

Periodic flooding restrains local succession of microphytobenthos in floodplain lakes

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With 5 figures and 3 tables

Abstract: Periodic flooding of river floodplains and connectivity of floodplain lakes and rivers is suggested to interfere with the succession of microphytobenthos. To analyse this we: 1. studied the impact of flooding on the relationship between irradiance level (depth) and microphytobenthic community composition; 2. sampled three lakes with different connection-disconnection patterns; and 3. studied seasonal variation in community composition in one floodplain lake subjected to several flooding events. Shortly after flooding and subsequent connection of floodplain lakes, microphytobenthic communities showed a uniform species composition. Disconnection of the lakes was followed by a succession of species according to local environmental conditions. However, assemblages were often set back before outgrowth of local species or divergence of community composition became prominent. It is therefore concluded that flooding and the associated connection-disconnection regime of floodplain waters overrule the selective effects of local environmental parameters.

Key words: Microphytobenthos, periphyton, sediment, succession, floodplain lakes, flooding, connection, community composition.

Introduction

In highly dynamic environments, microphytobenthic communities may be frequently disturbed (Biggs 1995) and mixed, potentially masking the relationships between local environmental gradients and microphytobenthic community composition (Soininen 2007). Floodplains of large lowland rivers are such highly dynamic environments: during flooding the floodplain becomes inundated and the floodplain lakes become connected to the main river. At that time the suspension and sedimentation of the sediment top layer is intense, while during low water the floodplain lakes become disconnected from the main stream and develop according to local conditions (Ward & Stanford 1995, Pithart 1999).

The present study aims to analyze how flooding of a river and the consequent connection of the floodplain lakes and the river interfere with the relationship between microphytobenthic community composition and local environmental conditions. We expect that during flooding the connection of the lakes will result in mixing and redistribution of species, leading to a uniform species composition. In disconnected floodplain lakes microphytobenthic communities may diverge according to local conditions.

To study the effect of these connection-disconnection patterns on microphytobenthic community composition, we sampled three lakes at different distances from the river Waal, the Netherlands, representing different connection-disconnection patterns. Secondly we studied seasonal variation in community composition.

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tion in one floodplain lake which was subjected to several flooding events. Finally we studied the relationship between a single environmental factor (irradiance level) and microphytobenthic community composition after flooding by sampling microphytobenthos along a depth gradient in a single floodplain lake. Irradiance level was chosen because of the relationship between microphytobenthic community composition and light quantity (Hill 1996, Dodds et al. 1999, Wellnitz & Rinne 1999, Tuji 2000, Kralj et al. 2006).

Material and methods

Study area

The sampled lakes are situated in floodplains of the river Waal, the main channel of the River Rhine in the Netherlands (Fig. 1). The plains are partly used for pasturing cattle and also serve as a foraging and resting place for birds. Clay deposits were exploited in the past and now a man-made semi-natural landscape dominates. The floodplain and the lakes are embedded between a low summer dike and a high winter dike, leading to semi-natural flood dynamics.

Three lakes were selected for the present study. Lake Och5 is a relatively large lake (ca. 800 m long, estimated average depth 2.5 m), which is always connected to the main stream of the river, and consequently, the water level fluctuates with the water level of the river. The sediment is composed of coarse sand. Lake DeO4 is small (50 × 50 m, average depth 2 m) and is connected during 50–150 days a year. It is dominated by macrophytes in summer, but the present study concentrates on unvegetated patches of the lake. The sediment is silty and rich in organic matter and tends to be anoxic. Lake DeO1 is a shallow lake (average depth 2 m) with highly fluctuating water levels caused by flooding, precipitation and evaporation, leading to highly variable dimensions of the lake (maximal size 200 × 50 m). In dry summers the lake evaporates completely, whereas in wet winters it becomes connected to neighbouring lakes. It is

connected during 2–20 days a year. The sediment is composed of fine sand and silt. When the river is flooded and the plains are inundated, all floodplain lakes become connected to the main stream, and after the flood they become disconnected again.

The time course of the sampling campaigns and the flooding regime of the river are illustrated in Fig. 2. The highest bars indicate the dates when the river water level is as high as or higher than the summer dike and the floodplains are inundated. The lower bars indicate after-flood recovery and onset of disconnection, the dates when river water level drops from flood-level to 1 meter below the level of the summer dike (original water level data were from Rijkswaterstaat, 2003). The moment each lake is connected, and becomes disconnected again, and consequently also the duration of the connection varies with distance to the river, height of the dikes, and other factors. The spatio-temporal characteristics of the impact of different flooding regimes are reflected in the dynamics of nutrients and conductivity (Fig. 3). The two southern lakes (DeO1 and DeO4) become NO_3 and SiO_2 depleted when they are isolated and are replenished when the plains are flooded. The parameters for the connected lake (Och5) follow those for the river.

