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Spatial distribution and abundance of *Unionidae* mussels in a eutrophic floodplain lake

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ABSTRACT

Although *Unionidae* mussels produce large biomass and reach high density in freshwater habitats, little is known about their ecology. We studied the distribution of 5 species of freshwater unionids in a eutrophic floodplain lake, on transects, along the lake shore and across the depth gradient. The clam distribution within the water body was not random: all species form a crowded zone along the lake shore, showing the highest density at ca. 0.5 m depth. The distribution of the most numerous species changed along the shore in *Anodonta anatina* and *Unio pictorum* but not in *A. cygnea*, whose numbers remained constant. The population numbers of the most numerous species showed a positive correlation with silt layer thickness. The generalized model of all the analyzed factors influencing the unionids' distribution confirmed this relation and indicated a trade-off between water depth and distance from bank, which might be responsible for the occurrence of the zone at some optimum depth. Unionids have an important influence on freshwater ecosystem functions, thus their zonation implies that their functions are also spatially structured.

Introduction

Ecology is often said to be concerned with understanding the environmental and biological factors responsible for the distribution and abundance of organisms. This task is especially relevant in view of the need to halt the dramatic decline of one of the most important groups of freshwater organisms—mussels of the family *Unionidae* (Strayer, 2008). The importance of unionids relies on specific functions that strongly influence the water ecosystem, such as water purifying (Pusch et al., 2001), nutrients loads and cycling within the water ecosystem (Strayer, 2014), and even outside it (Novais et al., 2015). Mediating nutrients heterogeneity can influence local biodiversity (Spooner et al., 2013) and also provide shelter or substrate for other organisms (Vaughn and Hakenkamp, 2001).

The reasons for the decline of freshwater mussels in the past were mainly large scale river training, with the dominating role of impoundments changing the water regime on a large scale (Vaughn and Taylor, 2001) as well as dramatic water pollution (Bogan, 1993; Naimo, 1995). The most important threat for the future seems to be invasions of alien species (Sousa et al., 2011). More studies are still needed on the decline of the freshwater mussel population integrity (Strayer, 2008), however the information on reference populations and their habitat is still scarce ('the Rivers of Eden' concept of Strayer, 2014). Under favorable conditions Unionids can reach a very high abundance and biomass thus, considering their strong relationship with the ecosystem (Vaughn et al., 2004), both their increase as well as decrease can markedly influence the ecosystem's functioning. The other important role of freshwater mussels is indication: a change in Unionids abundance and distribution may reflect less perceptible but important alterations to their habitat, such as a decrease of interstitial dissolved oxygen level (Sparks and Strayer, 1998; Geist and Auerswald, 2007), water turbidity (Österling et al., 2010), and a change of hydrological regime (Watters, 2000; Gates et al., 2015).

The distribution of freshwater mussels in different types of water bodies is still far from being described and understood (Strayer, 2008). It is worth noticing that the spatial distribution of mussels may have significant consequences for the ecosystem (e.g. biogeochemical hotspots, Atkinson and Vaughn, 2015), because the mussels' distribution influences the spatial distribution of their 'services', e.g. the material captured from the water column is usually deposited in the form of feces within mussel bed (nutrients 'focusing', Howard and Cuffey, 2006); also the nutrients accumulated by mussels are released (in the form of decomposing dead

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sperms, larvae, adults and/or proteins released by stressed individuals) within mussels beds (for a review see Strayer, 2014), creating benthic heterogeneity.

Another inadequately studied factor is interspecific competition (Bronmark and Malmqvist, 1982) and possible niche differentiation. Mussel species can differ in their vertical distribution (spatial distribution model, Warren, 2012) as a result of different adaptations or constraints related to the abiotic environment, and/or to avoid competition from other species. Examples of the different vertical distributions of mussels from lakes support this: for example, reported differences in vertical distribution between *Elliptio complanata* (Lightfoot, 1786) and *Anodonta grandis* Say, 1829 in Lake Bernard (Fig. 2 in Ghent et al., 1978), or between *Anodonta* sp. and *Unio* sp. in Kortowskie Lake (Widuto and Kompowski, 1968). However, unionids are also regarded as a guild of suspension-feeding organisms, for which substantial interspecific differences has not been satisfactorily demonstrated (Vaughn et al., 2008).

In lentic habitats some patterns suggesting depth optima for unionids inhabiting lakes have been described at 0.5–2 m depth (Dillon, 2004; Cyr, 2008, but see also Gołąb et al., 2010) but the data are still sparse and the specific factors regulating the vertical distribution of mussels remain to be discovered. Dillon (2004) suggested that because light, temperature, food and flow rate decline with depth, mussels should live as close to the lake surface as possible, and that mortality factors such as falling water level, thick ice or predation reduce their number in the shallows. Some other authors add the disturbing impact of waves (Cyr, 2008) or littoral zone sedimentation facilitating young recruitment (Cyr et al., 2012).

In fact, similar general factors (i.e. light, wave action, flow) are responsible for one of the most striking features of lentic habitats—zonation (Weaver and Clements, 1938; Nicholson and Aroyo, 1975; Wetzel, 2001). Following the arguments of Warren (2012) on the utility of species distribution models (SDM; used instead of defining ecological niche models ENM), the lake zonation can be easily and, for some purposes, sufficiently described on the basis of three simple variables reflecting the main environmental gradients of this type of habitat: (1) horizontal distance from bank; (2) if the lake is supplied by a river, the horizontal gradient along the directional movement of water through the lake; and (3) water depth.

