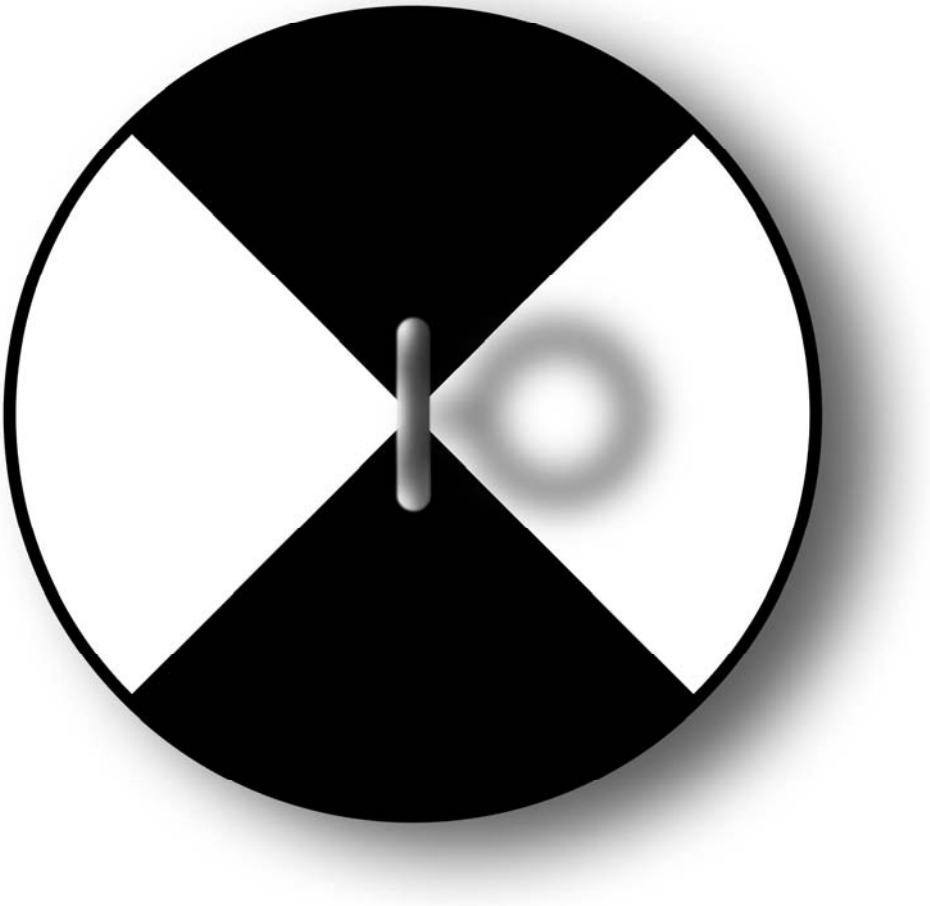
TRANSPARENCY OF FLOODPLAIN LAKES

a study of plankton and suspended matter along the lower Rhine



Promotor:	**Prof. dr. M. Scheffer** Hoogleraar Aquatische Ecologie en Waterkwaliteitsbeheer, Wageningen Universiteit, Wageningen
Co-promotoren:	**Dr. R.M.M. Roijackers** Universitair Docent, Leerstoelgroep Aquatische Ecologie en Waterkwaliteitsbeheer, Wageningen Universiteit, Wageningen **Dr. B. Ibelings** Onderzoeker, Nederlands Instituut voor Ecologisch Onderzoek (NIOO), Centrum voor Limnologie, Nieuwersluis
Promotiecommissie:	**Prof. dr. E. Van Donk** Nederlands Instituut voor Ecologisch Onderzoek (NIOO), Centrum voor Limnologie, Nieuwersluis; Radboud Universiteit, Nijmegen **Prof. dr. F. Berendse** Wageningen Universiteit, Wageningen **Prof. dr. J.T.A. Verhoeven** Universiteit Utrecht, Utrecht **Dr. ir. A.D. Buijse** Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterbehandeling (RIZA), Lelystad

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F.C.J.M. Roozen

TRANSPARENCY OF FLOODPLAIN LAKES

a study of plankton and suspended matter along the lower Rhine

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CHAPTER 1

General Introduction

Frank Roozen

General Introduction

1.1 The Lower Rhine and its floodplains

The River Rhine originates in Switzerland and discharges in the North Sea in The Netherlands. The river is mainly fed by glaciers in the Alps and further downstream by precipitation in its whole catchment area (185.000 km^2). In the Netherlands the Rhine has its highest discharge during the winter months due to precipitation (*Figure 1.1*). After entering the Netherlands near Spijk (Lobith), the Rhine splits up twice. About two-sixth of the total discharge at Lobith is transported by the most southern branch, the Waal, while the rest is transported northwards through the Pannerdensch kanaal. Near Arnhem, the water is divided over the Nederrijn/Lek and the IJssel, these branches transport two-ninth and one-ninth of the total discharge near Lobith respectively. The Nederrijn/Lek discharges in the North Sea, while the IJssel discharges in Lake IJsselmeer.

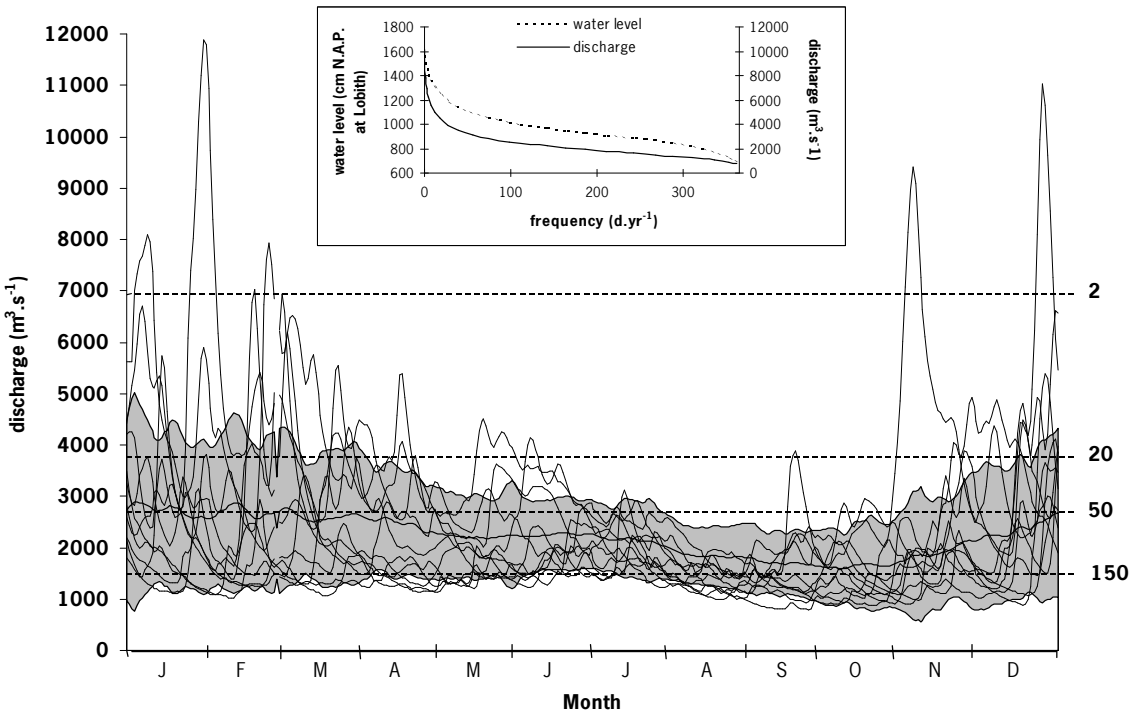

Figure 1.1 Annual discharge regime (daily average) of the Rhine (1991-1999). The shaded area indicates the average discharge ± SD. The horizontal dotted lines present the limits (Figures on the right of the y-axis) of the inundation frequency classes (d.yr^{-1}) used in this thesis. The inlay Figure shows the relation between river discharge and the inundation frequency (adjusted from Buijse et al., 2002).

Like in many (lowland) rivers, human interference during the last two centuries resulted in drastic changes in morphology and natural processes of the river Rhine, changing the river from a meandering, braided river into an artificial, cultivated and intensively managed landscape where only few stretches have been allowed to remain relatively natural. The floodplains along the Lower Rhine are nowadays constrained within high embankments to prevent flooding of the densely populated hinterland (*Figure 1.2*). Additional minor embankments separate the main channel from the present hydrological active floodplain, with the main hydrological connectivity between the river and its floodplain being restricted to groundwater pathways. This leaves no possibilities for morphologic alteration of the channel (like meandering) and no regeneration of floodplains can occur (Simons *et al.*, 2001). In fact, these natural riverine processes are considered to be the key elements for high levels of biodiversity, through creating the characteristic patch dynamics, spatial heterogeneity and mosaic structures that provide the specific habitats for characteristic floodplain species and result in high species richness (Schiemer, 1999). Consequently, the various forms of human interference have resulted in a loss of biodiversity and in the composition of the flora and fauna, due to an increased loss of habitat quality, terrestrialization and fragmentation of the river-floodplain system (Schiemer, 1999).

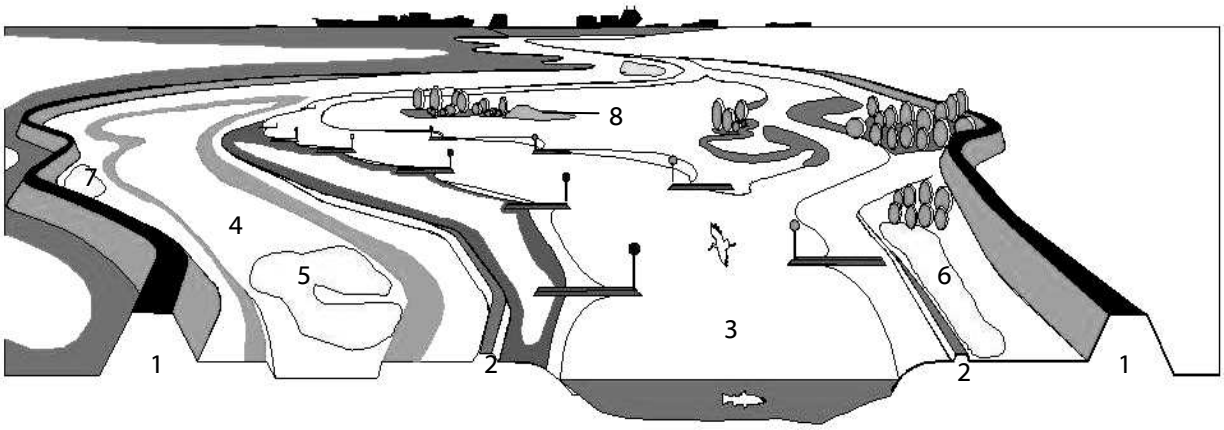

Figure. 1.2. Schematic view of lakes within the floodplain of the regulated Lower Rhine River during summer: 1, major embankments; 2, minor embankments; 3, main channel; 4, excavated floodplain; 5, new lake, excavated in the floodplain; 5-7, lakes protected by minor embankments; 8, unprotected lake.

Only during the last three decades has rehabilitation of the river system become a topic of interest (Raat, 2001). Various (inter)national and regional projects have been initiated to restore the quality of the river water (the Rhine Action Programme, IKSR, 1987; 'Salmon 2000' project,

Wieriks & Schulte-Wülwer-Leidig, 1997) and to prevent serious flooding at increased discharges in the future (Program 'Room for Rivers', Ministry of Transport, Public Works & Water Management, 2000). However, most of these programs and the related research activities, like programs in other countries, focus mainly on the river channel and permanent aquatic habitats, with only a few including the riparian zone and floodplains (e.g. Schiemer, 1995; Buijse *et al.*, 2002), like those about the spatial development of the active floodplains (plan 'Ooievaar', De Bruin *et al.*, 1987; 'Living Rivers', WWF, 1993). In the late 80-s and early 90-s, Van den Brink (1994) did focus on lakes in floodplains in the Netherlands and showed clear effects of the hydrological variability on the biotic, chemical and physical properties of the lakes in a wide range of different connectivities.

1.2 The ecology of floodplain lakes.

Stagnant water bodies in the river Rhine floodplains occur in a wide variety of morphological and hydrological types. Clear and turbid water bodies with and without aquatic macrophytes exist next to each other. These stagnant water bodies differ from water bodies outside the floodplains by their hydrological connectivity with the river. Inundation of the Lower Rhine floodplains occurs almost on a yearly basis, while seepage and infiltration in response to water level fluctuations in the river form a continuous influence on the communities in the floodplain lakes. During floods, sediments, nutrients and organisms are redistributed between the river water and the lake water, creating new initial conditions for the succession of the lakes during the following growing season. Hydrological connectivity between floodplain lakes and the river and flood pulses is considered to be a key factor in understanding the ecology of floodplain lakes (Heiler *et al.*, 1995; Schiemer, 1995; Coops *et al.*, 2000).

Due to the increased need for river restoration river ecosystems have received increased attention during the latest decades. Studies into the functioning of rivers resulted in various concepts and theories which proved influential for the present views and opinions (Buijse *et al.*, 2001) about these water systems. Some of these concepts and theories are of particular interest to isolated floodplain lakes. The flow pulse concept (Tockner *et al.*, 2000b) refers to the hydrological contact between a river and its floodplain lakes through groundwater and is mainly determined by changes in water level in the river in relation to the water level in the lakes and the hydrological resistance of the sediment (*Figure 1.3*). Effects on the ecological state of isolated floodplain lakes by the flow pulse are mainly influenced by the change in water level affecting chemistry and both

flora and fauna. Low water levels in the river might even lead to the desiccation of lakes with extreme consequences for aquatic species of macrophytes (Bornette and Amoros, 1996), fish and macro invertebrates (Williams *et al.*, 2004).

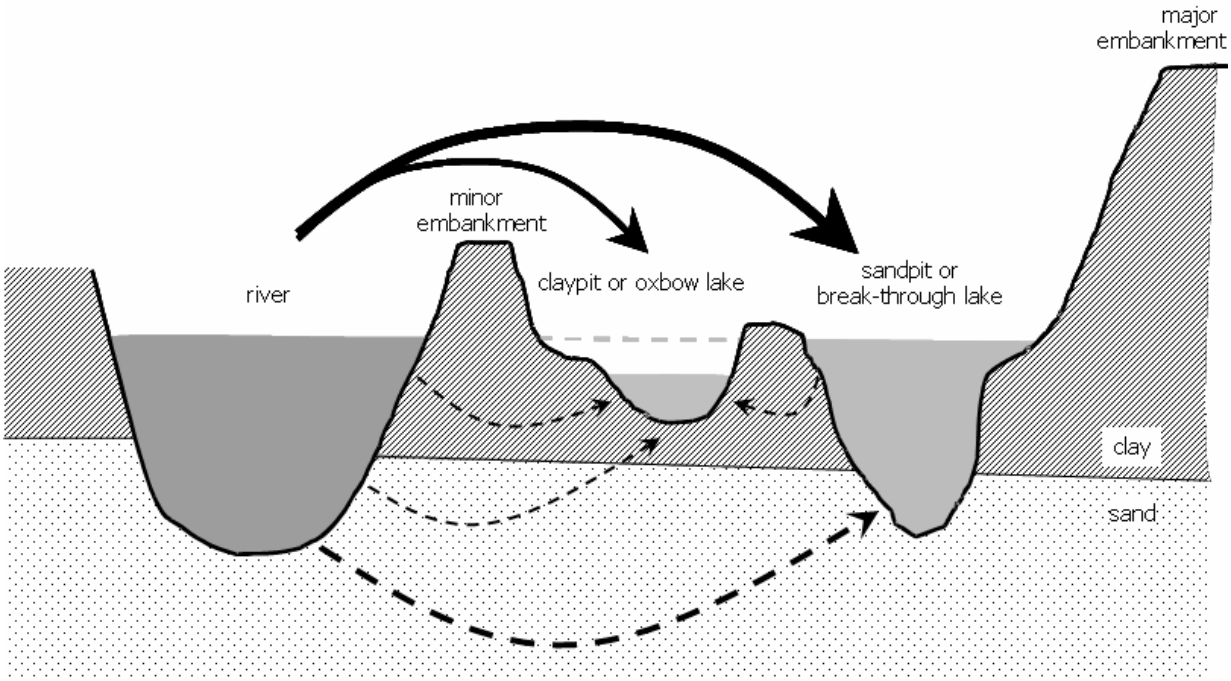

Figure 1.3. Schematic overview of the sediment composition of floodplains and the location of isolated floodplain lakes in relation to the type of sediment. The solid arrows indicate a flood pulse, while the dotted arrows indicate the flow pulse. The weight of the dotted arrows indicate the strength of connectivity, which is strongly determined by the sediment type. In this scheme the water level in the lakes is an indication of the differences in response - via the flow pulse - to an increase of the river water level. Due to the clayish sediment the water level rise in the clay pit remains behind the water level rise of the sandpit, which is in direct contact with the sandy layer (which has a lower hydrological resistance).

The Flood Pulse concept emphasizes the importance of the lateral river-floodplain connections in both tropical (Junk *et al.*, 1989) and temperate climates (Bayley, 1991; Junk, 1999). Flood pulses (*Figure 1.3*) allow an exchange of matter and organisms between the river and the floodplain (lakes), changing the ecological and chemical properties of the flooded lakes on a temporal scale. The frequency and duration of the flood determine the extend to which the water quality of the lakes is influenced by the river water. Floods enable the inoculation of plant seeds, plankton, macro invertebrates and migrating fish and can cause erosion or sedimentation of sediments depending on the magnitude (force) of the flood. In the Flood Pulse concept, based on natural river-floodplain systems, floodplain systems without embankments are considered to act as a

productive source for the river, where the flood pulses are not considered to be disturbances. Instead, significant departures from the natural hydrological regimes should be regarded as disturbances (Bayley, 1995). However, in this thesis, due to the various human interferences on the river-floodplain system of the Lower Rhine, inundations are considered to be *disturbances* on the ecology of the temporarily isolated floodplain lakes, which is in line with many other studies where floods are considered as a disturbance (e.g. Schiemer, 1995; Spink *et al.*, 1998; Hein *et al.*, 1999a).

Disturbances in population ecology can be defined as relative abrupt events (like inundations and desiccation) that alter the characteristics of the habitat; organisms can be removed from their habitat thus leaving space for (re)colonization by individuals from the same or other species (after Townsend, 1989). When considering a flood pulse to be a disturbance, then the Intermediate Disturbance Hypothesis (IDH) by Connell (1978) can be applied in this context. The IDH assumes that biodiversity is highest at an intermediate degree of disturbance. At a high degree of disturbance only the most adapted, rapid colonists are able to resist, resulting in a low diversity. At a low or no degree of disturbance only the best competing (most tolerant) species can resist, also resulting in a low diversity.

In this thesis, the validity of these concepts and theories (Flood Pulse concept, Flow Pulse concept, IDH, resistance and recovery) are tested for an important category of floodplain lakes along the Rhine branches.

1.3 Aim of thesis

The Memorandum 'Ruimte voor de Rivier' (Ministry of Transport, Public Works & Water Management, 2000) stated that because of the need for safety against flooding - like the ones which occurred in 1993 and 1995 - rivers must be given more space. One of the possible measures is the creation of new lakes by (local) excavation of floodplains. Shape and position of the new lakes are well designable during the development of the new situation. Following this, in the late 1990's the Dutch Institute for Inland Water Management and Waste Water Treatment (RIZA) started a research project to increase our understanding of the ecological functioning of floodplain lakes with the ultimate goal to develop practical recommendations and guidelines for ecological rehabilitation of floodplains along the Lower Rhine and the river Meuse. A number of sub-projects were initiated of which one aimed at the study of stagnant water bodies, the OER-

project (in Dutch: 'Onderzoek Ecologie Rivieruiterwaardplassen'). This project was to investigate the ecological functioning of floodplain lakes with the main project question being: 'How does morphometry (shape) and position (with respect to the inundation frequency) of floodplain lakes affect the development of the aquatic ecosystems?'

The OER project focused mainly on macrophytes (van Geest, 2005) and plankton dynamics (this thesis) in relation to hydrological variability and autogenic (ecological) processes, while fish dynamics in floodplains were analyzed in a different project by Grift (2001). The current thesis is based on four main research questions with respect to temporary isolated floodplain lakes:

1. *Is hydrological connectivity/isolation a major determinant of ecology and chemistry of floodplain lakes along the Lower Rhine?*
2. *Which are the major factors determining the ecological state of temporarily isolated floodplain lakes?*
3. *What determines plankton diversity in floodplain lakes?*
4. *How resistant are temporarily isolated floodplain lakes to inundations, and how rapid do they recover?*

ad 1. Connectivity/isolation

In the extensive study by Van den Brink (1994) hydrological processes initiated by the river (flood and flow pulse) have been shown to be a dominant force in shaping the ecology (aquatic communities) of floodplain lakes. Clear patterns in plankton and aquatic macrophytes abundances were presented which were strongly related to the degree in hydrological connectivity (*Figure 1.4*). However, in Van den Brink's study a rather extreme gradient in hydrological connectivity was studied: ranging from a maximum hydrological influence of the river in the permanently connected lakes to a minimum degree of connectivity in the lakes behind the major embankments (*Figure 1.4*). A consequence of this approach is that this wide ranging gradient in hydrology might conceal other (ecological) processes which are important for the development of the lakes in periods when no disturbance (inundation by the river) takes place, or when the lakes recover from a disturbance.

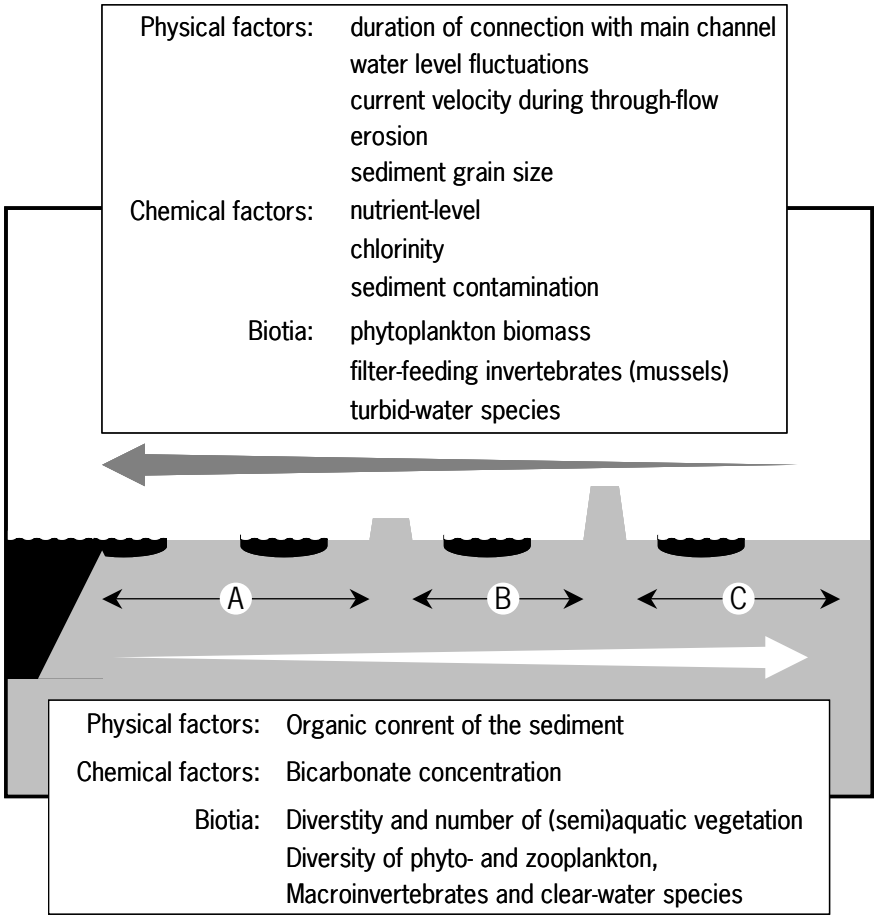

Figure 1.4. The effects of increased connectivity (grey arrow) and decreased connectivity (white arrow) on various physical, chemical and biological properties of floodplain lakes. The indicated areas A-C contain respectively: A) permanently connected lakes and lakes between the minor embankments and the river, B) temporarily isolated lakes between the minor and major embankments and C) lakes behind the major embankments (no inundation by the river) (after: Van den Brink, 1994).

Most floodplain lakes along the Lower Rhine are sand- and clay-mining pits (Jongman, 1992), which are situated between the minor and major embankments and are only temporarily connected to the river during high discharges of the river. The annual discharge pattern of the Rhine clearly shows that the timing of this inundation is more or less predictable, high discharges mainly occurring during winter and spring (*Figure 1.1*). However, there have also been some (rare) elevated discharges in summer, during the growing season, which are less predictable. Commonly, connectivity (by inundation) of the semi-isolated lakes in the floodplain is therefore considered to be of short duration, to occur rather simultaneously for all lakes, and mainly outside the growing season. Whether the effect of connectivity on the general ecology of our

subset of lakes is as apparent as presented by Van den Brink (1994) for the whole set of lakes is, however, questionable. Therefore, I hypothesize that the influence of hydrological connectivity (by inundation) on the ecological state of the lakes (e.g. transparency, chemistry, and plankton) during the growing season is of minor importance, while flooding mainly occurs outside the growing season.

ad 2. Why are some lakes clear while others are turbid?

When hypothesizing that the recent hydrological fingerprint of the river (*Figure 1.1*) is of minor importance to plankton and chemistry of the temporarily isolated floodplain lakes during the growing season (*ad 1*), I infer that these lakes might as well be considered to behave quite similar to 'normal' shallow lakes, even though these floodplain lakes are regularly affected by inundation events and strong water level fluctuations, in contrast to normal shallow lakes which are not. Plankton and turbidity of the floodplain lakes in the summer period will most likely be determined by autogenic ecological processes during the succession of the lakes driven by the seasonal cycle, and also by their morphometry (*e.g.* depth, size). I am interested in the major processes determining turbidity and plankton in these temporary isolated lakes, and hypothesize that autogenic (in-lake) processes are strongly determining these ecological properties of these lakes. For management purposes (creating and maintaining) these processes are also of importance.

ad 3. Plankton diversity in semi-isolated floodplain lakes

Natural river-floodplain systems are considered to be hot spots of biodiversity (Ward *et al.*, 1999), due to the variability in hydrology and disturbances of the lentic, lotic and semi-aquatic habitat types present. The intermediate disturbance hypothesis (IDH; Connell, 1978) predicts that the highest biodiversity will be present in habitats exposed to an intermediate disturbance regime. When connectivity is considered to be the major disturbance of floodplain lakes, this would suggest that the lakes with an intermediate connectivity would have the highest diversity, while permanently connected (highest connectivity) and isolated lakes (lowest connectivity) have the lowest diversity. River-regulation led to serious deterioration of this natural variability in hydrology resulting in losses in the biodiversity (Ward *et al.*, 1999). It can be expected then, that the diversity of plankton in the lakes studied, which are relatively little dynamic, is rather low. In his study of the Dutch floodplains along the Rhine and Meuse, Van de Brink (1994) showed an increase of both zoo- and phytoplankton diversity with decreasing connectivity, without an

optimum at an intermediate level of connectivity (*Figure 1.4*) as would have been expected on basis of the IDH. Moreover, in that study there seemed to be a negative relation between plankton diversity and plankton productivity. Considering the lakes in this study to be quite equal to normal shallow lakes (*ad 2*) I hypothesize that the diversity of plankton is rather low compared to more natural floodplains, because the dynamics and diversity of plankton during the growing season will be influenced similarly to other shallow lakes, whereas, again, river hydrology will be of minor importance.

ad 4. Resistance and recovery

The chemistry and biology of floodplain lakes are considered to be highly influenced by their connectivity with the river (Amoros & Roux, 1988; Van den Brink *et al.*, 1992; Tockner *et al*, 2000b). Floods allow an exchange of matter and organisms between the river and the floodplain (lakes), changing the ecological and chemical properties of the flooded lakes, but on a temporal scale. Also, many recent studies showed strong effects of connectivity on the chemical and biological properties of the floodplain lakes of temperate rivers (Van den Brink *et al.*, 1994; Heiler *et al.*, 1995; Spink *et al.*, 1998; Tockner *et al.*, 1999a; Buijse *et al.*, 2002). The timing of a flood is thought to be crucial for the effects on the water quality of the inundated lakes (Junk *et al.*, 1989; Bayley, 1991; Hein *et al.*, 1999a; Tockner *et al.*, 2000b). Despite all the interest in the effects of the river's hydrology on floodplains, there have been virtually no detailed studies addressing the dynamics of the ecosystem response upon retreat of the river after inundation (Pithart, 1999). The almost simultaneous inundation of the numerous floodplain lakes, which generally happens along the Dutch branches of the Rhine, can be used as an large ecological experiment that may reveal effects of disturbance. In this thesis, I attempt to take advantage of this annual natural experiment in floodplain systems and focus on the ability of the lake ecosystem to resist an effect due to a flood (resistance), and when disturbed by a flood, the speed with which the lake ecosystem returns to its pre-flood state (recovery). I hypothesize that the resistance of phyto- and zooplankton and chemistry is low, while an inundation replaces much of the original lake water and the recovery is rather rapid, due to the hypothesized low effect of river hydrology on the succession of the lakes during isolation.

1.4 Study area

Lakes sampled for this study are all situated within floodplains along the three branches of the Rhine in The Netherlands (*Figure 1.5)*. A total of 215 shallow lakes was sampled in 1999 (100) and 2000 (115) for analysis of the major factors that determine the macrophyte abundance.

