Original Research

Effects of High Water Levels on Bacterioplankton Abundance in the Danube River floodplain (Kopački Rit, Croatia)

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Abstract

Effects of high water levels on the abundance of colony-forming units of eutrophic and oligotrophic bacteria were investigated. Changes in their proportion were exploited as the biological indicator of organic substrate availability. It was also reconsidered, to a certain extent, which source (autochtonous or allochtonous) of organic substrate and bacteria prevails during floods. Water samples were collected from the surface and from the bottom during high water levels in the floodplain lake (Kopačko Lake) and the connecting channel (Hulovo Channel). The relative abundance of oligotrophs vs. eutrophs was considerably higher at the end of investigation, to which higher abundance of eutrophs preceded at Kopaèko Lake sampling station. Also in Kopačko Lake, a considerably higher abundance of bacteria was noticed in the bottom samples during first intensive flooding pulses. Elevated bacterial abundance was connected with the sufficiently intensive floods (eutrophs dominate) but also with the water properties established following the settling down of disturbed conditions (oligotrophs dominate). Greater abundance in the bottom samples established during the first intensive pulse suggests a sediment origin of bacteria, while considerable differentiation between oligotrophic and eutrophic bacteria suggests an establishment of lower quality of organic substrate at the end of the investigation.

Keywords: floodplain, high water level, bacterioplankton, r- and K- strategists, DOC bioavailability

Introduction

Floodplains are places where water and land meet to create extensive contact areas. Their characteristics mix and form new specific properties. A driving force of that process is the variation in water level, which is indicated in several studies [1-5]. The water inundating the floodplain resuspends the sediment deposits while at the same time causing an acceleration of detritus decomposition rates [6-9]. Burns and Ryder [10] have noted that during the flooding of sediments the loading of water with dissolved organic carbon (DOC) occurs and is accompanied with elevated activity of bacterial extracellular enzymes. The burst of the flooding pulse propels the bacterial activity and utilization of readily assimilable DOC through which goes the major carbon pathway [11]. It is simultaneously also the limiting factor of bacterioplankton growth [12]. According to Kritzberg et al. [13], both types of sources of organic carbon in ecosystems (autochtonous and allochtonous) are important for bacteria while higher bacterial abundance is commonly observed in relation to phytoplankton primary production [1, 14]. Lack of that relationship suggests the existence of some other than phytoplankton source of organic carbon that is biologically important for heterotrophic bacterioplankton. Allochtonous, a source of organic carbon in the water column can

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be a resuspended sediment [10] and/or a washout from the floodplain [1, 15].

There are two known major trophic groups of heterotrophyc bacteria. Regarding their capability to uptake organic matter, heterotrophs are separated into species with low nutrient affinity and rapid growth (r-strategist), which depends on high carbon concentration. These are named policarbophylls, copiotrophs or eutrophs. On the other hand, the species with high nutrient affinity and slow growth (K-strategists) that succeed on low concentrations of carbon are named oligocarbophylls or oligotrophs [16, 17]. The difference in the way of carbon consumption, between trophic groups of bacteria, could be exploited as an indicator of bioavailability of organic substrate [18-20], in the case of which a changing proportion of substrate labile fractions will result in different proportions of eutrophic and oligotrophic bacteria. Grossart & Ploug [21] reported about the shift of community structure from high growth efficiencies to low growth efficiencies in relation to substrate composition.

The purpose of this study was to determine the influence of high water levels on the abundance of colony-forming units in the Kopački Rit floodplain and to note temporal and spatial dynamics of proportions of oligotrophic and eutrophic bacteria as a biological indicator of carbon availability. We also tried to examine to a certain extent which source (autochtonous or allochtonous) of organic substrate and bacteria prevails during floods.

