating were advantageous for the older mussel age groups that were larger in size and of an even sex

ratio. The stability of the population inhabiting this habitat stemmed from the mussels exploiting more advantageous conditions for living as was manifested in the effective settling of larvae on substrate, an even sex ratio, higher survival, and good growth conditions for both juveniles and older age groups (strategy *K*).

The lotic and lentic environments that were more intensely heated were inhabited by unstable populations with a higher share of females, a shorter life span, and a lower individual mussel body weight. The survival of these mussel populations was only possible thanks to increased reproductive potential, including an increased share of females, and a lengthening of the reproduction cycle of the population during the season (strategy *r*). The higher metabolism rate of the mussels inhabiting these habitats generally resulted in increased energy consumption that was spent on reproductive processes and not on somatic growth.

Applying an alternative life strategy can result in phenotype differentiation among individual mussel populations located in temperature gradients. The highest heterogeneity was noted among the mussel population located in the post-cooling water discharge area. Stressful conditions, including permanently elevated water temperature (28°C), can cause mass deaths in the mussels located in this environment. It could also lead to the shrinkage of the area inhabited throughout the lake system. Similar changes in life strategy were noted in a *Mytilus galloprovincialis* population in a polluted zone of the Black Sea (Shurova and Stadnichenko 2002).

The consequences of the extended reproductive period in mussels inhabiting the ecosystem of the Konin heated lakes might be similar in other organisms under conditions of global climate change. Faster maturation, intensified reproductive processes, and increased numbers of generations might result in lowered individual weight, weaker condition, increased mortality, faster aging of the population, as is the case with the zebra mussel, and in consequence, the loss of many species.

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STRESZCZENIE

ROZWÓJ POPULACJI ZEBRA MUSSELS, *DREISSENA POLYMORPHA* (PALL.) W EKOSYSTEMIE PODGRZANYCH JEZIOR. II. STRATEGIE ŻYCIOWE

Celem pracy było zdefiniowanie mechanizmów formowania się struktury populacji *Dreissena polymorpha* (Pall.) zasiedlającej zróżnicowany termicznie i hydrodynamicznie ekosystem podgrzanych jezior. Zmiany w strukturze populacji oceniono na podstawie wieloletnich wyników badań zagęszczenia i biomasy. Stwierdzono, że warunki biotopów lenitycznych i lotycznych, o umiarkowanym stopniu podgrzania, sprzyjały występowaniu starszych grup wiekowych małży, o większych rozmiarach, jak też w równej proporcji płci. Stabilność struktur populacji zasiedlającej te środowiska wynikała z wykorzystania przez małże korzystniejszych uwarunkowań do przeżycia, manifestujących się efektywnym osiadaniem larw na substratach, równym stosunkiem płci, większą przeżywalnością oraz dobrą kondycją wzrostu młodzieży i starszych grup wiekowych (strategia K). W środowiskach lotycznych i lenitycznych intensywniej podgrzewanych stwierdzono natomiast niestabilne populacje, zwiększanie udziału samic, skracanie długości życia i zmniejszanie maksymalnej masy osobniczej małży. Przeżycie populacji małży w tych środowiskach było możliwe tylko w wyniku zwiększania potencjału reprodukcyjnego, w tym udziału samic, jak też zwiększania cykli rozmnażania się populacji (strategia r). W warunkach stresowych, m.in. długotrwałego podwyższenia temperatury wody (> 28°C), mogło następować masowe wymieranie małży w tych środowiskach, jak też i kurczenie się areału zasiedlenia całego systemu.