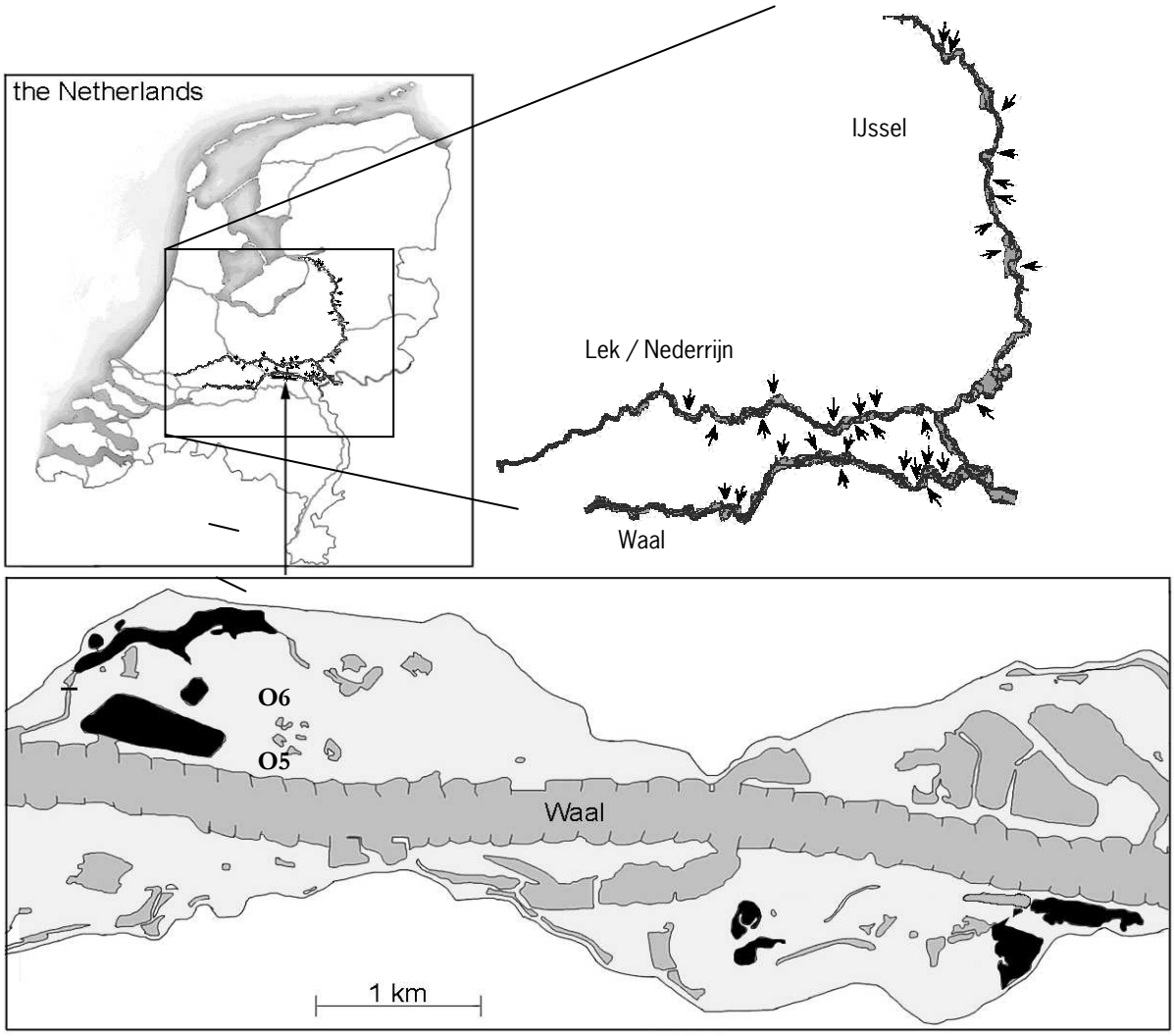

*Figure 1.5 The Netherlands with the location of the Rhine branches (upper left) and their floodplains (arrows) which were included in this study (upper right). The ten lakes sampled monthly for three years are displayed in black on the northern and southern bank of the river Waal (lower panel). The permanently connected lake Ochten 5 (**O5**) and the deep lake Ochten 6 (**O6**) are indicated.*

Among these lakes 93 lakes were sampled in parallel (only in 1999) for plankton and water quality assessments. All lakes were characterized by periodic disturbances by the river via surface overflow, yet none of the lakes were permanently connected to the river during the growing season. Lakes were selected a priori so that they covered the natural range in potentially important factors such as inundation duration, surface area, lake age, decrease in water level during the growing season, distance to the main channel, and land use on the adjacent land. Many of the lakes were created during the last century by extraction of clay and sand, whereas others are more natural such as oxbow lakes and break-through lakes (which are formed during dike-bursts). Ten lakes in two floodplains along the river Waal (*Figure 1.5*, lower panel) have been subject to a 3-year monthly monitoring programme from 1998 until 2000. Eight of these ten lakes were also included in the set of 93 lakes that were sampled once in 1999. The two other lakes (Ochten 5 and Ochten 6, *Figure 1.5*) are deep (>10 meters) and one of these (Ochten 5) is permanently connected to the river Waal.

1.5 Outline of thesis

In recent years interest has grown in restoring floodplain functions by reconnecting the floodplain with the main channel of regulated rivers. However, scientific insight into the effects of such increased 'connectivity' on the ecology of formerly isolated floodplain lakes is still poor. The present thesis is focussed on the main factors influencing the ecological processes in temporarily isolated floodplain lakes (*Figure 1.6*). The hydrological variability of a natural river system is supposed to be a dominant factor in determining the ecological processes in the floodplain lakes. However, the floodplain lakes in this study are party of a strongly altered (unnatural) river-floodplain system and are not as different from normal shallow lakes apart from the hydrological influence of the river.

This thesis is composed of 7 chapters. Most of the chapters are articles which are published in or submitted to international scientific journals. *Chapters 2-4* are dealing with the effects of the hydrological variability and in-lake processes on the ecological state of the temporarily isolated floodplain lakes during the end of the growing season, in a period of isolation from the river. In *Chapter 2* the focus is on lake transparency and plankton, while in *Chapter 3* the focus is on the aquatic macrophytes. The patterns of diversity at 2 trophic levels, phytoplankton and zooplankton, are explored in *Chapter 4*. Using a sub-set of lakes from *Chapter 2*, attempts are also made to find the factors that create the diversity patterns that are found. *Chapter 5* deals with the

resistance and recovery of floodplain lakes during and after inundations by the river, using plankton and chemical data from a 3-year monthly monitoring program of 10 lakes. *Chapter 6* studies the effect of sediment resuspension by benthivorous fish on the phytoplankton abundances in a floodplain lake. *Chapter 7* briefly reflects on two future developments that will be important in the management of floodplain lakes along the lower Rhine river.

Figure 1.6 Schematic overview of processes and interactions in temporarily isolated floodplain lakes, in relation to turbidity and the diversity of plankton communities. The different arrows correspond with different chapters in this thesis.

CHAPTER 2

Lake age and water level affect turbidity of floodplain lakes along the Lower Rhine

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Lake age and water level affect turbidity of floodplain lakes along the Lower Rhine.

2.1 Introduction

In the Netherlands numerous new water bodies will be excavated in the floodplains of the River Rhine over the coming years. Size, depth and connectivity to the river of these future lakes can in part be designed, raising the question how these aspects of lake morphometry affect water clarity and biodiversity. Previous studies on ecosystem dynamics in floodplain lakes stress the dominant effect of periodic inundations by the river (Amoros & Roux, 1988; Zsuffa, 1997), summarized in the Flood Pulse Concept of Junk *et al.* (1989). Particularly pronounced and well-studied are the effects of extensive flooding periods during the growing season on lakes in the Amazon floodplains (Engle & Melack, 1993; Junk, 1997; Ibanez, 1998). Strong riverine effects are also reported for temperate rivers such as the Austrian / Romanian parts of the River Danube (Hein *et al.*, 1996; 1999a; Tockner *et al.*, 1999a; Oosterberg *et al.*, 2000) and the Australian River Murray (Burns & Walker, 2000).

Surprisingly, most studies on floodplain lakes largely neglect the wealth of literature on shallow lakes regarding the role of internal processes such as top-down control of plankton (Carpenter *et al.*, 1985, Jeppesen, 1998), sediment resuspension (Carrick *et al.*, 1993; Breukelaar *et al.*, 1994) and mechanisms related to the presence of submerged macrophytes (Hootsmans, 1991; Van den Berg *et al.*, 1998).

In this study we analyze data from a large set of lakes in the floodplains of the lower River Rhine in order to estimate the relative importance of river dynamics and in-lake processes on lake transparency. Our lakes are inundated with river water during periods of high discharge. Such inundation can result in migration of fish (Grift, 2001) as well as input of suspended materials and nutrients (Junk *et al.*, 1989). Aquatic vegetation may also be affected by inundation duration (Van Geest *et al.*, 2003). On the other hand, the effect of the river on the biota in these lakes may be less than in those on which much of the Flood Pulse literature has been based (Junk, 1999), as inundations of our lowland lakes are almost entirely restricted to the winter (Van den Brink, 1994; Middelkoop & Van Haselen, 1999), when the rates of ecophysiological processes (e.g. photosynthesis and respiration) are low. Therefore, we hypothesize that river dynamics

characteristic for the Lower Rhine are of minor importance to the transparency of the lakes in summer, but in-lake processes are.

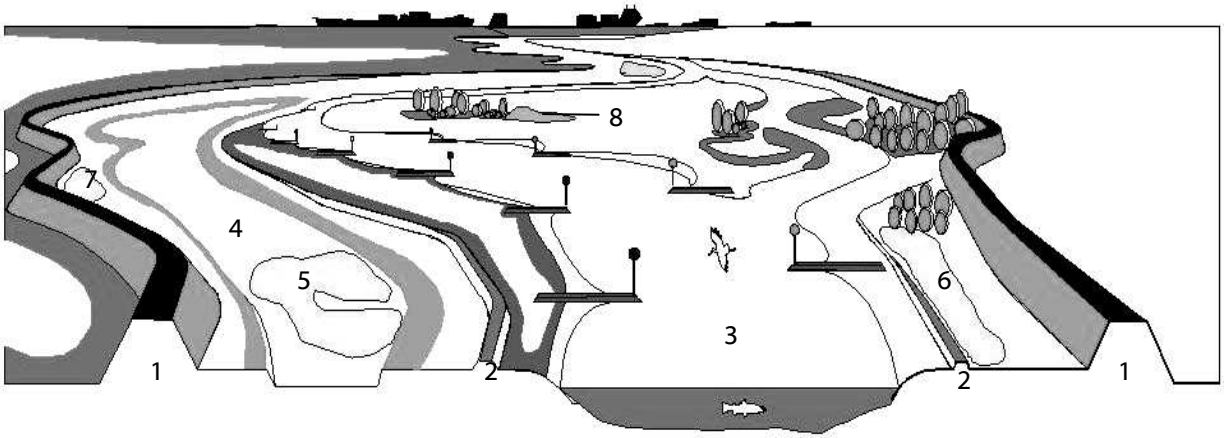

Figure 2.1. Schematic view of some lakes within the floodplain of the regulated Lower Rhine River during summer: 1, major embankments; 2, minor embankments; 3, main channel; 4, excavated floodplain; 5, new lake in excavated floodplain; 5-7, lakes protected by minor embankments; 8, unprotected lake.

2.2 Methods

2.2.1 Study area

The study was carried out in the Dutch part of the River Rhine, in July-August 1999. After the Rhine enters The Netherlands near Lobith, the river is divided into the Waal, the Neder-Rijn and the IJssel. At Lobith, the mean discharge is 2,300 m^3 s^{-1}, from which two thirds is channelled through the Waal, two ninths through the Neder-Rijn and one ninth through the IJssel (Middelkoop & Van Haselen, 1999). Highest discharge normally occurs during winter and lowest during autumn but, depending on climate, occasional floods may occur at any time of the year. The 93 floodplain lakes included in this study are divided over 31 floodplain sections along the three Rhine branches, with 40, 31 and 22 lakes along the Waal, Neder-Rijn and IJssel, respectively. All sampled floodplain lakes are situated between the main channel and the major embankments (*Figure 2.1*). All lakes are shallow, with a mean depth in August between 0.08 and 5.40 m, and 90 percent of the lakes are smaller than 10 ha (*Table 2.1*).

Table 2.1 Descriptive statistics of some lake-characteristics, vertical light attenuation (K_d), and the concentrations of chlorophyll-a, inorganic suspended solids (ISS) detritus and dissolved organic carbon (DOC).

			percentile			
Variable	n	min.	25%	50%	75%	max.
Ln(age)	93	0.69	3.50	4.30	5.49	5.71
Surface area (ha)	93	0.10	0.33	0.94	2.83	19.78
Mean water depth (m)	93	0.08	0.5	0.88	1.48	5.4
Water level drop (m wk^{-1})	93	-0.41	0.02	0.05	0.09	0.54
Shoreline index (m^{-1})	93	0.02	0.04	0.06	0.11	0.38
Distance to river (m)	93	10.0	96.5	280	609	1210
Maximum fetch (m)	93	16.0	93.8	173	331.3	1430
Calcium (mg L^{-1})	93	25.1	46.9	55.7	73.3	144
N-total (mg L^{-1})	93	0.48	0.93	1.11	1.45	3.63
P-total (mg L^{-1})	93	0.02	0.12	0.18	0.23	1.27
K_d (m^{-1})	93	0.95	3.26	4.69	6.76	13.3
Chlorophyll-a (μg L^{-1})	93	2.96	25.4	56.3	96.9	595
ISS (mg L^{-1})	93	3.45	12.0	19.9	30.4	72.6
Detritus (mg L^{-1})	93	0.22	5.12	7.06	10.6	134.5
DOC (mg L^{-1})	93	5.56	8.30	9.86	12.4	23.1

Lake sediments consist of silt and/or clay, whereas the three river branches have sediments consisting of mainly sand and clay. All lakes are influenced to a various extent by inundation from the adjacent river (Buijse *et al.*, 2002). We estimated average annual inundation duration in five classes, on the basis of the geographical height of the floodplains and the long term (1900 – 1995) average water level dynamics of the rivers (*Table 2.2*). For each class the median value of the range is used in the statistical analyses:

Table 2.2 Inundation duration ranges with the median values used in the statistical analyses.

Class	*duration range (days $year^{-1}$)*	*median (days $year^{-1}$)*
1	*< 2*	*1*
2	*2-20*	*11*
3	*20-50*	*35*
4	*50-150*	*100*
5	*> 150*	*258*

2.2.2 Field and laboratory procedures

In each lake water was sampled using a transparent plastic tube (length 2 m, diameter 10 cm). The lakes were sampled from a boat, taking five to seven samples from the middle of the lake to the shore. The samples were mixed in a 30 L tank, from which all sub-samples were taken. Five liters was taken for analyses of total N and total P, DOC, chlorophyll-a and suspended materials.

Another 25 L was concentrated through a 55 μm zooplankton net and stored in formalin. A 1-L flask was filled directly from the lakes for analyses of chloride, bicarbonate and calcium in the field using field kits. Lake transparency was characterized as Secchi depth (m^{-1}) and the vertical light attenuation (K_d, m^{-1}). The latter was measured with two Bottemanne light-sensors at two different depths in the water column. The highest sensor was just beneath the water surface and the second 30 cm lower. Both sensors were connected to a GRANT 1202 Squirrel Meter/Logger, reading signals every five seconds during one minute, the mean K_d of one minute readings was used.

Chlorophyll-a was measured in triplicate after filtration over Whatmann GF/F filters. Ethanol was used as extraction fluid, and acid was used to correct for phaeopigments (Moed & Hallegraeff, 1978). Dissolved organic carbon (DOC) was analyzed on filtered (0.2 μm membrane filter, Schleicher & Schuell) water samples using a TOC-analyzer (model 700, OI-Analytical). Suspended solids were analyzed from a known volume of the 5-L water samples, collected on pre-weighed (GF/F filters, Whatmann), dried and stored for 24 h at 105 °C, weighed, combusted for 3 h at 530 °C and weighed again. Control filters were processed similarly with each measurement.

Vegetation mapping was done in July and August. Each sample was taken in a plot containing a homogeneous vegetation type according to the phytosociological classification described in Schaminée *et al.* (1995), with the quantity of samples varying between four and 31 plots per lake. Submerged plants were collected using a rake, and for each species the percentage cover projected on the bottom was estimated visually using a seven-point scale (< 1%, 1-5%; 6-15%, 16-25%; 26-50%; 51-75%, 76-100%). In each plot, the total percentage cover of submerged, floating and helophyte vegetation was estimated. Based on these data, the surface area covered by submerged and nymphaeid vegetation and the percentage of unvegetated area in the whole lake was calculated as a percentage of the surface area of the lake. A more detailed description can be found in van Geest *et al* (2003).

Water level of the lakes was measured in July, August and October 1999 using marked poles in or near the lakes as a reference. Mean lake depth was calculated using depth measurements at different points in the lakes in July during the vegetation mapping, and was calculated for August using water level measurements of July and August. Lake size, as well as the shortest distance

from the river, was calculated using GIS-maps. We expressed the decrease in surface area from July to October as the draw-down area, where the water surface area in July was used as a reference and complete sediment exposure to the air in October equaled 100 % draw-down. Age of the lakes was determined by using historical geographical maps. The presence of cattle at the time of sampling was noted.

2.2.3 Data analysis

To estimate the respective contributions of chlorophyll-a, inorganic suspended solids and detritus to vertical light attenuation coefficient (K_d) and inverse Secchi depth (1/Sd), we used regression models as described by Kirk (1994). Kirk (1994) showed that K_d and 1/Sd are roughly linear combinations of the concentrations of algal chlorophyll-a, detritus and inorganic suspended solids. The parameter values used were obtained from Buiteveld's model (1995), which has been tuned to a large (521 – 761 lakes) and diverse set of Dutch lakes. Model 2 incorporates DOC as a variable, which was obtained by converting analytical DOC as measured to spectrometric values through regression from field data (de Lange, 1999) with the model $DOC_{spect.} = 0.245\ DOC_{analyt}$ ($n=18$, $R^2 = 0.31$, $p < 10^{-6}$).

$$K_d = 0.81 + 0.02 \text{ chlorophyll-a} + 0.028 \text{ ISS} + 0.043 \text{ detritus} \quad (1)$$

$$K_d = 0.63 + 0.02 \text{ chlorophyll-a} + 0.025 \text{ ISS} + 0.049 \text{ detritus} + 0.050 \text{ DOC} \quad (2)$$

$$1/Sd = 0.13 + 0.010 \text{ chlorophyll-a} + 0.070 \text{ ISS} + 0.068 \text{ detritus} \quad (3)$$

To predict the potential for wind-resuspension for each lake during the period of sampling, a model (4) by Carper & Bachmann (1984) was used. The model calculates wavelength (L_w, m) as a function of fetch (F, km) and wind velocity (W, m s^{-1}):

$$L_w = 1.56\left(0.77W \tanh\left(0.077\left(9.8\frac{F}{W^2}\right)^{0.25}\right)\right)^2 \quad (4)$$

Using data from a lake with sand/clay sediments, much like our floodplain lakes, Carper & Bachmann (1984) showed that resuspension occurs only when the wavelength as computed by equation 4 exceeds twice the lake depth ($L_w > 2D$).

To study relationships between lake turbidity, suspended materials and environmental variables, multiple regression analysis were performed. To test the robustness of the regression models, both forward and backward regression were calculated. Forward regression is a variable selection

procedure in which variables are sequentially added to the equation, as long as they correlate significantly ($p<0.05$) to the residual variance in the dependent variable. With the backward regression analyses all independent variables are initially entered in the equation, and are sequentially removed from the equation until only the independent variables which contribute significantly ($p<0.05$) to explaining the variance in the dependent variable remain. When both approaches result in different models, this suggests that different (mutually correlated) sets of independent variables may explain the patterns. All regression analyses were performed with 14 variables (*Table 2.3*), unless otherwise indicated. Secchi depth was not included in these regression analyses, because in some of the lakes the bed was visible. Eliminating these lakes would result in misrepresentation of lakes in the data-set as the class of transparent shallow lakes would be eliminated. The submerged vegetation cover was arcsine transformed before use in the regression analyses.

Table 2.3 15 Independent variables used in regression analyses to vertical light attenuation, inorganic suspended solids and chlorophyll-a.

Variable	Comments
Ln(age, years)	Natural logarithm of the lake age
Mean lake depth (m)	Calculated from five to 10 measurements in each lake
Water level fluctuation (m $week^{-1}$)	Calculated from water level decrease between July and August
Calcium (mg L^{-1})	
Inundation duration (days $year^{-1}$)	Long year average (1900-95)
Maximum fetch (m)	Largest linear distance from bank to bank
Wind speed (m s^{-1})	Data from Royal Dutch Meteorological Institute
Lake surface area (ha)	Obtained from GIS maps
Relative shoreline length (m^{-1})	Ratio lake circumference to lake surface area (shoreline index), obtained from GIS-maps
Distance to river (m)	Nearest distance of the lake to the river
Draw down area (%)	Percentage of lake area decrease from July to October
Submerged vegetation cover (%)	Absolute cover of submerged vegetation
Floating vegetation cover	Cover < 1% is poor and = 1% is rich in floating vegetation
Helophyte cover (category)	Cover < 1% is poor and = 1% is rich in helophytes
Unvegetated water area (%)	100% minus the sum of the covers of all vegetation types, except the helophytes

2.3 Results

Most of the lakes sampled were small (< 10 ha) and shallow (< 2.5 m), with relatively stable water levels (*Table 2.1*). Transparency, as well as the concentrations of chlorophyll-a and inorganic suspended solids (ISS), varied widely between lakes (*Table 2.1*) although most were rather turbid at the time of sampling. The lakes also differed widely in aquatic plant abundance. Floating vegetation and helophytes tended to be either absent or abundant. The bimodality in these vegetation variables caused their frequency distributions to differ significantly from a normal distribution. The abundance of these groups were therefore replaced in further regression analyses by binary variables (less than 1% cover = 0 and from 1% cover = 1). The arcsine transformed variable 'submerged vegetation abundance' in this data set was not significant different ($p = 0.10$) from a normal distribution (Kolmogorov-Smirnov test). Therefore, unlike the larger data set of *Chapter 3*, there was no bimodality in submerged vegetation in this data set. A thorough account of the vegetation patterns and their relationship to environmental conditions is presented in *Chapter 3*.

2.3.1 Relationship of water level dynamics and lake properties to turbidity

As a first step we analyzed how various aspects of turbidity were related to hydrological dynamics, e.g. inundation and lake water level fluctuations and to general lake characteristics such as age, size, distance to river and vegetation abundance (*see Table 2.3*). Multiple regression analyses showed that the vertical attenuation coefficient (K_d) and chlorophyll-a decreased with lake depth and submerged and floating vegetation cover (*Table 2.4a*). In addition, both variables increased with lake age, and K_d also with water level constancy. So younger lakes and lakes with a greater drop in water level are more transparent. Forward regression differed slightly from the backward regression for $K_{d,}$ not including the floating vegetation and lake age (*Table 2.4a*). Inorganic suspended solids concentration decreased with lake depth, drop in water level and the abundance of helophytes. When we substituted the different vegetation variables with the arcsine transformed percentage of unvegetated lake area, this variable replaced the variable 'helophytes' in the model for inorganic suspended solids in *Table 2.4a*. The models for K_d and chlorophyll-a changed in a similar way, unvegetated lake area replacing the vegetation variables of the models in *Table 2.4a*. For chlorophyll-a, lake age disappeared from the model (*Table 2.4b*).

The ratio between chlorophyll-a and inorganic suspended solids gives an indication of the relative importance of both variables in determining lake turbidity. Spearman's correlation analyses (*Table 2.5*) indicated that, with increasing turbidity (as K_d), this ratio (and thus the relative contribution of chlorophyll-a to turbidity) increases.

Table 2.5. Spearman's rank correlations between the ratio of chlorophyll-a inorganic suspended solids (ISS) and five independent variables. All correlations significant (two-tailed) at the 0.01 level, except for [a)] at the 0.05 level.

	Variable	Corr. Coef.
Chlorophyll-a / ISS	K_d (m^{-1})	0.381
	Lake age (y)	0.215 [a)]
	Draw down area (%)	0.381
	Submersed vegetation (%)	- 0.269
	Vegetation rich/poor (binary)	- 0.322
	Water level fluctuation (m wk^{-1})	0.315

The chlorophyll-a to inorganic suspended solids ratio was also positively related to lake age and to the drop in water level, and negatively to vegetation abundance. Thus the increase in turbidity related to age and lack of vegetation seems predominantly due to variation in phytoplankton biomass rather than inorganic suspended solids. The relative clarity of lakes with a marked drop in water level in summer seems largely due to low inorganic suspended solids concentration.

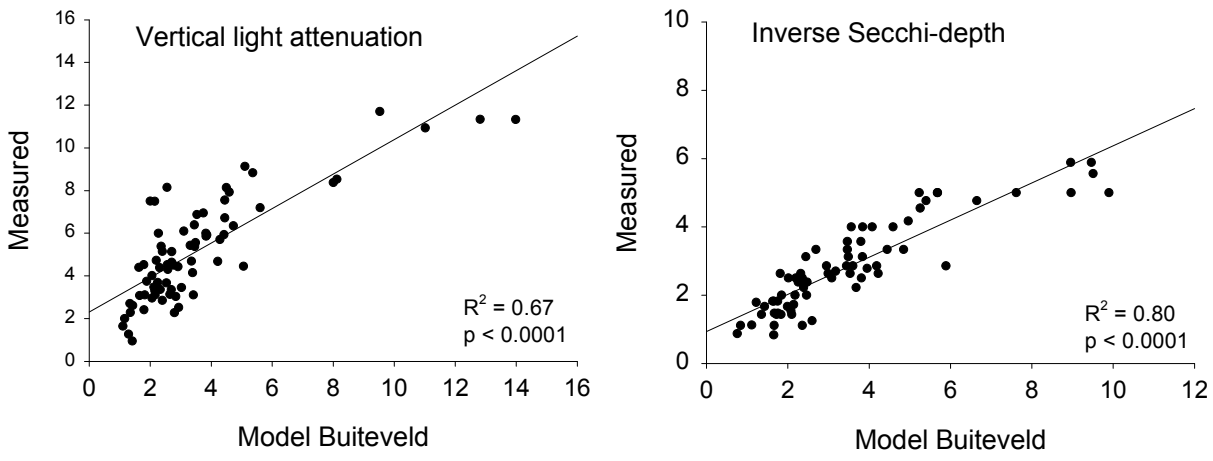

Figure 2.2. Relationship between values calculated with the model of Buiteveld and the measured values for a) vertical light attenuation (m^{-1}) and b) inverse Secchi depth (m^{-1}). Solid lines represent linear regression.

2.3.2 Contribution of inorganic suspended solids, phytoplankton and DOC to the light climate

Buiteveld's model (1995) could explain inverse Secchi depth (excluding lakes with bottom visibility) and K_d quite well from the concentrations of inorganic suspended solids, detritus and chlorophyll-a (*Figure 2.2*).

Calculations with the model suggest that inorganic suspended solids explained on average 50% of the inverse Secchi-depth, but only for 18% to K_d, which was largely determined by chlorophyll-a (41%) (*Figure 2.3*). Although DOC, when viewed in isolation, correlated positively to K_d (Pearson $r = 0.444$, $p < 0.0005$), multiple regression (not shown) indicated that it explained hardly any variance in K_d. When included, DOC accounted for only 4.5% of the K_d in our lakes in Buiteveld's model (not shown).

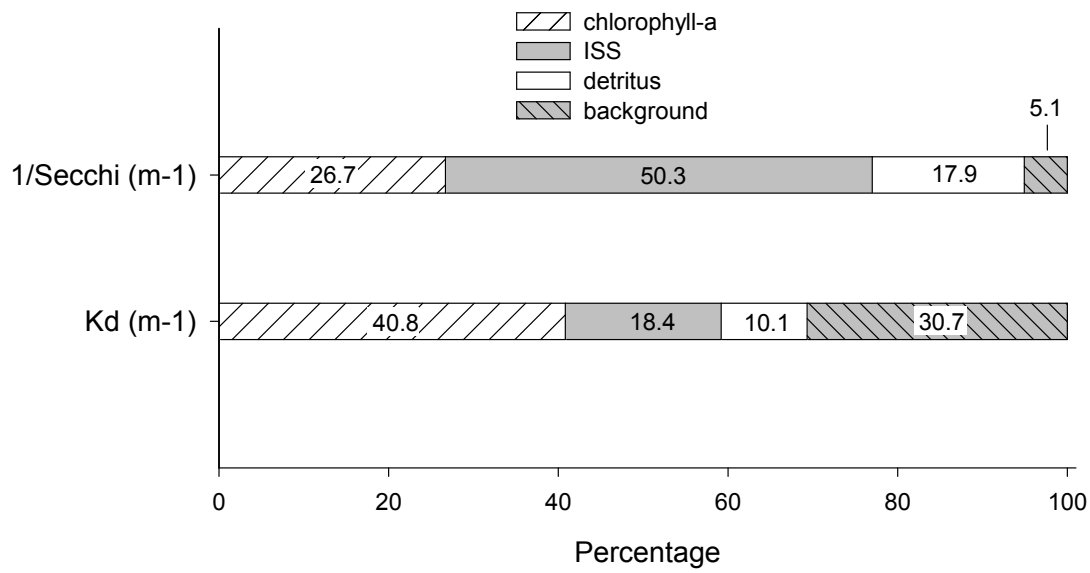

Figure 2.3. Average contribution (%) of chlorophyll-a ($\mu g\ L^{-1}$), inorganic suspended solids (ISS, $mg\ L^{-1}$), detritus ($mg\ L^{-1}$) and background turbidity (m^{-1}) to the inverse Secchi depth (1/Secchi) and to the vertical light attenuation coefficient (K_d) in our data-set, calculated with the model of Buiteveld (1995).

2.3.3 Chlorophyll-a relationship to other water quality parameters

No correlations were found between chlorophyll-a concentration and the abundance (individuals L^{-1}) of different functional groups of zooplankton ($p > 0.05$), except for a positive correlation with rotifers (Pearson $r = 0.379$, $p < 0.01$). Only 32% of the lakes had *Daphnia*, and no significant differences in chlorophyll-a concentrations in lakes with and without *Daphnia* were observed.