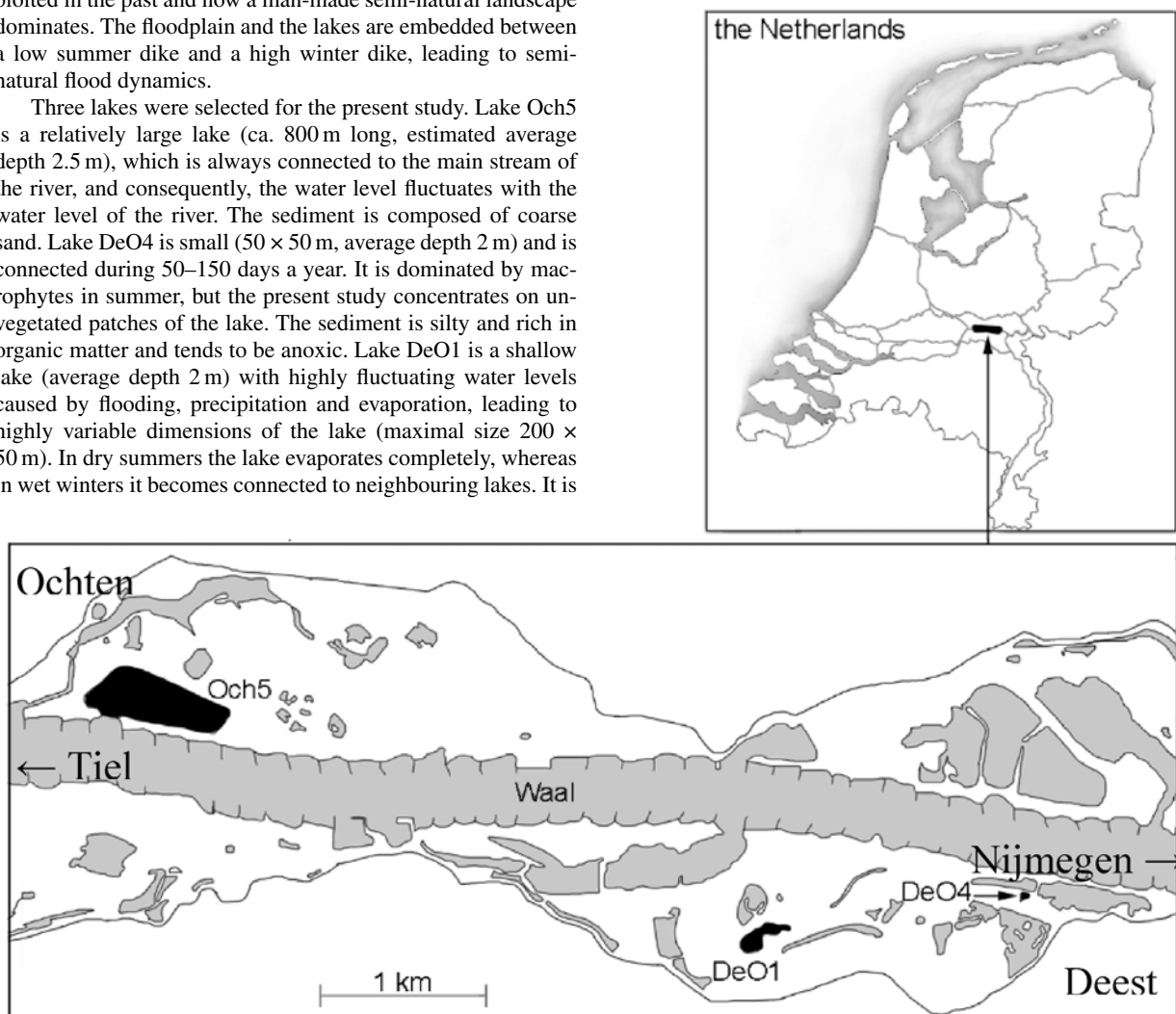


Fig. 1. Locations of the sampled floodplains lakes (black) of the River Waal (The Netherlands, 51° N 5° E).

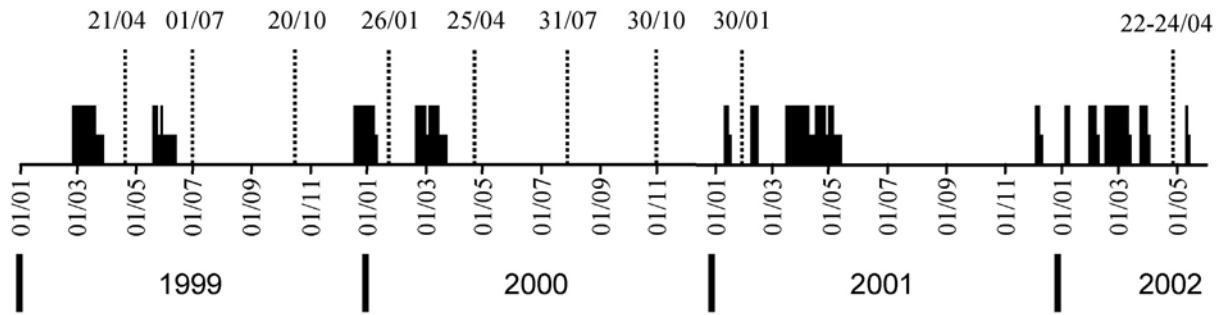


Fig. 2. Time course of the samplings and flooding history of the river. The vertical dotted lines indicate the sampling dates. The highest bars indicate the dates when the river water level was as high as or higher than the summer dike and the floodplains were inundated. The lower bars indicate after-flood recovery and onset of isolation, the dates when river water level dropped to 1 meter below the height of the summer dike (original water level data were from Rijkswaterstaat 2003).