Of course, the list of environmental and biotic factors responsible for actual ecological niches and resulting spatial distribution of the unionid species within a lake is probably very long, requiring a lot of effort to be properly analysed. Among them, one of the most important ecological factors related to the distance to the shore is wave action, which creates enough turbulence not only to influence the shore vegetation (Keddy, 1984), but also re-suspend particulate material (Hilton et al., 1986), which can be a substrate both for anchoring and source of organic matter as food for mussels. Distance along the flow can reflect, for example, the sedimentation (Hilton et al., 1986) or inflow of various exogenous chemically – or biologically – active compounds (Richardson and Mackay, 1991). Depth influences a lake's vertical zonation through its well-known effects on primary production, oxygen content, toxic compounds etc. (Wetzel, 2001). This list should be supplemented by the sediment layer, whose role is not obvious: it can be a typical anchorage substrate for mussel adults and juveniles (Cyr et al., 2012); however, it can be also a negative component interfering with their feeding (Kat, 1982) or related to the absorption of ammonia (Wetzel, 2001).

If there is a strong link between the basic lake environmental gradients and other, perhaps more complex ecological factors, then even without knowing all the underlying processes, it should be possible to predict the distribution and abundance of unionids simply on the basis of the above-mentioned three measurements, which can operate like the Cartesian coordinate system for a three-dimensional space of a lake. In this study we sought to determine the relation between these basic environmental gradients and the distribution and abundance of different species of unionids in one of their typical habitats—a floodplain lake.

Despite the fact that almost every large river valley contains sometimes hundreds of floodplain lakes, this habitat is an understudied one; most of the published papers focus on water quality, especially in reference to plankton, with larger attention devoted to fish (e.g. Miranda, 2005), and single studies of other groups, e.g. birds (Cintra, 2015). In Europe, floodplain lakes are usually under the protection of the Habitat Directive, due to their large decrease during extensive river training works. Halt of the lateral erosion causes that floodplain lakes are no longer created, with existing ones disappearing, together with mussels inhabiting them, due to biological succession (Zając, 2002).

A floodplain lake offers a perfect site for a study into the ecology of lentic environments: these types of lakes are small and their general morphological, hydrological and biological processes are similar (e.g. zonation). A floodplain lake is an important habitat for bivalves (Brock and Van Der Velde, 1996; Zając, 2002). We have made an extensive study of the abundance and distribution of 5 species of unionids in the Zalew Pińczowski. This floodplain lake offers a very interesting perspective for research of unionids because it comprise all species which occur in this type of habitat in Central Europe. The aim of the study was to demonstrate, that, in an eutrophic habitat, unionids are non-randomly distributed within the lake, and their occurrence can be defined using simple habitat factors. We also wanted to test whether the simple measures of environmental gradients are suitable to find interspecific niche differences in freshwater mussels, which would be reflected in their spatial distribution (Warren, 2012). Following this approach, we analyzed distribution of different species in relation to depth, distance from and along the shore, and sediment layer and, considering the very eutrophic character of the lake and existing small flow of the water homogenising the distribution of resources, we did not expect differences in the distribution of the mussels, when their food is not a limiting factor (Vaughn et al., 2008).

Material and methods

Study site

Zalew Pińczowski (Fig. 1) is an old riverbed left after straightening of the main channel. Construction work was completed in 1973. At the time of this study the water body was in an early stage of succession (sand bottom, no vegetation). The old riverbed is blocked from the east by a road bank and its maximum damming height is 185.80 m a.s.l., with no possibility of regulating the water

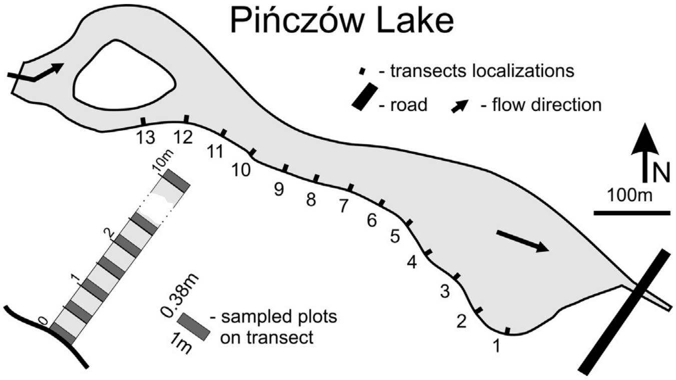

Fig. 1. General view of Zalew Pińczowski lake, showing transects localizations and transect sampling scheme.