Table 2.6. Regression models for chlorophyll-a, calculated from 15 independent variables shown in Table 2.3 and inorganic suspended solids (ISS) (models I_a and I_b). Model I was calculated with a backward regression method, whereas model II was calculated with a forward regression method. All corresponding $p < 0.05$.

Dependent Variable	Const	Mean lake depth (m)	Subm. veg. (cat)	Float veg. (cat)	Lake age (y)	ISS (mg L^{-1})	R^2
I. Chlorophyll-a (μg L^{-1})	97.9	-29.1	-65.8	-65.4	21.7		0.18
II. Chlorophyll-a (μg L^{-1})	30.4					2.32	0.10

By contrast, chlorophyll-a and inorganic suspended solids were strongly correlated (Pearson $r = 0.508$, $p < 0.0005$). Offering inorganic suspended solids concentration as an independent variable in the multiple regression analysis for chlorophyll-a resulted in an equation with only inorganic suspended solids in the case of forward regression (*Table 2.6*, model II). Backward regression (*Table 2.6*, model I) resulted in the same model as shown in *Table 2.4*.

2.3.4 Potential wave resuspension

Using the model of Carper & Bachmann (1984) we calculated that, at the average wind speed measured on the day of sampling and the day before (source KNMI), a total of 21 lakes could potentially have experienced sediment resuspension. Of these 21 lakes, 12 were rich in vegetation, implying a greatly reduced chance of resuspension (Jackson & Starrett, 1959; Dieter, 1990; Scheffer *et al*, 1994; van den Berg *et al*, 1998). The remaining nine lakes which may be expected to have experienced wind resuspension on the day of sampling, did indeed have significantly (t-test, $p < 0.02$) higher inorganic suspended solids concentrations (34.5 mg L^{-1}) than the rest of the lakes (22.8 mg L^{-1}).

2.4 Discussion

Transparency in these lakes increased with lake depth and vegetation cover. In addition, younger lakes and those with strong fluctuation in water level were more transparent on average. We first focus on these general relationships between transparency on one hand and water level dynamics and lake properties on the other hand, and subsequently discuss mechanisms that may be responsible for explaining variation in inorganic suspended solids and chlorophyll-a concentration.

2.4.1 Clarity of the lakes and water level dynamics

Inundation did not seem to be important for lake transparency in our data set. However, the drop in water level was positively related to lake transparency (*Table 2.4*). Water level fluctuations in these lakes are largely the result of groundwater contact (seepage and infiltration) with the nearby river, as is quite common for floodplain lakes along gravel rivers (Heiler *et al*, 1995; Ward & Stanford, 1995; Tockner *et al*, 1999a). The chlorophyll-a to inorganic suspended solids ratio was higher in lakes with a marked drop in water level and larger drawdown areas (*Table 2.5*). Water level change did appear in the regression models for inorganic suspended solids, but not in the models for chlorophyll-a. This suggests that lakes with stronger fluctuations in water level tend to be relatively clear due to a lower concentration of inorganic suspended solids. Our data do not support the idea that phytoplankton biomass is enhanced by fluctuating water level due to intensive release of nutrients along the moving littoral (Wood, 1951).

For the Danube, Tockner *et al.* (1999a) introduced a conceptual model linking hydrological connectivity with ecological processes. Using this model for our data set, some of our lakes can be considered to be in the disconnected phase (I). Marked declines in water level suggest that many other lakes can be considered to be in the second phase, where in our case hydrological connectivity is through groundwater transport. According to Tockner *et al.* (1999a), lake transparency should be high while nutrient concentration should be low to medium. In the lakes we studied lake transparency was rather low, however, and nutrient concentrations were rather high (*Table 2.1*), indicating that the division by Tockner *et al.* (1999a) is not supported by this set of lakes along the lower Rhine.

2.4.2 Clarity of the lakes and lake properties

The positive relationship found between lake depth and transparency is classical. Large data sets show that lakes tend to be more turbid when they are shallow. This may be explained by the fact that in deep water, resuspension and sediment nutrient release are less intense and light limitation prevents high algal concentration (Scheffer, 1998). The positive effect of vegetation on lake transparency is also well known (Canfield *et al.*, 1984; Jeppesen *et al.*, 1990; Scheffer 1998). Many different mechanisms can be involved in this clearing effect (Scheffer, 1999). Macrophytes increase lake transparency by stimulating sedimentation and preventing resuspension (Jackson & Starrett, 1959; James & Barko, 1994; van den Berg *et al.*, 1998). Vegetation provides a refuge for zooplankton against fish predation, allowing zooplankton to suppress phytoplankton biomass (Timms & Moss, 1984; Stansfield *et al.*, 1997). Further, macrophytes compete with phytoplankton

for nutrients and light (James & Barko, 1994; Scheffer, 1998) and may suppress phytoplankton by excreting allelopathic substances limiting algal growth (Hootsmans, 1991; Scheffer, 1998). Although the correlation of clarity to vegetation abundance in our data suggests that such mechanisms may be at work, it is not *a priori* obvious which mechanisms are most important as the relative importance of the different clearing mechanisms related to vegetation can differ widely between lakes (Scheffer, 1999). The fact that the ratio between chlorophyll-a and inorganic suspended solids was negatively correlated to submerged vegetation abundance (*Table 2.5*), however, implies that the negative effect of vegetation is greater on the phytoplankton than on inorganic suspended solids. This suggests that nutrient competition, shading, refuge effects or allelopathy may be more important than the effects of macrophytes on resuspension and sedimentation in these lakes.

The higher light attenuation (K_d) and chlorophyll-a concentration in older lakes could be related to the fact that, with time, lakes tend to accumulate organic matter and nutrients (Carpenter, 1981) as well as clays and silt (Middelkoop, 1997). However, none of the fractions (ISS, TSS, detritus and chlorophyll-a) was directly correlated to lake age (not shown), except for DOC (Pearson's r 0.27, $p < 0.01$). In contrast, total phosphorus concentration did show a significant positive correlation with flood duration ($r = 0.29$, $p<0.005$), suggesting that riverine material may represent an important nutrient input as is probably a common situation in floodplain lakes (Zsuffa, 1997). In line with these results, Van den Brink (1994) found that many frequently-flooded floodplain lakes of the Rivers Rhine and Meuse were loaded with phosphate, and showed that regeneration of P from the sediment can be an important source of nutrients in periods of nutrient depletion. Importantly, during the field sampling many aquatic macrophytes had already started to decay and nutrient concentrations were rather high in most lakes (*Table 2.1*). This may explain the weak relations with nutrients we found in our data set.

2.4.3 Inorganic suspended solids

Inorganic suspended solids concentrations were remarkably high in most lakes, contributing an estimated 50% to the inverse Secchi depth of the lakes on average. Much clay and silt is imported to the lakes when the floodplains become inundated in winter (about 10 mm settled material; Middelkoop, 1997). However, the settling rate of this kind of material is high and the last inundation was months before the sampling took place, implying that other processes must be

responsible. Likely candidates are resuspension of lake sediments by waves or benthivorous fish, bank erosion by waves or cattle and surface runoff during heavy rainfall.

Runoff is unlikely, as there was no heavy rain during the sampling period. Presence of cattle was correlated to inorganic suspended solids concentrations. However, when offered to the analysis, backward multiple regression eliminated cattle as a significantly explanatory variable. This is due to the fact that cattle were correlated with other independent variables in the model. Specifically, lakes with cattle tend to be shallower, and the shallow lakes were more turbid in general (*Table 2.4*). In addition, cattle are more often present around the older lakes (not shown), which tend to be more turbid than younger lakes.

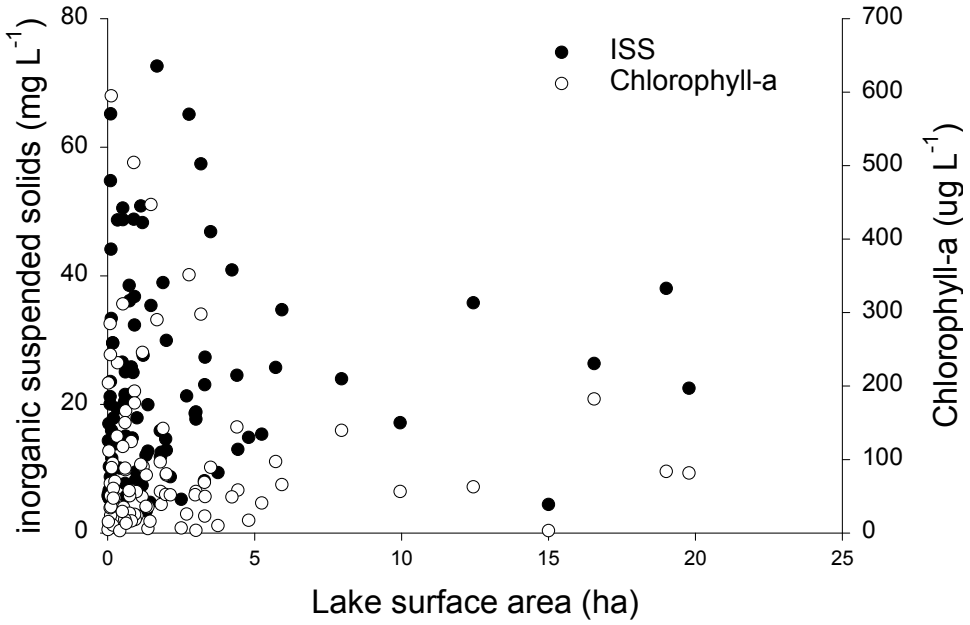

Figure 2.4. Relation between lake surface area (ha) and concentrations inorganic suspended solids (ISS, mg L^{-1}) and chlorophyll-a (μg L^{-1}), showing that small lakes in which wind resuspension is unlikely can nonetheless have very high concentrations inorganic suspended solids (and chlorophyll-a), suggesting fish driven resuspension.

Resuspension of lake sediments by waves (e.g.: Carper & Bachmann, 1984; Bengtsson & Hellström, 1992; Gons *et al.*, 1996) or fish (*e.g.*: Meijer *et al.*, 1990; Havens, 1991; Lammens & Hoogenboezem, 1991; Breukelaar *et al.*, 1994) is certainly the most commonly recognized cause of a high concentration of inorganic suspended solids in lakes. For wind-induced resuspension, surface area (i.e. actual wind fetch) is an important factor. Mazumer *et al.* (1990) showed that very small lakes (< 10 ha) are less susceptible to wind mixing, and thus to resuspension due to wind. The highest inorganic suspended solids concentration was found in the smallest lakes (*Figure 2.4*),

suggesting a minor importance of wind-induced resuspension in most of these lakes. Furthermore, using the model of Carper & Bachmann (1984), and assuming vegetation-rich lakes to be protected against wind effects, we excluded waves as a likely cause of resuspension in 84 of the 93 lakes studied. Therefore, the high inorganic suspended solids concentration in most lakes must largely be explained by another resuspension process, which can lead to high suspended sediment concentration in even the smallest lakes (*Figure 2.4*).

Resuspension by benthivorous fish is a likely mechanism. The concentration of suspended solids in small shallow lakes is often closely related to the biomass of benthivorous fish (Meijer *et al.*, 1989; Meijer *et al.*, 1990a; Havens, 1991; Breukelaar *et al.*, 1994), and various enclosure studies have demonstrated the potentially strong sediment resuspension by benthivorous fish (Havens, 1991; Breukelaar *et al.*, 1994; Roozen *et al.*, *Chapter 6*).

Although we have no data on fish density in most of our lakes, it is known that fish biomass tends to be particularly high in floodplain lakes (Bayley, 1991), and this has been confirmed for floodplain lakes along the lower River Rhine (Grift, 2001). In our data set the concentration of inorganic suspended solids is higher in unvegetated lakes. This is in line with the idea that benthivorous fish are responsible for much of the resuspension, since these fish tend to be rare in vegetated lakes. A census of fish communities in Dutch floodplain lakes by Grift (2001) showed that the presence of vegetation is the most important factor determining the nature of the fish communities, benthivorous fish being relatively scarce in vegetation-rich lakes but abundant in poorly vegetated lakes. This fits with earlier work showing that Dutch shallow lakes without submerged macrophytes are typically dominated by adult benthivorous bream, resuspending sediment while feeding on benthic invertebrates (Lammens, 1989; Lammens & Hoogenboezem, 1991). Therefore, it may well be that the high concentrations of inorganic suspended solids in poorly vegetated lakes is related to the relatively high abundance of benthivorous fish. Whether fish suppresses the vegetation or vegetation suppresses the fish is presently not clear. Fish is able to prevent germination of vegetation by disturbing the sediment (Ten Winkel & Meulemans, 1984), but fish is hypothesized to be able to distinguish between vegetation poor and rich lakes during winter inundation. The fish-resuspension hypothesis is also in line with our finding; that lakes with a larger drop in water level contained a lower concentration of inorganic suspended solids (*Table 2.4*). Low water levels may result in fish kills, as confirmed by the frequent occurrence of dead fish on the dried up areas of the lakes.

2.4.4 Phytoplankton

Phytoplankton abundance is the other important seston component affecting water clarity in our data-set. All regression analyses suggest that lake depth and vegetation abundance are important drivers of phytoplankton biomass (as chlorophyll-a). As discussed earlier (for K_d) this is well in line with results from previous work. The way in which macrophytes affect phytoplankton abundance can hardly be inferred from our results. Correlations to total-P and total-N tell little, as those concentrations are dominated by the fractions of P and N contained in algal cells, making causality difficult to unravel.

Also the importance of top-down effects of zooplankton on phytoplankton could not be demonstrated here. Lakes with high *Daphnia* abundance were not more clear or turbid than lakes with low abundance, only indicating that top-down effects might not have been very important at the time of sampling. Unfortunately our data do not allow extensive grazing pressure calculations, so no conclusions on the zooplankton-phytoplankton relationships could be drawn.

The strong positive correlation between chlorophyll-a and inorganic suspended solids is remarkable. We know of no direct effects of phytoplankton on inorganic suspended solids or *vice versa*, with the notable exception that suspended solids will reduce the light available for algae. However, such shading would lead to a negative correlation. Another possible explanation for the correlation would be that phytoplankton and inorganic suspended solids are affected by a common factor. Benthivorous fish are an obvious candidate because, as argued, resuspension by fish is probably an important process in the lakes. Many studies show that benthivorous fish can enhance phytoplankton concentrations (Andersson *et al.*, 1978; Breukelaar *et al.*, 1994). This effect is usually ascribed to the release of nutrients from sediment and to fish excretion (Andersson *et al.*, 1978; Qin & Threlkeld, 1990; Cline *et al.*, 1994; Attayde & Hansson, 1999). The fact that benthivorous foraging, rather than nutrient excretion or planktivory, may be the dominant mechanism stimulating phytoplankton biomass has been demonstrated in elegant *in-situ* mesocosm experiments by Havens (1991). The observation that wind resuspension can stimulate chlorophyll-a concentration (Carrick *et al.*, 1993; Ogilvie & Mitchell, 1998) suggests that, indeed, resuspension *per se* can be a key-process for planktonic communities in shallow lakes. However, the relative importance of nutrient release by resuspension and actual physical resuspension of settled algal cells remains uncertain (Schelske *et al.*, 1995).

In conclusion, we found that older lakes tend to be more turbid than younger lakes and that this increase in turbidity is largely determined by phytoplankton. Surface inundation in winter had no

obvious impact, but water level fluctuations through groundwater transport tended to be related to higher water clarity. The latter effect was due to decrease in inorganic suspended solids rather than chlorophyll-a. Water clarity was also strongly related to vegetation abundance and water depth as found in many earlier studies. Phytoplankton biomass was less influenced by the river, but rather by the lake properties depth and age, and by submerged and floating vegetation. Indirect evidence indicated that inorganic suspended solids concentrations in these floodplain lakes were highly determined by sediment resuspension by benthivorous fish in the largely unvegetated lakes. The strong positive relation of chlorophyll-a with inorganic suspended solids suggests that resuspension by benthivorous fish is also an important mechanism determining phytoplankton biomass.

2.5 Acknowledgments

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CHAPTER 3

Vegetation abundance in lowland floodplain lakes determined by surface area, age and connectivity

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Vegetation abundance in lowland floodplain lakes determined by surface area, age and connectivity.

3.1 Introduction

In recent years interest has grown in restoring floodplain function by reconnecting the floodplain with the main channel of regulated rivers. However, scientific insight into the effects of such increased 'connectivity' on the ecology of formerly isolated floodplain lakes is still poor. Previous work on the composition and succession of aquatic vegetation in floodplain water bodies predominantly stresses the role of river-related hydrological dynamics as the major driving force for vegetation abundance and composition (Junk *et al.*, 1989; Van den Brink *et al.*, 1991; Amoros & Bornette, 1999). However, various other abiotic variables may strongly influence the aquatic vegetation. The age of lakes, surrounding land use and seepage from hill slope aquifers have been found to affect the successional stage and nutrient content of the water along the River Rhône (Bornette *et al*, 1998). Geomorphological conditions have been addressed as an important factor determining the impact of inundations. The erosive power of the overflowing water is high in straight, formerly-braided channels, resulting in sediment scouring and macrophyte removal. This creates recruitment opportunities for new plant individuals. In contrast, oxbow lakes with high sinuosity experience only moderate erosive forces, resulting in a very soft substratum of organic matter, which impedes recruitment of new individuals (Henry *et al.*, 1996).

Research on macrophytes other than in floodplains has a long history and addresses a much broader range of environmental factors. Many studies stress the importance of water depth and transparency (Canfield *et al.*, 1985; Chambers & Kalff, 1985a; Skubinna *et al*, 1995), but also the effects of slope (Duarte & Kalff, 1986a), wave action (Strand & Weisner, 1996), bird grazing (Lauridsen *et al.*, 1993), periphyton (Weisner *et al.*, 1997), and sediment characteristics (Chambers & Kalff, 1985b) have been shown to be important in many lakes. It has also become clear over the past decade that submerged macrophytes play a key role in the regulation of ecosystem processes, particularly in shallow lakes (Jeppesen *et al.*, 1997). This insight has sparked extensive recent work on the dynamics of vegetation in a wide range of shallow lakes (Scheffer, 1998). In these studies however, the role of fluctuations in water level is hardly addressed.

The objective of the present study is to unravel the combined effects of hydrological dynamics, lake morphometry, lake age and land use on macrophyte occurrence in a large set of shallow floodplain lakes along the lower Rhine.

3.2 Methods

The aquatic vegetation of a total of 215 shallow lakes was sampled in the Lower Rhine floodplains in the Netherlands in 1999 (100) and 2000 (115), including 93 lakes in which the plankton and water quality were analyzed in parallel (Roozen *et al.*, 2003). All lakes were characterized by periodic inundation by the river via surface overflow, yet none of the lakes were permanently connected to the river during the growing season. Lakes were selected *a priori* so that they covered the natural range in potentially important factors such as inundation duration, surface area, lake age, decrease in water level during the growing season, distance to the main channel, and land use on the adjacent land.

3.2.1 Sampling of vegetation

In July and August 1999, submerged and floating vegetation was sampled in 916 quadrates distributed over 100 of the 215 water bodies. Each sample was taken in a quadrate containing a homogeneous vegetation type. The surface area of the quadrates varied from 1 m^2 for submersed vegetation up to 4 m^2 for nymphaeids. In each lake, the number of quadrates located in submerged and nymphaeid vegetation and areas poor in vegetation was chosen in proportion to the estimated area occupied by these types. The number of quadrates per lake varied between 4 and 31, depending on the complexity of the vegetation structure and surface area of the lake. Submerged plants were collected using a rake. The percentage cover projected on the bottom was visually estimated for each species using a seven-point scale (< 1%, 1-5%; 6-15%, 16-25%; 26-50%; 51-75%, 76-100%). In each quadrate, the total percentage cover of submerged plants, floating plants, helophytes and filamentous algae was estimated. The surface area covered by submerged and nymphaeid vegetation and the percentage of vegetation-poor area in the whole lake was calculated based on cover percentages and transformed to the lake surface area. Additionally, the cover of large emergent species (helophytes such as *Typha* and *Phragmites*) was estimated separately as a percentage of the surface area of the lake in July.

In July and August 2000 the remaining 115 lakes were studied following an almost identical procedure. However, the smallest lakes were now surveyed by wading rather than by boat. In the

small lakes no quadrates were sampled, but the total cover of different vegetation types and unvegetated areas was visually estimated.

3.2.2 Abiotic variables

Table 3.1 gives an overview of the abiotic variables measured and their ranges, the number of lakes sampled and year of sampling. For all lakes, estimates of inundation duration, surface area, and shoreline length were obtained from GIS-maps (RIZA, Arnhem, The Netherlands). Inundation duration is defined as the long term (1900 – 1995) average number of days per year during which the floodplain lakes were connected with the main channel. The relative shoreline length was calculated by the ratio of shoreline length to surface area. The drawdown area was estimated visually in the field and is defined as the percentage of the surface area of the lake bottom in July which became exposed in October. The approximate age of lakes was derived from historic topographical maps. Reliable estimates of the age of the lakes could be made up to 300 years; older lakes were classified being 300 years. The uncertainty of the lake age estimation was about one year for lakes with an age between 1 – 20 years, 3 - 7 years for lakes with an age between 20 – 90 years, and 10 - 25 years for lakes older than 90 years. During the fieldwork the prevailing land use in the adjacent floodplain (presence of trees, cattle access, use of manure) was recorded. For these variables the following categories were used: presence of trees: (0, shoreline length for < 25% covered by trees; 0.5, shoreline covered for 25 – 75% by trees; 1, shoreline covered > 75% by trees); cattle grazing: (0, cattle access to 0 – 25% of perimeter; 0.5, 25 – 75% of perimeter; 1, > 75% of perimeter; use of manure: (0, no manuring of adjacent land; 0.5, > 0 – 50% of adjacent land; 1, 51-100% of adjacent land).

For the 100 floodplain lakes sampled in 1999, the texture of the upper 0 – 0.5 m (in some cases extended to 1.0 m) of the sediment was visually determined from a core. In most lakes, two to ten sediment cores were taken: at least one in the centre and one on the shoreline. In the dataset the presence of sand and clay in the upper 10 cm of the cores was documented for each lake. From the other 115 lakes sampled in 2000, no data for sediment composition were obtained. For 95 of the 100 floodplain lakes sampled in 1999, samples for total N and total P in the water phase were taken according to Roozen *et al.* (2003).

For the 100 floodplain lakes sampled in 1999, water depth was measured at several (5 - 31) locations in each lake. To obtain an estimate of the decline in water level in these lakes during the growing season, additional measurements were made in July, August and October 1999. Based on

these data, mean lake depth in July and drawdown area of the lakes at the end of the growing season, when the lowest level occurred (October), was calculated. In the additional 115 lakes, the area of the lake bottom exposed was estimated visually in October 2000. A rough estimate of the water level in May was obtained from the vegetation zonation on the shoreline.

Table 3.1 Number of lakes, minimum, maximum and 25, 50 and 75 percentile values of environmental variables; a): only sampled in 1999; other variables were determined in both 1999 and 2000.

			percentile			
variable	n	min.	25%	50%	75%	max.
Inundation duration ($d.y^{-1}$)	215	1	11	11	35	258
Drawdown area (%)	215	0	0	0	10	100
Water level drop May – Oct (m) [a)]	99	0.1	0.49	0.94	1.35	2.3
Surface area (ha)	215	0.01	0.19	0.73	2.13	44.6
Mean lake depth (m)	215	0.13	0.66	0.99	1.42	5.16
Relative shoreline length (m^{-1})	215	146	440	726	1,208	11,905
Age (y)	215	1	40	85	250	300
Presence of clay [a)]	99	0	1	1	1	1
Presence of sand [a)]	99	0	0	0	1	1
Presence of trees	215	0	0	0	0.5	1
Use of manure	215	0	0	0.5	1	1
Cattle grazing	215	0	0	0.5	1	1
Total N ($mg\ L^{-1}$)	94	0.48	0.93	1.12	1.46	3.63
Total P ($mg\ L^{-1}$)	94	0.02	0.12	0.18	0.24	1.27

3.2.3 Data analysis

The percentage cover of submerged, floating-leaved and helophyte vegetation relative to the total water surface area in July was used in the analyses for each lake. The nymphaeids were the only floating-leaved plants included in the analysis, because non-rooted floating-leaved species like *Hydrocharis morsus-ranae* L. were very rare and lemnids dominated only at the end of the growing season (i.e. after the sampling period) in a few lakes. Filamentous algae were also rare and were therefore excluded from the analysis. We checked for normality of distribution of the cover-values of the vegetation growth forms by means of the Kolmogorov-Smirnov test.

Correlations among abiotic and biotic variables were determined using a Spearman rank correlation test. Because abundance of vegetation growth forms tended to fall into two distinct classes (abundant or rare/absent, see Results), we used multiple logistic regression (Jongman *et al.,* 1995) to evaluate the relationship between the probability of being abundant for different

vegetation growth forms and abiotic environmental variables. The general expression for this probability is:

$$P(x) = \frac{e^{(b_0 + b_1 x_1 + b_2 x_2)}}{1 + e^{(b_0 + b_1 x_1 + b_2 x_2)}}$$

where b_o, b_1, and b_2 are regression coefficients. The parameters were estimated by means of the maximum-likelihood principle. Eight independent variables were used in the multiple logistic regression analysis (*Table 3.2*). Inundation duration, drawdown area, surface area, mean lake depth and lake age were ln(x+1)-transformed. For each analysis both forward and backward multiple logistic regressions were done. Further, in cases where independent variables were excluded from the model, but were correlated to other independent variables that were included, we performed alternative analyses to check if the excluded variable could contribute significantly to the model if its correlated 'competitor' was removed. We also checked if the year of sampling influenced the results by including this variable in the multiple logistic regression analysis.

Table 3.2 Eight independent variables used in multiple logistic regression analysis to predict submerged vegetation dominance and nymphaeid and helophyte occurrence.

Variable	unit	comments
Ln (Inundation duration + 1)	$d.y^{-1}$	long term average 1900 – 95
Ln (Drawdown area + 1)	%	% of surface area of lake in October that has been drawn down compared to the surface area in July
Ln (Surface area + 1)	ha	surface area of lake at start of growing season
Ln (Mean lake depth + 1)	m	calculated from 5 – 31 measurements in each lake
Ln (Age + 1)	y	for accuracy: see Methods
Use of manure	categories	see Methods
Presence of trees	categories	see Methods
Cattle grazing	categories	see Methods

3.3 Results

The lakes varied widely in inundation duration (< 2 up to > 150 days y^{-1}), surface area (0.01 – 45 ha), mean depth (0.13 – 5.16 m), age (1 up to ≥ 300 years), and concentrations of total N (0.48 – 3.6 mg L^{-1}) and total P (0.024 – 1.3 mg L^{-1}) (*Table 3.1*). Submerged macrophyte cover was negatively correlated with mean lake depth, surface area, inundation duration and lake age and positively with relative shoreline length and drawdown area (*Table 3.3*). Nymphaeid cover was positively correlated with lake age (*Table 3.3*, *Figure 3.1*), showed an optimum at 0.5 to 1.0 m with respect to mean lake depth (*Figure 3.2*), and was negatively correlated with the occurrence of

sandy bottoms (*Table 3.3*). Helophyte cover was negatively correlated with the decline in water level through the growing season, mean lake depth, surface area and, positively, with lake age (*Figure 3.1*) and relative shoreline length (*Table 3.3*).

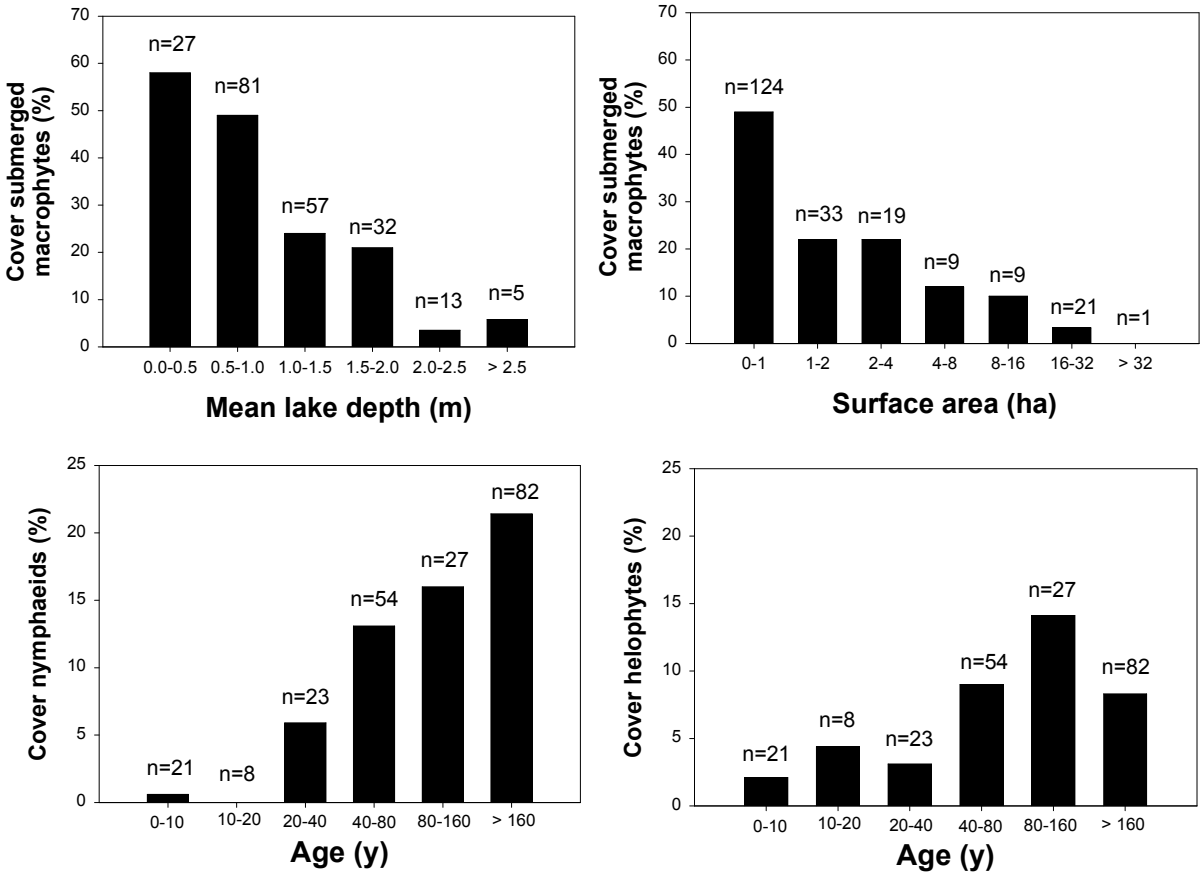

Figure 3.1 Cover of submerged macrophytes, nymphaeids and helophytes in relation to age, mean depth and surface area of the lakes.