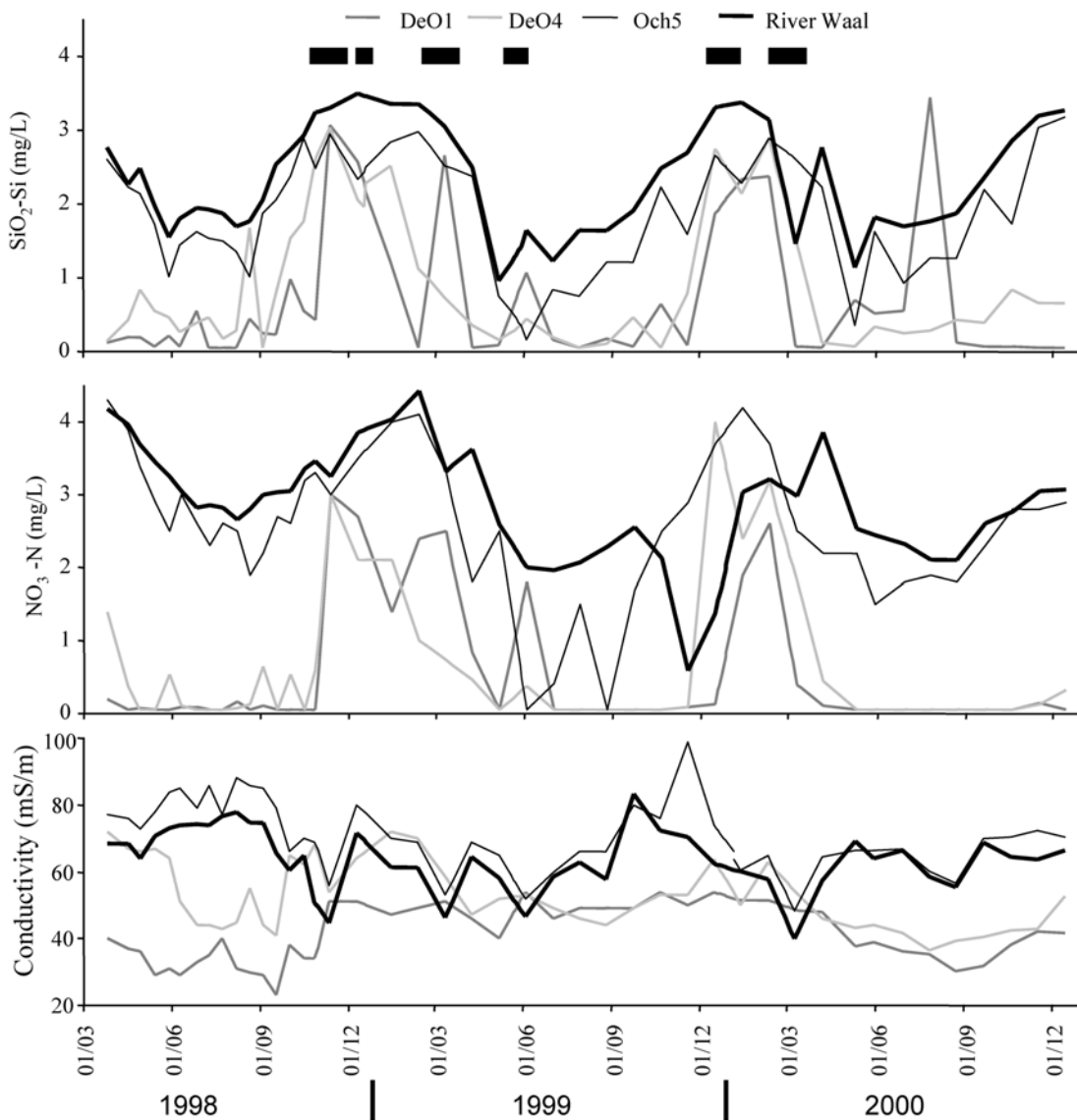


Fig. 3. Concentrations of SiO_2 and NO_3 and conductivity in the three floodplain lakes DeO1, DeO4 and Och 5 (connected) from 1998 to 2000 (data from RIZA) and for the main stream river of the river Waal (bold black line, data from Rijkswaterstaat 2003). The black bars at the top of the figure indicate the periods of time that the river inundated all of the floodplains.