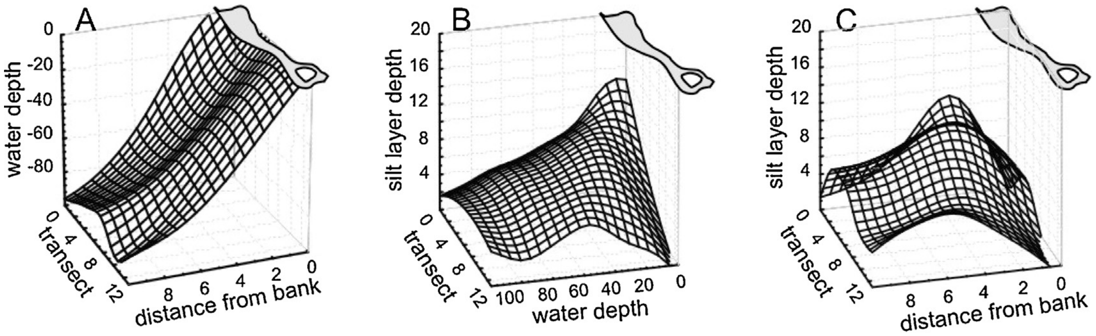

Fig. 2. Shape of Zalew Pińczowski bank and distribution of mud within the studied area. The presented figures are surfaces generated by spline procedure (Statistica 12.0), fitting water depth and silt layer measurements for 273 sampling plots distributed on 13 transects along the southern bank (20 plots per transect, every 0.5 m, perpendicular to bank, lake outline given above).

level. The lake covers 11.35 ha, its maximum depth is 1.54 m, and its volume is 160,000 m^3. It is supplied by the channel following the previous course of the river, with water intake from the new main river channel, 1.8 km from the lake. Water supply to the lake is $Q = 0.17\ m^3/s$; flow is detectable only in the channel supplying water (0.07 m/s). The main part of the lake contains almost still water; water movement there is caused rather by wind and temperature differences. Water exchange takes 8 days (for more details, see Strużyński, 2007).

The profile of the lake bank is artificial on the north side (concrete slabs) and natural on the south bank. The south bank descends more or less monotonically to 1–1.2 m depth, where it becomes approximately flat (Fig. 2a). On the slope are silt deposits ranging in thickness from 0 to 37 cm; over large areas the layer is thin (mean 5.97 cm, SD = 6.08; silt layer <5 cm thick in 62% of all 273 sampled plots; 5–15 cm thick in 32% of plots; >15 cm thick in only 6% of plots; Fig. 2b), tending to form a thicker alluvium ca. 5 m from bank (Fig. 2c). The silt contains 5.9% organic matter as determined by ashing a silt sample's previously dried constant weight. It is a colloid composed of loess particles originating from loess soils occurring in the Nida Valley. The colloid is deposited on fine sand.

In Zalew Pińczowski lake the water pH is very high (mean 8.69, range 8.62–8.74 during summer, depending on site and time of measurement). Water conductivity was measured at 465 μS/cm (limestone and gypsum areas in catchment). The water is highly eutrophic (mean chlorophyll content 104 μg/L (range 37.6–143.2 μg/L), without phosphorus. Mean oxygen content was 18.7 mg/L, ranging from 15.5 mg/L before dawn (3:00 a.m.) near the bottom, to 22.2 mg/L in the afternoon (2:00 p.m.) near the surface (measurements made 3 September 2002 on transect nos. 3 and 4; Fig. 1).

The amplitude of changes in the water level was 51 cm (30 August 2003: 71 cm; 8 October 2002: 122 cm). The ice layer during a period of typical winter frost (−20 °C to −10 °C) was 51 cm thick (24 January 2006, our measurement).

The lake bank is overgrown with a narrow strip of *Phalaris arundinacea* Linnaeus, 1753 and *Glyceria maxima* (C.J. Hartman) O.R. Holmberg, 1919, with some areas covered by *Carex acuta* Linnaeus, 1753. The water vegetation shows zonation: to a distance of 2.5–4 m (mostly ca. 3 m) from bank there was a compact carpet of *Ceratophyllum demersum* Linnaeus, 1753, mixed with *Elodea canadensis* Michaux 1803 and *Hydrocharis morsus-ranae* Linnaeus, 1753, in more or less equal proportions. This type of vegetation was extremely dense, growing from the bottom to the surface, filling 100% of the area of this zone. From this zone to 6 m from bank was a strip of dispersed stems of *Potamogeton* sp. (<5 stems/m^2). The vegetation was developed along the southern shore of the broad eastern part of the lake and was not present in the narrow western part.

Field protocol

The data were collected on 8–12 August 2003. Along the southern bank of Zalew Pińczowski lake, 13 transects, each 10 m long, were demarcated perpendicular to the bank at intervals of 50 m. The transect of 10 m length covered the whole bank slope: from the edge of the emergent vegetation to practically the flat bottom of the lake. On each transect water depth and the silt layer were measured every 0.5 m. At the same points bottom samples were collected from an area of 0.385 × 1 m using a dredge rake 38.5 cm wide with nylon netting (3 mm mesh) (273 samples taken, 21 bottom samples on each transect; Fig. 1). All the bottom sediment was taken to a 20 cm depth and sieved, with the mussels retained in the rake netting. Where sampling points were overgrown with vegetation, or where twigs or large pieces of litter were present (which could interfere with sediment sampling by blocking the entrance to the rake netting), that material was gently removed prior to sampling and checked to avoid overlooking small mussels.