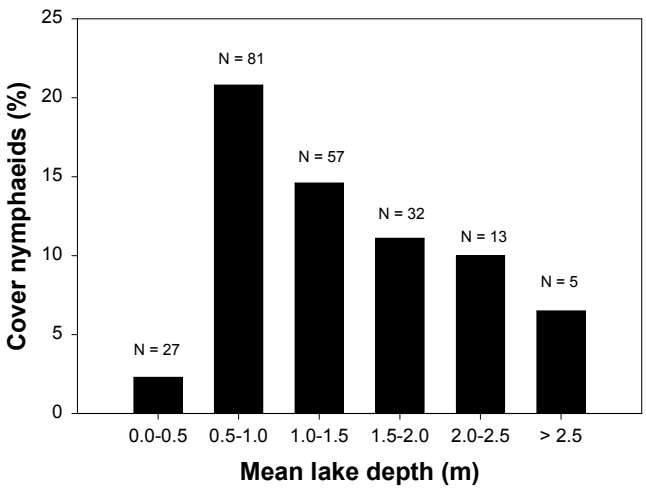

Figure 3.2. Average cover of nymphaeids in relation to mean depth per lake.

Many variables in the dataset were correlated (*Table 3.3*). Such multi co-linearity occurred among morphometric variables like mean lake depth, surface area and relative shoreline length, as well as indicators of abundance of submerged macrophytes, nymphaeids and helophytes. Therefore, the correlations with macrophyte abundance cannot be evaluated straightforwardly.

After arc-sin transformation of the percentage cover of the three growth forms, all of them still deviated significantly from a normal distribution ($p < 0.001$). Indeed, there was a tendency for each of these three groups to be either rare or abundant in a lake. The frequency distribution of the cover of submerged macrophytes in the lakes was particularly bimodal (*Figure 3.3*). In view of this we categorized lakes into rich or poor for submerged macrophyte, nymphaeid and helophyte cover, and used multiple logistic regression for further analysis. For both nymphaeids and helophytes the cut level for separating vegetation cover into two classes was taken at 1%. Based on the shape of the curve for submerged macrophytes (*Figure 3.3*), the data were analyzed for cut levels of, respectively, 20, 30, 40 and 50%.

Table 3.4 Results of backward logistic regression analyses for dominance of submerged vegetation (cut level of cover 20%) and occurrence of nymphaeids and helophytes (cut level of cover 1%). In these analyses Secchi-depth is included as abiotic variable in addition to the variables listed in Table 3.2;

Variable	Coefficient	S.E.	p	R
a. Dependent variable: submerged vegetation dominance				
Mean lake depth [a]	-7.4846	1.8573	< 0.001	-0.3658
Secchi-depth	0.0702	0.0168	< 0.0001	0.3801
b. Dependent variable: nymphaeid occurrence				
Age [a]	1.3594	0.3277	0.0001	0.3794
Secchi-depth	0.0254	0.0102	0.0310	0.1981
Constant	-7.2095	1.9237	0.0002	
c. Dependent variable: helophyte occurrence				
Age [a]	1.3570	0.3716	< 0.001	0.3260
Mean lake depth [a]	-4.7845	1.2994	< 0.001	-0.3292
Secchi-depth	0.0519	0.0145	< 0.001	0.3199
Presence of trees	-1,7456	0.8836	< 0.05	-0.1336

[a] *ln(x+1)-transformed*

We used multiple logistic regression to analyze the combined effect of independent variables on the probability of dominance of submerged macrophytes, and the occurrence of nymphaeids or helophytes. First, we used the abiotic variables listed in *Table 3.2* together with Secchi-depth as

explanatory variables. In these analyses a) the probability of dominance by submerged macrophytes was positively related to Secchi-depth and negatively related to mean lake depth, b) the probability of nymphaeid occurrence was positively related to Secchi-depth and lake age, and c) the probability of helophyte occurrence was positively related to lake age and Secchi depth, and negatively related to mean lake depth and the presence of trees (*Table 3.4*). However, because water transparency might be rather the effect than the cause of aquatic vegetation abundance during the sampling period of our lakes *(see* Discussion), we kept the variable 'Secchi-depth' out of further logistic regression analyses. During subsequent logistic regression analyses, only the abiotic variables listed in *Table 3.2* were included. In all cases backward and forward multiple logistic regression gave similar results. For each group the results of backward analysis are presented in *Table 3.5*.

Table 3.5 Results of backward logistic regression analysis for dominance of submerged vegetation (cut level of cover 20%) and occurrence of nymphaeids and helophytes (cut level of cover 1%); In these analyses only abiotic variables listed in Table 3.2 are included (Secchi-depth is excluded).

Variable	Coefficient	S.E.	p	R
a. Dependent variable: submerged vegetation dominance				
Surface area [a]	-1.4994	0.3528	0.0001	-0.2322
Mean lake depth [a]	-2.7894	0.7694	0.0003	-0.1934
Age [a]	-0.4271	0.1453	0.0033	-0.1493
Inundation duration [a]	-0.3869	0.1329	0.0036	-0.1474
Constant	6.0926	1.0015	0.0001	
b. Dependent variable: nymphaeid occurrence				
Age [a]	0.9080	0.1655	0.0001	0.3075
Mean lake depth [a]	7.1784	2.3792	0.0026	0.1546
Mean lake depth [a,b]	-3.7647	1.4711	0.0105	-0.1237
Constant	-7.6505	1.3464	0.0001	
c. Dependent variable: helophyte occurrence				
Age [a]	1.0279	0.1711	0.0001	0.3404
Presence of trees	-1.5689	0.4993	0.0017	-0.1636
Cattle grazing	-1.4571	0.4549	0.0014	-0.1676
Surface area [a]	-0.7398	0.2706	0.0063	-0.1364
Use of manure	-0.9295	0.4230	0.0280	-0.0981
Mean lake depth [a]	-1.4422	0.6957	0.0382	-0.0884

[a] *ln(x+1)-transformed;* [b] *the square-value of variable*

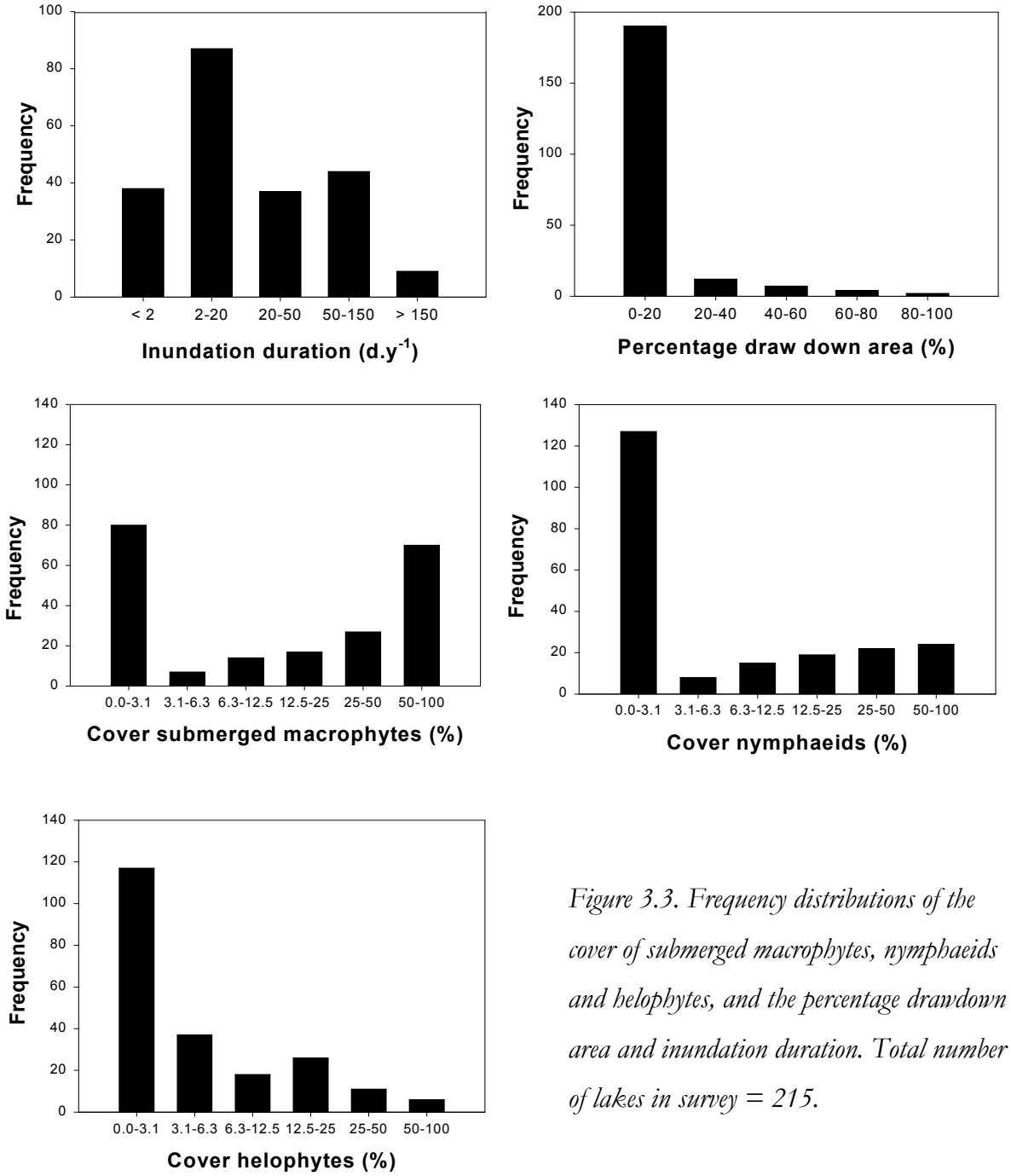

Figure 3.3. Frequency distributions of the cover of submerged macrophytes, nymphaeids and helophytes, and the percentage drawdown area and inundation duration. Total number of lakes in survey = 215.

The probability of submerged macrophyte dominance decreased with increasing surface area, mean lake depth, lake age and inundation duration (Figures 3.1 & 3.4; Table 3.5a). Surface area and mean depth of the lakes explained the largest proportion of the variance, whereas age and inundation duration were less important, although highly significant (*Table 3.5a*). The general shape of the fitted response of submerged macrophytes to mean lake depth and surface area

corresponded well to patterns shown by quadrates of the raw data, indicating that the logistic regression model is well suited to describe the pattern (Figure 3.4).

Note that the quadrates of the raw interpolated data confirmed that (as assumed in the models) the effects of different factors are multiplicative. This implies that, for instance, the critical depth for macrophytes depends on the age and size of a lake. In small lakes submerged macrophytes dominated at greater depth than in large lakes (*Figure 3.4*). Further, small old lakes were more often dominated by submerged macrophytes than large old lakes (*Figure 3.4*), and small lakes with high inundation duration were more often dominated by submerged macrophytes than large lakes with high inundation duration (results not shown).

Because surface area was correlated with relative shoreline length (*Table 3.3*), we offered the latter variable as a substitute for surface area in an alternative regression analysis. Indeed, in the absence of surface area, relative shoreline length was included as a highly significant variable in the model equation ($p < 0.001$). This means that the negative correlation between surface area and submersed vegetation dominance can also be explained as a positive correlation between relative shoreline length and submerged vegetation dominance or a combination of both abiotic variables. We also checked if the variable mean lake depth could be substituted for the correlated variable percentage drawdown area (*Table 3.3*). However, the latter variable did not contribute to the model significantly.

Nymphaeid occurrence was positively related to lake age and mean lake depth (*Table 3.5b*). The quadratic term in the model implies an optimum of nymphaeids roughly at 1.5 m with respect to mean lake depth (*Figure 3.2*).

In alternative analyses, the independent variable age in the model was substituted by relative shoreline length and inundation duration, respectively, as these variables were correlated with lake age (*Table 3.3*). The regression for relative shoreline length was not significant, whereas the correlation for inundation duration was significant ($p < 0.01$), indicating that a high inundation duration may have a positive effect on nymphaeid occurrence.

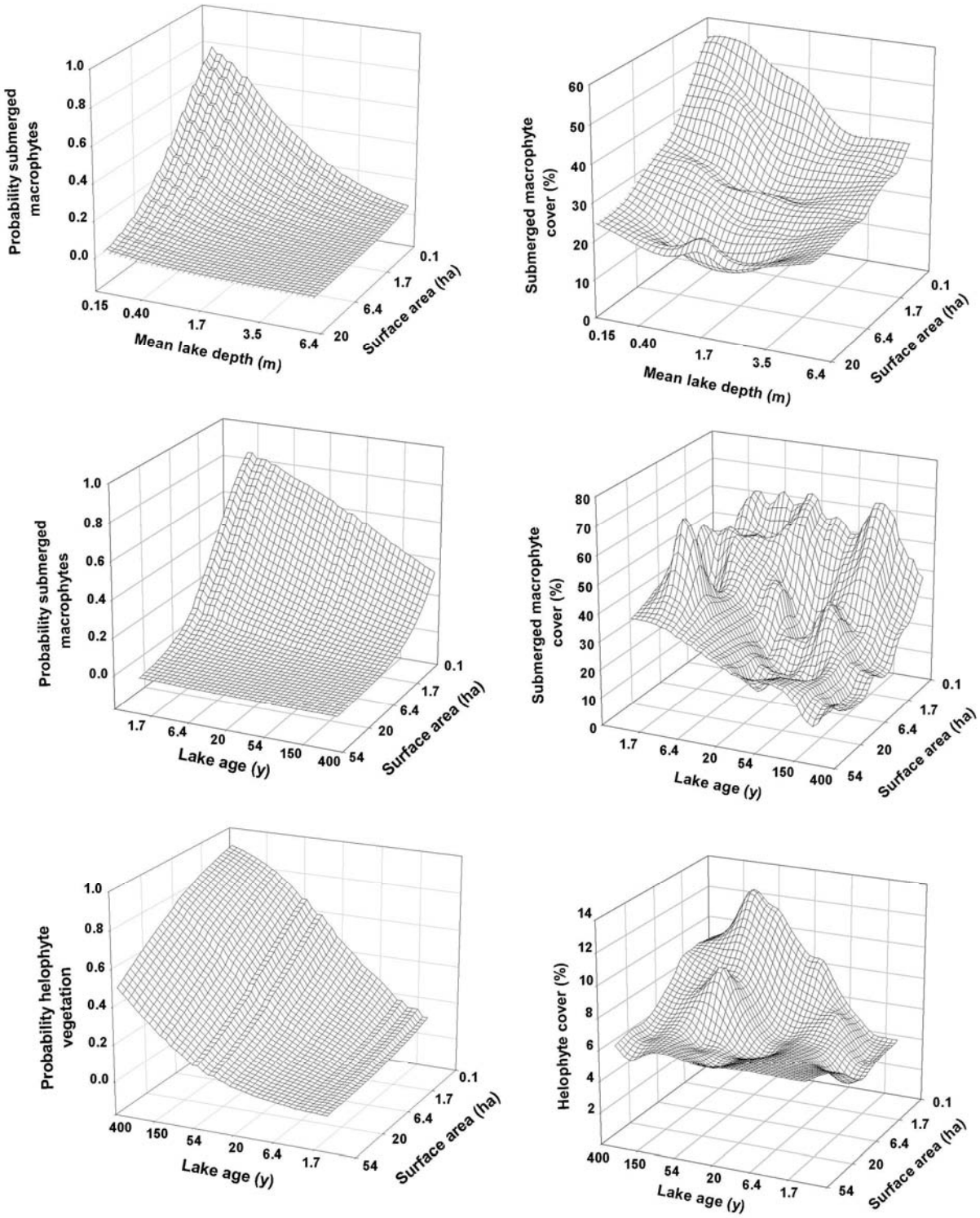

Figure 3.4. Modeled response of submerged macrophytes and helophytes in relation to age, surface area and mean lake depth as compared with a response surface computed from the raw coverage data by means of interpolation (inverse distance to a power; submerged macrophytes: smoothing factor 0.2; helophytes: smoothing factor 0.4)

Helophyte occurrence was found to increase with age and decrease with the presence of trees, cattle grazing, surface area, use of manure and mean lake depth in multiple logistic regression (*Figure 3.4*; *Table 3.5c*). As for submerged macrophytes, the effects of these variables were multiplicative. For instance, in small lakes helophytes occurred at younger age than in large lakes (*Figure 3.4*), and in shallower lakes helophytes occurred at younger age than in deep lakes (not shown). In an alternative analysis, the variable surface area was substituted by the strongly correlated variable relative shoreline length (*Table 3.3*). As with submerged macrophytes, this variable was accepted as highly significant in the model equation ($p < 0.001$), indicating that helophyte occurrence could be affected by a surface area *per se* or by relative shoreline length. We also checked if the variable age could be substituted for the correlated variables inundation duration and relative shoreline length (*Table 3.3*). However, neither of these substitutions contributed significantly to the model.

To check whether there were significant differences between the two years of sampling, we offered the sampling year as an additional independent variable to the regression analysis. Although the year of sampling was included as an additional variable in the models for submerged and nymphaeid macrophytes, it contributed less to the explained variance than the variables already listed in *Table 3.5*, indicating that the results were not strongly biased by the year of sampling.

During logistic regression analysis, submerged vegetation dominance was not significantly related to nutrient concentrations in the water column of the lakes. Many lakes with total P concentrations higher than 0.1 mg L^{-1} were still dominated by submerged macrophytes (*Figure 3.5*).

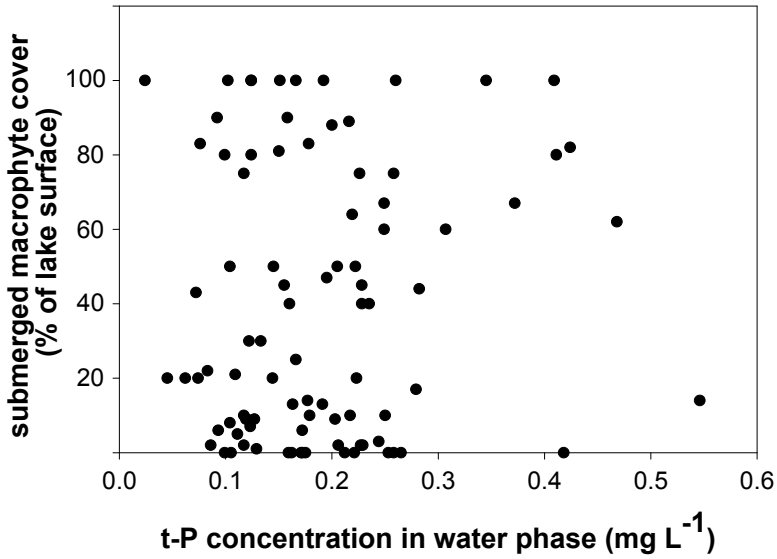

Figure 3.5. Relationship between total P concentration (mg L^{-1}) and submerged vegetation cover (% of surface area) in the lakes. Three outlayers with total P values between 0.6 – 1.3 mg P L^{-1} with submerged macrophyte cover ≤ 10% have been removed.

3.4 Discussion

The results show that both extremes of vegetation cover can be found among lakes of the Lower Rhine floodplains. Water bodies completely covered by macrophytes and those without vegetation lie next to each other in floodplain areas, a phenomenon also described for the Danube delta (Coops *et al.*, 1999) and the Rhône (Bornette *et al.*, 1998). In our data set the frequency distribution of submerged macrophyte cover in lakes was bimodal indicating the tendency to be either abundant or almost absent (*Figure 3.3*). Such bimodality could result from the existence of contrasting states under similar environmental conditions, which has been demonstrated to occur in shallow lakes outside floodplain areas (Scheffer, 1998; Jeppesen *et al.*, 1997), and has also been described more recently for lakes in regularly inundated floodplain areas along the Danube (Dokulil & Janauer, 2000) and the river Murray in Australia (Ogden, 2000).

Many studies show the large effect of water clarity on submerged macrophyte cover (e.g. Canfield *et al.*, 1985; Middelboe & Markager, 1997; Hudon *et al.*, 2000). Accordingly, Secchi-depth was strongly correlated with vegetation abundance in our lakes (*Table 3.3*). However, we did not consider turbidity as an independent variable in our analysis of vegetation abundance. The rationale is that causality is likely to be complicated. In shallow lakes submerged macrophyte cover strongly affects turbidity (Jeppesen *et al.*, 1997), due to a suite of mechanisms including lower resuspension, increased zooplankton grazing pressure and competition for nutrients

between macrophytes and algae (Scheffer, 1998). Since, in this study, the sampling period for turbidity occurred in the period when submerged macrophyte cover peaked, water clarity may largely be a result rather than a cause of submerged macrophyte cover.

Although we found relationships between vegetation structure and the relative impact of river hydrodynamics ('hydrological connectivity'), this aspect appeared less dominant than has been concluded in previous studies (Van den Brink *et al.*, 1991; Bornette *et al.*, 1998; Heiler *et al.*, 1995; Bornette *et al.*, 1998). In contrast, we found strong relationships between vegetation structure, morphometry and lake age, which have previously received little attention. Obviously, causality cannot be inferred from statistical relationships. In the sections below we discuss how our results, with respect to hydrological connectivity, land use, morphometry and lake age, may be interpreted in the light of previous work.

3.4.1 Hydrological connectivity

Inundation duration was negatively correlated with submerged macrophyte dominance, as found in earlier studies (Van den Brink *et al.*, 1991; Heiler *et al.*, 1995). Winter inundation is unlikely to have much direct impact on the vegetation, as in these temperate lakes plants over winter largely as dormant underground structures. The negative correlation between inundation duration and macrophyte dominance found by Van den Brink *et al.* (1991) could be due to the fact that winter inundation duration is related to (1) the occurrence of summer inundations within the study period, which have deleterious effects on macrophyte growth in floodplain lakes (Brock *et al.*, 1987); (2) higher nutrient load in the recent past, which is in agreement with the positive correlation between total-P concentration and inundation duration (Roozen *et al.*, 2003); (3) higher salinity (Van den Brink *et al.*, 1992), which can reduce growth of submerged macrophytes (Van den Brink & Van der Velde, 1993).

By contrast, no correlations between percentage drawdown area and the abundance of submerged macrophytes, nymphaeids or helophytes were found in the regression analysis (*Table 3.5*). This does not imply that drawdown is an unimportant process for these growth forms. Note that the number of lakes in the data set with a considerable drawdown area in the study period is very low (*Figure 3.3*), which makes the effects of drawdown hard to detect.

3.4.2 Land use

The negative correlation between the occurrence of helophytes and the presence of trees may be explained by competition for light and altered sediment characteristics. Trees (mainly *Salix* species) often grow in the shallow littoral, thereby occupying space which otherwise could be dominated by helophytes. Cattle grazing can obviously eliminate helophytes through a direct reduction in above ground biomass (Hroudová *et al.*, 1996) and by the destruction of rhizomes by trampling. The cause of the negative relationship between the use of manure and helophyte occurrence is obscure. Eutrophication seems an unlikely candidate, since submerged macrophytes are more sensitive yet show no relationship with manure use (*Table 3.4*, *3.5*). Perhaps the relationship with observed manure use is caused by the fact that manured fields had been used for cattle grazing in the years before the survey. Indeed, cattle grazing and manure use are highly correlated in our data-set (*Table 3.3*).

3.4.3 Nutrient content

It is often observed that submerged macrophyte abundance decreases with total-P content of the water, probably due to light limitation caused by algal growth (Jeppesen *et al.*, 1990; Scheffer, 1998). Surprisingly, logistic regression analysis showed that neither total-P nor total-N were significantly related to dominance by submerged macrophytes. Many floodplain lakes in our data-set were still dominated by submerged macrophytes at a total-P concentration up to 0.4 mg L^{-1} (*Figure 3.5*). This value is much higher than found in a large study of Danish lakes outside floodplain areas (i.e. 0.08–0.15 mg L^{-1}, Jeppesen *et al.*, 1990). This discrepancy may be related to the fact that our data-set contains many very small lakes which have a higher chance of being dominated by submerged vegetation. Also Mjelde & Faafeng (1997) reported dense submerged macrophyte cover over a wide range of total P concentration (0.03 – 0.70 mg P L^{-1}) in relatively small shallow lakes, although the surface area range in their dataset (6-112 ha) is larger than in ours (0.01 - 45 ha). The effect of lake morphometry on submerged macrophyte dominance is discussed below.

3.4.5 Morphometry

Small shallow lakes with a high relative shoreline length supported the highest abundance of submerged macrophytes in our data-set (*Table 3.3*, *Figures 3.1* & *3.4*). It has often been shown that the abundance of submerged macrophytes decreases with water depth, largely due to light limitation (Canfield *et al.*, 1985; Chambers & Kalff, 1985a; Skubinna *et al.*, 1995). On the contrary,

the pronounced negative relationship between lake surface area and submerged macrophyte dominance is novel. The effects of surface area on plant abundance have received hardly any attention in literature. Ogden (2000) reported a similar pattern for floodplain lakes along the Murray and Ovens River in Australia, but did not separate the effects of water depth and surface area. Further, in lakes outside floodplains lake area effects have hitherto been explained largely as a result of a positive correlation between lake size and depth (Duarte *et al.*, 1986b; Gasith & Hoyer, 1997). In our dataset surface area and depth had separate effects on submerged macrophyte cover. Several mechanisms can be hypothesized to explain a negative effect of lake size on submerged plant dominance.

1. Fish-kills may occur more frequently in small lakes, because there is a higher risk of oxygen depletion (Jeppesen *et al.*, 1990). In the wake of such events, submerged macrophytes may develop.
2. Smaller lakes tend to have a higher ratio of shoreline to surface area. Because shorelines act as a refuge for zooplankton (Lauridsen & Lodge, 1996; Nurminen *et al.*, 2001), this may favor transparency and hence growth of submerged macrophytes (Jeppesen *et al.*, 1990).
3. A large relative shoreline length may also favor recruitment and survival of pike (*Esox lucius* L.), a piscivore able to reduce recruitment of planktivorous fish (Berg *et al.*, 1997; Søndergaard *et al.*, 1997; Jacobsen *et al.*, 1997), leading to clear water through a trophic cascade, stimulating plant growth.
4. Submerged macrophytes tend to remain present throughout the winter period in sheltered, small water bodies (Van Wijk, 1988), giving them an advantage in spring.
5. Colonization, starting from the shallow 'hot spots' along the shoreline, may take several years to complete in large lakes (Van den Berg, 1999). Because the colonization with submerged macrophytes is a sensitive phase (Scheffer *et al.*, 1993a), the chance for a switch from vegetation-poor to a vegetation-rich lake during a period of favorable conditions for submerged macrophyte growth could be lower in large lakes.
6. Macrophyte growth in large lakes can be hampered by wind-stress (Hudon *et al.*, 2000; Spence, 1982).
7. Turbidity due to wind-induced resuspension is less in small lakes (Jeppesen *et al.*, 1990; Strand & Weisner, 1996; *Chapter 6*).

Testing these hypotheses requires further research, but some indications can be derived from our data. As was concluded in *Chapter 2*, wind is unlikely to be responsible for most of the resuspension related turbidity in our lakes (*mechanism 7*), because of small lake size and low exposure. Also, the effect of wind-stress on macrophytes (*mechanism 6*) seems unlikely to be important in these lakes. Indeed, in much larger shallow eutrophic lakes in the Netherlands, submerged plants have been observed to occur preferentially at exposed, rather than sheltered sites (Scheffer *et al.*, 1992). By contrast, the pike hypothesis (*mechanism 3*) is supported by the observation that the fish community in small floodplain lakes with high cover of submerged macrophytes and helophytes is often dominated by pike, whereas larger lakes without vegetation are almost exclusively dominated by benthivorous bream (*Abramis brama* L.) (Grift *et al.*, 2002). Fish-kills during periods of low water (*mechanism 1*) are also frequently observed in the studied floodplains (Scheffer *pers. obs.*), and Grift *et al.* (2001) reported high mortality rates of bream in floodplain lakes during periods of low water level. In conclusion, the first five mechanisms remain likely candidates for the floodplain lakes studied.

In this data-set, nymphaeid abundance was not related to lake size, but showed a distinct optimum with respect to mean lake depth (*Table 3.5b*, *Figure 3.2*). This depth zonation pattern is in accordance with observations by Van der Voo & Westhoff (1961), who reported also for Dutch floodplain lakes a depth range for nymphaeid occurrence from 0 – 3 m with an optimum in abundance between 0.8 and 1.2 m.