Sampling

To study if a relationship between irradiance level and micro-phytobenthic community composition was established 22–24 days after flooding a depth gradient (of 10, 75 and 200 cm) in a single lake (DeO1) was sampled twice with a two days interval in spring 2002 (Table 1a). Secondly, to study the effect of differences in the frequency and duration of connection all three lakes were sampled twice, in spring 1999 and in spring 2000, at a depth of 10 cm (Table 1b,c). Finally, temporal variation within one lake (DeO1) was studied. This lake was sampled in all seasons for two subsequent years (1999 and 2000) at a depth of 10 cm, creating large differences in the time between sampling and the latest flooding, varying from 19 days in January 2001 to 232 days in November 2000 (Table 1b,c).

At each sampling date conductivity, pH, temperature and light attenuation was measured (Table 1). Replicate cores were taken from the sediment using cut-off polypropylene syringes with a sharpened edge (Terumo®, diameter 1.5 cm, volume 50 ml), at a distance of 10–30 cm parallel from each other. The cores were completely filled with sediment and water and closed with a stopper and transported to the laboratory in cooled containers. In the laboratory, slices of the top 3 mm of the cores were cut after pushing the sediment upwards with the syringe stopper. Slices of 3 to 6 replicate cores were pooled and composite samples diluted (200 ml filtered lake water per slice).

This slurry was stirred with a magnetic stirrer and an aliquot of homogenized slurry was fixed with Lugol's iodine.

In the depth gradient 6 additional cores per depth were taken to measure chlorophyll *a* in the top 3 mm slices of each individual core according to Lorenzen (1967). The chlorophyll-*a* data were tested for significant differences by One-Way ANOVA followed by a Post Hoc test (SNK).

Identification and counting

The fixed samples were first examined at a magnification of 1000× with a light microscope (Olympus BH2) and species were identified as intact cells, according to Bourrelly (1966–1970), Krammer & Lange-Bertalot (1986–1991), Anagnostidis & Komarek (1988) and Cox (1996). Some species were grouped into a single taxon because Cox's key does not allow determination to the species level, e.g. for *Nitzschia* we distinguished several size groups rather than individual species.

Chlorophyll-containing algal cells that were alive when sampled were counted on temporary slides at 400× magnification. Single-celled taxa were enumerated and for filamentous cyanobacteria and chlorophytes a 50 µm length of filament was counted as one individual. Algal cells were identified to the lowest taxonomic level possible. Per sample 4–8 sub-samples were counted, adding up to a total of 500–600 single cells or filaments.

Table 1. Dates of the sampling campaigns and physico-chemical characteristics of the sampling sites. a) depth gradient in lake DeO1. b) & c) three lakes representing differences in inundation-isolation pattern and seasonal variation in lake DeO1.

a	10 cm DeO1 spring 2002	75 cm DeO1 spring 2002	200 cm DeO1 spring 2002	10 cm DeO1 spring 2002	75 cm DeO1 spring 2002	200 cm DeO1 spring 2002
Date (m/d/y)	22/04/02	22/04/02	22/04/02	24/04/02	24/04/02	24/04/02
time after last flooding (days)	24	24	24	26	26	26
temperature at sed. surf. (°C)	17	14.9	11.7	20.2	17.2	15.2
pH at sed. surf.	9.3	9.3	9.12	9.25	9.36	9.03
O ₂ (mg/L)	14	15.3	12.45	14.9	13.8	11.25
O ₂ (%)	135	151	118	160	145	112
Conductivity (mS/m)	36.8	36.8	37.7	36.8	36.9	38.1
% of incidence irradiance	76.5	13.4	0.47	67.7	5.4	0.04
mg chl <i>a</i> / m ² (± 1SD)	177 ± 39	115 ± 23	45 ± 12	143 ± 31	69 ± 15	43 ± 16
b	Och5 spring 1999	DeO4 spring 1999	DeO1 spring 1999	DeO1 summer 1999	DeO1 autumn 1999	DeO1 winter 2000
Date (m/d/y)	21/04/99	21/04/99	21/04/99	01/07/99	20/10/99	26/01/00
time after last flooding (days)	0	34	34	34	145	22
temperature at sed. surf. (°C)	11.3	13.6	12.8	18.9	5.9	1.9
pH at sed. surf.	8.02	8.37	8.38	8.15	8.75	7.94
Conductivity (mS/m)	69.0	56.1	43.2	46.0	50.8	51.1
% of incidence irradiance	69.0	78.8	76.7	77.0	65.3	73.6
c	Och5 spring 2000	DeO4 spring 2000	DeO1 spring 2000	DeO1 summer 2000	DeO1 autumn 2000	DeO1 winter 2001
Date (m/d/y)	25/04/00	25/04/00	25/04/00	31/07/00	06/11/00	30/01/01
time after last flooding (days)	0	44	44	141	232	19
temperature at sed. surf. (°C)	12.8	14.8	14.7	25.6	7.3	1.6
pH at sed. surf.	8.20	9.2	8.51	9.4	8.55	8.04
Conductivity (mS/m)	76.2	42.5	42.6	32.3	40.7	43.0
% of incidence irradiance	78.2	72.0	81.8	80.2	72.2	80.6