Materials and Methods

Study Area

Kopački Rit is a Nature Park located in eastern Croatia (45°34´ latitude, 16°24´ longitude-near the town of Osijek) in the corner which is surrounded by the Danube and Drava (Fig. 1). It covers a surface of almost 240 km^2. About one half of the area, which is not protected by the embankment, is inundated by the Danube. The floodplain is divided into the northern and the southern parts, where the flooding pulses enter through the Vemeljski Dunavac (the northern part) and the Hulovo Channel (the southern part). The Hulovo Channel flows into Kopačko Lake. Our investigation was conducted in Hulovo Channel and Kopačko Lake. Sampling station Hulovo-I is located in the middle of the channel Hulovo-II is on outflow toward Kopačko Lake. The stations are separated from the main Danube flow. Hulovo-I is approximately 3 km, Hulovo-II 6 km and Kopačko Lake sampling station is about 6.5 km away. During high water level the depth of the Hulovo Channel and Kopačko Lake can reach 6 and 5 m, respectively. The south part of the floodplain is characterized as eutrophic [22].

The start of flooding is at +250 cm at the Danube water level measuring station-Apatin (G. Palijan, personal observation). The Danube water enters the channels which fill in the lakes of the floodplain. When the river level reaches +400 cm at Apatin (Fig. 2), water in the channels and lakes starts to overflow the surrounding lowland area of Kopački Rit, which is covered with forests mainly consisting of white willow (*Salix alba* L.), black poplar (*Populus nigra* L.) and pedunculate oak (*Quercus robur* L.) and with vast stands of emergent macrophytes, mainly common reed (*Phragmites communis* Trin.) and bulrush *(Carex* sp*)*. The area covered with water during low and high water phases varies substantially, about 10 times [23].

High water levels, during which the investigation was performed, can be separated into two distinct types. The first one, when the water entering the floodplain does not overflow the surrounding lowland area of Kopački Rit but stays instead in the channels and lakes of the floodplain (low flood intensity), and the second one when the water overflows the same (high flood intensity) (Fig 2). The first type of flood occurred during March, May and October 2003, whereas the second flood type occurred during April and June 2004. During May and July 2004 water was withdrawing to the river. Furthermore, the flood during October 2003 occurred after almost five months of drought, during which time the water level in the floodplain decreased considerably.

Sampling

Sampling was carried out monthly from March 2003 until July 2004 only during high water levels when the Danube inundates the floodplain. Two water samples were collected from each sampling station: from the surface and from the bottom. All chemical variables (pH, electrical conductivity, dissolved oxygen, ammonia, nitrates+nitrites, total N and total P) were determined in the laboratory according to APHA [24] standard methods. Concentrations of oxidized forms of inorganic nitrogen (nitrates+nitrites) were added to the Kjeldahl nitrogen concentration to obtaine the concentration of total nitrogen, whereas total phosphorus was determined after sulfuric-nitric acid digestion.

Concentrations of chlorophyll a were determined spectrophotometrically [24] after filtration through glass fibre filters (Whatman, GF/C).

The physical parameters determined in the field were: depth, temperature and transparency (by Secchi disc-30 cm diameter).

Bacterial Abundance

The water samples collected for bacteriological examinations were taken in 200 mL sterilized bottles and transported to the laboratory in a cooler at the sampling temperature. The number of colony forming units (CFU) was determined by means of two media different in their content of organic matter. Eutrophs were cultivated on MPA (nutrient agar-Biolife) plates poured in triplicate and

Fig. 1. Study area of the Danube River floodplain Kopački Rit. Region enclosed with a dashed line is protected as a Nature Park. Sampling stations: H1=Hulovo-I, H2=Hulovo-II, KL=Kopačko Lake. Stars mark the embankment of the Danube and Drava.

oligotrophs on technical agar (Biolife) suplemented with 0.1xMPA [18, 20]. Incubations were conducted at 25°C. According to Kuznetsov and Dubinina [25], the colonies were counted after three days on MPA and after three weeks on diluted MPA. Abundance of colonies on plates is expressed as log CFU/mL. Except freeliving bacterial cells, the cells which were attached to particles were also considered as bacterioplankton, so that the number of colonies corresponds to the abundance of freeliving bacterial cells and to the abundance of particles with attached bacteria. In waters with high amount of suspended particles (as in disturbed system of the floodplain) more than 80% of bacterioplankton can be attached to particles [11]. Secondary production in the floodplain is also higher in the attached than in the free-living bacteria [32].

The colonies on diluted MPA are not tested for growth on richer media, so it could not be stated that they are strict oligotrophs [17], although they are for the purpose of this research considered oligotrophs.