Statistical analysis

The frequency of unionids found in the bottom samples shows a typical Poisson distribution, with zero prevailing and small numbers of mussels (1, 2, 3...); that is why nonparametric tests are used here to analyse their occurrence. The relation of mussel number to water depth has a typical quadratic shape. The Poisson distribution of the response variable disallows the use of any parametric test to examine the data fit to the quadratic function. Instead, following the methods used in quantifying stabilising (quadratic) natural selection (Broodie et al., 1995), we transformed the predictor data (e.g. water depth, distance from bank) as deviation from the mean by subtracting the mean from each of the predictor observations ($X_{obs} - X_m$). When these deviations were squared they were transformed to positive values reflecting the difference between a given value and the mean. A negative relation between N mussels and squared deviation from the mean implies that the quadratic function is convex (highest numbers of mussels found at depths close to the mean). A positive relation between N mussels and squared deviation from the mean implies that the quadratic function relating them is concave (highest number of mussels found at depths far from the mean). Because the relations between N mussels and squared difference in depth are linear after squaring, they can be tested with nonparametric tests assuming a linear relation, such as the Spearman rank correlation.

Spatial autocorrelation tests whether similar (or dissimilar) values of given variable cluster together in space. The species distribution in Zalew Pińczowski lake (Table 1) was explored using the global Moran's *I* statistic (Moran, 1948), which tests spatial autocorrelation: whether there are relationships between location and

Table 1
Basic data on the occurrence of *Unionidae* in Zalew Pińczowski lake, from 273 sampling plots on 13 transects perpendicular to the shore line, each 10 m long; bottom samples were collected from 0.385 m^2 patches every 0.5 m from bank; *—$p < 0.05$.

	N ind. in all samples	% Of empty samples	Density per 1 m^2	SD	Range	Mean water depth	SD	Range	Md	Autocorrelation *Moran's I*
A. anatina	142	48	3.55	5.07	0–34	55.2	23.60	6–115	55	0.244^*
A. cygnea	138	49	2.57	3.411	0–18	59.1	23.29	12–120	60.5	0.144^*
P. complanata	8	97	0.09	0.515	0–5	60.7	24.64	19–84	66.5	0.022
U. pictorum	121	56	2.34	3.794	0–21	59.2	21.56	16–115	60	0.200^*
U. tumidus	24	91	0.257	0.867	0–5	55.2	32.38	24–88	55	0.005

attribute values, using SAM 4.0 (Rangel et al., 2010). Positive spatial auto-correlation occurs when IM is close to +1 (values are clustered together), negative when is close to −1 (dissimilar values are next to each other); value of 0 indicates no autocorrelation.

It is reasonable to assume that the distribution of mussels within the lake can be caused by collinear and/or multiple factors, even within the simplified system of analysis of their distribution, e.g. the relation between mussel occurrence and the silt layer might be a coincidence related to the quadratic relation of both mussel number and silt to the same variable, water depth. In order to tackle this problem, we calculated a generalized linear model (GLZ), with the number of mussels of a given species as the response variable having a Poisson distribution, and distance from the southern corner (transect location, Fig. 1), distance perpendicular to the bank, water depth and silt layer thickness as predictors. Results of this analysis enable an assessment of the relative strength and direction of the analyzed relationships separately for given species, having controlled influences of other variables.

In Fig. 6 we have presented the number of individuals for two species in relation to the two basic dimensions of the lake's ecological gradients: distance along the shore and distance from the shore, as examples of visualizing models of mussels distribution. To visualize the generalised mussels distribution we used spline 3D surfaces fitted to actual quantitative data on their occurrence in 273 sampling plots on 13 transects along the shore, using the Statistica 12 package.

Results

Among the *Unionidae* we recorded the following five species: *Anodonta anatina* (Linnaeus, 1758), *A. cygnea* (Linnaeus, 1758), *Pseudanodonta complanata* (Rossmässler, 1835), *Unio pictorum* (Linnaeus, 1758) and *U. tumidus* Retzius, 1788. Basic data describing their occurrence are presented in Table 1. Although almost all of the studied species showed a significant positive autocorrelation, indicating that nearby locations of similar attribute values are more spatially clustered than randomly distributed, the values of the global Moran's *I* are small (Table 1). The significance of Moran's *I* is probably caused by the large sample size ($N = 273$) but its value indicates a low level of autocorrelation.

Distribution along flow

The total number of the two most abundant species recorded in each of the analysed 13 transects decreased along the course of the shore; their number correlated negatively and significantly with transect number (i.e. the distance from the southern corner of the lake; Fig. 3): *A. anatina* ($r_S = -0.61$, $n = 13$, $p = 0.027$) and *U. pictorum* ($r_S = -0.64$, $n = 13$, $p = 0.018$). However, *A. cygnea*, also among the most numerous species, showed virtually no pattern along the shoreline ($r_S = 0.04$, $n = 13$, $p = 0.886$). The least numerous species, *U. tumidus*, showed some negative tendency of number of individuals per transect, but it did not change significantly along the shore ($r_S = -0.39$, $n = 13$, $p = 0.191$). The situation was similar for *P. complanata* ($r_S = -0.48$, $n = 13$, $p = 0.099$).

The only environmental factor that showed a similar negative trend along the lake shore was mean silt depth per transect ($r_S = -0.55$, $n = 13$, $p = 0.049$). Mean silt depth per transect was significantly correlated with the number of mussels per transect for both *A. anatina* ($r_S = 0.57$, $n = 13$, $p = 0.002$) and *U. pictorum* ($r_S = 0.60$, $n = 13$, $p = 0.031$).

