HYDROECOLOGICAL CONDITIONS OF FUNCTIONING OF INVERTEBRATE GROUPS IN OXBOW LAKES WITH DIFFERENT HYDROLOGICAL CONNECTIVITY TO RIVERBED

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Biotope of oxbow lakes is a combination of lotic and lentic features. That forms unique habitats assigned to protection within the Habitats Directive Natura 2000 as subtype "Oxbow lakes and small reservoirs" (code 3150-2). Phytosociological indicators of that habitat are submerged unattached macrophytes (*Potamion* and partly *Nymphaeion*), floating attached as well as floating unattached macrophytes (*Lemnetea*). Those unique plant communities in oxbow lakes are accompanied by fauna of equally unique structure. Particularly interesting are benthic fauna communities, which condition indicates the ecological state of aquatic ecosystems. Their presence and structure in oxbow lakes depend on the connectivity with the main river. Benthic fauna is particularly abundant in the contact zone between riverine and oxbow waters while limited hydrological connectivity lowers its density. In cut-off oxbow lakes, which undergo quick succession and shallowing, plants constitute alternative habitat for benthofauna (Strzałek, Koperski 2009). Thanks to "ecological plasticity" some species may survive in anaerobic conditions, which occur in lentic oxbows mainly during summer.

Irrespective of the fact, that the distinguished hydrodynamic types of oxbow lakes favour the occurrence of specific hydrobionts, those reservoirs are important ecological centres, so called **"hot spots"**, on a scale of a river valley or even a region, which form diverse habitats for numerous flora and fauna representatives (Ward, Stanford 1995, Bornette et al. 1998). Relationships between riverbed and river valley are reflected by complex functions, such as production, decomposition and consumption, which are influenced by systematic floods and oscillations of water level (Sparks et al. 1990). According to the **"flood pulse"** theory, alternating periods of floods and streamflow drought favour decomposition and the circulation of nutrients, which increase biological diversity and productivity of ecotones water/land (Zalewski 2006).

Scientific studies conducted so far have revealed that the following factors influence he taxonomic and functional structures of invertebrates in oxbow lakes:

1. hydrological connectivity between the river and oxbow lake, which determines the rate of water and matter exchange;
2. environmental conditions;
3. presence of vegetation and artificial substrate as habitats for invertebrates.

Hydrological connectivity seems to be the key factor which influences ecological state of an oxbow ecosystem. Differences in surface contact with the main river obviously have impact on taxonomic and functional structures of zoocenoses. Cut-off and eutrophicated oxbow lakes were predominated by Chironomidae or Crustacea (mainly *Asellus aquaticus* L.). In partly open and open oxbows the main component of benthic fauna were Crustacea representatives while in oxbows connected with the main river by melioration ditches the main role played Ephemeroptera larvae. Hydrological connectivity between river and adjacent wetlands reflects in the biodiversity of a river valley. The highest Shannon index (around 1) was recorded for open oxbow lakes and often it was higher than in the main river. In turn, the lowest diversity values were noted in closed oxbows, where the Shannon diversity index usually did not exceed 0.5 (Obolewski 2011). It turns out, that invertebrate diversity slightly increases with increasing hydrological connectivity while the invertebrate abundance has unimodal distribution (Tockner et al. 1999b, Ward 1998, Amoros, Bornette 2002, Ward et al. 2002, Whiles, Goldowitz 2005, Gallardo et al. 2008, Obolewski 2011). The most optimal connection is a partial one – semi-lotic – or alternatively the full contact. Most of the studies conducted so far have revealed that such types of hydrological connectivity favour habitat diversity within one reservoir. As a result, considerable amount of benthic invertebrates appears. Moreover, hydrological connectivity improves environmental conditions in oxbow lakes (Glińska-Lewczuk 2009).

In semi-open oxbows the highest abundance of macrozoobenthos is usually recorded in the oxbow arms, which are in contact with the main river. A considerable number of taxa are observed in such ecosystems but the total density is low: not exceeding 2000 indiv.m^{-2}. The open oxbow lakes, with moderate flow velocity, the distribution of consecutive invertebrate taxa is more even, however benthic invertebrates tend to group in the oxbow arms. Benthofauna diversity in such oxbows is moderate (around 20 taxa) while density reaches 2000 indiv. m^{-2}. In turn, the benthic fauna in cut-off oxbow lakes is of low diversity; however its abundance can vary considerably, reaching even a few thousand indiv. m^{-2} (Gallardo 2009, Obolewski 2011). Limited water flow (i.e. stable conditions) favours Crustacea, mainly A.

aquaticus (Obolewski 2011), which domination increases with hydrological connectivity and reaches its maximum at the level of 50%.

Hydrological connectivity within a river valley may be treated as a key parameter which influences qualitative and quantitative structure of benthic invertebrates. Regardless of the oxbow-river connection, the abundance of invertebrates in oxbows is usually considerably higher than in watercourses (5-fold in semi-lotic oxbows, 6-fold in lentic and 8-fold in lotic oxbows). Any rapid events within riverbed, which are followed by the elimination of some invertebrate fauna components in the river, can be interacted by organisms inhabiting oxbow lakes. Therefore, the wetlands within a floodplain are **"biological centres"** of recolonization for river valleys.