Statistical Analysis

All data, except pH, were logarithmically transformed to fulfill the terms of statistical analyses. The results were considered significant if $P<0.05$. Dimensionality of biotic and abiotic variables was reduced by means of principal component analysis (PCA). The parallel analysis (PA) was used as a stopping rule in PCA [26-28] after which VARIMAX rotation of significant principal components was performed. Significant loadings were determined by the Broken-Stick method [29]. Communality values are used to show which variables have the best representation by the significant components.

A multiple regression analysis was performed in order to investigate the influence of high water levels on bacterial abundance. Principal component scores were used as independent variables whereas bacterial abundance of oligotrophs and eutrophs were used separately as dependent variables.

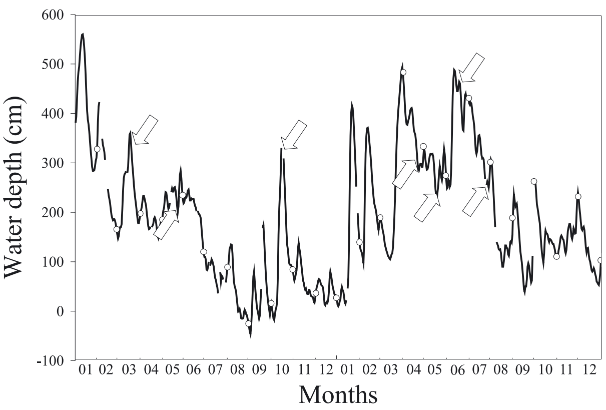

Fig. 2. Water level of the Danube during 2003 and 2004 at the Apatin water level measuring station. Circles mark the end of the month, while arrows mark samplings. During March, May and October 2003 floods of low intensity occurred, while during April and June 2004 floods of high intensity occured and the water flooded lowland areas of the floodplain.

Results

Physical and Chemical Properties

Investigation was performed during high water levels. Dimensionality of biotic and abiotic variables was reduced by PCA. The first three components, which are significant according to PA, account for 76.2% of variation (Table 1) and reveal two groups of samples (Fig. 3).

The first group (noted as A) consists of the samples from April and June 2004 together with the samples from Kopačko Lake during May 2004, while the rest of the samples from May 2004 and all samples from July 2004 and May 2003 make the second group (noted as B).

The first axis is positively correlated with dissolved oxygen concentration, transparency, nitrates+nitrites concentration and total nitrogen, while it is negatively correlated with water temperature. The second axis is positively correlated with transparency, water depth and pH while negatively with ammonia concentration. Chl-a, electrical conductivity and total phosphorus are positively correlated with the third axis, which does not have significant negative loadings (Table 2). Communality values indicate that the water temperature, transparency, depth, ammonia, nitrates+nitrites, total nitrogen and phosphorus have the best representation by the significant components (Table 2).

Bacterial Abundance

The abundance of colony forming units was in the range from $7.3*10^2$ to $6.5*10^8$ CFU/mL for eutrophs and $3.7*10^3$ to $4.9*10^9$ CFU/mL for oligotrophs. Increased numbers of bacteria were present during June 2004 in

Table 1. Eigenvalues and percents of explanation of variability among measured variables accounted by the first five principal components. Axes with eigenvalues greater than that from the PA are considered for interpretation (bold values).

PC	Eigenvalues	% of variation	Cumulative% of variation	Eigenvalues from the Parallel Analysis
1.	**3.88**	35.3	35.3	2.19
2.	**2.81**	25.5	60.8	1.81
3.	**1.69**	15.4	76.2	1.54
4.	0.85	7.7	83.9	1.35
5.	0.51	4.6	88.6	1.18

Hulovo-I and in Kopačko Lake, and during April 2004 in Hulovo-II sampling station (Fig. 4). Considerable difference between the number of eutrophs and oligotrophs appeared during July 2004 in the Hulovo-I and Kopačko Lake sampling stations. At Kopačko Lake sampling station, a considerable difference was also noticed in the number of CFUs from the surface and the bottom samples collected in October 2003 and April 2004 (Fig. 4a and c). Moreover, CFU from the bottom samples, especially from Kopačko Lake, predominate in the majority of samples. Higher counts from the bottom samples on that sampling station are partially exceeded by the counts from the surface samples during May 2004 and completely exceeded during June and July 2004. During June 2004, eutrophs dominate, after which their abundance ceases and finally, during July 2004, oligotrophic bacteria were more abundant (Fig 4c). Oligotrophs are more abundant in the majority of samples at the Hulovo Channel sampling stations (Fig. 4a and b).