The following community characteristics were calculated: Number of taxa, Shannon-Wiener diversity index H' (Shannon & Weaver 1963), evenness J' (Pielou 1966) and Bray-Curtis similarity index S' (Bray & Curtis 1957, according to Clarke & Warwick 1994). The Bray-Curtis similarity index S' was calculated for all pairs of samples using the expression

$$S'_{jk} = 100 * \left(1 - \frac{\sum_{i=1}^n |y_{ij} - y_{ik}|}{\sum_{i=1}^n (y_{ij} + y_{ik})} \right)$$

With $i(n)$ = number of taxa, j = community j , k = community k , y_{ij} = fraction of taxon i in community j , y_{ik} = fraction of taxon i in community k , S'_{jk} = similarity value between communities j and k . S' can range from 0% to 100% for communities with respectively none and all taxa in common. Values of > 60% generally are regarded as indicating replicate samples (Engelberg 1987, Gauch 1982).

Results

Characterization of microphytobenthic communities on floodplain lake sediments

Diatoms always dominated the communities (64–99%), except for the winter sample of 2001 (44%), which was dominated by chlorophytes (53%) (Table 2). At the other sampling dates relative abundance of chlorophytes ranged from 1–18%, while cyanobacterial abundance ranged 0–26% (Table 2). Hardly any community was clearly dominated by one or a few taxa: the highest relative abundance of a single taxon was 43.7%, while the mean of highest relative abundances in all samples was $22.1 \pm 10.7\%$. (Table 2). Diatoms were mainly represented by members of the motile *Nitzschia* and *Navicula* genera. In all except one sample the taxon *Navicula capitatoradiata / gregaria* was present at more than 5% abundance, and was the most abundant taxon in 11 of 18 samples. Genera like *Achnanthes* and *Gomphonema* that grow attached to solid substrates were scarcely represented, except in sites that were isolated for longer periods of time (Table 2).

Relationship between irradiance level and microphytobenthos

The percentage of solar irradiance at the water surface reaching the sediment surface ranged from 77% at 10 cm water depth to < 0.5% at a depth of 200 cm (Table 1a). Accordingly, chlorophyll-*a* concentrations decreased significantly ($p < 0.05$) with increasing depth on both sampling dates (Table 1a). Despite the large differences in irradiance and chlorophyll-*a* between depths, differences in species composition were small (Fig. 4), reflected by similarities of 44–78% (Table

3a). Yet, the lowest similarities were observed between the shallowest and deepest sites (44–53%) (Table 3a). Moreover, similarities between the same depth at the two sampling dates were higher than those between different depths at the same sampling day (Table 3a). The number of taxa increased with increasing depth (from 45 ± 4 to 58 ± 4 taxa) (Table 2), as well as the relative abundance of planktonic diatoms like *Asterionella* and *Fragilaria* (from $14.3 \pm 2.2\%$ to $26.4 \pm 0.4\%$) and the relative abundance of chlorophytes (from $3.0 \pm 2.3\%$ to $13.6 \pm 6.0\%$).

Effect of differences in inundation-isolation pattern

The location of the three lakes causes differences in frequency and duration of flooding and isolation. Consequently, the time after the last flooding varied from 0–34 days and from 0–44 days in 1999 and 2000, respectively (Table 1b,c). Yet, communities in the three lakes were very similar in 1999 (53–58%), and quite similar in 2000 (32–46%) (Fig. 5, Table 3b). The lower similarities in 2000 coincided with a longer time after the last flooding.

Sampling one lake (DeO1) in all seasons for two subsequent years (1999 and 2000) at a depth of 10 cm, created large time intervals between sampling and the last flooding, varying from 19 days in January 2001 to 232 days in November 2000 (Table 1b,c). Prolonged disconnection coincided with lower similarities: the similarity between spring 2000 (44 days post flooding) and summer 2000 (141 days post flooding) was only 24% (Table 3c), suggesting that the longer isolation time allowed divergent development of the community. The lowest similarities were observed when reconnection occurred by a new flooding, between winter 2001 (19 days post flooding) and spring, summer and autumn 2000 (44, 141 and 232 days post flooding, respectively) (Table 3c).

In all other cases similarities were higher, but nevertheless, we did find seasonal differences in species composition (Table 2). In winter *Hantzschia amphioxys* (abundance of 18 and 8% in 1999 and 2000) and *Luticola mutica* (abundance 7 and 1.2%) were typical, only occurring in very small abundances in the other seasons (< 0.8%). *Amphora libyca* had its highest abundance in autumn of both years (0.6 and 2.1%). *Gomphonema* spp. had its highest occurrence in both summers (5.7 and 9.1%). The seasonal variation in species composition was similar for all sampling years, confirmed by the high similarities between the DeO1 spring samples from 1999, 2000 and 2002 (53–64%, Table 3c).