Vertical distribution and water depth optimum

The most numerous species showed an evident tendency toward a square function relation between the number of individuals in a given sampling plot and water depth, indicating some optimum at 0.4–0.6 m depth (Fig. 4a–d). All the studied species except for the least numerous one, *P. complanata*, showed significant negative correlations between their number in 273 bottom samples and the squared difference between actual depth and mean depth: *A. anatina* ($r_S = -0.47$, $p < < 0.0001$), *A. cygnea* ($r_S = -0.47$, $p < < 0.0001$), *U. pictorum* ($r_S = -0.48$, $p < < 0.0001$), and *U. tumidus* ($r_S = -0.24$, $p < 0.0001$), and nonsignificant for *P. complanata* ($r_S = -0.06$, $p = 0.35$).

Distance from bank

Because water depth is highly correlated with the distance from bank ($r_S = -0.92$, $n = 273$, $p < < 0.0001$), a similar square function pattern could also be found in the relation between mussel distribution and distance from bank. All the studied species, except for the least numerous one, showed significant negative correlations between their number in 273 bottom samples and the squared difference between actual and mean distance from bank: *A. anatina* ($r_S = -0.47$, $p < < 0.0001$), *A. cygnea* ($r_S = -0.43$, $p < < 0.0001$), *U. pictorum* ($r_S = -0.44$, $p < < 0.0001$), *U. tumidus* ($r_S = -0.18$, $p = 0.003$), and nonsignificant for *P. complanata* ($r_S = -0.03$, $p = 0.57$).

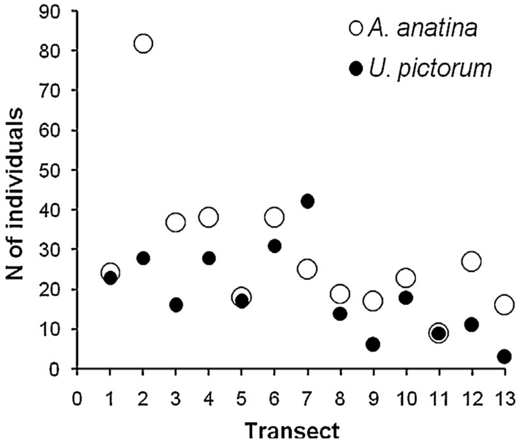

Fig. 3. Distribution of the two most numerous *Unionidae* species along the bank of the floodplain lake.

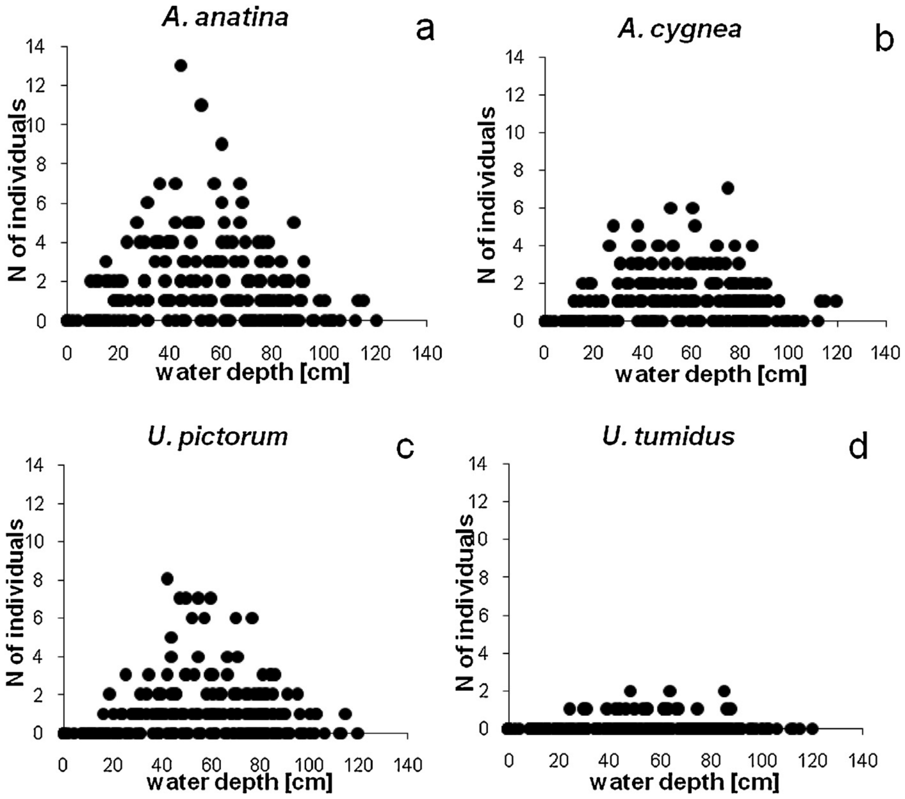

Fig. 4. Vertical distribution of *Unionidae* in Zalew Pińczowski lake: number of individuals found in a given sampling plot versus water depth of that plot (*P. complanata* not shown due to small number and lack of statistical significance).