3.4.6 Lake age

The decline of submerged macrophytes and the increase of nymphaeids and helophytes with age are in line with the 'classical' sequence of aquatic vegetation succession (Pearsall, 1920; Hutchinson, 1975). Submerged macrophytes may accelerate the succession by altering net sedimentation, nutrient cycling and accumulation of organic matter, leading to a gradual enrichment of the sediment (Carpenter, 1981). In floodplain lakes these processes are accompanied by additional accumulation of fine materials (silt, clay) deposited during floods. The fine materials gradually decrease the porosity of the bottom, leading to a considerable reduction in groundwater exchange between river and lakes (Wood & Armitage, 1997). As a consequence, the amplitude of water-level fluctuations and the associated risk of desiccation of macrophyte seeds and seedlings decreases with lake age. At the same time, a low oxygen concentration resulting from organic matter accumulation stimulates germination of some late successional

macrophyte species, such as *Nuphar* (Smits, 1994), whereas low redox potential in the increasingly organic sediments could hamper growth of submerged macrophytes (Barko & Smart, 1986). Also, increased internal phosphorus loading from the gradually enriched sediments may stimulate phytoplankton, resulting in light limitation for submerged (but not for floating) plants. Eventually, a decrease in lake depth can further promote the transition to helophyte vegetation. Unlike in many other floodplains, such as those along the Rhône (Amoros & Bornette, 1999), the process of reduced hydrological connectivity in floodplain lakes along the Lower Rhine caused by accumulation of fine materials and organic matter is hardly reversed by bed erosion resulting from scouring overflows.

3.4.7 Combined effects of morphology, river dynamics and ageing

The results consistently show that the different environmental factors that affect vegetation abundance should not be viewed separately as 'limiting factors'. Rather the sensitivity to one factor always depends on the values of other factors. This is an implicit assumption of the logistic model but the Figures of the raw data (*Figure 3.4*) confirm this pattern. This implies, for instance, that small lakes tend to remain dominated by submerged macrophytes up to a greater depth than large lakes, and helophytes colonize smaller lakes faster.

Perhaps the most remarkable result from our analysis is that, independently of depth, lake surface area and age are such important factors determining vegetation structure. Nutrient loading is unlikely to differ substantially among our lakes, because they are all inundated almost every year. The relatively minor role of river dynamics may largely be due to the fact that, unlike in other floodplain systems (Bornette *et al.*, 1998; Heiler *et al.*, 1995), our lakes are rarely inundated during the growing season and experience only moderate currents during inundation periods. Nonetheless Van den Brink *et al.* (1991), who investigated floodplain lakes along the Lower Rhine, found much stronger correlations to connectivity. This may be due in part to the fact that they also included in their survey permanently connected and never inundated lakes behind the major embankments in the hinterland. In addition, in their dataset lake morphometry was strongly correlated to connectivity, leading to potentially spurious results.

Our results have important practical implications for future management of the Lower Rhine floodplains. New water bodies will be excavated in the floodplains over the coming years in a campaign aimed at enhancing the water storage, discharge capacity and conservation value of the

floodplain. Size, depth and connectivity to the river of these prospected lakes can in part be designed (Coops *et al.*, 2000). Our results suggest that the chance of new lakes becoming rich in vegetation is higher if many small lakes, rather than fewer large ones, are created. Also, the clear succession in vegetation structure patterns with age implies that, in these floodplains where natural erosion by scouring water is virtually absent, regular re-excavation of lakes may be essential if the aim is to promote biodiversity of the river – floodplain system.

3.5 Acknowledgments

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CHAPTER 4

Predation may reverse diversity-productivity patterns in lake plankton

Roozen F.C.J.M., Peeters E.T.H.M., Bransen F., Ibelings B., Roijackers R.M.M., Buijse A.D. & Scheffer M.

Predation may reverse diversity-productivity patterns in lake plankton.

4.1 Introduction

Patterns in the distribution of species richness (or biodiversity) over different habitats and their possible explanations have remained a central theme in ecology for a long time. Perhaps the best-studied pattern is the humped shaped relationship of species richness to productivity. Species numbers tend to increase with productivity until they reach an optimum beyond which they decline with a further rise of productivity (Grime 1973, Huston 1979; Tilman 1982; Rosenzweig 1992; Mittelbach *et al.* 2001). This pattern is found in many different communities ranging from terrestrial plants (Al-Mufti *et al.* 1977; Tilman, 1988) and desert rodents (Abramski & Rosenzweig, 1984, Rogovin *et al.* 1994) to oceanic benthos (Rex, 1981), coral reefs (Huston, 1985) and plankton in lakes (Dodson *et al.*, 2000) and oceans (Belgrano & Brown, 2002), and is also very robust against the choice of different surrogates for productivity and diversity (Proulx & Mazumder, 1998). In spite of the ubiquity of the humped pattern, there is no general consensus about the mechanisms causing it. Especially the explanations for loss of species at the high productivity end of the spectrum have been under debate (*e.g.* Abrams, 1995).

Also, few empirical studies have explored the relationship between species richness of different trophic levels. It has been suggested that diversity of higher trophic levels will tend to peak at higher productivity levels than those of lower trophic levels (Huston, 1994). The idea is that organisms of a higher trophic level derive their energy less efficiently due to energy loss from one trophic level to the next, and therefore require higher levels of primary productivity to maintain sufficient growth rates and large enough population sizes to recover from disturbances and random fluctuations in population size (Huston, 1994). Unfortunately, we have few data to explore the link of diversity between different trophic levels. Obviously, it would be useful to have a deeper understanding of this link. If there are general patterns, those could help to estimate overall biodiversity from information limited to one trophic level only. Also, if diversity on different trophic levels is causally linked this would imply that loss of species due to human impacts could cascade through trophic levels.

The complex interaction between different trophic levels is relatively well understood for shallow lakes (*see* Jeppesen, 1998 and Scheffer, 1998 for an overview). However, most of the intense research in these ecosystems has been focused on reducing algal biomass, and aspects of biodiversity have remained relatively little explored. Here we analyze communities of phytoplankton and zooplankton in a set of 71 shallow floodplain lakes, to see how diversity at these two adjacent trophic levels is related to productivity. We interpret the results against the current understanding of food web interactions in shallow lakes to infer how top-down effects may modify patterns predicted from current bottom-up based theory.

4.2 Methods

4.2.1 Study area

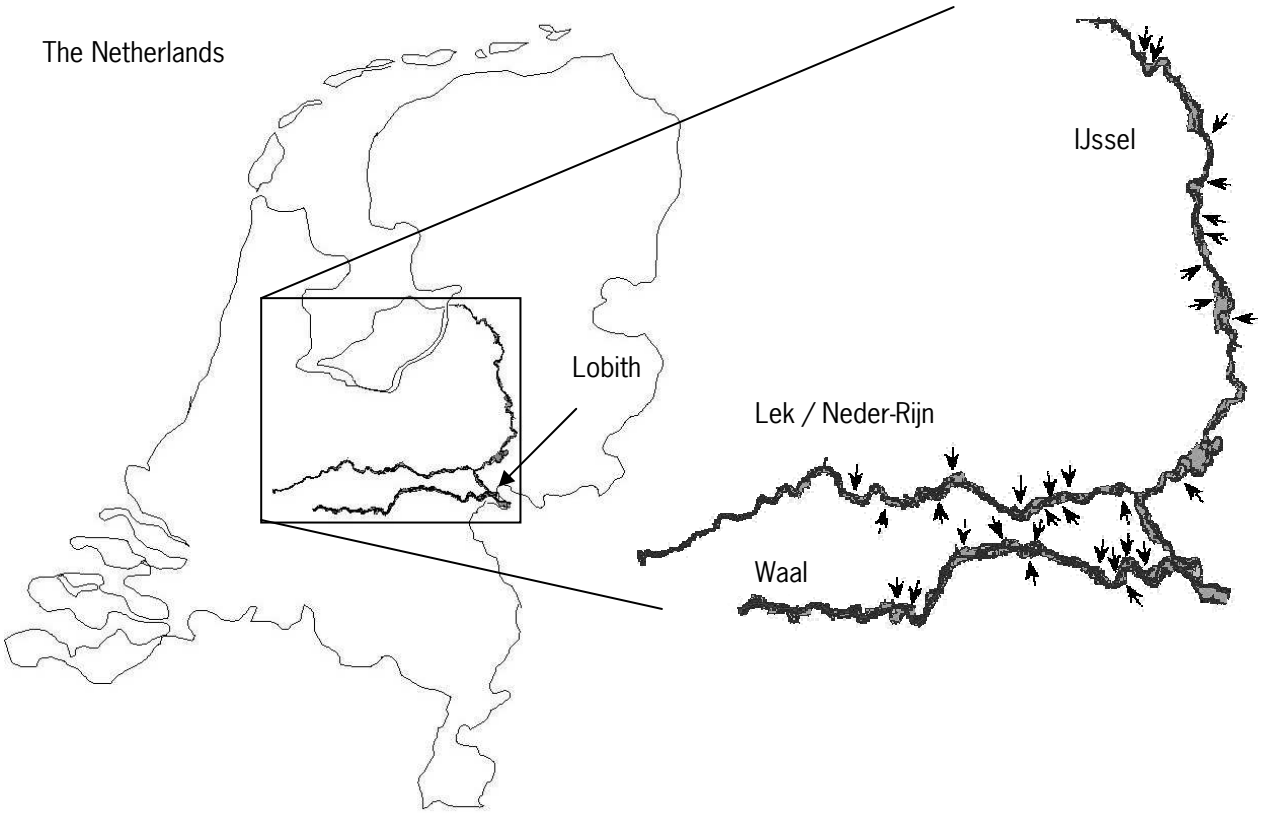

Figure 4.1. Map of the Netherlands with the sampled sections of the three Rhine branches. Arrows indicate the locations of the sampled floodplains.

The study was performed in the Dutch part of the River Rhine, in July-August 1999. After the Rhine enters The Netherlands near Lobith, the river is divided into the Waal, the Neder-Rijn and

the IJssel. At Lobith, the mean discharge is 2,300 $m^3.s^{-1}$, from which two thirds is channeled through the Waal, two ninths through the Neder-Rijn and one ninth through the IJssel (Middelkoop & Van Haselen, 1999). Highest discharge normally occurs during winter and lowest during autumn, but depending on the climate, occasional floods may occur at any time of the year. The 71 floodplain lakes included in this study are divided over 31 floodplain sections along the three Rhine branches, with 28, 24 and 19 lakes along the Waal, Neder-Rijn and IJssel respectively (*Figure 4.1*). All sampled floodplain lakes are situated between the main channel and the major embankments. All lakes are shallow, with a mean depth in August less than 1.5 meter. Lake sediments consist of mainly silt and/or clay. All lakes are influenced to various extents by the adjacent river through winter inundation.

We divided the average annual inundation duration in 5 classes on the basis of the geographical elevation of the floodplains and the long term average water level dynamics of the rivers. For each class the median value of the range is used in the statistical analyses:

Class	*duration range ($d.yr^{-1}$)*	*median ($d.yr^{-1}$)*
1	*< 2*	*1*
2	*2-20*	*11*
3	*20-50*	*35*
4	*50-150*	*100*
5	*> 150*	*258*

4.2.2 Field and laboratory procedures

Each of the 71 lakes was sampled once in August 1999. In addition we sampled 10 lakes on a monthly basis for 3 years (1998-2000; *Chapter 5*). We used a transparent plastic tube (length two meters, diameter of 10 cm) and sampled the lakes from a boat, taking 5-7 samples from the middle of the lake to the shore. The samples were mixed in a 30 liter tank, from which all sub-samples were taken. Five liters were taken for analyses of total N and total P, DOC, chlorophyll-a and suspended materials. For phytoplankton analysis a one liter sample was taken and fixed in 3% lugol's solution (final concentration). For analysis of zooplankton a composite sample of 25 liter was filtered over a 55 μm zooplankton net and fixed in 5% formaldehyde (final concentration). A one-liter flask was filled directly from the lakes for analyses of chloride and bicarbonate in the field using field kits. Lake transparency was characterized as Secchi depth (m^{-1}) and vertical light attenuation (K_d, m^{-1}). The latter was measured with two Bottemanne light-sensors at two different depths in the water column. One sensor just beneath the water surface,

and the other 30 cm lower. Both sensors were connected to a GRANT 1202 Squirrel Meter/Logger, reading signals every 5 seconds during one minute. The K_d was calculated as the mean of the readings during the measurement. Chlorophyll-a was measured in triplicate after filtration over Whatmann GF/F filters. Ethanol was used as extraction fluid, and acid was used to correct for phaeopigments (Moed & Hallegraeff, 1978).

Dissolved organic carbon (DOC) was analyzed on filtered (0.2 μm membrane filter, Schleicher and Schuell) water samples using a TOC-analyzer (model 700, OI-Analytical). Inorganic and organic suspended solids (resp. ISS and detritus) were analyzed from a known volume of the five liter water samples, collected on preweighed (GF/F filters, Whatmann), dried and stored for 24 hours at 105 °C, weighed, combusted for 3 hours at 530 °C and weighed again. Control filters were processed similarly with each measurement. Zooplankton and phytoplankton samples were analyzed using an inverted microscope (Reichert) at a magnification of 128x (zooplankton) and 500x (phytoplankton).

Vegetation mapping was done in July and August 1999 (Van Geest *et al.* 2003). Each sample was taken in a plot containing a homogeneous vegetation type according to the phytosociological classification described in Schaminée *et al.* (1995), with the quantity of samples varying between 4 and 31 plots per lake. Submerged plants were collected using a rake, and for each species the percentage cover projected on the bottom was visually estimated using a 7-point scale (< 1%, 1-5%; 6-15%, 16-25%; 26-50%; 51-75%, 76-100%). In each plot, the total percentage cover of respectively submerged, floating and helophyte vegetation and of filamentous algae was estimated. Based on these data, the surface area covered by submerged and nymphaeid vegetation and the percentage of open water (i.e. unvegetated area) in the whole lake was calculated as a percentage of the total surface area of the lake (Van Geest *et al.* 2003).

Water level of the lakes was measured in July, August and October using marked poles in or near the lakes as a reference. Mean lake depth was calculated using depth measurements at different points in the lakes in July, and was computed for August using water level measurements of July and August. Lake size, as well as their shortest distance from the river was calculated using GIS-maps. We expressed the decrease in surface area from July to October as the draw-down area, where the water surface area in July was used as a reference and complete sediment exposure to

the air in October equaled 100 % draw-down. Age of the lakes was determined by using historical geographical maps.

4.2.3 Measures of diversity and terminology

Phytoplankton and zooplankton diversity can be expressed in various forms. We used the number of taxa, which is a practical proxy of taxonomic richness, and is more robust to problems of identification than species richness (Bengtsson, 1998). We also calculated the Shannon diversity (Shannon, 1948) on the base of numbers of individuals (ind L^{-1}):

$$H'' = - \Sigma (n_i/N) \log2 (n_i/N) \quad (1)$$

where n_i is the density measure of the i-th taxa and N is the total number of taxa.

To explore whether differences in Shannon diversity were affected by patterns of taxa dominance, we used the evenness (or equitability) of the taxa distribution, (E) (Reynolds, 1997):

$$E = H'' / H''_{max} \quad (2)$$

where H''_{max} is the theoretical maximum of SW-diversity in any sample, expressed as

$$H''_{max} = \log_2 s \quad (3)$$

where s is the number of taxa in the sample.

For simplicity we will use the generic term 'taxonomic richness' when we refer to our statistics on the number of taxa, and 'SW-diversity' for Shannon diversity index. Also we will use the term 'diversity' for short in cases where we refer to patterns that occur in Shannon diversity and number of taxa.

4.2.4 Data transformation and analysis

The original vegetation abundances (in percentages) were arcsine transformed (Lubberstedt *et al.* 1998) in order to stabilize variance. To obtain an indicator of nutrient availability which is not too biased by algal biomass itself (Scheffer, 1998) we also computed the ratio of total nitrogen and total phosphorus (both mg L^{-1}) to the chlorophyll-a (µg L^{-1}) concentration, respectively

Table 4.1. Means (+SE) and ranges of 30 environmental variables used in the statistical rank-correlation analyses.

factor	Mean (± SE)	range
Hydrological variables		
Inundation duration (d y^{-1}) [a)]	60.3 (9.43)	1.00 - 258
Water level May-October	0.95 (0.06)	0.17 - 2.30
Draw down area (%)	0.26 (0.03)	0.00 - 1.11
WL (m wk^{-1}) [a)]	0.07 (0.01)	-0.05 - 0.23
Morphometric variables		
Mean lake depth (m) [a)]	0.73 (0.05)	0.08 - 1.48
Lake surface (ha) [a)]	2.16 (0.44)	0.01 - 19.8
Lake circumference (m)	8.83 (1.13)	0.41 - 46.0
Shore (m) [a)]	0.09 (0.01)	0.02 - 0.38
Distance to river (m) [a)]	332 (34.8)	10 - 1210
Vegetation variables		
Vegetation rich/poor (-) [a)]	0.63 (0.06)	0.00 - 1.00
Helophytes (arcsin (%))	0.22 (0.03)	0.00 - 1.11
Submerged (arcsin (%))[a)]	0.71 (0.06)	0.00 - 1.57
Floating (arcsin (%))[a)]	0.30 (0.04)	0.00 - 1.11
Open water (arcsine (%))	0.54 (0.06)	0.00 - 1.57
Chemical variables		
EC (µS cm^{-1})	536 (12.7)	334 - 959
pH (-)	8.12 (0.06)	7.07 - 9.91
Chloride (mg L^{-1})	69.3 (1.78)	40.8 - 118
HCO_3^- (mg L^{-1}) [a)]	185 (9.81)	83.0 - 383
TN/chlorophyll-a (-)	0.06 (0.01)	$4.3.10^{-3}$ - 0.64
TP/chlorophyll-a (-)	0.01 (0.00)	$3.5.10^{-4}$ - 0.08
Turbidity variables		
Sd (m)	50.3 (4.04)	17.0 - 170
K_d (m^{-1})	5.13 (0.32)	0.95 - 13.3
ISS (mg L^{-1}) [a)]	23.6 (1.69)	4.42 - 65.2
Detritus (mg L^{-1}) [a)]	11.1 (1.96)	0.22 - 134
DOC (mg L^{-1})	11.2 (0.42)	5.70 - 23.1
Chlorophyll-a (µg L^{-1}) [a)]	97.1 (13.9)	2.96 - 595
Other variables		
Lake age (ln(y)) [a)]	4.11 (0.17)	0.69 - 5.71
River branch (-)	1.87 (0.10)	1.00 - 3.00
Distance from Lobith (km)	59.3 (3.40)	18.0 - 133
Water temperature (°C) [b)]	18.6 (0.24)	15.0 - 23.0

[a)] *are offered to the regression analyses*
[b)] *is offered to the regression analysis of phytoplankton only.*

TN/chlor-a and TP/chlor-a. Non-parametric correlation calculations between phytoplankton and zooplankton variables and 30 explanatory variables presented in *Table 4.1*, as well as backwards multiple regression analysis were performed using SPSS for Windows release 10.1.0 from SPSS Inc. (2000). The correlations were performed to find patterns in the data, not for finding causal relations. For this reason it was not necessary to perform a sequential Bonferroni

test (to limit comparison-wise error rates). ANOVA was performed using SPSS and Sigma plot 2000 for Windows, version 6.00 from SPSS Inc. was used for model fitting.

4.3 Results

A total of 55 different phytoplankton and 45 zooplankton taxa were found in the 71 sampled floodplain lakes. Only 12% of the phytoplankton taxa and 17% of the zooplankton taxa were found in more than 50% of the lakes. The relative abundance of motile phytoplankton taxa was highest in the lakes with low inorganic suspended solids concentrations (*Figure 4.2*), which were generally the lakes rich in aquatic vegetation (Roozen *et al.* 2003). Means and ranges of the taxonomic richness, the SW-diversity and evenness of the plankton communities were rather comparable for phytoplankton and zooplankton (*Table 4.2*).

Table 4.2. Means (± SE) and ranges of the taxonomic richness, SW-diversity and evenness for phytoplankton and zooplankton in the total set of 71 floodplain lakes.

	Mean (± SE)	range
Phytoplankton		
# genera	10.3 (0.53)	3 - 24
SW-diversity	2.12 (0.09)	0.59 - 3.70
Evenness	0.66 (0.02)	0.22 - 0.93
Zooplankton		
# genera	11.3 (0.42)	4 - 19
SW-diversity	2.47 (0.07)	1.20 - 3.65
Evenness	0.72 (0.02)	0.34 - 0.90

Analysis of the data from the 10 monthly sampled lakes indicates that taxa richness which we used as an indicator of taxonomic richness at the genus level is linearly related to species richness in these floodplain lakes (*Figure 4.3*).

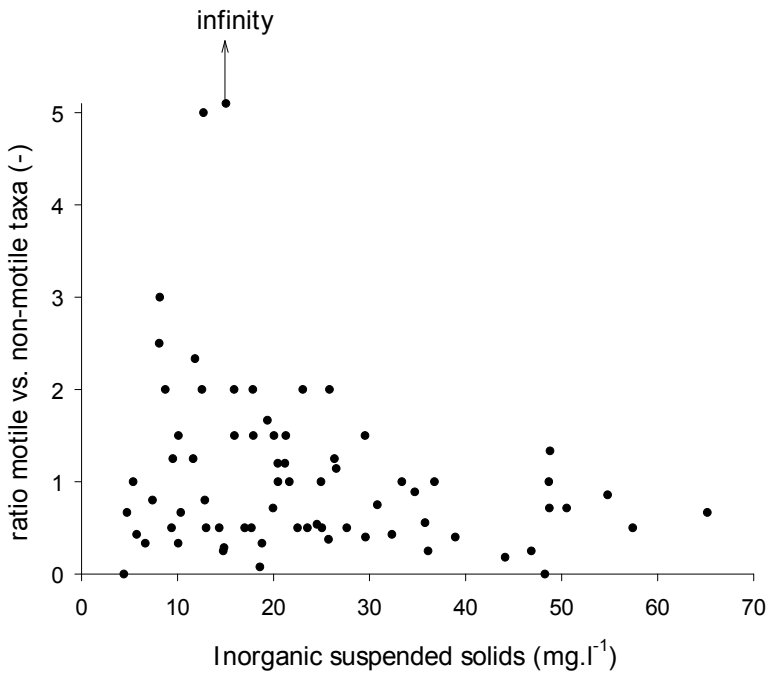

Figure 4.2. Relation of inorganic suspended solids concentrations and the ratio of abundances of motile to non-motile phytoplankton taxa.

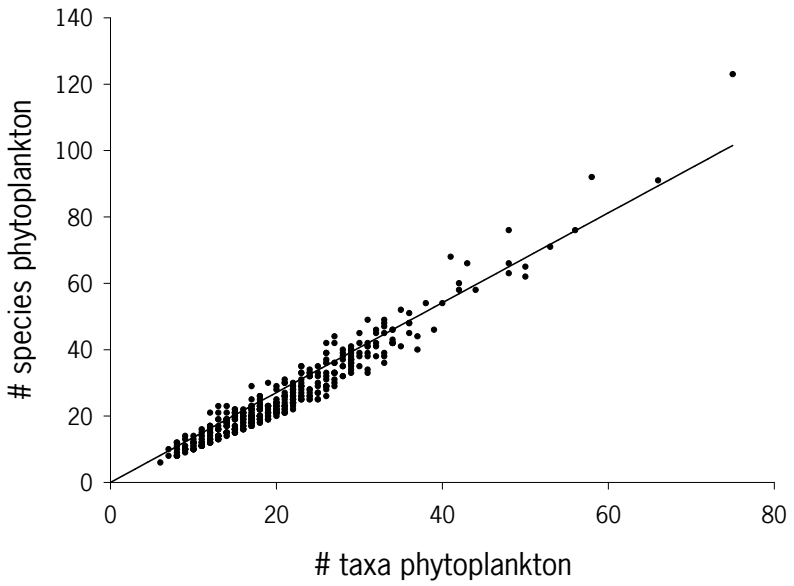

Figure 4.3. Relation between the phytoplankton taxa richness and species richness. The solid line represents the linear regression ($p < 0.0005$, $R^2_{adj} = 0.98$).

4.3.1 Pair wise correlations

Pair wise rank-correlation analysis (*Table 4.3*) showed that taxonomic richness of phytoplankton and zooplankton were negatively correlated, and the overall diversity of phytoplankton and zooplankton showed rather different correlations with environmental variables. Despite the large range of hydrological dynamics in these riverine lakes, correlations with hydrological variables were not significant, with the notable exception of phytoplankton richness which correlated positively to the water level decrease. Lake size (ha) and average lake depth (m) were positively correlated with phytoplankton taxonomic richness and SW-diversity. By contrast, zooplankton SW-diversity and taxonomic richness were not related to lake size or depth. SW-diversity of both phytoplankton and zooplankton were strongly related to the presence of vegetation. Phytoplankton taxonomic richness was negatively related to vegetation abundance, while no correlation was found for the evenness. By contrast, zooplankton diversity indicators were generally positively correlated with vegetation abundance. Chemical variables also correlated with plankton diversity measures. Phytoplankton evenness decreased with the electric conductivity (EC) and bicarbonate (HCO_3^-), while it increased with the pH. Zooplankton taxonomic richness decreased with increasing EC-values. Taxonomic richness of phytoplankton and zooplankton decreased with increasing total nitrogen concentrations, while no correlations were found for total phosphorus. The ratios TN/chlor-a and TP/chlor-a were positively correlated with indices of zooplankton diversity, while phytoplankton diversity indicators showed little relationship to these ratios. Turbidity related variables were negatively correlated with zooplankton diversity indicators. By contrast phytoplankton diversity indicators were hardly correlated with turbidity related variables, with the exception of a strong negative correlation between DOC and phytoplankton taxonomic richness. Phytoplankton evenness and SW-diversity decreased with lake age.

Table 4.3. Rank-correlations between phytoplankton and zooplankton taxonomic richness, SW-diversity and evenness and different environmental variables. Only the environmental variables with significant correlations are presented (all tested variables are presented in Table 4.1).

Factor	Phytoplankton			Zooplankton		
	# taxa	Diversity	Evenness	# taxa	Diversity	Evenness
Hydrological variables						
Water level May-October	0.336					
Morphometric variables						
Mean lake depth (m)	0.377	0.287				
Lake surface (ha)		0.255				
Vegetation variables						
Vegetation rich/poor	- 0.289			0.311	0.299	0.249
Helophytes (arcsin (%))	- 0.372	- 0.367				
Submerged (arcsin (%))	- 0.356			0.370	0.287	
Floating (cat)				0.261		
Open water (arcsin (%))	0.455	0.243		- 0.340	0.290	
Chemical variables						
EC (µS cm^{-1})			- 0.339	- 0.300	- 0.315	- 0.272
pH (-)			0.344			
HCO3- (mg L^{-1})		- 0.329	- 0.363			
TN (mg L^{-1})	- 0.255			- 0.317		
TN/chlorophyll-a (-)				0.350	0.459	0.419
TP/chlorophyll-a (-)	- 0.257			0.365	0.515	0.469
Turbidity variables						
Sd (m)				0.376	0.363	0.246
Kd (m^{-1})				- 0.297	- 0.315	- 0.237
DOC (mg L^{-1})	- 0.434	- 0.285				
Chlorophyll-a (µg L^{-1})				- 0.369	- 0.445	- 0.384
Other variables						
Lake age (ln(y))		- 0.293	- 0.275			
Water temperature (°C)	0.255	0.286				
# taxa zooplankton	- 0.289					

All significant at $p < 0.01$, except for a), where $p < 0.05$.

4.3.2 Multiple regressions

To explore the relationship between diversity and environmental conditions further multiple regression analyses (*Table 4.4*) were performed. These analyses suggested that vegetation cover had an important negative effect on phytoplankton taxonomic richness and SW-diversity. Evenness and SW-diversity of phytoplankton decreased with lake age. The positive relation of phytoplankton taxonomic richness with lake depth, found in the pair wise correlations was also found in the multiple regression. In contrast to phytoplankton diversity, zooplankton taxonomic richness increased with submerged vegetation cover, while a negative relationship to the duration

of inundation appeared. No significant models for zooplankton SW-diversity and evenness were found.

Table 4.4. Regression models for the taxonomic richness, SW-diversity and evenness of phytoplankton (A) and zooplankton (B). All models are calculated through backward regression analyses. The models are calculated with the variables offered as presented in Table 4.1. For zooplankton, analyses with the given significance levels resulted in no models for the SW-diversity and evenness.

	Coeff.	p	R^2_{-adj}
A. phytoplankton			
Taxonomic richness			
(Constant)	9.01	$1.9.10^{-7}$	0.233
Average lake depth (m)	3.81	$1.1.10^{-2}$	
Submerged vegetation cover (arcsin (%))	- 2.80	$1.1.10^{-2}$	
SW-diversity			
(Constant)	3.50	$1.2.10^{-16}$	0.255
Lake age (ln(y))	- 0.32	$2.0.10^{-4}$	
Vegetation rich/poor (-)	- 0.46	$1.8.10^{-2}$	
Floating vegetation (cat)	0.45	$2.7.10^{-2}$	
Evenness			
(constant)	0.87	$4.2.10^{-17}$	0.136
Lake age (ln(y))	$-4.9.10^{-2}$	$5.7.10^{-3}$	
B. zooplankton			
Taxonomic richness			
(constant)	10.6	$3.4.10^{-17}$	0.139
Inundation duration (d y^{-1})	$-1.0.10^{-2}$	$4.5.10^{-2}$	
Submerged (arcsin (%))	1.83	$4.3.10^{-2}$	

4.3.3 Non linear relationships

Exploration of possible non-linear relationships indicated that taxonomic richness of phytoplankton showed a humped relationship with the LN transformed chlorophyll-a concentration (*Figure 4.4*, upper panel). Most taxa are found in lakes with chlorophyll-a levels around 60 μg L^{-1} (Ln(60) ≈ 4.1 on the horizontal axis) while lakes with higher or lower chlorophyll concentrations have a lower taxonomic richness. The best model describing the pattern in this relation was the Gaussian regression model (*Table 4.5a*; *Figure 4.4*, upper panel).