Table 3. Bray-Curtis similarity indices (S'). a) depth gradient in lake DeO. b) & c) three lakes representing differences in inundation-isolation pattern and seasonal variation in lake DeO1. Values of >60 % (bold) generally are regarded as indicating replicate samples (Engelberg 1987, Gauch 1982).

a	10 cm DeO1 22/04/02	75 cm DeO1 22/04/02	200 cm DeO1 22/04/02	10 cm DeO1 24/04/02	75 cm DeO1 24/04/02		
10 cm DeO1 04/22/02	x						
75 cm DeO1 04/22/02	73.8	x					
200 cm DeO1 04/22/02	44.1	54.0	x				
10 cm DeO1 04/24/02	58.3	55.0	52.2	x			
75 cm DeO1 04/24/02	70.9	77.7	62.5	59.0	x		
200 cm DeO1 04/24/02	47.9	64.6	67.5	52.6	66.8		
b	DeO1 spring 1999	DeO4 spring 1999	Och5 spring 1999	DeO1 spring 2000	DeO4 spring 2000		
DeO1 spring 1999	x						
DeO4 spring 1999	58.3	x					
Och5 spring 1999	52.6	58.2	x				
DeO1 spring 2000	60.3	42.7	42.7	x			
DeO4 spring 2000	58.3	53.9	48.8	45.6	x		
Och5 spring 2000	45.2	26.9	30.5	31.6	46.4		
c	DeO1 spring 1999	DeO1 summer 1999	DeO1 autumn 1999	DeO1 winter 2000	DeO1 spring 2000	DeO1 summer 2000	DeO1 autumn 2000
DeO1 spring 1999	x						
DeO1 summer 1999	50.0	x					
DeO1 autumn 1999	57.1	54.6	x				
DeO1 winter 2000	43.7	49.3	46.3	x			
DeO1 spring 2000	60.3	50.2	43.0	41.4	x		
DeO1 summer 2000	21.0	34.7	25.0	27.1	24.4	x	
DeO1 autumn 2000	52.4	56.9	45.5	47.3	55.5	43.9	x
DeO1 winter 2001	16.8	23.3	23.6	37.4	20.2	16.2	23.2
10 cm DeO1 04/22/02	63.9	49.1	51.6	36.6	53.1	17.4	46.6
10 cm DeO1 04/24/02	63.5	44.8	57.3	37.7	55.1	15.8	44.2

Discussion

The microphytobenthic communities sampled at different depths, in different floodplain lakes and in different seasons were quite similar. Although in field studies there is always a potential for covariation, it is hypothesized that during flooding when the three lakes become connected, water bodies are thoroughly mixed and species are redistributed, leading to a uniform species composition, resetting local succession. Only when the lakes become disconnected and mixing of water bodies does not take place for some time, local environmental variables will cause microphytobenthic community composition to diverge. This hypothesis is consistent with the concepts formulated by Ward & Stanford (1995) and Pithart (1999) on riverine invertebrates and phytoplankton, respectively. Hence floodplain lakes may exemplify the environments where 'spatial factors' (Biggs 1995, Soininen 2007) overrule the effects of local physical and chemical parameters.

Roozen (2005) reported rapid divergence of nutrient regimes and plankton development after isolation of floodplain waters from the lower sections of the rivers Rhine and Meuse. A diverging water chemistry of disconnected floodplain lakes was also evident from the seasonal dynamics of nutrients and conductivity in the present study (Fig. 3). Mixing of the floodplain lakes is reflected by a uniform water chemistry and by a uniform species composition, demonstrated by the high values of similarity between communities. Similarity values of >60 % indicate replicate samples (Gauch 1982, Engelberg 1987) and this value was often reached or exceeded. The communities were dominated by *Nitzschia* and *Navicula*, unattached diatoms, which are susceptible to displacement (Cattaneo & Kalff 1978, Peterson et al. 1990). Genera like *Achnanthes* and *Gomphonema* that grow attached to solid substrates were scarcely represented, except in sites that were disconnected for longer periods of time. The species *Hantzschia amphioxys* and *Luticola mutica* were