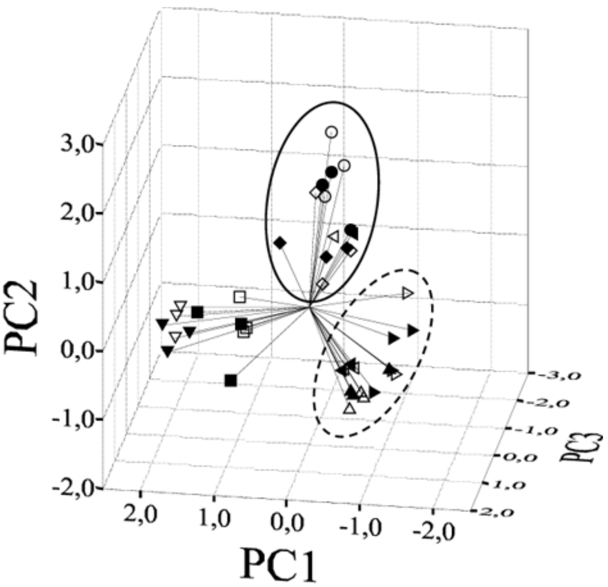

Fig. 3. 3D PCA plot consisting of PC1, PC2 and PC3. Lines are projections of the points into the origin. Oval with full line comprises group A while a dashed oval comprises the group B. The symbols represent: ▽▼-March 2003, △▲-May 2003, ■□-October 2003, ◇◆-April 2004, ◁◀-May 2004, ○●-June 2004 and ▷▶-July 2004; black symbols=bottom samples, white symbols=surface samples. Samples collected during March and October 2003 are pointed in differnt directions although they seem to be close to each other.

Table 2. Loadings and communalities of measured variables on the first three principal components. Significant loadings according to the Broken-Stick method are in bold.

Variables:	PC1	PC2	PC3	Comm.
Dissolved oxygen	**0.67**	0.31	-0.051	0.548
Chlorophyll a	-0.338	-0.006	**0.751**	0.678
Water temperature	**-0.919**	0.026	-0.275	0.92
Secchi disc transparency	**0.522**	**0.722**	-0.112	0.806
Water depth	0.29	**0.848**	-0.204	0.845
pH	-0.022	**0.811**	0.153	0.682
Electrical conductivity	0.025	-0.219	**0.792**	0.675
Ammonia	0.266	**-0.777**	0.312	0.773
Nitrates+Nitrites	**0.887**	0.159	-0.101	0.822
Total nitrogen	**0.939**	-0.169	-0.038	0.912
Total phosphorus	0.25	-0.005	**0.813**	0.723

Distribution of maximal counts of CFU into the groups of samples established by the PCA is presented in Table 3. The maximal counts on Hulovo-I sampling station belong to oligotrophs exclusively. In Hulovo-II the eutrophs dominated only during one month, while in Kopačko Lake the eutrophs dominated in the majority of samples. Thus, slowly growing strains (oligotrophs) dominate in the Hulovo Channel while rapidly growing bacteria (eutrophs) prevail in Kopačko Lake (Table 3).

Multiple regression analysis performed to investigate the influence of high water levels on bacterial abundance did not show any significant relationship between dependent and independent variables. Both regression models, for eutrophs and oligotrophs, were insignificant; P=0.772 and P=0.194, respectively.

Elevated abundance of CFU occurred in relation to different types of floods (see Study area section). During October 2003 the floodplain was inundated after five months of isolation. The flood was of low intensity (Fig. 2). During April 2004, similar bacterial dynamics to that during October 2003 occurred (Fig. 4b and c) although the water samples were collected under the different hydrological conditions. These samples were collected in the period after the flooding of lowland areas of the floodplain (Fig 2). Finally, samples in June 2004 were collected, as the ones in April, after flooding of lowland areas of the floodplain but immediatelly after the innundation (Fig 2). Resulting bacterial dynamics are different from the ones in April 2004. Eutrophic bacteria dominate at Kopačko Lake sampling station, whereas oligotrophs are more abundant in the Hulovo Channel sampling stations as was already mentioned (Fig. 4). These flooding pulses have finally resulted in a development of exclusively oligotrophic bacteria in July 2004 at all sampling stations.