Silt

The number of clams recorded in samples (including samples with no clams) usually showed a positive and significant correlation with silt layer thickness, except for *U. tumidus*, which showed no significant relationship (Table 2). However, excluding the sampling plots where no clams were found (zero values of response variable) made the previously significant relations completely nonsignificant, suggesting that the positive relations between clam frequency and silt layer reflected only binomial differences between sites having no clams and the other sites.

Interspecific differences in distribution

There was virtually no difference between *Unionidae* species in the water depth of occupied plots; they all lived at similar depths (Fig. 5; $H(4,433) = 3.05$, $p = 0.549$) and in silt of similar thickness (Fig. 5; $H(4,433) = 3.48$, $p = 0.481$).

Table 2

Correlations between the number of *Unionidae* individuals found in a particular sampling plot and silt layer thickness at the same point. The first analysis includes all samples (also with empty samples, with no mussels found); the second analysis is based only on the samples where mussels were found (empty samples without mussels excluded), r_S—Spearman's rank correlation coefficient.

N individuals/plot vs:	All samples			Only samples with mussels		
	n	r_S	p	n	r_S	p
A. cygnea	273	0.29	<0.0001	138	0.10	0.24
A. anatina	273	0.24	<0.0001	142	−0.07	0.41
P. complanata	273	0.13	0.03	8	0.42	0.31
U. pictorum	273	0.30	<0.0001	121	0.06	0.52
U. tumidus	273	0.05	0.39	24	0.01	0.97

However, silt layer thickness showed a quadratic relation to water depth and the distance from bank (Fig. 2b, c). The correlation between silt layer thickness and the squared difference between actual and mean depth ($r_S = -0.35$, $n = 273$, $p \ll 0.0001$) was of the same type as the correlation for silt thickness and distance from bank ($r_S = -0.34$, $n = 273$, $p \ll 0.0001$).

The GLZ models analysing mussel numbers in relation to other measured environmental factors (Table 3) revealed that: (1) *A. anatina* and *U. pictorum* differed in their number in relation to transect location along the flow; (2) *A. anatina, A. cygnea* and *U. pictorum* showed a trade-off between distance from bank (always negative) and water depth (always positive); (3) in *A. anatina, A. cygnea* and *U. pictorum* there was a significant positive relation between silt

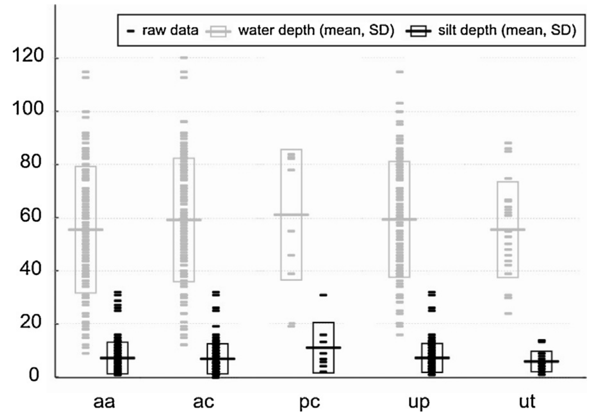

Fig. 5. Distribution differences in water depth and silt layer depth between *Unionidae* species found in Zalew Pińczowski lake: aa—*Anodonta anatina*, ac—*A. cygnea*, pc—*Pseudanodonta complanata*, up—*Unio pictorum*, ut—*Unio tumidus*.

Table 3
Results from generalized linear model (GLZ) of mussel number as response variable versus all analyzed variables as predictors: distance along lake bank, distance of sample from bank, depth at which the sample was collected, and silt layer thickness; standardized estimates in bold indicate opposing relations between distance from bank and water depth.

Mussels number vs		Estimate	SE	Wald statistic	*p*	Estimate/SE
A. anatina	Transect	−0.08	0.015	32.5	<0.00001	−5.70
	Distance	−0.33	0.052	41.4	<0.00001	**−6.43**
	Water depth	0.03	0.005	51.0	<0.00001	**7.14**
	Silt layer depth	0.03	0.008	10.1	0.001	3.18
A. cygnea	Transect	0.01	0.017	0.6	0.46	*ns*
	Distance	−0.22	0.056	15.6	0.00008	**−3.95**
	Water depth	0.03	0.005	31.7	<0.00001	**5.63**
	Silt layer depth	0.04	0.010	18.8	0.00001	4.34
P. complanata	Transect	−0.14	0.111	1.6	0.20	*ns*
	Distance	−0.38	0.336	1.3	0.25	*ns*
	Water depth	0.05	0.032	2.7	0.10	*ns*
	Silt layer depth	0.11	0.043	7.1	0.008	2.66
U. pictorum	Transect	−0.07	0.018	16.4	0.00005	−4.05
	Distance	−0.15	0.059	6.4	0.011	**−2.53**
	Water depth	0.02	0.006	19.7	0.00001	**4.44**
	Silt layer depth	0.04	0.010	21.1	<0.00001	4.59
U. tumidus	Transect	−0.06	0.053	1.2	0.27	*ns*
	Distance	−0.17	0.180	0.9	0.34	*ns*
	Water depth	0.02	0.017	1.8	0.17	*ns*
	Silt layer depth	−0.01	0.037	0.0	0.88	*ns*

layer thickness and number of individuals. *Unio tumidus* showed no significant relation to any of the studied predictors.