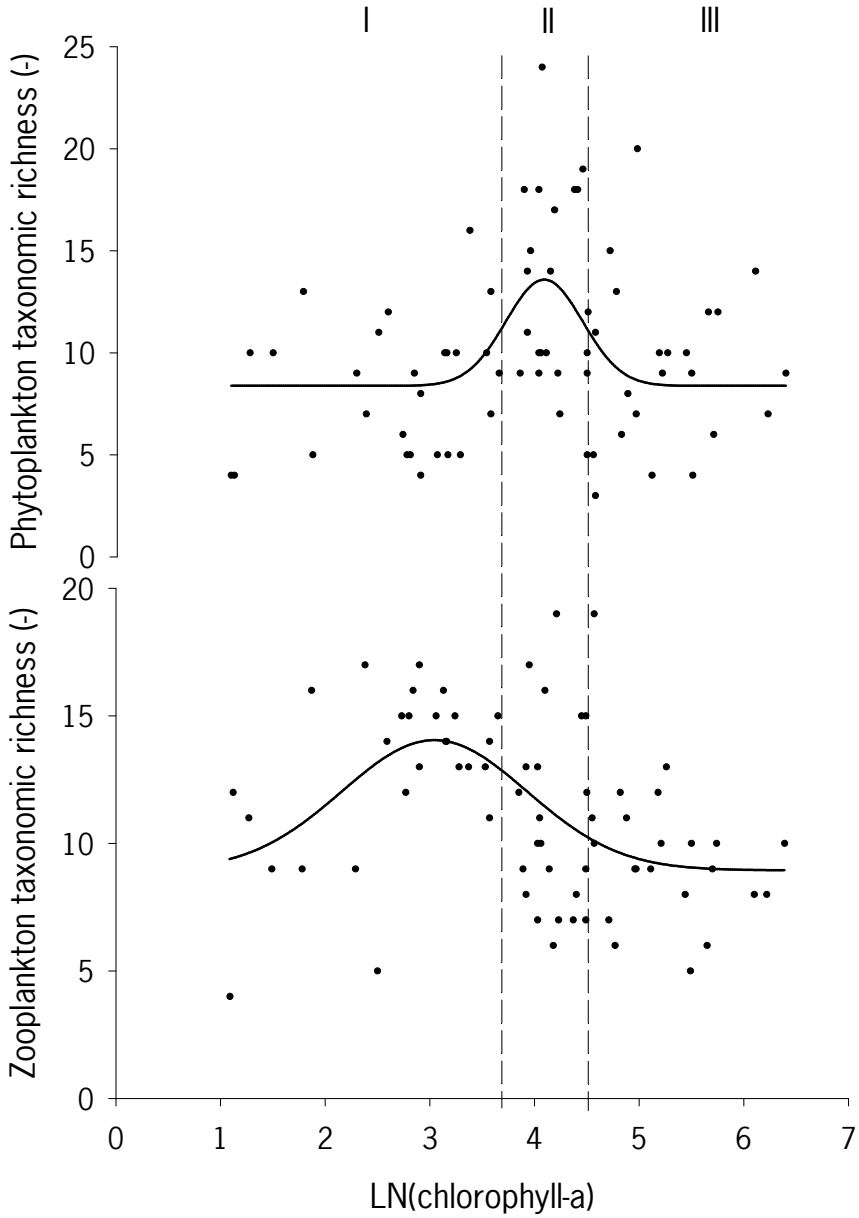

Figure 4.4. Relation between the phytoplankton taxonomic richness (upper panel) and zooplankton taxonomic richness (lower panel) with the LN transformed chlorophyll-a (µg L^{-1}) concentrations in the 71 sampled lakes. The vertical dashed lines represent the boarders between three sub-sets of lakes (I, II and III), where the left boarder is at 40 µg L^{-1} and the right boarder at 90 µg L^{-1} chlorophyll-a. The solid line in the upper panel represents the Gaussian (4) regression models as presented in Table 4.5.

To explore possible explanations of this humped pattern we arbitrarily divided the lakes into three groups corresponding to the hump, and the groups on the left and right hand side respectively. Within ANOVA, Tukey's-b post-hoc tests (*Figure 4.5*) showed that the left hand region contains mostly transparent, vegetation rich lakes whereas the right hand region is

characterized by turbid lakes with high ISS and DOC (not shown) concentrations and little vegetation. Lakes in the hump are not very turbid, but poor in vegetation.

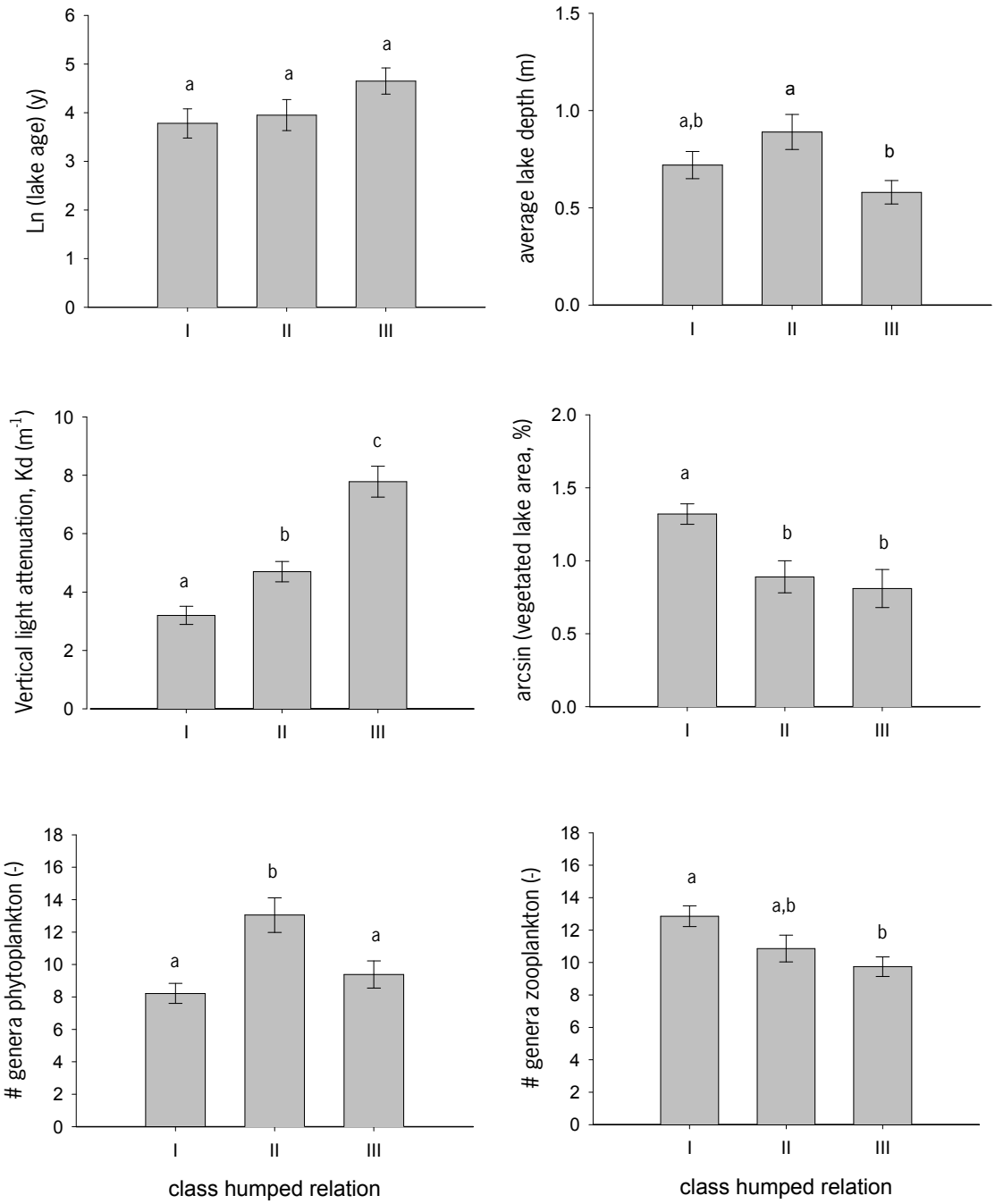

Figure 4.5. Means of lake age (y), average lake depth (m), vertical light attenuation (K_d), vegetated lake area (%) phytoplankton and zooplankton taxonomic richness (-) in the three regions of phytoplankton biomass (I, II and III). Similar symbols 'a…c' indicate homogeneous groups that are not different at the 95% level (Tuckey test).

By contrast, zooplankton taxonomic richness is highest in the low chlorophyll lakes which are usually vegetated and clear. A closer look suggests that the relationship of zooplankton taxonomic richness to the chlorophyll-a level is also humped and could also be described by a Gaussian regression model (*Table 4.5b*; *Figure 4.4*, lower panel). The maximum richness occurs at lower chlorophyll levels than the maximum for phytoplankton taxonomic richness. However, at the very lowest chlorophyll levels in our data set there seems to be a decline again in zooplankton taxonomic richness. Indeed, linear regression of the lakes on the left side of the maximum suggested by the Gaussian regression confirms that taxonomic richness tends to drop in situations with very low chlorophyll levels (*Figure 4.6*).

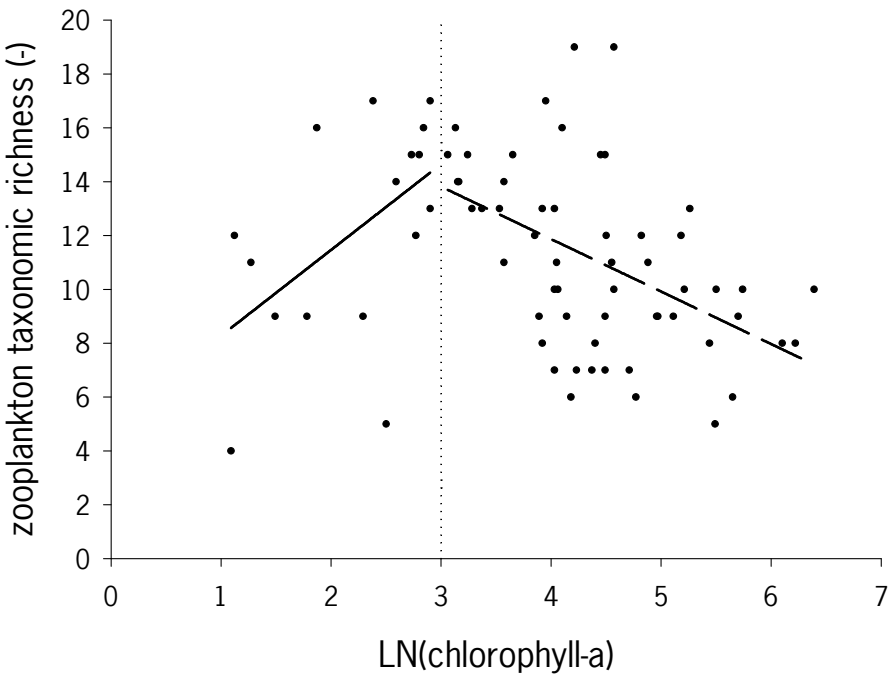

Figure 4.6. Relation between the zooplankton taxonomic richness and the LN transformed chlorophyll-a (µg L^{-1}) concentrations in the 71 sampled lakes. The solid line on the left side of the dotted line x = 3 represents the linear regression model y = 5.09 + 3.19x, with p = 0.036 and R^2_{adj} = 0.22, and the dashed line on the right side of the line x = 3 the linear regression model y = 19.7 – 1.95x, with p = 0.0002 and R^2_{adj} = 0.22.

Table 4.5. Models describing the relation between chlorophyll-a concentration and the taxonomic richness of A) phytoplankton and B) zooplankton. The values between brackets are p-values corresponding to the parameter values.

type	Model	a	B	x_0	y_0	R^2_{adj}	p
	A. phytoplankton						
Constant:	$y = y_0$	-	-	-	7.49 (0.0006)	0	-
Linear:	$y = y_0 + ax$	0.65 (0.137)	-	-	7.48 (<0.0001)	0.02	0.137
Gaussian (3 par.):	$y = ae^{\left[-0.5*\left(\frac{x-x_0}{b}\right)^2\right]}$	11.1 (<0.0001)	2.61 (<0.0001)	4.31 (<0.0001)	-	0.07	0.0331
Gaussian (4 par.):	$y = y_0 + ae^{\left[-0.5*\left(\frac{x-x_0}{b}\right)^2\right]}$	5.2 (0.0002)	0.37 (0.0074)	4.08 (<0.0001)	8.38 (<0.0001)	0.16	0.0019
	B. zooplankton						
Constant:	$y = y_0$	-	-	-	14.3 (0.0001)	0	-
Linear:	$y = y_0 + ax$	3.19 (0.036)	-	-	5.09 (0.13)	0.22	0.036
Gaussian (3 par.):	$y = ae^{\left[-0.5*\left(\frac{x-x_0}{b}\right)^2\right]}$	12.9 (<0.0001)	2.72 (<0.0001)	3.07 (<0.0001)	-	0.18	0.0005
Gaussian (4 par.):	$y = y_0 + ae^{\left[-0.5*\left(\frac{x-x_0}{b}\right)^2\right]}$	5.1 (<0.0001)	0.88 (0.0036)	3.04 (<0.0001)	8.95 (<0.0001)	0.22	0.0002

4.4 Discussion

It has been suggested that maximum taxonomic richness of herbivores should tend to occur at a higher productivity level than that for plants (Huston, 1994). Although this has been confirmed by a study of plankton in 33 mainly large North American lakes (Dodson *et al.*, 2000), our results suggest an opposite pattern. This may well represent a general pattern for shallow lakes, as a recent Danish study of 71 mainly shallow lakes using TP as productivity indicator also suggests that zooplankton diversity is highest in low productive lakes whereas phytoplankton diversity has an optimum at high TP levels (Jeppesen *et al.* 2000). In the following sections we first reflect briefly on gradients of productivity and disturbance in our data, and subsequently discuss which processes could be responsible for the humped diversity relationships we found.

4.4.1 Productivity gradients

Although all our floodplain lakes are frequently (1-2 a year) inundated by nutrient rich river water, productivity of plankton varied widely between lakes. In shallow lakes, nutrient loading from the sediment to the water column is important and many studies show that total-P concentrations in the water are enhanced by benthivorous fish (Lamarra, 1974; Andersson *et al.*, 1988; Havens, 1993; Breukelaar *et al.*, 1994; Van Donk *et al.* 1994). Submerged vegetation by contrast may reduce nutrient availability in the water column and further limit phytoplankton productivity by intercepting light and excreting allelopathic substances (*see* Scheffer, 1998 for an overview). Also phytoplankton losses through sinking tend to be higher in vegetated water columns implying a relative advantage for motile species as reflected by our data as well as other studies (Schriver *et al.* 1995; Van den Berg *et al.* 1998). It seems likely that in line with the general observations on shallow lakes the large variation in chlorophyll concentrations among our lakes is due to a large extent by differences in abundance of vegetation and benthivorous fish (Roozen *et al.* 2003). The fish and vegetation effects may be largely 'bottom-up' i.e. affecting phytoplankton productivity through availability of nutrients and light. This implies that it is not unreasonable to interpret our chlorophyll gradient (which is highly correlated with total-P and total-N, Pearson r resp: 0.44 and 0.64, both $p < 0.01$) as a productivity gradient.

4.4.2 Disturbance gradients

Even though chlorophyll concentrations may be correlated with bottom-up factors, top-down control is also likely to vary systematically over the chlorophyll gradient. There is abundant evidence that predation on zooplankton by fish tends to be lower in vegetation stands than in open water, and consequently grazing pressure by zooplankton on phytoplankton follows the opposite pattern (*see* Jeppesen, 1998 and Scheffer, 1998 for an overview). As we will argue below, the plankton diversity patterns seem likely to be highly influenced by this correlated top-down gradient. While top-down impacts on species richness can be interpreted much like the impacts of other 'disturbances' (Huston, 1994; Abrams, 1995; Proulx & Mazumder, 1998) hydrological dynamics such as inundation frequency are often considered the dominant mechanism of disturbance in floodplain ecosystems (Hein *et al.* 1999a; Tockner *et al.* 1999a, 2000b; Ward *et al.*, 1999). It is at first sight surprising that we did not find any correlation between plankton diversity and hydrology, except between phytoplankton taxonomic richness and water level change between May and October. However, all our lakes became completely isolated from the river after winter inundation 3-4 months before sampling, which may be long enough for

phytoplankton succession to lead to a community composition which is essentially independent of the inundation event (*see Chapter 5*)

4.4.3 The humped diversity-chlorophyll relationships

The explanations of humped relationships between taxonomic richness and productivity remain controversial (e.g. Abrams, 1995), but the dominant idea in brief is that few species can survive the unfavorable conditions at the low productivity end of the spectrum while at the high productivity end competitive exclusion leaves only a small dominant subset. Especially older lakes (Middelkoop, 1997) which tend to have high DOC, total nitrogen and chlorophyll-a concentrations (Roozen *et al.* 2003) have a low evenness in phytoplankton taxonomic composition suggesting that the community becomes dominated by fewer groups. One could also imagine that resources are homogeneously distributed due to the apparently intense resuspension process in the ISS-rich shallow lakes at the high-chlorophyll end of the range. Increasing resource homogeneity has been an important argument for loss of species richness at high productivity (Tilman & Pacala, 1993). Although, the systematic link of homogeneity to productivity is questionable (Abrams, 1995) the correlation may well exist in our specific case, however our data do not allow to test this. In summary, the explanations for the humped chlorophyll-diversity relationship in phytoplankton of floodplain lakes seem rather in line with ideas that already dominate the literature.

At first sight the humped relationship of zooplankton taxonomic richness to chlorophyll may seem classical along the same lines of reasoning. However, in view of the abundant shallow lake ecology literature, competitive exclusion seems a rather unlikely mechanism for explaining the low zooplankton diversity in high chlorophyll lakes. Rather intense predation by fish may limit the range of zooplankton species that occur in such highly productive lakes (Brooks & Dodson, 1965; Jeppesen, 1998; Scheffer, 1998). Indeed, competitive exclusion among zooplankton species seems more likely at the low chlorophyll end of the range. Here the presence of vegetation as a refuge makes predation-sensitive cladocerans (with taxa like *Daphnia*) less likely to be suppressed by fish predation, allowing it to become abundant and potentially out compete a range of zooplankters that are less efficient at reducing biomass of algal food sources over a wide size-range (Brooks & Dodson, 1965). Indeed, our results showed a clear trend of higher abundances of cladocerans in low-chlorophyll-a lakes (Spearman R^2=-0.335, p=0.004). Also *Daphnia* showed higher abundances in low-chlorophyll-a lakes, however this trend is not significant (Spearman

R^2=0.125, p=0.3). We also know from *Chapter 2* that the unvegetated lakes were the most turbid and also seemed to contain the highest abundance of benthivorous fish, while the composition of fish communities in the floodplain lakes are highly determined by the presence/absence of vegetation (Grift, 2001).

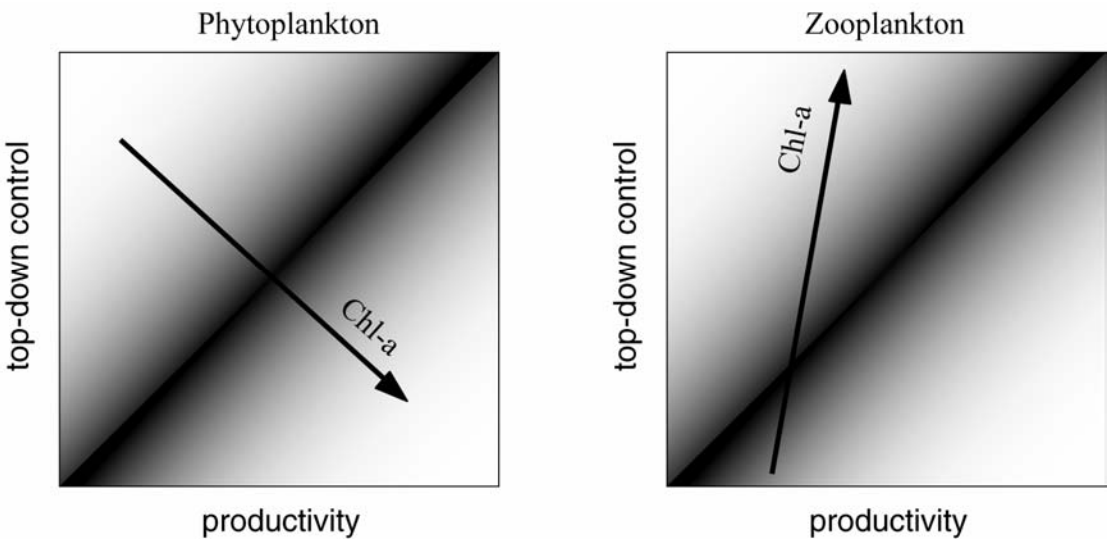

Figure 4.7. Theory and observations suggests that the optimum taxonomic diversity (shading) will occur at higher productivity levels if disturbance due to predation or other processes is more intense. In our shallow lakes intensity of top-down control is likely to be correlated negatively to productivity for phytoplankton, but positively for zooplankton (arrows). This suggests that the decrease of zooplankton taxonomic richness at high chlorophyll-a levels occurs despite (rather than due to) high productivity, and is caused by strong top-down control ('disturbance') rather than competitive exclusion.

While this explanation seems completely at odds with the 'classical explanations' for the humped diversity pattern along the productivity gradient, things can be reconciled if we interpret top-down control as a form of 'disturbance' and take the latter into account explicitly. Theory and observations (Huston, 1994) suggests that the optimum taxonomic diversity will occur at higher productivity levels if disturbance (e.g. predation pressure) is more intense. As argued intensity of top-down control of zooplankton by fish is likely to rise steeply towards higher chlorophyll levels in our systems. If one plots this correlation of productivity to (top-down) disturbance in Huston's diversity graphs (*Figure 4.7*, right hand panel) it becomes clear that the humped relationship along a productivity gradient may be related to seemingly opposed mechanisms. By contrast top-down control of phytoplankton decreases with productivity, leading to a humped

pattern for 'classic' reasons which are merely emphasized by the (top-down) disturbance effects (*Figure 4.7*, left-hand panel).

Since the classical work of Paine (1966) hypotheses about keystone-predation effects on species richness have been important in ecological thinking. However, systematic links between bottom-up and top-down control of biodiversity are only recently being explored (Leibold, 1996; 1999). For shallow lake ecosystems we know that top-down control on different trophic levels changes profoundly over a productivity gradient, and that the loss of vegetation structure with eutrophication plays a crucial role in moderating top-down effects (Jeppesen, 1998; Scheffer, 1998). It is therefore not surprising that effects of predators and vegetation structure seem important for explaining the humped diversity relationships we find. Although this may be typical of shallow lake ecosystems, strong trophic cascade effects may actually occur in a surprisingly wide range of terrestrial and aquatic ecosystems (Pace *et al.*, 1999). This suggests that it may be worthwhile to explore if shifts in top-down control and vegetation structure are more often involved in causing diversity patterns along productivity gradients.

4.5 Acknowledgements

This project was performed in co-operation and financed by RIZA Institute for Inland Water Management and Waste Water Treatment. Fieldwork would not have been possible without the help of Suzanne Graas, Bart Groeneveld, and Fred Bransen who also helped during evening filtration sessions. Frits Gillissen helped a great deal in nutrient and DOC analysis, and finally we like to thank Ronald Gylstra for his great help with statistical analysis of the data set and Miquel Lürling for his suggestions which improved the manuscript.

CHAPTER 5

Fast response of lake plankton and nutrients to slow ecosystem components: effects of river inundations on floodplain lakes

Roozen F.C.J.M., Peeters E.T.H.M., Roijackers R.M.M., Van der Wyngaert I., Wolters H., de Coninck H., Ibelings B.W., Buijse A.D. & Scheffer M.

Fast response of lake plankton and nutrients to slow ecosystem components: effects of river inundations on floodplain lakes.

5.1 Introduction

In shallow lakes dynamics of plankton and nutrients in the water column are thought to reflect almost instantaneously the condition of slow ecosystem components such as fish, macrophytes and sediment pools of nutrients which constitute as it were 'the memory' of the ecosystem (Scheffer, 1998). Floodplain lakes offer a wonderful opportunity to test the idea. Incidental massive inundations with river water reset the water column of all lakes to the same state in terms of chemical composition and plankton.

Indeed, the chemistry and biology of floodplain lakes are considered to be highly influenced by their connectivity with the river (Amoros & Roux, 1988; Van den Brink *et al.*, 1992; Tockner *et al.*, 2000b). Various important theories address this relationship. The flood pulse concept emphasizes the importance of the lateral river-floodplain connections in both tropical (Junk *et al.*, 1989) and temperate climates (Bayley, 1991; Junk, 1999). Floods allow an exchange of matter and organisms between the river and the floodplain (lakes), changing the ecological and chemical properties of the flooded lakes, but on a temporal scale. Tockner *et al.* (2000b) extended this concept by including the flow pulse, i.e. connectivity between floodplain lake and river below bank full. Also, many recent studies showed strong effects of connectivity on the chemical and biological properties of the floodplain lakes of temperate rivers (Van den Brink *et al.*, 1994; Heiler *et al.*, 1995; Spink *et al.*, 1998; Tockner *et al.*, 1999a; Buijse *et al.*, 2002; Van Geest *et al.*, 2003; Roozen *et al.*, 2003). The timing of a flood is thought to be crucial for the effects on the water quality of the inundated lakes (Junk *et al.*, 1989; Bayley, 1991; Hein *et al.*, 1999a; Tockner *et al.*, 2000b). Inundations of the floodplain lakes by the lower River Rhine are almost entirely restricted to the winter and spring (Van den Brink *et al.*, 1994; Middelkoop & Van Haselen, 1999). For this river, Van den Brink *et al.* (1994) described a conceptual model for the impact of hydrology on both chemistry and biology of floodplain lakes, mainly based on differences in hydrological connectivity (*see Chapter 1*). In their view, especially the frequency and duration of inundation are thought to be especially important for the floodplain lakes along the lower Rhine.

Despite all this interest, there have been virtually no detailed studies addressing the dynamics of the ecosystem response upon retreat of the river after inundation (Pithart, 1999). The main focus of the present study is to unravel the impact of a flood event by river water on several aspects of the ecosystem of floodplain lakes, during and after such an event: how do floodplain lakes respond to inundations by the river and upon retreat of the flooded water? The almost simultaneous inundation of the numerous floodplain lakes can be viewed as an informative massive ecological experiment that may reveal effects of disturbance, one of the main themes in ecology since classic contributions of Connel (1978) and others. In fact, the article which is considered to mark the start of ecology as a science (Forbes, 1887) is largely about the intriguing dynamics of the ecosystem of a floodplain lake after inundation. In this study, we take advantage of this annual natural experiment in floodplain systems. We analyzed data from a three-year (1998-2000) monthly monitoring program of ten lakes in two floodplain areas along the river Waal. The two floodplains are situated only five km from each other, but are influenced differently by the river Waal. The lakes near Deest are inundated only via overbank floods, while the lakes near Ochten are inundated already at lower water levels through a sluice gate (from November until March).

5.2 Methods

5.2.1 Study areas

The river Waal is the main branch of the lower River Rhine after its division into three branches, discharging 65% of the Rhine water (Van den Brink *et al.*, 1994). The average discharge of the Waal is 1450 m^3s^{-1} (Middelkoop & Van Haselen, 1999). On average, two peaks of discharge occur every year; in winter due to high precipitation and low evaporation in the catchment area, and in spring due to melting of snow in the Alps (Middelkoop & Van Haselen, 1999).

From March 1998 to December 2000, ten floodplain lakes (*Figure 5.1*; *Table 5.1*) along the river Waal (Netherlands) were sampled monthly. The ten studied floodplain lakes are situated in two different floodplains; five lakes are within the floodplain Afferden and Deest (from now on referred to as Deest) on the south bank of the Waal near river km 899, and five lakes are situated within the more downstream floodplain of Ochten on the north bank of the Waal near river km 905. The lakes near Deest are inundated only via overbank floods, while the lakes near Ochten are inundated already at lower water levels via a temporarily opened sluice gate (from November until March) in the minor embankment.