Discussion

Despite the fact that all samples were collected during high water levels, the PCA revealed a grouping of samples based on their biotic and abiotic properties (Fig. 3). Considering measured variables, the samples collected during or closely after the flooding of lowland areas of the floodplain (group A) and the samples collected for a

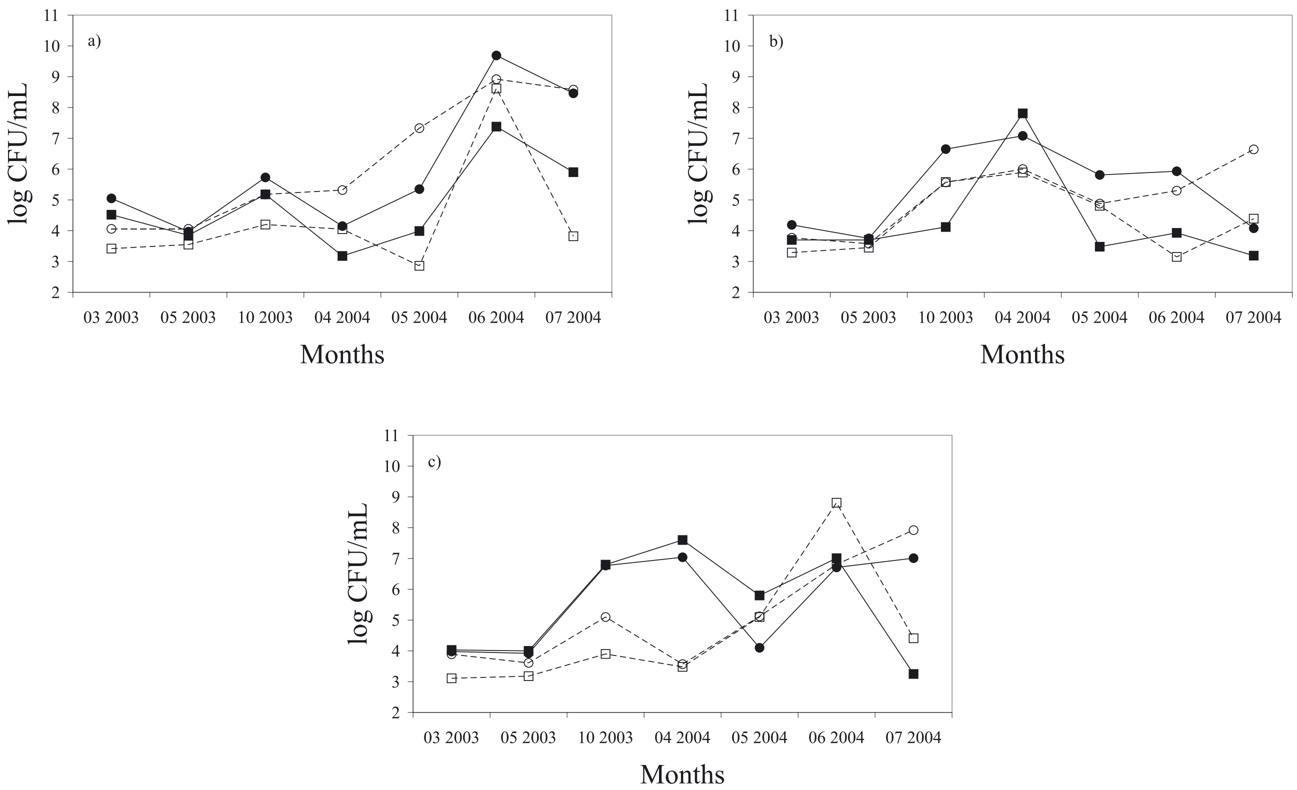

Fig. 4. Values of CFU number in: a) Hulovo-I, b) Hulovo-II and c) Kopačko Lake sampling stations. Squares=eutrophs, circles=oligotrophs; black symbols=bottom samples, white symbols=surface samples. Considerable differences emerge between samples from the surface and the bottom in October 2003 and April 2004 in Kopačko Lake and between number of eutrophs and oligotrophs in July 2004 in Hulovo-I and Kopačko Lake sampling stations.