Discussion

Unionids, as indicated by the Moran statistics, do not occur randomly within Zalew Pińczowski. Contrary to our expectations, the vertical distribution of the unionids in Zalew Pińczowski lake shows a very distinct pattern (quadratic) versus depth and distance from bank, which can be interpreted as a kind of optimal zone which spreads along the lake shore, however at a different distance as regards different species. An 'optimum' or quadratic pattern also overlaps with the zone of silt sedimentation, though for three species the number of mussels shows a significant relation with silt thickness, independent of the relations to the other measured variables (Table 3). Only *U. tumidus* showed no relation to any of the measured variables.

The relation with silt thickness can be understood on the basis of sedimentation processes: small particles of sediment should be expected to settle in the same places where young individuals would be deposited just after leaving the fish host (Cyr et al., 2012). Other factors may also be relevant, such as slight disturbances from water currents or deposition of organic matter. Large silt deposits are frequently associated with un-ionized ammonia NH_3, which is toxic to mussels (Augspurger et al., 2003). Un-ionized ammonia is produced during the decomposition of organic matter in oxygen-poor conditions; an oxygen deficit can limit the occurrence of *Unionidae* in old river beds (Zając, 2002). In Zalew Pińczowski lake, however, oxygen conditions deteriorate with water depth at night, but are sufficient throughout the whole water column from surface to bottom (own unpubl. data).

Although the 'optimal' zone was the same along the whole lake bank for all species except *P. complanata*, the abundance of individuals changed: *A. anatina* (Fig. 6a) and *U. pictorum* decreased in abundance along the lake bank, whereas *A. cygnea* maintained a quadratic pattern and stable number (Fig. 6b). This decrease suggests that the general character of the lake differentiates the niches of *A. anatina* and *U. pictorum* (high abundance and high peak at 'optimal' water depth in the wide 'lake-like' part of the waterbody; Fig. 6a) from that of *A. cygnea* (a flatter distribution with regard to depth and stable numbers along the bank*;* Fig. 6b). The negative correlation between silt layer thickness with distance along the shore cannot explain the decrease of these two species, because the relation between *A. anatina* and *U. pictorum* abundance and distance along the shore is significant when controlled for the amount of silt in GLZ analyses (Table 3). It is also characteristic that the bank profile does not change that much along the shore.

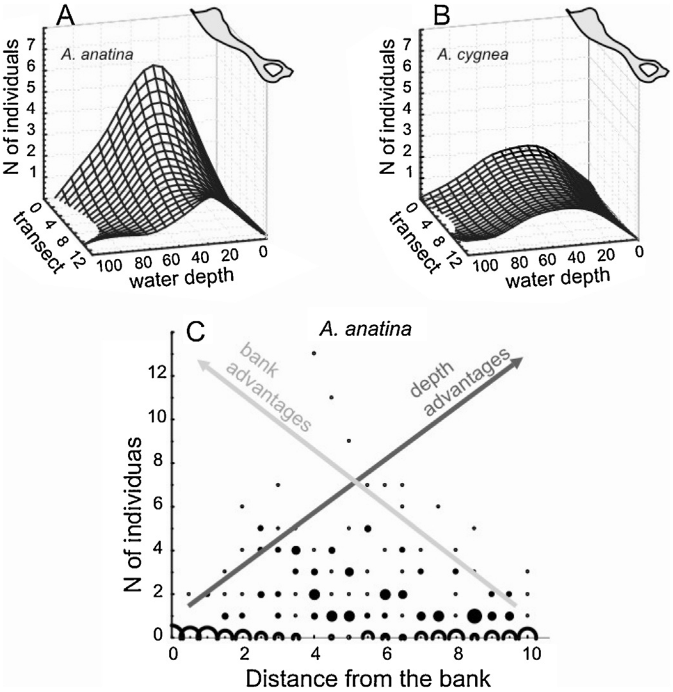

Fig. 6. 'Cartesian' (length along the shore and distance from bank) distribution models of *A. anatina* and *A. cygnea* in Zalew Pińczowski lake: a—*A. anatina* shows a distinctive depth optimum but its abundance decreases upstream and then again increases slightly near the island (lake outline shown for comparison along the 'transect' axis); b—*A. cygnea* show a flatter depth optimum and little decrease in abundance upstream; c—putative model of environmental gradients influencing the 'optimum' distribution of *A. anatina*; size of dots is proportional to the number of overlapping points.

The low numbers of *U. tumidus* and *P. complanata* imply that they do not prefer the habitat conditions (still water, highly eutrophic), although *U. tumidus* also shows the depth optimum found for the other species. *U. tumidus* is one of the dominating species in the main channel of the Nida River (Korzeniak et al., 2004). In the Szeszupa River, which flows through a system of five lakes, *U. tumidus* was dominating, in contrast to the lakes, lying in the same river continuity (Lewandowski, 1990). *P. complanata* generally seems to differ from all the other analyzed unionids. Haukioja and Hakala (1974) reported that the depth distribution of *P. complanata* differed from other unionids inhabiting their study site. *P. complanata* was found to be the dominating species in an oligotrophic lake by Ożgo M. (pers. comm.).