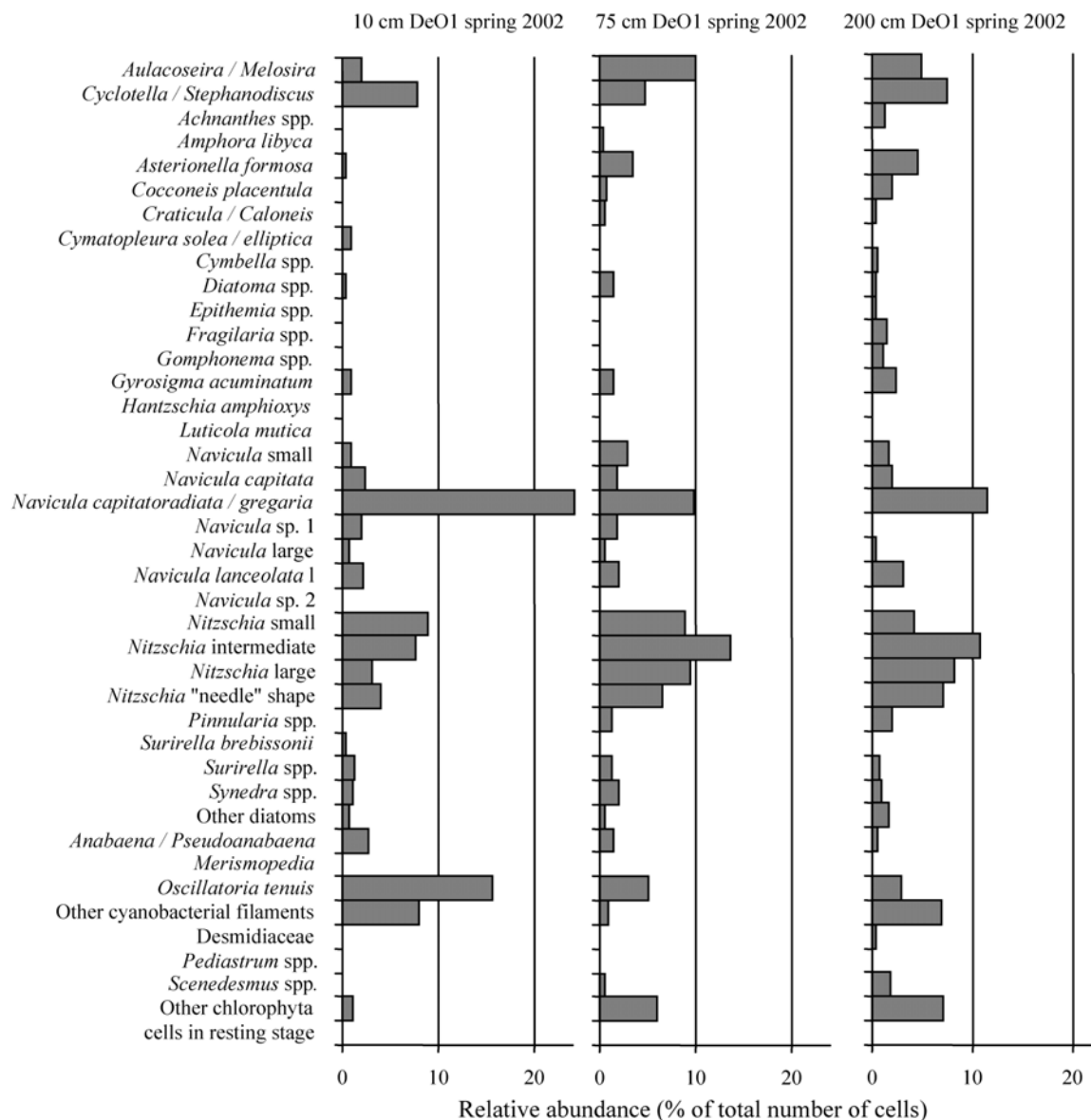


Fig. 4. Relative abundance of species (based on cell numbers) in the depth gradient sampled on 22.04.2002. 10 cm, 75 cm and 200 cm: sampling depth.

found in post-flood samples. These species are known as cosmopolitan aerophylous species mainly occurring as soil diatoms in prolonged dry or temporarily wet environments (Krammer & Lange-Bertalot 1988, Flechtner et al. 1998, Van de Vijver & Beyens 1999). The presence of these species is indicative of terrestrial sediment being washed into the floodplain lakes (Medioli & Brooks 2003). In agreement, De Fabricius et al. (2003) found high abundances *H. amphioxys* and *N. mutica* (a synonym of *L. mutica*) coinciding with high flow conditions.

Colijn & Dijkema (1981), Underwood (1994) and Thornton et al. (2002) found that at high densities mi-

crophytobenthic communities on dynamic intertidal mudflats were clearly dominated by one or a few species (relative abundance of >65% in Thornton et al. 2002). In dense communities the most competitive species would be expected to drive less competitive species to extinction, and resources are partitioned among species whose realized niches do not overlap completely. However, this advanced state of succession requires prolonged interaction, and therefore, temporal heterogeneity (like disturbance) may prevent that this state is reached (Begon et al. 1996). This may explain why in our study many different species could coexist at low and high densities and the highest den-

