



Impact of environmental factors on bacterial communities in floodplain lakes differed by hydrological connectivity



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ABSTRACT

We analysed total bacterial number and mean volume of cells at three sites in each of ten floodplain lakes in the Middle Basin of the Biebrza River, North-Eastern Poland to test bacterioplankton communities change according to the distance to the river. The composition of the bacterial communities was determined by fluorescent in situ hybridization method. Total number of bacteria in the lakes ranged from 4.0 to 7.48 cells $\times 10^6 \text{ mL}^{-1}$ with dominance by Actinobacteria, the contribution of which was positively correlated with water level. Old river channels (side-arms) featured Alpha- and Gammaproteobacteria. The community of Betaproteobacteria was limited by concentration of dissolved organic carbon. Archaea, in spite of a minor role (<3.65% of DAPI-4',6-diamidino-2-phenylindole) in the communities, showed a positive relation to floodplain lake isolation. Multivariate analysis demonstrated that bacterioplankton in riverine lakes was similar to that in rivers, while lakes with limited water exchange showed a similarity to fertile lakes. Water level and nutrients were among the factors determining bacterial community structure.

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Introduction

Floodplains are important and complex systems but fundamental studies on their ecology, and particularly microbial ecology, are scarce because so few intact floodplains now persist. They comprise a range of habitats subject to a continuum of hydrological conditions as the rivers meander, and old meanders are isolated to different degrees. Side arms, oxbow lakes, and paleomeanders, represent lotic, lentic and semi-aquatic habitats, potentially provide 'hot-spots' of biodiversity (Ward, 1998). Natural floodplain lakes serve as sinks, sources or transformers of dissolved and particulate organic matter, inorganic elements and thus contribute greatly to the self-purification ability of a river (Tockner et al., 1999; Besemer et al., 2005). Hydrological connectivity is key to the

functioning of floodplain systems through both surface and groundwater inflow.

Formation of oxbow lakes leads to characteristic natural biological and hydrological features (Amoros and Bornette, 2002; Tockner et al., 1999), changing the lotic to a lentic character, owing to the increased water residence time. The lakes accumulate organic matter and become shallow, with decreasing biodiversity due to progressive domination of species tolerant of changed environmental quality (e.g. Obolewski, 2011; Wilk-Woźniak et al., 2014). Floodplain lakes are short-lived as they fill with sediment and vegetation.

The community structure of all these systems is built on microorganisms (Lew et al., 2010). Temperature, nutrient, organic carbon, flood pulses, and light exposure are key bottom-up factors controlling bacterial dynamics in aquatic systems (Amado et al., 2006, 2013; Almeida et al., 2015). Bacteria are the most important consumers of the organic carbon carried in running waters and thus play a significant role in the aquatic carbon cycle. They metabolize not only detritus from dead organisms, but also organic wastes from excretions or photosynthetic extracellular release (Ziembinska et al., 2012). Heterotrophic bacteria are a valuable

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nutritional resource for higher organisms and this pathway, called the microbial loop, profoundly increases the productivity of the entire system (Besemer et al., 2005; Obolewski, 2011; Granado and Henry, 2014; Wilk-Woźniak et al., 2014). The structure and composition of microbial communities thus reflects the condition of a given ecosystem (Gołaś et al., 2009).

We tested two hypotheses that: (1) bacterial communities change according to the distance to the river, because of different flood duration and intensity among lakes and (2) loss of lotic conditions causes the bacterial communities in floodplain lakes similar to fertile lakes. Transport of riverine bacterial cells between lakes can be substantial, depending on season and lake water retention time (Bergström and Jansson, 2000; Lindström et al., 2006). We used the Biebrza River (NE Poland) floodplain—one of the last remnants of natural floodplains and one of the largest wetland complexes in Europe. There are a few natural, relatively unpolluted, undisturbed watercourses in Europe (Besemer et al., 2005), but only the Biebrza floodplain has a well-preserved system of natural cut-off channels, by-passes, oxbows and active meanders that are suitable for examination of natural processes of mixing and dispersion of microbial communities (Grabowska et al., 2014; Wassen et al., 2002).

Material and methods

Study area

The catchment of the Biebrza River floodplain in North-Eastern Poland (22°30'–23°60'E and 53°30'–53°75'N) occupies 7057 km², and the floodplain covers an area of 1950 km². The Middle Basin is approximately 33 km long and spreads along the floodplain between the villages of Osowiec and Sztabin. The river flows through boggy meadows and marshes, meanders considerably and forms numerous old riverbeds and floodplain lakes in different stages of succession (Wassen et al., 2002). A distinct feature of the Middle Biebrza's hydrosystem is the natural landscape and flood-pulse pattern, because the floodplain has been nearly entirely preserved and has never been dammed, diverted, regulated or embanked. The Biebrza's floodplain wetlands are protected under the Ramsar Convention Bureau (1997).