Interestingly, in the flowing water of a lake outlet, *A. anatina* and *U. pictorum* occupied different sites within and along the channel, indicating different ecological niches: *U. pictorum* dominated near the lake, whereas *A. anatina* was more abundant ca. 0.5 km downstream and then decreased (Bronmark and Malmqvist, 1982). In a study by Norelius (1967), *A. cygnea* and *A. anatina* decreased but *U. pictorum* increased along the course of a lake outlet. Those two situations are difficult to compare directly with our outcomes from Zalew Pinczowski lake because, there, the distribution of mussels was studied in running water and in an outlet, not within the lake. However, Bronmark and Malmqvist (1982) suggested that the distribution of mussels along the course of the flow was related to food availability (see also Richardson and Mackay, 1991). Taking this into account, the increase in the numbers of *A. anatina* and *U. pictorum* along the flow in Zalew Pinczowski lake might be explained by higher primary and near-bank production of food within the wide lake-like part of this water body. This would imply that *A. cygnea* relies on a different food source, which is accessible across the whole lake.

We do not know exactly which factors determine optimum depth, although the mechanism proposed by Dillon (2004), i.e. light, temperature, food decline with depth, mortality factors stronger in shallows, seems likely. We should note that the depth optimum in Zalew Pińczowski lake is much shallower than in lakes of glacial origin (0.5 m vs 1 m). Widuto and Kompowski (1968) reported a similar peak density for *U. tumidus* and *U. pictorum* in the eutrophic Kortowskie Lake in Poland. As shown in Table 3, the abundance of all species except for *U. tumidus* was positively correlated with sites of silt deposition. Mussel abundance was negatively correlated with distance from the bank (all other things being equal, they occurred more frequently closer to the bank). In terms of depth (all other things being equal) they preferred deeper locations. This creates opposing optimum-forming factors (Fig. 6c).

What lies behind these factors? It is easy to imagine that a changing water level promotes higher mussel abundance at a greater depth. If a lake's water level fluctuates within a range of ca. 0.5 m, depending on drying vs. precipitation, then it can be assumed that the mussels will escape from near-shore shallow areas, where they are threatened with desiccation during contraction of the water body. The water level of Zalew Pińczowski lake can change significantly, and quickly, especially in the summer (see methods). Such natural and regular changes in the water level, ranging from 30 to 50 cm within a month, have been documented for old riverbeds in this area (Bielański et al., 2005). Other depth-related factors include ice thickness (a 0.5 m layer of ice contains all the water volume 0–5 m from the shore; Fig. 2a) and predation from white storks *Ciconia ciconia*, the otter *Lutra lutra*, and muskrat *Ondatra zibethicus* (unpublished observations, Zając, 2014) in shallow areas after contraction of the water body. On the other hand, since different kinds of microorganisms and organic matter particles or even dissolved organic matter can be food for mussels (Strayer, 2008), and since the biomass of immersed vegetation is high near the bank, the near-bank area is likely to be a significant source of POM and microorganisms washed outward from the area overgrown with plants by waves (Hilton et al., 1986). This can be regarded as a factor promoting the shoreward direction of mussel occurrence. Such a scenario is supported by data from Cvancara (1972), who found that mussel abundance differed in depth at different parts of Long Lake: they occurred at a 4–12 m depth on a sandy/gravel bank, but only to a 1 m depth on the other side of the lake, where mud and aquatic plants predominated. The relationship with depth does not have to be associated only with food. A higher temperature and oxygenation in the shallows should provide better growth conditions for mussels; on the other hand, a night-time oxygen deficit at deeper localities and the presence of NH_3 might be a disadvantage to them. Further detailed, small-scale studies of these matters of speculation are required.

It was pointed out by Vaughn et al. (2008), that "healthy mussel communities typically occur as multispecies assemblages". Taking this into consideration, we also observed regular recruitment of juvenile mussels from all species in our lake, so we can conclude that we have described a healthy mussel community which should be typical for well-preserved floodplain lakes. The large density of mussels in a certain zone within the lake also implies that specific functions played by mussels within a lacustrine habitat are also spatially restricted into the same narrow zone. It opens interesting perspectives for further research. According to our results, the mussels' ecosystem functions (e.g. water purification, nutrients cycling) co-occur in Zalew Pińczowski lake with fine sediment focusing, which is also a significant abiotic mechanism of nutrient cycling (Mackay et al., 2012). Zonation of the mussels' distribution may also interact with important biotic factors (e.g. parasite occurrence, Müller et al., 2015), or lacustrine biodiversity (e.g. the relation with bitterling *Rhodeus sericeus*, Smith et al., 2004).

The possibility of defining this zone using simple 'xyz' measurements provides the possibility of saving efforts in the process of environmental impact assessment and in the monitoring of effects of investment/conservation actions. The frequently applied relocation of mussels threatened by construction zones, should not only use these results for the effective finding of mussels for relocation but, even more importantly, for elaboration of the criteria for selecting a suitable relocation site, taking into account the variable success of this action (Cope and Waller, 1995). The spatial distribution demonstrated here is concordant with the findings of Aldridge (2000), who postulated that sediment removal from watercourses should be restricted to the middle part of the channel; accordingly, numerous projects of oxbow lakes restoration, aimed usually at removal of organic matter from the waterbody, should comply with this standard.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.limno.2016.02.002.

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