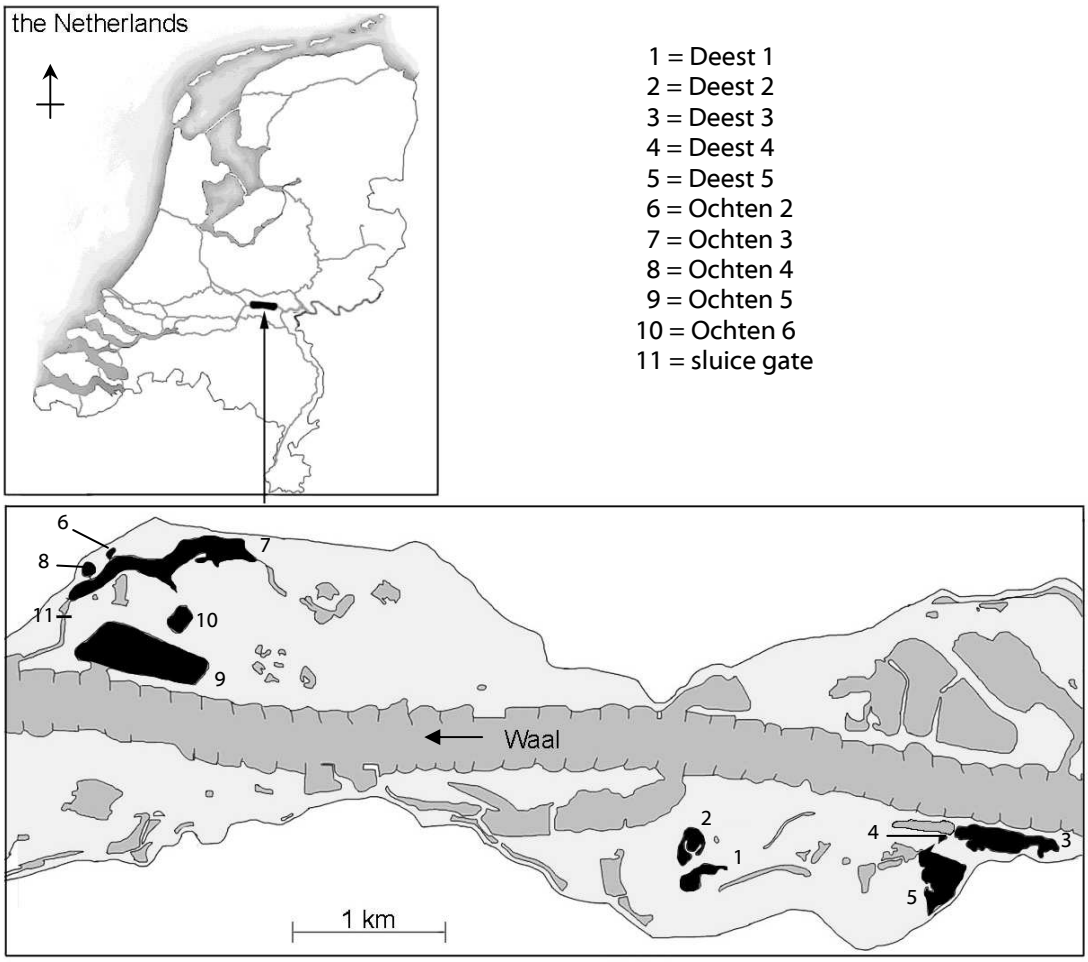

Figure 5.1. Overview of the Netherlands and the sampled floodplain lakes in the floodplains of Ochten and Deest (above and below the river respectively) along the river Waal. The arrow indicates the flow-direction of the river Waal. (after E.M. de Haas & B. Reuvers)

While, as all lakes, the floodplain lake ecosystems are driven by seasonal cycle of the local weather conditions (e.g. *Figure 5.2*), their dynamics are also strongly affected by the hydrology of the river. *Figure 5.3* shows the water levels of the floodplain lakes near Deest and the river Waal at km 899 (upper panel) and the water levels of the floodplain lakes near Ochten and the river Waal at km 905 (lower panel). Before the start of the monitoring, the last flood occurred from February 28th until March 4th 1997. The lines indicating the water levels of the river (*Figure 5.3*) show that within the monitoring period, four periods of high discharges occurred, the first starting in November 1998. The Figures also show that some of the lakes closely follow the water level of the river

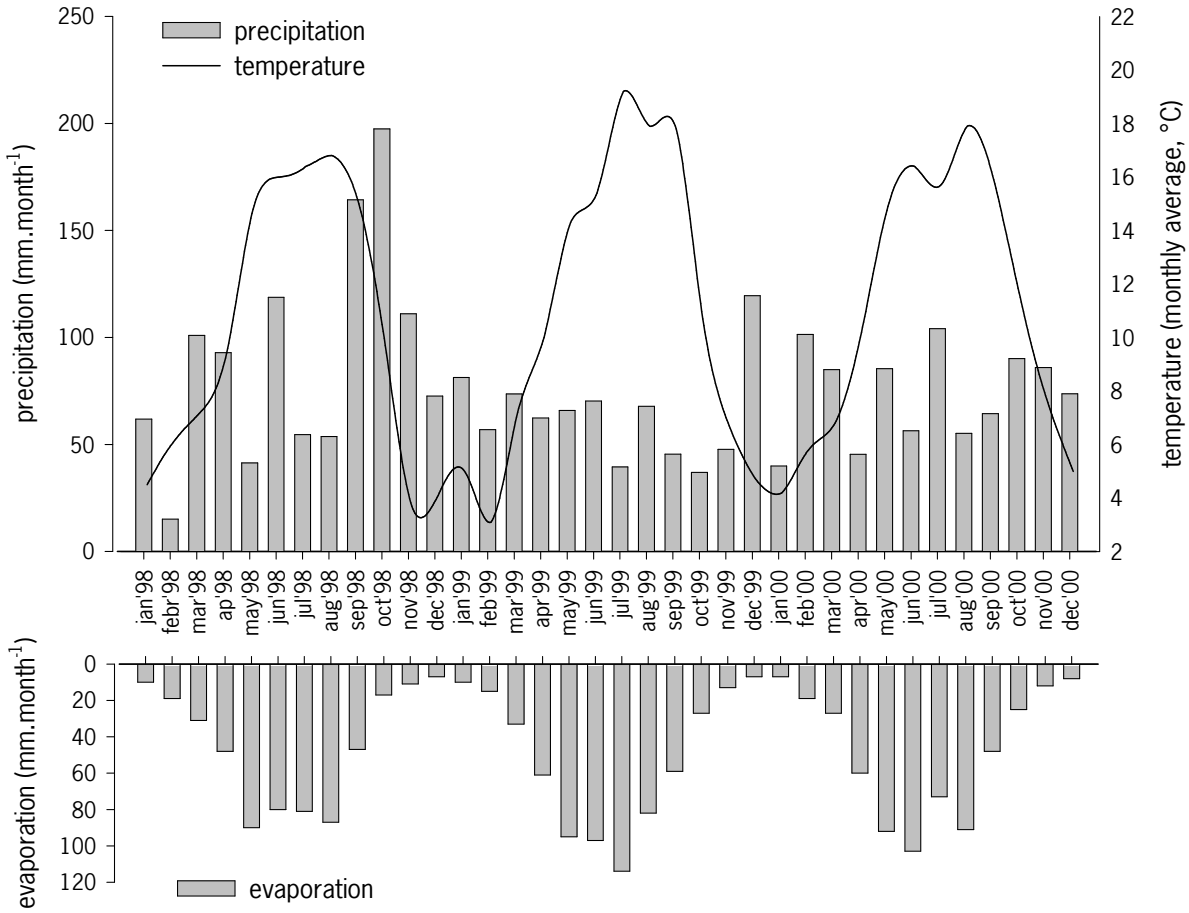

Figure 5.2. Monthly average precipitation (bars up), evaporation (bars down) and temperature (solid line) over the monitoring period 1998-2000. The values are obtained from the Royal Dutch Meteorological Institute (KNMI) and calculated from daily registrations: 1) for precipitation and sun-hours at two different meteorological stations at Tiel and Zetten and 2) for evaporation from registrations of the station at Herwijnen. All stations are in the vicinity of the floodplains.

(Deest 1 and Ochten 5), while others follow with some delay, caused, among other things, by differences in permeability of the soil and the distance to the river.

The timing and duration of inundations of the lakes near Deest is determined by the lowest threshold between the river and the floodplain. The lakes Deest 1, 2 and 5 are inundated at a water level in the river of 8.40 m + NAP (standardized water level in relation to the sea) and Deest 3 and 4 at a water level of 10.0 m + NAP (*Figure 5.3*, upper panel).

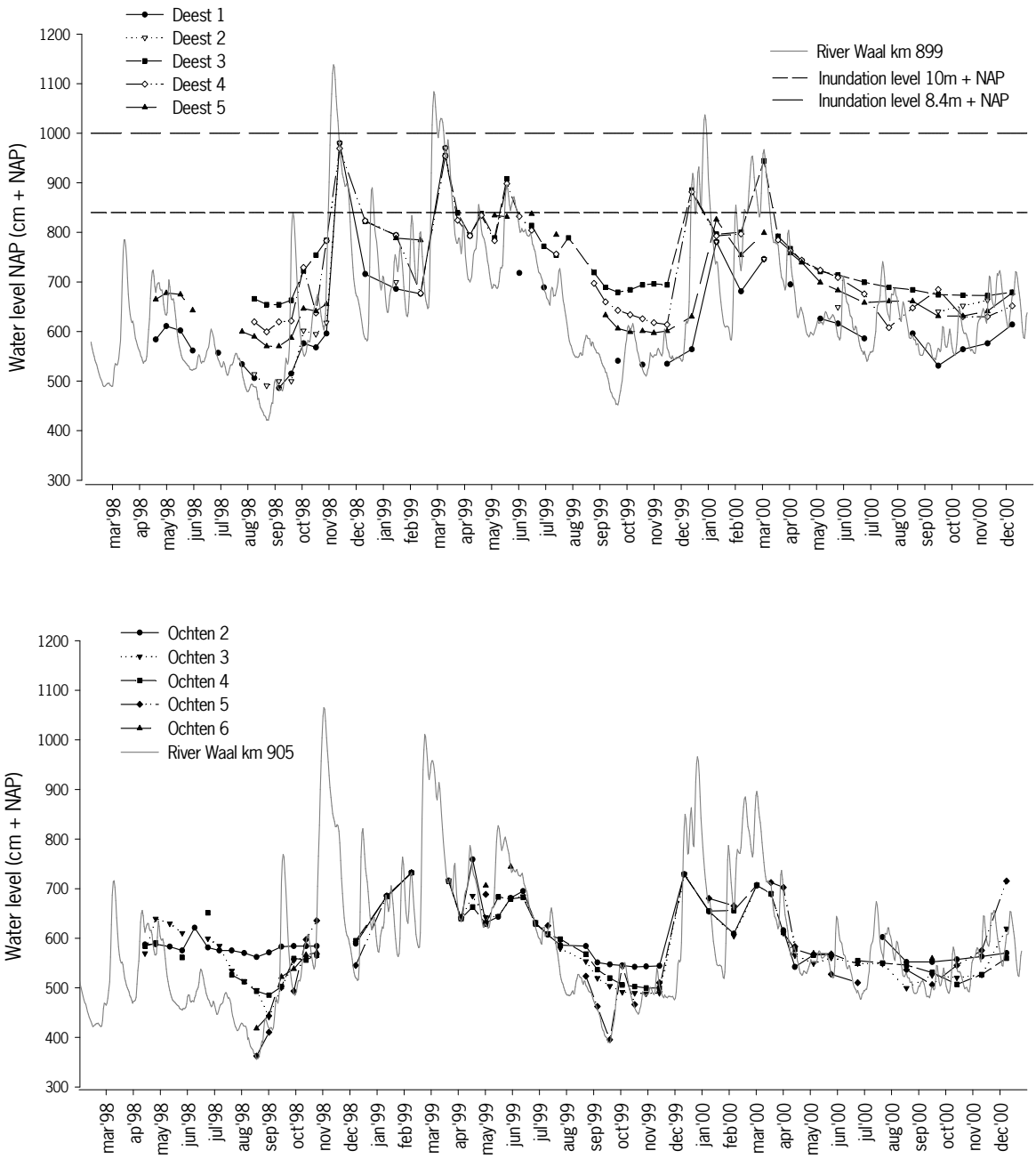

Figure 5.3. Water levels of the river Waal and the ten studied lakes. The top panel shows the river water level at Waal km 899 and the lakes in the floodplain of Deest. The horizontal lines indicate the river water level at which the lakes Deest 1, 2 and 5 are inundated (lower dashed line) and at which lakes Deest 3 and Deest 4 are inundated (upper dashed line). The lower panel shows the river water level of the Waal at km 905 and the lakes in the floodplain of Ochten.

This means that these two groups of lakes were inundated respectively twelve and three times during the three years of monitoring. The rapid outflow of the all the lakes in this floodplain occurred down to a water level of 8.0 m + NAP. Inundations of the lakes near Ochten could not be calculated exactly, due to the presence of a sluice gate in the minor embankment. The sluice gate opened each year in November or earlier when high discharges occurred, and closed again in March or at the end of high discharges between March and November. Ochten 5 was permanently connected to the river, and Ochten 3, 2, 4 and 6 became connected in this order at an increasing discharge of the river. Calculations on the hydrological data revealed that all lakes are mainly fed by river water (above and below ground) or rain water, and the contribution by ground water (from the hinterland) was low (unpublished results).

5.2.2 Data collection

Hydrochemical, hydrological data and suspended solids concentrations in the river were obtained from the Institute for Inland Water Management and Waste Water Treatment (RIZA). Meteorological data were obtained from the Royal Dutch Meteorological Institute (KNMI). No data were available on phyto- and zooplankton composition in the river.

At each lake a mixed water sample (30 L) was taken with a transparent tube (length 1.5m, diameter 8 cm) from a boat. All sub-samples were taken from the mixed sample, and stored in different flasks. Phytoplankton samples were stored in a 1 liter flask containing 3% lugol's solution (final concentration), zooplankton samples (25 liter) were filtered over a 55 µm zooplankton net and fixed in 5% formaldehyde (final concentration). Phytoplankton abundance and composition were analyzed microscopically using an inverted light microscope (Olympus IMT-2), at 630x magnification and zooplankton abundance and composition were analyzed to the species level also with an inverted microscope (Olympus IMT-2), at 200x magnification. Macro-ions and nutrients were analyses conform Dutch standard procedures (standard NEN-norms). Inorganic suspended solids were analyzed from a known volume of the five liter water samples, collected on pre-weighed (GF/F filters, Whatmann), dried for 24 hours at 105 °C, weighed, combusted for 3 hours at 530 °C and weighed again. Control filters were processed similarly with each measurement. An overview of various water quality variables are presented in *Table 5.2*.

5.2.3 Statistical analyses

Dissimilarities between the lakes were calculated for macro-ions, nutrients (both in *Table 5.2*), phytoplankton and zooplankton (both at the level of genus) using the Multi-Variate Statistic Tool pack, version 3.11f, by Kovach Computing Services. Standard Euclidean distances (dissimilarities) were calculated by centroid cluster analyses on $\log_{10}$ transformed data. For both individual floodplains the dissimilarity of each pair of lakes was calculated (resulting in 10 pairs of lakes for each floodplain) and averaged. The average dissimilarities with their standard errors of both floodplains were plotted against time. Differences in dissimilarities between and within floodplains are tested with non parametric tests (Wilcoxon and Mann-Whitney U test respectively), using the statistical tool pack SPSS® version 10.1.0 (SPSS Science, Briljant Software & Techniek, Mijdrecht, The Netherlands).

Principal Component Analyses (PCA; Jolliffe, 1986; Ter Braak, 1995) was performed to detect relations between the river discharge and the chemical condition (macro-ions and nutrients) of the river water. Standardized PCA resulted in several axes, and each axis contained variables that are comparable in their occurrence. Each variable was assigned to the axis for which their correlation coefficient was highest.

The principal response curves (PRC) analysis is a multivariate method designed to test and display changes relative to a well defined reference across time. The method is based on reduced rank regression that is adjusted for changes across time in the control treatment. This allows the method to focus on time-dependent treatment effects (Ter Braak & Šmilauer, 1995). In other words, PRC is a RDA (Redundancy Analysis) analysis using nominal variables denoting sampling date as covariables and the product of sampling date and treatment levels (in our case the different lakes) as nominal explanatory variables (*see* Van de Brink & Ter Braak, 1997; 1999 for more details). The method has been developed for analyses of ecotoxicological studies. It was first applied to the results of ecotoxicological experiments evaluating the effects of pesticides on freshwater ecosystems (Van de Brink & Ter Braak, 1999) but rapidly terrestrial ecosystems (Smit *et al.*, 2002) and the analysis of ecological field experiments (Frampton *et al.*, 2001) followed. PRC has only been applied to experimental data with the exception of a monitoring study by Leonard *et al.* (2000). This study, however, also dealt with an ecotoxicological topic, the effect of endosulfan exposure on macro invertebrate communities. The theory of the PRC-analysis is given in Van der Brink & Ter Braak (1997; 1999).

The PRC-method is applied to find the effect of floods on ecosystem variables of different floodplain lakes. In present study, the control for each analysis was defined as the means of the variables sampled in November 1998, during the first inundation of all the studied lakes. The argument for this was that during inundation, the water quality of the lakes is supposed to be homogeneous due to the simultaneous flooding by the river (Pithart, 1999). These mean values from November 1998 were used as a control for every sampling date during the monitoring, in order to find the resistance against and recovery after inundation. Values on the y-axis (the calculated canonical coefficient) of the PRC are not presented, while these are not relevant for showing the patterns the lakes follow in relation to the reference line (x=0). The 'species' weight (b_k) must be interpreted as the affinity of the taxon with the principal response curves (Van de Brink & Ter Braak, 1999), and implies that when lakes develop in the positive direction in the PRC curve the variables with a positive species weight increase in importance (contribution), and *vise versa*. Due to the large number of genus used in the analyses, the species weights for phytoplankton are not presented. The PRC-analyses were performed with the same variables as were used for calculating the dissimilarities, except for the macro-ions, where Manganese strongly determined the analyses and therefore was deleted from the analysis. No statistical analyses could be performed on the PRC, because there were no replicates. Patterns are therefore interpreted visually.

5.3 Results

5.3.1 River water analysis

PCA on macro-ions in the river water resulted in four axes that together explained 79% of the variance in time (*Table 5.3*). All macro-ions, except manganese, were strongly negatively correlated to the river discharge and were grouped on the first axis which corresponds to the salinity of river water. Manganese was positively correlated to the second axis which was linked to the river discharge and inorganic suspended solids concentrations.

PCA also showed a strong link between nutrients in the river water and discharge (*Table 5.3*). Nutrients which both had no significantly correlation to discharge, except SO_4 (negatively correlated to discharge), were assigned to the third and fourth axis. The third and fourth axis showed seasonal patterns, (*Figure 5.4*). Variables assigned to the third axis (NH_4 and PO_4) were highest in spring and lowest in autumn, whereas variables assigned to the fourth axis (NO3 and SiO_2) were highest in the winter.

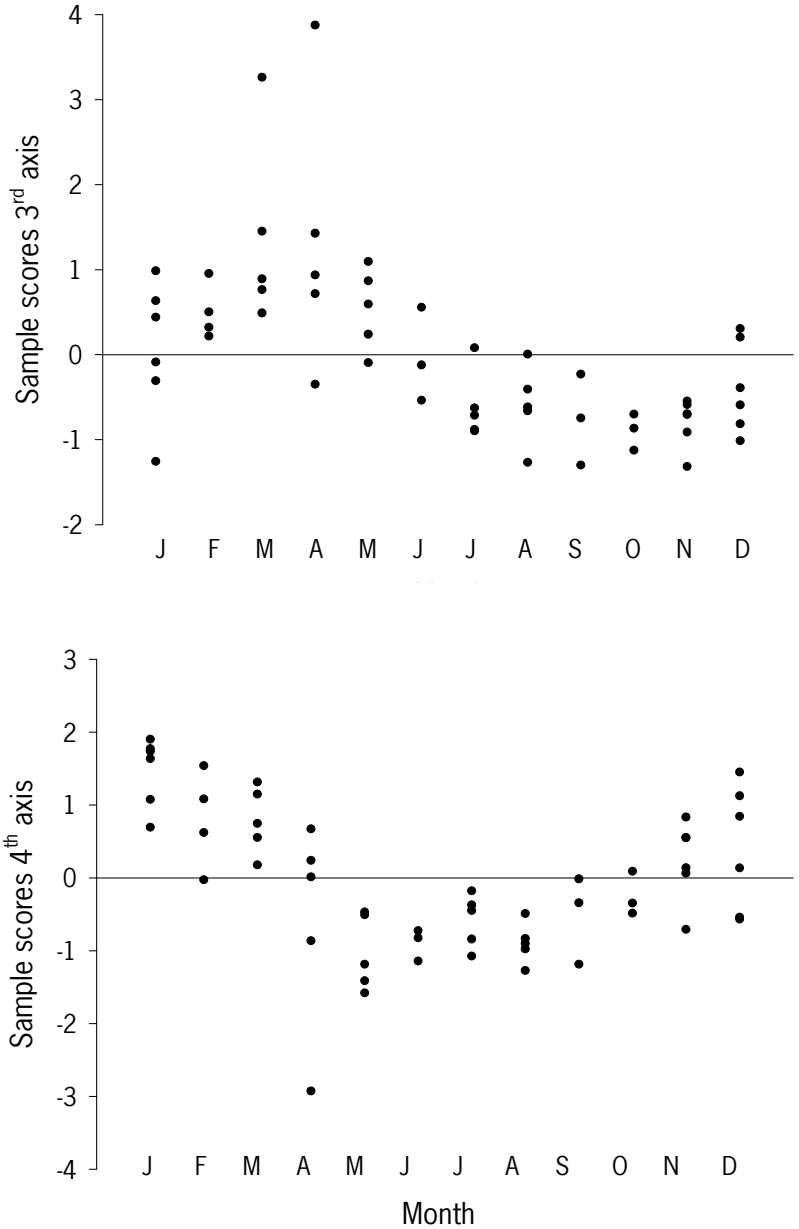

Figure 5.4. The sample scores of the 3rd axis (left panel) and 4th axis (right panel) from the PCA-analysis of the river hydrological data (see also Table 5.3), plotted against the months of the year. Clearly visible are the seasonal patterns of both axis.

Table 5.3. Principal component analyses of the chemical quality and the concentration inorganic suspended solids (ISS) of River Rhine. The most significant correlations ($p < 0.001$) are printed in ***bold****.*

	Axis 1 (38%)	Axis 2 (18%)	Axis 3 (11%)	Axis 4 (11%)
Discharge ($m^3.s^{-1}$)	**-0.663**	**0.622**	0.053	0.150
ISS ($mg.l^{-1}$)	-0.353	**0.855**	0.097	-0.051
Macro-ions				
Cl ($mg.l^{-1}$)	**0.964**	-0.108	-0.051	0.000
Ca ($mg.l^{-1}$)	**0.772**	-0.028	0.322	0.170
K ($mg.l^{-1}$)	**0.949**	0.004	-0.113	0.028
Mg ($mg.l^{-1}$)	**0.682**	-0.099	0.365	0.111
Na ($mg.l^{-1}$)	**0.950**	-0.148	-0.086	-0.136
Mn ($\mu g.l^{-1}$)	-0.204	**0.916**	0.043	-0.045
Nutrients				
NH_4-N ($mg.l^{-1}$)	0.170	0.148	**0.822**	0.072
NO_3-N ($mg.l^{-1}$)	0.252	0.092	0.327	**0.810**
PO_4-P ($mg.l^{-1}$)	0.299	0.184	**-0.725**	0.431
SO_4 ($mg.l^{-1}$)	**0.788**	-0.211	0.060	0.127
SiO_2 ($mg.l^{-1}$)	-0.189	0.123	-0.308	**0.825**

5.3.2 Influence of inundation on chemistry

The (relative) change in concentrations of macro-ions from the last sampling before the November 1998 flood to the following sampling (during flood) demonstrates that the least connected lakes were affected most by the flood (*Figure 5.5*). Like the PCA on river water, the permanently connected lake Ochten 5 (*Figure 5.5*, lower panel) shows a decrease in concentrations of most macro-ions at higher discharge (flood), indicating dilution *of the river water*.

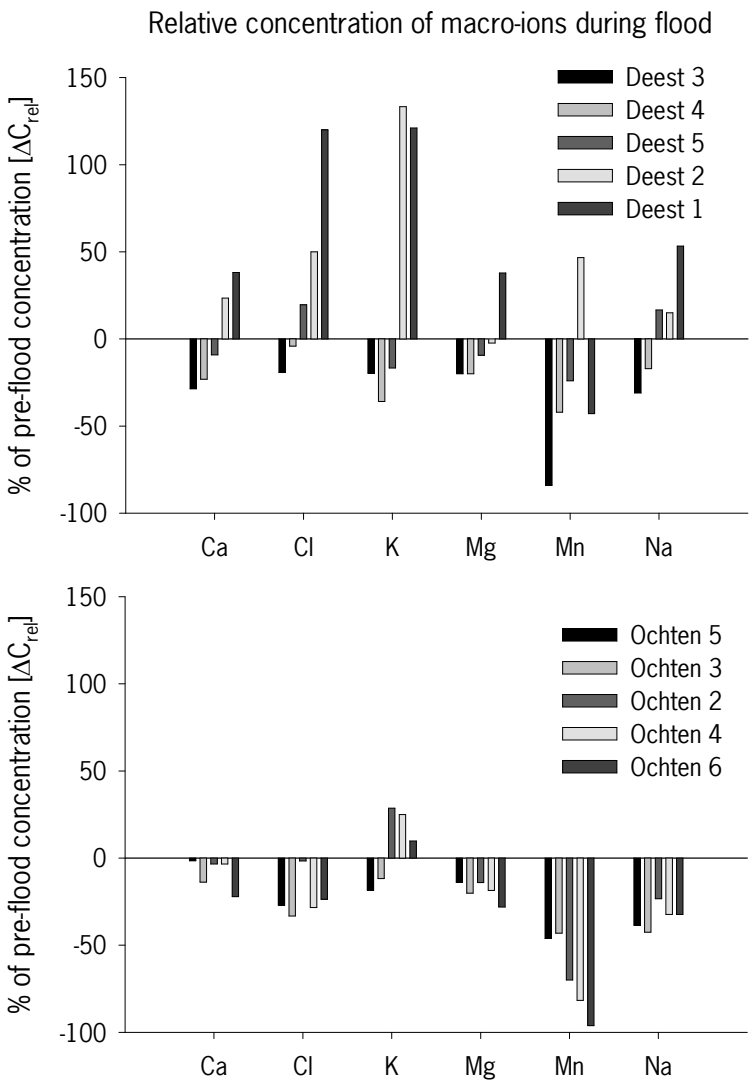

Figure 5.5 Relative change [ΔC_{rel}] in concentration of macro-ions in the floodplain lakes near Deest (upper panels) and Ochten (lower panels) between two consecutive sampling dates; the first date (C_1: October 29th, 1998) before the flood and the second (C_2: November 11th, 1998) during the flood. For each floodplain the lakes are ordered from the one with the highest connectivity on the left to the one with the lowest connectivity on the right. Values are calculated with the formula: ($[\Delta C_{rel}]=[C_1]-[C_2])\backslash[C_1]*100\%$. Positive values indicate an increase in concentrations in the lakes compared to the pre-flood situation, whereas negative values indicate a decrease.

Comparing concentrations of nutrients in lakes during a flood with the pre-flood situation (*Figure 5.6*) showed an increase in concentrations nitrate, phosphate and silicate during the flood, while ammonium and sulphate decreased in most cases.

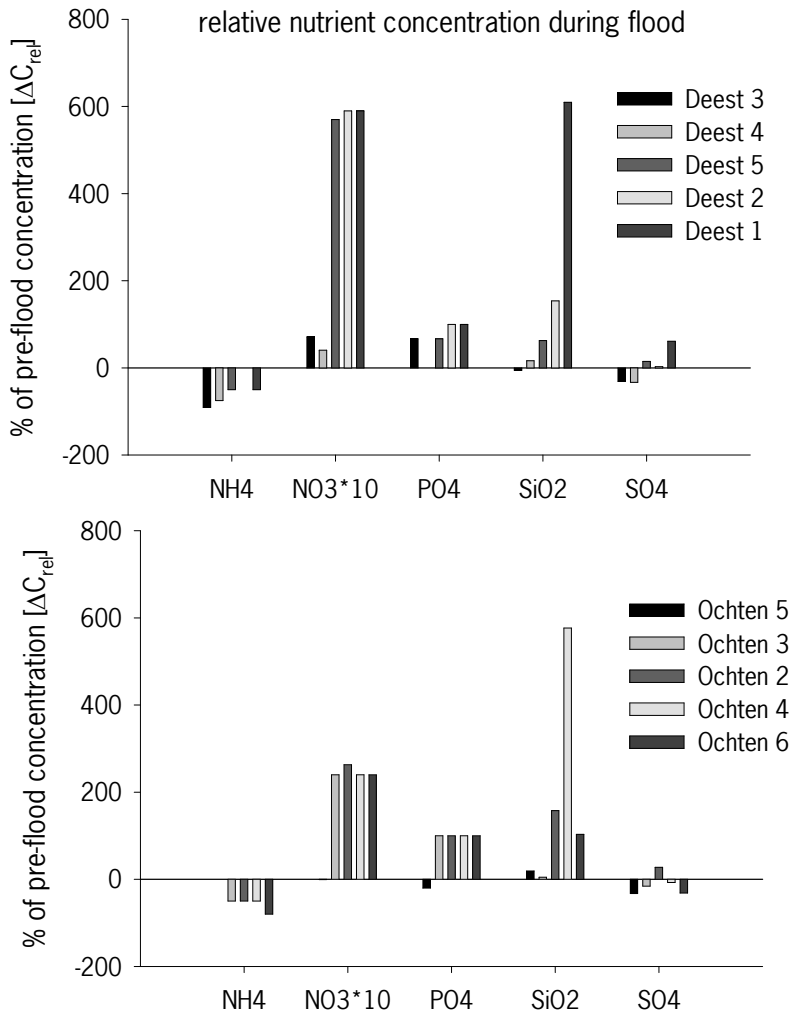

Figure 5.6 Relative change [ΔC_{rel}] in concentration of nutrients in the floodplain lakes near Deest (upper panels) and Ochten (lower panels). Values of NO_3 have to be multiplied by 10. For more information see *Figure 5.5.*

5.3.3 Dissimilarities

Before the November 1998 inundation the lakes in the floodplain of Deest were significantly more dissimilar with respect to the macro-ions than the lakes in the floodplain of Ochten *(Figure 5.7a*; Wilcoxon: n=8, p=0.012). During the November 1998 inundation all lakes became highly similar. The impact on the lakes near Deest was even more severe than on those near Ochten. The higher dissimilarities before November 1998 for the Deest floodplain were not obtained again in 1999 and 2000 (*Table 5.4*). This is also illustrated in *Figure 5.5*, where variations in response to flood were higher in the upper panel (Deest). Lakes in both floodplains started to diverge after the 1998 inundation, but the inundation in March 1999 set back this diversification process for both floodplains as did the January 2000 flood (*Figure 5.7a*). Differences in

dissimilarities between the floodplains after the 1998 flood were not significant for nutrients. The dissimilarity of both floodplains based on nutrients (*Figure 5.7b*) differed significantly in 1998 before the November flood (Wilcoxon: n=8, p=0.012), Deest showing less similar lakes. This difference between the floodplains continued in 1999, but not in 2000 (*Table 5.4*). Remarkable was the difference between the floodplains during the period from November 1998 until March 1999. The individual development of the lakes in the floodplain of Ochten remained behind the development of the lakes near Deest, resulting in significantly lower diversity in the lakes in this floodplain, due to the permanently opened sluice gate at Ochten (Mann-Whitney U test: n=4, p=0.03).