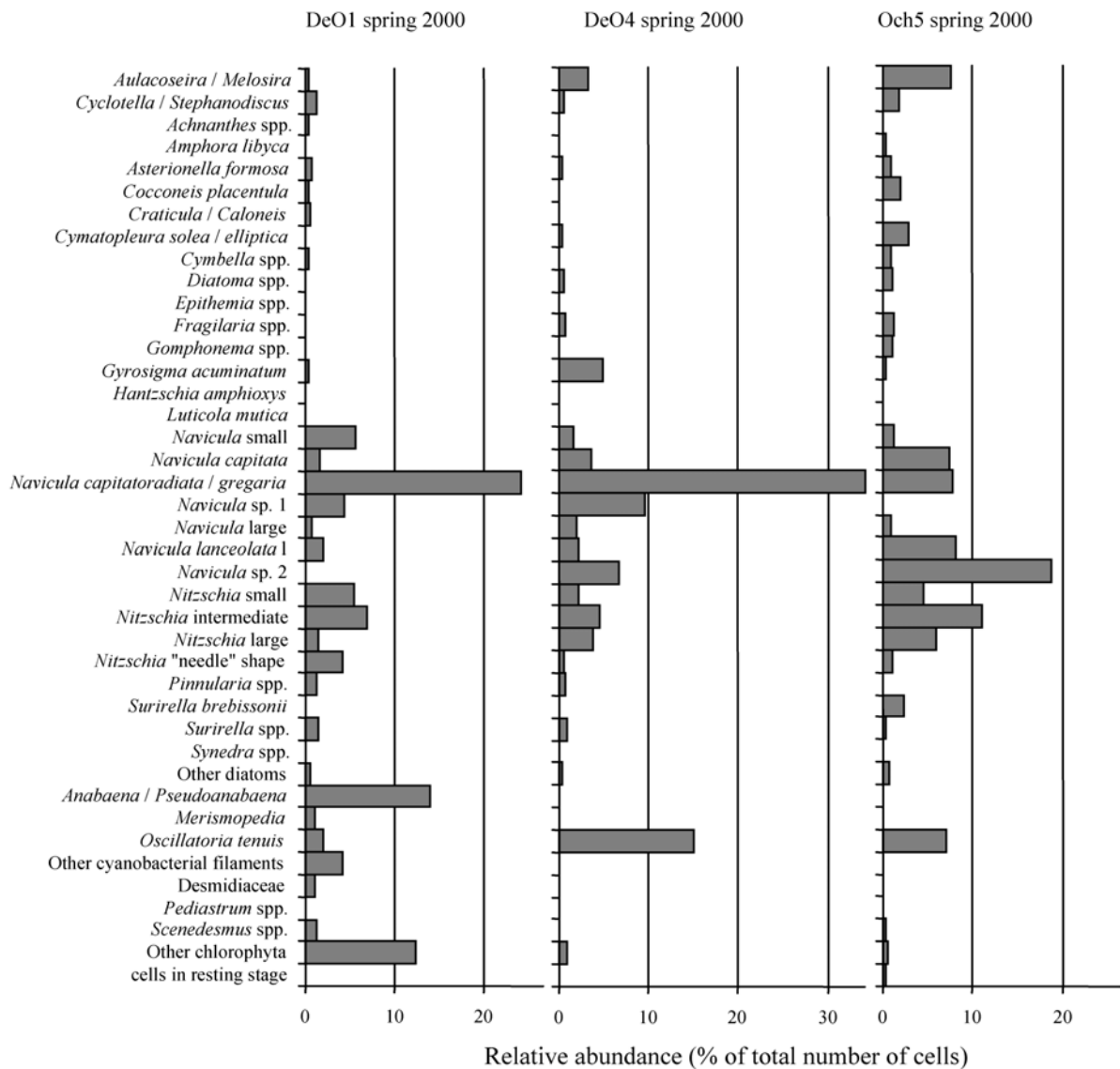


Fig. 5. Relative abundance of species (based on cell numbers) in the three lakes in spring 2000.

sity for a single taxon was 44%, substantially lower than the 65% reported by Thornton et al. (2002).

When lakes become disconnected and disturbance and mixing do not take place for a prolonged period of time, animal communities (Ward & Stanford 1995) and phytoplankton (Pithart 1999) develop differently according to local conditions in riverine micro-habitats. In the present study similar results were observed for microphytobenthos, indicated by the lower similarities between the three lakes in spring 2000 (max. 44 days of isolation) compared to spring 1999 (max. 34 days of isolation). Likewise, low similarities during prolonged isolation and high similarity caused by the next flooding in lake DeO1, indicate that seasonal succession is disrupted by flooding. A typical example of

that was the winter 2000 sample that was dominated by resting cells of chlorophytes (relative abundance of 44.5%). In the depth gradient, sampled 24–26 days after flooding, higher abundances of phytoplankton species at deeper sites were observed, due to a higher volume of water overlying the bottom.

In conclusion, floodplain lakes of large lowland rivers are thoroughly mixed at intervals and microphytobenthic species are extensively redistributed, leading to a uniform species composition. Yet disconnection of the floodplain lakes, triggers succession of species according to local environmental conditions. However, this divergence of community composition and diverging water chemistry is restricted to stable periods of disconnection from the river.

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