Table 3. Distribution of maximal counts of eutrophic and oligotrophic bacteria in groups of samples reveald by PCA. Black symbols=group A, white symbols=group B; circles=oligotrophs, squares=eutrophs;

Sampling station:	05 2003	04 2004	05 2004	06 2004	07 2004
Hulovo-I	○	●	○	●	○
Hulovo-II	○	■	○	●	○
Kopačko Lake	□	■	■	■	○

certain period after the flooding (group B) create two distinct groups.

Several studies pointed out the importance of hydrologic factors, primarily the variation in the water level, in creating different characteristics of floodplains [1-5]. The obtained results in this study suggest that not only difference between periods of high and low water levels but also oscilations during the period of high water level, can create changes in the properties of water and in bacterial abundance. After distinction of abundance of oligotrophic and eutrophic bacteria on the basis of groupation revealed by the PCA (Table 3), it is possible to assume that the oscilation in intensity of high water level produces differences that were recorded in abundance of CFU. According to Table 3, group B comprised almost exclusively the oligotrophs, while eutrophs dominated group A. Considering loadings on the principal components (Table 2, Fig. 3), it is possible that water transparency, depth and pH have a major influence on bacterial development in group A, whereas water temperature, total phosphorus, electrical conductivity, chl-a and ammonia concentration possibly have a major influence on bacterial development in group B. Nevertheless, the multiple regression models did not confirm any significant relationship between the measured variables and bacterial abundance.

Considering the fact that multiple regression failed to explain the variability in number of CFUs, it can be concluded that bacterial density during the time of elevated water levels was under the control of some variable (-s) other than those which were measured. An alternative to that is that the elevated bacterial abundance was not of autochthonous water column origin. There are two scenarios possible. The first one is that the bacteria are imported into the water column from the surrounding lowland areas of the floodplain [2, 15]. There could have been a possibility of that during April 2004 because samples were collected when the water level was decreasing and withdrawing to the channels and lakes, but not during June 2004 when the water was entering the floodplain (Fig. 2). In that case, an allochthonous origin from the surounding lowland areas of the floodplain is excluded. The second possibility is that the bacteria originated from perturbed sediment. The higher bacterial abundance recorded in the bottom samples from Kopačko Lake and Hulovo-II sampling stations during April 2004 support that hypothesis (Fig. 4). The divergence between samples from the surface and the bottom was not repeated in the flooding pulse during June 2004. Instead, the abundance of oligotrophs and eutrophs diverges, more or less at all sampling stations, indicating the change in bacterial dynamics established by different pulses. The abundance of CFU in June 2004 corresponds to the values usually reported for sediments [30]. It seems that the flooding pulses release bacteria from the sediment developed in substantial biofilm consortia that overgrow every available surface under the water [31], and equalize their distribution through the water column. Different effects of flooding pulses during April and June 2004 on the bacterial abundance (Fig. 4) are probably due to the different hydrological situations. The sampling in April 2004 occurred during a certain period after the flood, whereas during June 2004 it occurred immediately after the flooding (Fig. 2). More intensive hydrological conditions during June 2004 resulted in similar bacterial distribution through the entire water column (i. e. no differentiation between the surface and the bottom samples; Fig. 4).

The established situation in Kopačko Lake during October 2003 (Fig. 4) supports the possibility that the sediment is the source of bacteria. Compared with other months, the bacterial abundance in the bottom samples from October 2003 is similar to the bacterial abundance during April and June 2004 (Fig. 4b and c) although abiotic water properties are different according to results of PCA (Fig. 3). The fact that there was no flooding of lowland areas during October 2003 suggests that the source of bacteria must have been intrinsic (i. e. sediment). Contrary to that, the flood in May 2003 created physical and chemical properties similar to those during May and July 2004 (group B; Fig. 3), although bacterial abundance between May 2003, May 2004 and July 2004 was different (Fig. 4). Such results suggest the importance of floodplain isolation in establishing elevated bacterial abundance. During drought accumulated nutrients could support bacterial development. It is therefore possible that the influence of flooding on bacterial abundance is determined not only by flood type (intensity) but also to which extent the floodplain was isolated prior to flooding. During drought, established difference in the water level between river and the floodplain facilitates the development of flooding properties that are more similar to the second, more intensive type of flood. The flooding pulses in March and May 2003, with intensities similar to that in October 2003 (Fig. 2), do not produce equal effects considering water properties and bacterial dynamics as pulse in October 2003 (Fig. 3 and 4), probably because they did not occur after the period of drought.