Oxbow-river hydrological connectivity triggers water movement of different scale and wavy motion, which considerably alter habitat conditions. Intensive water movement prevents the deposition of sediments while stable waters favour the existence of isolated still water pools. Moreover, water flow and waves equalize water temperature and differences in other parameters between consecutive zones of an oxbow environment. They also favour the inflow of food, oxygen and outflow of metabolic products. In terms of water movement, it is clear to divide oxbow lakes into lotic and lentic. More complex situation is observed in semi-open oxbows, which combine the features of both closed and open reservoirs.

Apart from the type of oxbow-river connectivity, the level of connection should be also considered, since it influences the volume of flowing water as well as the velocity and distribution of currents. The strength of currents varies between the oxbow types but also within the same type of such reservoirs. Strong currents occur in open arms of an oxbow lake and in the surface zone. Therefore, habitats differ between lotic reservoirs (favoured by rheophilic organisms), lentic oxbows (preferred by rtheoxenic species) and many intermediate environments. That has been confirmed by the research on invertebrates in a lotic oxbow lake, where fauna more abundantly inhabited the zone of river water inflow. The more intensive water flow, the higher abundance of benthofauna species, particularly Crustacea, and their biomass, mostly of Oligochaeta, Hirudinea and Crustacea. In case of Diptera larvae, Trichoptera, Ephemeroptera and Mollusca, their abundance and biomass varied considerably. Water flow in the studied oxbow also influenced invertebrates being a part of periphyton. Water movement particularly favoured Nematoda, which feed in many ways and Protista, predominated by sedimentators - Peritricha (Piesik 1992).

Suspended material and re-suspended bottom sediments are for them the source of food.

The studies carried out on **floodplain water bodies** have proved that water quality directly and indirectly influence hydrobiont communities (e.g. Wang et al. 2007). Flooded wetlands are supplied with nutrients from natural and artificial sources, both external (inflow) and internal (productivity) and their highest content is observed in cut off reservoirs (Tockner et al. 1999). The lack of **flood pulse** increases the rate of sediment deposition and eutrophication. Additionally, anthropogenic influences such as agricultural use and urbanization result in higher trophy of floodplain areas. Sedimentation of heavy particles and their immobility cause that small water bodies and oxbow lakes are so called ecological traps for contaminants migrating within a river valley. Therefore, oxbow lakes are sometimes used as settling basins but the accumulated matter is also a source of food for a wide range of invertebrates. In turn, epiphytic invertebrates, like Peritricha (Protista) and Rotifera (sedimentators), feed on fine particles suspended in water (Piesik 1992). In spite of small size, their considerable density cause that they are able to eliminate most of the suspended matter and improve light conditions in a reservoir. Those processes are intensified thanks to filtrators, represented in periphyton mainly by *Chydrous sphaericus* O.F. Müller.

Water quality has undeniable influence on living organisms and either favours their development or leads to their elimination from aquatic environment. Many studies aim at the assessment of relationships between abiotic factors and macroinvertebrates (e.g. Sadin 2003, Gallardo et al. 2008). More dynamic thermics of water in oxbow lakes, comparing to other aquatic ecosystems, determines the abundance of invertebrate communities. In this aspect, biodiversity in floodplain areas can be closely connected with global climatic changes (Burgmer et al. 2007).

Apart from physical factors, habitat conditions of invertebrates also significantly depend on chemical properties of water. The most important influence on taxonomic and functional structure of the discussed communities has been recorded for nitrogen compounds and sulphates (Blumenshine et al. 1997, Gallardo et al. 2008). Nitrites are soluble compounds, common in riverine waters, and therefore can be used as an indicator of water quality and integrity of aquatic ecosystems (Smith et al. 2007). As a transitional form of nitrogen in geochemical transformations, nitrites influence biodiversity and abundance of invertebrate fauna. Their presence is a sign of dynamic changes in floodplain areas. Low oxygen concentration, particularly in lentic oxbow lakes, results in the occurrence of

toxic ammonia, which eliminates the presence of most of invertebrate species. At higher oxygen concentration the nitrate nitrogen is formed, which can be assimilated by aquatic plants. In such conditions a rich food base and habitats favourable for invertebrates appear. The role of nitrite nitrogen in the functioning of invertebrate communities indicates the need of better hydrological connectivity in floodplain areas. Another important chemical parameter in oxbow waters is the concentration of sulphates. The lack of oxygen, particularly in wetlands with limited hydrological connection to the main river, causes the transformations of sulphur compounds and hydrogen sulphide appears, toxic for benthofauna. In turn, sulphate ions can be assimilated by vegetation, which favours their development. Then, the atrophy of plants is followed by the release of sulphur in the form of hydrogen sulphide. In lentic and semi-lotic (one closed arm) oxbow lakes that chemical compound appears regularly.

Conclusions

1. Oxbow lakes are a transitional form between river and lake ecosystems which are important in increasing biodiversity of river valleys and contribute to the recolonization of zoocenoses in riverbed. That role is determined by the following factors: (1) hydrological connectivity and the rate of water exchange; (2) hydrochemical conditions;.
2. The main factor which influences zoocenoses in oxbow lakes is the oxbow-river hydrological connectivity. Semi-lotic and lotic connections with moderate water flow seem to be the optimal types.
3. Oxbows function as biogeochemical filters and the content of nutrients in their waters increase with limited hydrological oxbow-river connectivity. Dynamic hydrochemical changes in those ecosystems influence invertebrate communities. Dissolved oxygen concentration is the most important for snails while benthic invertebrates in general are mainly influenced by dissolved nitrogen and sulphur compounds.

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