The middle Biebrza River water levels fluctuate within a range of 264 cm (Chormański et al., 2011). The average flow at the gauge in Osowiec is 22.78 m³ s⁻¹ with a range from 3.08 to 360.00 m³ s⁻¹ (Grabowska et al., 2014). There are long spring floods and low water stages during summers. During the spring floods, the river forms a vast shallow impoundment, locally up to 1 km in width, which lasts for several months. Prolonged spring floods promoted hydraulic and ecological connectivity among all water ecosystems in the floodplain in 2011, 2012 and 2013 and lasted for 42%, 35% and 48% of the year, respectively. Stages below the low water level in 2011 lasted 8% of the year, in 2012, 23%, and in 2013, 19%. Low water periods enhanced the isolation of lentic wetlands.

The eleven sampling sites were chosen subjectively for their accessibility and embraced a range of morphometric (e.g. area, connectivity to adjacent river channel), hydrological and water quality variables. Lakes with active inlets and outlets have a shorter water residence time than lakes without inlets or outlets. Based on the typology of floodplain lakes proposed by Amoros and Roux (1988), the analysed water bodies were classified into four types with different hydrological connectivity and water retention patterns:

- eupotamic—the main river channel (the Biebrza River);
- parapotamic—lotic side-channels (by-passes) with flowing water: Stara Rzeka (STR), Mostek (MOS) and Czerwony Domek (CZD);

- plesiopotamic—semi-lotic abandoned meanders, permanently connected with the river by a downstream arm: Bocianie Gniazdo (BOC), Klewianka (KLE), Tur (TUR) and Glinki (GLI) and
- paleopotamic—lentic side channels and depressions filled with stagnant water and isolated from the river unless flooded: Budne (BUD), Bednarka (BED) and Fosa (FOS), (Fig. 1).

The frequency and duration of the connection, and the amount of inflowing water, depend on the water level of the river, the height of the inflow and the morphology of the river banks.

Three sampling sites on each water body were chosen: A—on the upstream arm, B—in the middle part or the most distant part of a lake in relation to the river channel, C—on the downstream arm. Water for microbiological and chemical analyses was taken from the subsurface layer (ca. 0.2 m depth), sampled simultaneously, twice a year, in June and September in 2011–2013.

Hydrological and physico-chemical measurements

We recognised four water level categories: low water, rising, high water and receding water phases, based on the data provided by the Institute for Meteorology and Water Management in Poland (IMGW) for the Biebrza River. The measurement protocol was described by Grabowska et al. (2014). The fluctuations in the water level in the floodplain lakes were assumed to be identical to those in the river channel.

In situ measurements of dissolved oxygen (DO), pH, electrical conductivity (SEC), temperature and chlorophyll-*a* concentration were made with a YSI 6600R2™ calibrated multi-probe (USA). Water transparency was measured with a Secchi disk (20 cm in diameter). Concentrations of phosphates, nitrates, nitrites and ammonium ions were determined by standard analytical methods (APHA, 1989). Chemical oxygen demand (CODCr) was analysed with the dichromate method. Total organic carbon levels were determined in unfiltered samples. Dissolved organic carbon (DOC) was quantified after the samples had been passed through nitrocellulose membrane filters with a pore size of 0.45 μm (Millipore). Carbon analyses were made by high-temperature combustion (Shimadzu TOC 5000 analyser, Japan) and performed according to the protocol described by Dunalska (2009).

Total bacterial number and mean volume of cells

Floodplain samples were taken in triplicate to determine the variability of counts. Total bacterial number was determined by epifluorescence microscopy (Porter and Feig, 1980). Triplicate subsamples were fixed with neutralized formaldehyde (pH 7.4; final concentration 4%) and stored at 4 °C to perform the analysis. Staining was performed within 2 weeks of sampling. Subsamples were stained with 4',6-diamidino-2-phenylindole (DAPI; final concentration 0.01 μg mL⁻¹) for 15 min in the dark. The samples were then gently filtered through 0.2-μm black Nuclepore filters (type GTTP, Millipore) and enumerated under an Olympus epifluorescence microscope. More than 1000 bacterial cells in 20 objective fields were counted. The mean volume (μm³) of cells in a water sample was measured by automatic image analysis (Świątecki, 1997).

Fluorescent in situ hybridization

Samples for community analysis were fixed with freshly prepared buffered paraformaldehyde (pH 7.4) to a final concentration of 2% (vol:vol) and stored for several hours at 4 °C. The samples were filtered through white polycarbonate filters (0.2-μm type GTTP, Millipore), rinsed with sterile water, dried at room

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