Aspetsberger et al. [32] found that during inundation of the Danube floodplain near Vienna, a major source of particulate organic carbon was of lower bioavailability and it was imported from the river. Our investigation does not exclude that possibility but it strongly suggests that the source of carbon is more intrinsic. Some authors also have reported that organic carbon availability declined downriver and with high discharge [33, 34]. Their results suggest that the quality of organic carbon imported during inundation into the Kopački Rit floodplain could be considered of lower bioavailability. Also, such results could not explain almost constant higher abundance of eutrophic bacteria in Kopačko Lake (Fig. 4c, Table 3) and they suggest the existence of some other source of more labile DOC. Phytoplankton primary production probably is not the source of DOC because chlorophyll a concentrations during investigation were below 30 μg/L in the majority of samples (data not shown).

The previous discussion took into consideration the bacterial abundance in all samples except those from group B. The samples were collected while water was withdrawing to the Danube. The attribution of this group was almost exclusively the dominance of oligotrophs (Table 3, Fig. 4). The fact that oligotrophs are more abundant than eutrophs suggests that the concentration of available DOC was low. A change of community structure in dependence of DOC quality and concentration is already known [21, 35, 36]. According to Castillo [2] changes in the structure of bacterial community can be induced by the development of more efficient bacteria which respond to changes in sources of DOC. Grossart and Ploug [21] reported that on riverine aggregates the high growth efficiencies decrease after a few days of incubation, which is the consequence of a shift in bacterial community and substrate composition. Also, Siuda and Chrost [37] state that increases of particulate organic matter content cause adaptation of planktonic bacteria to live in particle attached forms and are mainly responsible for secondary production. Higher secondary production of attached bacteria is noted in the Danube floodplain near Vienna [32]. It is possible that in samples from group B, a similar situation occurred where the bacterial community with high growth efficiency (K-strategists, oligotrophs) was developed on suspended particles.

After the resources were decreased, the abundance of r-strategists decreased and K-strategists prospered. It seems that the quantity of bioavailable organic substrate is increased by flooding pulses (eutrophs dominate in group A). After it is depleted, indigenous bacterial assemblage starts to cope with newly created conditions. The number of oligotrophic bacteria increases upon the eutrophic, which finally results in their dominance. This tendency can be observed in Table 3, where gradually the maximal counts have oligotrophs at all sampling stations. Occasionally reported higher counts of CFU of rapidly growing bacteria during summer [38, 39] was observed only in Kopačko Lake during June 2004, whereas in the rest of the samples they were exceeded by the slowly growing bacteria as it was the case during July 2004. The difference in the abundance of eutrophic and oligotrophic bacteria during July was considerable (Fig. 4).

It can be suggested that the oscillation in the water level depletes labile fraction of organic carbon by consecutive flooding which resuspends detrital material and accelerates decomposition rates of it. The changes in composition of culturable fraction of bacterial community suggests a change in the proportion of bioavailable carbon. Resuspension during floods enables a greater development of eutrophic bacteria, while with resuspended detrital particles a transfer of attached bacteria to water column occurs being probably the reason of highly elevated number of CFU during that time (group A). In periods after floods, while water was still high but stagnant or decreasing (group B), the abundance of CFU was probably under the control of established water properties, although multiple regression did not establish significant a relationship of oligotrophic bacteria and measured variables.

If we suppose that the resuspension was a major source of bacteria, then the results of bacterial dynamics suggest that the quantity of bioavailable organic carbon was higher in the lake than in the channel sediment and its concentration decreased during the investigation, especially in Kopačko Lake.

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