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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

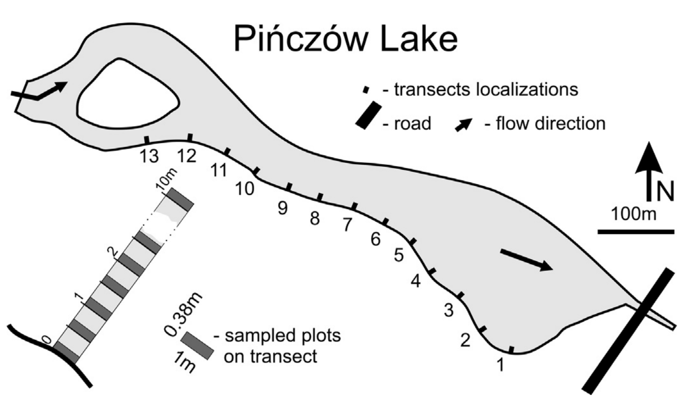

Fig. 1. General view of Zalew Pińczowski lake, showing transects localizations and transect sampling scheme.