*Table 5.4. Non-parametric comparisons of the annual mean dissimilarity values between the floodplains (Wilcoxon test for related samples, above the diagonal) and within the floodplains (Mann-Whitney U test, below the diagonal). Significant differences are marked with * p<0.05, ** P<0.001.*

	Ochten'98	Ochten'99	Ochten'00	Deest'98	Deest'99	Deest'00
Macro-ions						
Ochten'98	X			0.013*		
Ochten'99	0.87	X			0.64	
Ochten'00	0.54	0.44	X			0.48
Deest'98				X		
Deest'99				0.017*	X	
Deest'00				0.006**	0.84	X
nutrients						
Ochten'98	X			0.007**		
Ochten'99	0.31	X			0.041*	
Ochten'00	0.35	0.10	X			0.16
Deest'98				X		
Deest'99				0.16	X	
Deest'00				0.72	0.48	X
phytoplankton						
Ochten'98	X			0.72		
Ochten'99	0.60	X			0.012*	
Ochten'00	0.13	0.11	X			0.019*
Deest'98				X		
Deest'99				0.069	X	
Deest'00				0.60	0.017*	X
zooplankton						
Ochten'98	X			0.14		
Ochten'99	0.54	X			0.35	
Ochten'00	0.92	0.35	X			0.019*
Deest'98				X		
Deest'99				0.14	X	
Deest'00				0.77	0.045*	X

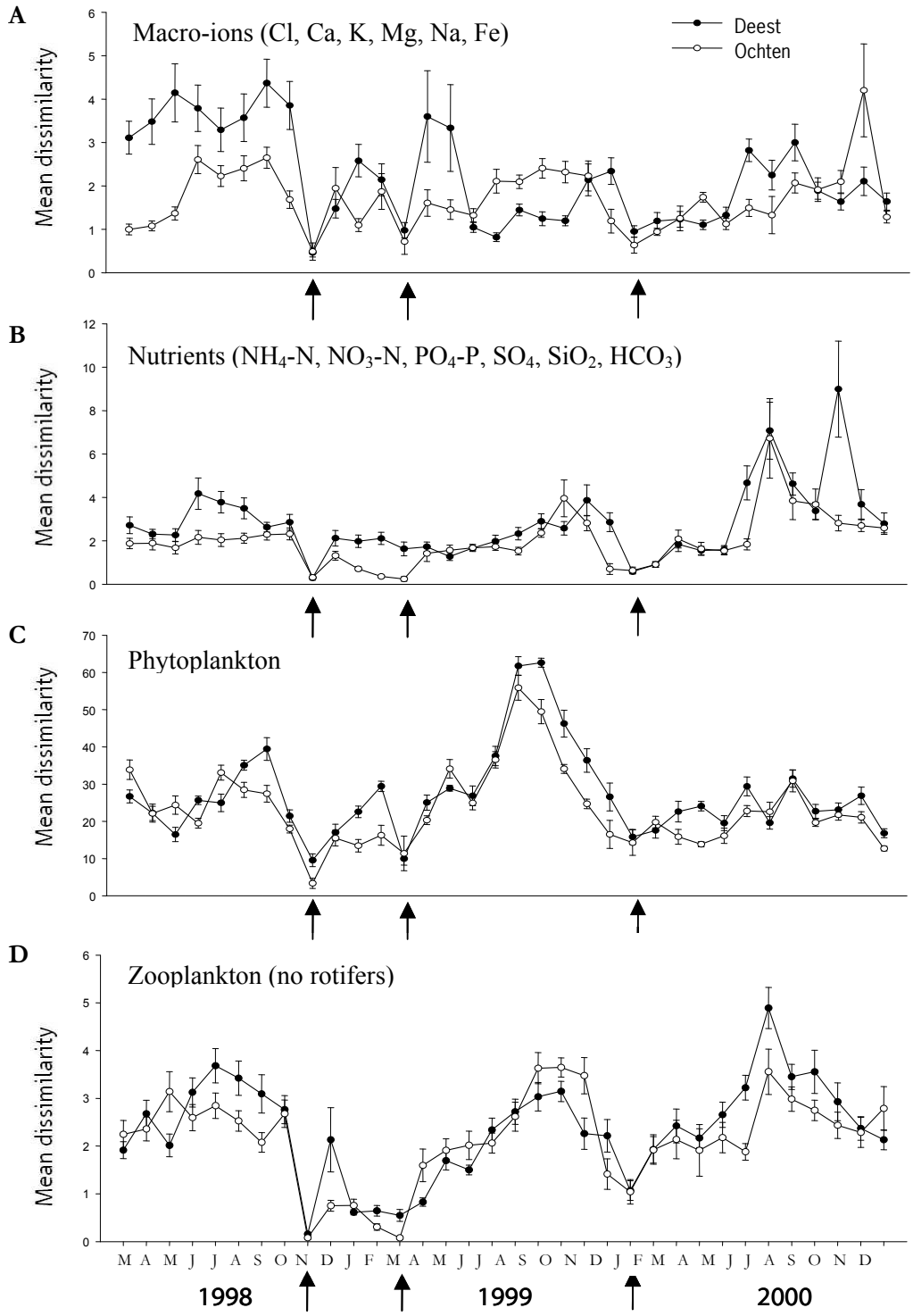

Figure 5.7. Results of the dissimilarity analyses (standard Euclidean centroid cluster analyses with log10 transformed data) of the: a) concentrations of macro-ions and b) concentrations of nutrients, both presented in Table 5.2 and c) phytoplankton abundances (genus) and d) zooplankton abundances (genus). The closed circles indicate the floodplain of Deest, while the open circles indicate the floodplain of Ochten. Arrows indicate start of overbank inundations.

Dissimilarities of the lakes based on phytoplankton were comparable for both floodplains in 1998 and were significantly higher in Deest in 1999 and 2000 (*Figure 5.7c*, *Table 5.4*). Lakes in Deest differed in 1999 more from each other than in 1998 and 2000 (*Table 5.4*). Dissimilarities based on zooplankton were comparable with phytoplankton patterns (*Figure 5.7d*, *Table 5.4*). Lakes in both floodplains started to become different after the early spring inundation in March 1999, due to their individual successional development. In 2000 no phytoplankton seasonal development seemed to happen at all.

5.3.4 Principal response curves

The PRC on macro-ions shows clear effects of floods on the macro-ion concentrations of each lake (*Figure 5.8a*). The horizontal axis (when y = 0) is the reference and was based on the mean concentrations of the sampled macro-ions in all lakes in November 1998. Therefore, all lakes in November 1998 were clustered around the x-axis. Similar clusters of the lakes are also found for March 1999 and January 2000, coinciding with two other periods of high river discharge. The PRC also clearly shows the effect of the open sluice gate at Ochten by clustering the lakes near Ochten around the permanently connected lake Ochten 5, apart from the lakes in Deest (*Figure 5.8a*). Variation in water quality between the lakes was highest before the November 1998 flood, and was not observed after that flood. Species weights of variables (*Figure 5.8a*) indicates that iron (Fe) is more related to the lakes in Deest and, while its weight is close to 0 (the reference), Fe can be related to inundations. Sodium (Na), chloride (Cl) and calcium (Ca) seemed to be more related to the lakes in Ochten, during isolation.

PRC on nutrients also shows the importance of the permanently opened sluice gate. (*Figure 5.8b*). Lakes near Ochten remained scattered close to the reference line (horizontal axis), indicating that nutrient concentrations in the river remained more constant compared to the macro-ions. Lakes near Ochten showed a response to connectivity already in December 1999, whereas lakes near Deest followed a month later (*Figure 5.8b*); again the effect of the presence of the sluice gate. The seasonal pattern found in the PRC was mainly caused by SiO2 and NO3, which are important during the winter periods as indicated by the species weights. Running the PRC-analyses without these nutrients resulted in a completely different curve without a seasonal pattern and the differences between the floodplains in the period from November 1998 until March 1999 disappeared. The permanently connected lake Ochten 5 (mostly resembling the river water) showed a similar seasonal pattern in nutrient composition suggests that, indeed as presented in *Table 5.3*, nutrients in the river water are more affected by seasonality than by discharge.

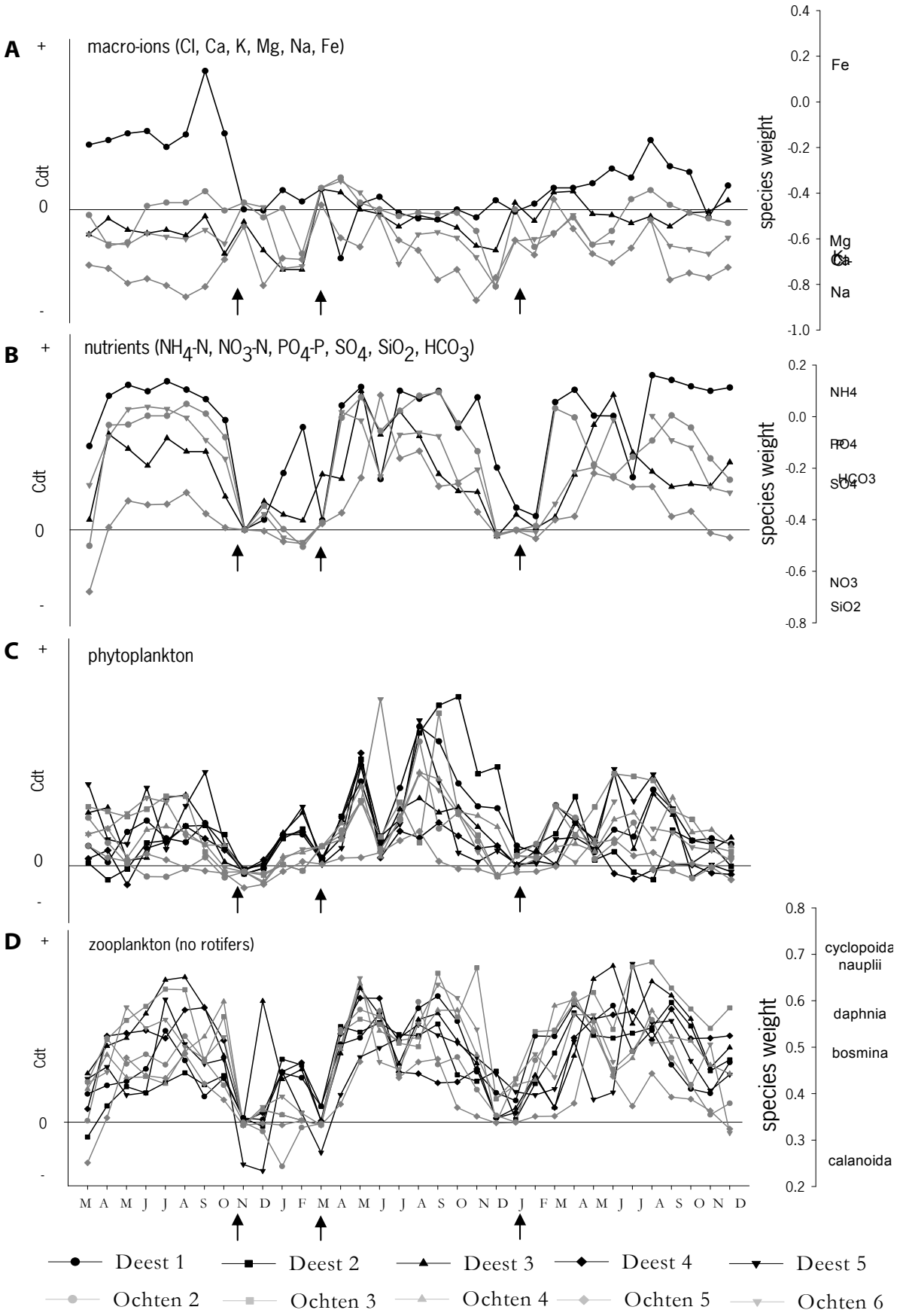
A
macro-ions (Cl, Ca, K, Mg, Na, Fe)
Cdt
species weight
Fe
Mg
Na
B
nutrients (NH4-N, NO3-N, PO4-P, SO4, SiO2, HCO3)
NH4
PO4
HCO3
SO4
NO3
SiO2
C
phytoplankton
D
zooplankton (no rotifers)
cyclopoida
nauplii
daphnia
bosmina
calanoida
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
Deest 1
Deest 2
Deest 3
Deest 4
Deest 5
Ochten 2
Ochten 3
Ochten 4
Ochten 5
Ochten 6

Figure 5.8. Results of the Principal Response Curve analyses by lake for: a) concentrations of macro-ions and b) concentrations of nutrients, both presented in Table 5.2, c) phytoplankton abundances (genus) and d) zooplankton abundances (genus). The y-axis represents the canonical coefficient, which is simplified by only presenting the positive (+) and negative (-) direction. The species weights (see text) for the macro-ions, nutrients and zooplankton are also presented. For phytoplankton these are left out due to the large amount of species. Arrows indicate start of overbank inundations.

PRC-analyses showed that the effects of the floods on both phyto- and zooplankton were clearly visible by the scattering of the lakes near the horizontal (reference) axis (*Figures 5.8c* and 5.*8d*). Remarkable are the patterns in summer 1999 for both phytoplankton and zooplankton, where in respectively June and July dips in the developments of the community structure of the lakes are observed. After these 'dips' the lakes seem to pick up their individual development again.

5.4 Discussion

Our results allow a remarkable glimpse of how slow and fast components interact in these ecosystems. The rapid divergence of plankton and nutrient dynamics to apparent local idiosyncratic conditions in the different lakes is a clear feature of our time series. However, the natural experiments we studied are far from 'controlled' experiments, and the interpretation of the dynamics in the seasonal and heterogeneous field situation has obvious caveats. Here we discuss some major uncontrolled sources of variation.

5.4.1 What river water brings into the lakes

The impact of inundation of a lake ecosystem should depend on the organisms and chemical compounds the river brings in (e.g. Flood Pulse). The composition of river water has a seasonal component, but also changes with the discharge. Thus floods do not simply bring in average river water and plankton. The biological activity of river phytoplankton (and consequently its abundance) is low during winter due to low temperatures and low irradiance levels partly caused by the high turbidity of the river water (Cole *et al.*, 1992; Riedler & Schagerl, 1998; Hein *et al.*, 1999b). Also chemical composition of the river water changes over time. Our data indicate that the concentrations of most macro-ions are lower during periods of high river discharges. Such a pattern is also observed for heavy metals in the Lower Rhine (Middelkoop, 1997), specific conductance in the Danube (Tockner *et al.*, 1999a), and for macro-ions in a steep headwater basin (Tsujimura *et al.*, 2001). Only manganese (Mn) correlated positively to the river discharge,

meaning that this macro-ion was not diluted at high discharges. Its positive relation with inorganic suspended solids (*Table 5.3*: both increased with increasing discharge) indicates that manganese was strongly influenced by resuspension from the floodplain during the flood.
The mean nutrient concentrations in the river did not seem to differed between periods of normal and high discharge. Tockner *et al.* (1999a) found that nitrate was positively correlated to discharge in the river Danube. Silicate concentrations in the river were extremely high all year round and increased with increasing discharge. A positive relation between discharge and silicate concentration was found here as well, although the relation was weak. Most nutrients in the data set showed a clear seasonal pattern, which might conceal patterns caused by floods (Junk, 1999) or *vise versa*.

Our time series analyses clearly illustrate how differently timed floods bring in different river water and seston. Comparing the position of the clusters in the PRC curves at the winter inundation of November 1998 versus the spring inundation of March 1999 shows that the phytoplankton composition became quite different at those two events, and also the macro-ions showed a clear difference. This finding is in line with the common notion that timing of a flood is essential for the effect on water quality and biota in floodplain lakes (Junk *et al.*, 1989; Bailey, 1991; Hein *et al.*, 1999a; Tockner *et al.*, 2000a; Grift, 2001). Differences in response of lake chemistry (*i.e.* development in time in relation to the reference, PRC) to floods in different years indicates that year to year variations in hydrochemistry can be important for the effect of flooding, when also the magnitude of a flood may determine the extent of the effect.

5.4.2 Degrees of isolation

The lakes we studied differ in the degree of isolation from the river. Comparison of the pre- and post-flood concentrations of nutrients and macro-ions in the different lakes, showed that the degree of connectivity (or isolation) is important for, at least, the short-term relative impact of a flood on the water quality in the lake. The most isolated lakes in both floodplains were affected more by the incoming flood water. This is in line with the general observation that systems with the least exchange with the river water show the most divergent chemical properties (Robinson *et al.*, 2002).

The connection of the floodplain of Ochten to the river through a sluice gate resulted in a continuous contact with the river between the November 1998 and March 1999 inundation,

while the lakes near Deest were isolated during that period. This explains why our data indicate that the lakes near Deest started a clear individual development after November 1998, while the lakes near Ochten remained relatively comparable to the river (reference in the PRC). Another effect of sluice gate in Ochten was the early onset of the visible effects of entering river water in December 1999 which was followed by an inundation response of the lakes near Deest only one month later, when the actual flooding occurred. While most studies have focused on the effect of the frequency and duration of flood pulses (Van den Brink *et al.*, 1992; 1994; Tockner & Schiemer, 1997), our results show that less obvious hydrological connections can have a large impact on the dynamics of floodplain lakes. Obviously, the pre- and post-flood connections between some lakes and the river, make it more difficult to interpret the floods as controlled experiments.

5.4.3 Does inundation really reset lake plankton and chemistry?

Another aspect which makes the effect of inundation less controlled than one could wish is the fact that flooding does not necessarily replace all the lake water and its plankton. Inundation certainly had a large effect. The lakes invariably converged in chemical composition at inundation events.

Nonetheless, the results also show that with respect to macro-ions the lakes were not completely similar during the flooding of November 1998. This could indicate incomplete mixing of the lake water with the flood water causing differences in concentrations between the lakes, but may also be due to spatial and temporal differences in the quality of the flood water (Asselman & Middelkoop, 1998).

The effect of inundation on plankton is more difficult to interpret than the effect on chemistry. In temperate regions, the annual light and temperature cycles interfere with the flood pulse (Sommer *et al.*, 1993; Junk, 1999). Indeed, the effects of the flood pulses in November 1998 and January 2000 on our plankton data are hard to distinguish from the effect of seasonality. Still, the impact of the river water on community structure of both plankton groups is illustrated by the observation (PRC) that the lakes near Deest started to diverge immediately after the November 1998 flood, while the lakes near Ochten which kept hydrological contact to the river, remained relatively similar to the riverine lake Ochten 5. Other studies also show a strong but not complete homogenizing effect of river water on plankton. For instance, Speas (2000) also found an

increased, but not complete similarity of the zooplankton community composition in floodplain waters of the Colorado River as a result of a flood.

5.4.4 Recovery dynamics

While there are obviously profound effects of floodplain inundation on the chemistry and plankton communities of floodplain lakes, perhaps the most remarkable result from our study is the finding that plankton and chemistry of the lakes remain quite different in the face of such a seemingly overwhelming event. Therefore, the idea that all flooded lakes which are inundated by the same river are being reset to a comparable 'zero' point, e.g. become essentially uniform and contiguous, from which the diversification starts after isolation (Ward & Stanford, 1995; Pithart, 1999) is obviously an oversimplification. The slowest recovery after a flood was found for the macro-ions. The initial differences between the lakes in macro-ions, especially for the lakes near Deest, where rather large, and this must have been the result of divergence during the relatively long period without inundation prior to our monitoring period (about 20 months). The inundation of the lakes in Deest prior to the monitoring was in March 1997, and lasted only a few days. Lakes near Ochten received river water closer to the monitoring period, due to the opened sluice gate in winter. This difference in connectivity between the two floodplains resulted in different dissimilarities for both floodplains. Before November 1998, the variation between the lakes in Deest was highest (highest dissimilarity), largely due to the young lakes Deest 1 and Deest 2, which have the lowest connectivity (by means of overbank connectivity, not by ground water). This extent of variation was never reached again after the following inundations. The macro-ions were also the only variables that did not show a clear seasonal pattern. These macro-ions are little influenced by biological processes and therefore rather reflect processes of dilution and transport. Our macro-ion results thus indicate that the input of river water does indeed replace much of the lake water and its seston, and that the role of river water is large relative to that of rain and groundwater, implying a potentially long lasting effect of inundations on macro-ions.

Nutrients, on the other hand needed little time to recover from a flood, as illustrated especially well by the swift return of the lakes to the seasonal pattern after the spring flood in March 1999. A similar rapid return of nutrients to 'business as usual' has been reported by Naselli-Flores & Barone (1997), who showed that the flooding of lake Arancio in southwest Sicily (Italy) did not markedly affect the seasonal trends of nutrients after the flood.

Also, the effect of the flood on the (dis)similarity of the plankton composition in our study was short lasting. The diversification of zooplankton in the lakes started immediately after the floods. Similarly, phytoplankton diversification of the lakes began immediately after isolation in both 1999 and 2000, and the communities converged rapidly due to succession as also described for other isolated floodplain lakes in temperate regions (Hein *et al.*, 1999b; Tockner *et al.*, 1999b). While the rapid recovery of plankton was a clear pattern in our time series, it does not necessarily reflect a universal pattern. For instance, a flood in spring in the Lower Oder valley resulted in an effect on the zooplankton community structure, which lasted the entire summer period (Schröder, 1999).

The exceptional position of the two young lakes Deest 1 and Deest 2 in the second half of 1999 (PRC-curves) should most probably not be ascribed to the flood pulse, but to the lake hydrology during isolation, i.e. the groundwater flow-pulse (*sensu* Tockner *et al.*, 2000b) related to the young age of these lakes The water level in these two lakes respond strongly to fluctuations in the level of the nearby river. This led to very low water conditions during the summer of 1999. Such extreme water level changes in a lake may have a large effect on phytoplankton dynamics (Nõges & Nõges, 1999; Roozen *et al.*, 2003).

Overall, the fact that nutrients and plankton diverge much faster than macro-ions to their idiosyncratic state for the different lakes, indicates that ecological processes are indeed responsible for the rapid divergence.

5.4.5 Synchronization of plankton dynamics

A remarkable feature (however, no proof) of the time-series revealed by the PRC analysis was the synchronization of the dynamics of phytoplankton and zooplankton communities in June-July 1999. A closer look at the data (not shown) shows that the synchronous dips in curves correspond to *Daphnia* spring peaks and subsequent clear water phases. In 2000 such events occurred asynchronously in the different lakes spread over a period of 4 months, while in 1999 all communities were apparently synchronized. Of course, our data do not allow a diagnosis of the reason why the 1999 inundation acted as a synchronizer whereas the 2000 inundation did not. However, it seems reasonable to assume that inundations may have a larger impact in spring (as in 1999) when the plankton populations already started their succession and nutrients become exhausted than in winter (as in 2000) when plankton abundances and productivity are low in the lakes and the river.

5.4.6 Synthesis, a slow-fast view of lake response

The large differences between the lakes we studied may seem remarkable, as the ecosystem dynamics are abruptly interrupted at times by an external disturbance (inundation), which destroys part of the information of the lake history (Reynolds & Lund, 1988; Garci de Emiliani, 1993). Obviously, the recovery after such disturbances depends on what remains of communities (as described in the Patch Dynamics Concept by Townsend 1989), what is brought in by the river, and on the local conditions determining the relative competitive power of the introduced and autochthonous species (Reynolds, 1993; Sommer *et al.*, 1993). Although we do not really know what is left of the local plankton communities after inundation, our results suggest that the water-column may not completely be reset to an identical state. Also, lake sediments usually contain substantial 'seed banks' of zooplankton resting stages (Hairston, 1996; Brendonck & de Meester, 2003) and phytoplankton cells (Reynolds, 1997). This results in different starting conditions influencing the successional development of the lakes when isolated.

Perhaps more importantly, the succession of phytoplankton is a fast process. The few months in a plankton growing season accommodate dozens of generations of phytoplankton. Correcting for generation times of the organisms this corresponds to decades in grasslands, and to centuries in forests (Sommer, 1991; Sommer *et al.*, 1993; Reynolds, 1993). Therefore, the development of plankton communities while driven in part by seasonal rhythms and weather will be highly determined by the local conditions set by slow variables such as the nutrient content stored in top-sediments, fish stock and vegetation of the lake (*see* Scheffer 1998 for an overview). Obviously, river induced inundation and desiccation of floodplain lakes may still affect the 'slow' fish (Bayley, 1995; Grift, 2001) and vegetation (Bornette *et al.*, 1998; van Geest, 2005). This is essentially because the frequency of the floods occurs roughly on the same time-scales as their dynamics. If time-scales of physical and biological dynamics are too disjunct, biology becomes less sensitive to the physical forcing (Steele & Henderson, 1994). Thus, the fact that we see fast recovery of plankton after inundation events does not exclude an overall long term effect of such disturbances on the ecosystem. Indeed, in the long term the regime to which the plankton dynamics of each lake converges may be determined in part by the effect of river dynamics on vegetation and fish communities.

5.5 Acknowledgements

This project was performed in co-operation and financed by RIZA Institute for Inland Water Management and Waste Water Treatment. I wish to thank Prof. dr. Jos Verhoeven for his advice and discussions concerning the analysis of the chemical dataset, and dr. Paul v.d. Brink on his advice concerning the performance of the Principal Response Curve method.

CHAPTER 6

Fish-mediated resuspension of algal cells boosts phytoplankton biomass and alters community structure in shallow lakes

Roozen F.C.J.M., Lürling M., Vlek H., Ibelings B. & Scheffer M.

Fish-mediated resuspension of algal cells boosts phytoplankton biomass and alters community structure in shallow lakes.

6.1 Introduction

Fish and macrophytes are major players in the mechanisms that drive shallow lakes to either a clear or a turbid state. The clear-water state may be stabilized by submerged macrophytes (Scheffer *et al.*, 1993b; Scheffer, 1998). By contrast, planktivorous and benthivorous fish push a system towards the turbid state. Benthivorous fish can consume or uproot submerged macrophytes (Ten Winkel & Meulemans, 1984) but also affect them indirectly through their negative effect on transparency. Benthivorous fish select food from the sediment by sucking in sediment and rejecting all items except retained food particles to the water column (Lammens & Hoogenboezem, 1991). As a result, benthic feeding hampers sediment consolidation (Delgado *et al.*, 1991; Scheffer *et al*, 2003), and causes a reduction in water column transparency Breukelaar *et al.* (1994).

Many studies have shown that benthivorous fish may enhance phytoplankton biomass (*e.g.* Meijer *et al.*, 1990a; Breukelaar *et al.*, 1994; Nalewajko & Murphy, 1998; Zambrano & Hinojosa, 1999). This may appear counter-intuitive since the fish increase turbidity and reduce the availability of light for photosynthesis (Hellström, 1991). Several mechanisms have been proposed to explain positive effects of fish on algal biomass, some work top-down by reducing larger zooplankton (*e.g.* Jeppesen *et al.*, 1999), others. bottom-up. Benthic feeding has been shown to release nutrients from the sediments into the water column stimulating the growth of phytoplankton (*e.g.* Havens, 1991; Shormann & Cotner, 1997). Resuspension of settled algal cells by the feeding activity of benthivorous fish has been suggested as another, but little studied mechanism that enhances phytoplankton biomass (Scheffer, 1998). Since, sedimentation of viable cells from the water column can be a major loss process for phytoplankton in shallow mixed water columns (Reynolds *et al.*, 1982) resuspension should contribute to the pelagic biomass of - especially larger - algal species. Most resuspended algae originate from a thin sediment surface layer, in which the biomass of larger algae may exceed the biomass in water column by one or two orders of magnitude (Carrick *et al.*, 1993). The potential impact of resuspension of this top layer is demonstrated by the observation that during periods of strong winds a large increase in algal

biomass may occur (Carrick *et al.*, 1993; Schelske *et al.*, 1995; 2000). The resuspension hypothesis is further corroborated by enclosure experiments where artificial mixing increased the chlorophyll-*a* concentrations (Ogilvie & Mitchell, 1998).

Resuspension of settled algae may also change the community composition of the phytoplankton. Ogilvie & Mitchell (1998) and Havens (1991) observed dominance of motile cryptophytes in small enclosures in the absence of fish, or when fish could not reach the sediment, but green algal dominance in the lake and enclosures when fish was able to reach the sediment.

Green algae, but especially diatoms are known for their relatively high sedimentation velocities of up to a few meters per day (Burns & Rosa, 1980; Visser *et al.*, 1996) and are dependent on turbulent mixing and/or repeated resuspension to be maintained in the water column. Diatoms have been observed to increase in biomass during high wind speeds (*e.g.* Schelske *et al.*, 2000).

We hypothesize that resuspension of settled planktonic algae by benthivorous fish is an important mechanism that enhances algal biomass and changes the phytoplankton community structure in shallow lakes. To test this hypothesis, we first analyzed the data of a survey of 93 floodplain lakes along the River Rhine in The Netherlands on the concentrations of chlorophyll-*a*, inorganic suspended solids, and the ratio of motile *vs.* non-motile algae. Subsequently, we performed enclosure experiments in a clear floodplain lake to examine the impact of benthivorous fish (carp) with and without access to the sediment on water transparency and algal community composition. The results of these studies underline the role of resuspension by benthivorous fish in floodplain lakes along the branches of the Dutch Rhine river.

6.2 Methods

6.2.1. Multi-lake survey

Study area

The multi-lake survey was carried out in the Dutch part of the River Rhine, in August 1999 (for extensive description see Roozen *et al.*, 2003). After the Rhine enters The Netherlands near Lobith, the river is divided into the Waal, the Neder-Rijn and the IJssel. At Lobith, the mean discharge is 2,300 m^3 s^{-1}, from which two thirds is channeled through the Waal, two ninths through the Neder-Rijn and one ninth through the IJssel (Middelkoop & Van Haselen, 1999). All sampled floodplain lakes are situated between the main channels and the major embankments. All lakes are shallow, with a mean depth in August between 0.08 and 5.40 m, and 90 percent of

the lakes are smaller than 10 ha. Lake sediments consist of silt and/or clay. The 93-floodplain lakes included in this study are divided over 31 floodplain sections along the three Rhine branches, with 40, 31 and 22 lakes along the Waal, Neder-Rijn and IJssel, respectively (*Figure 6.1b*).

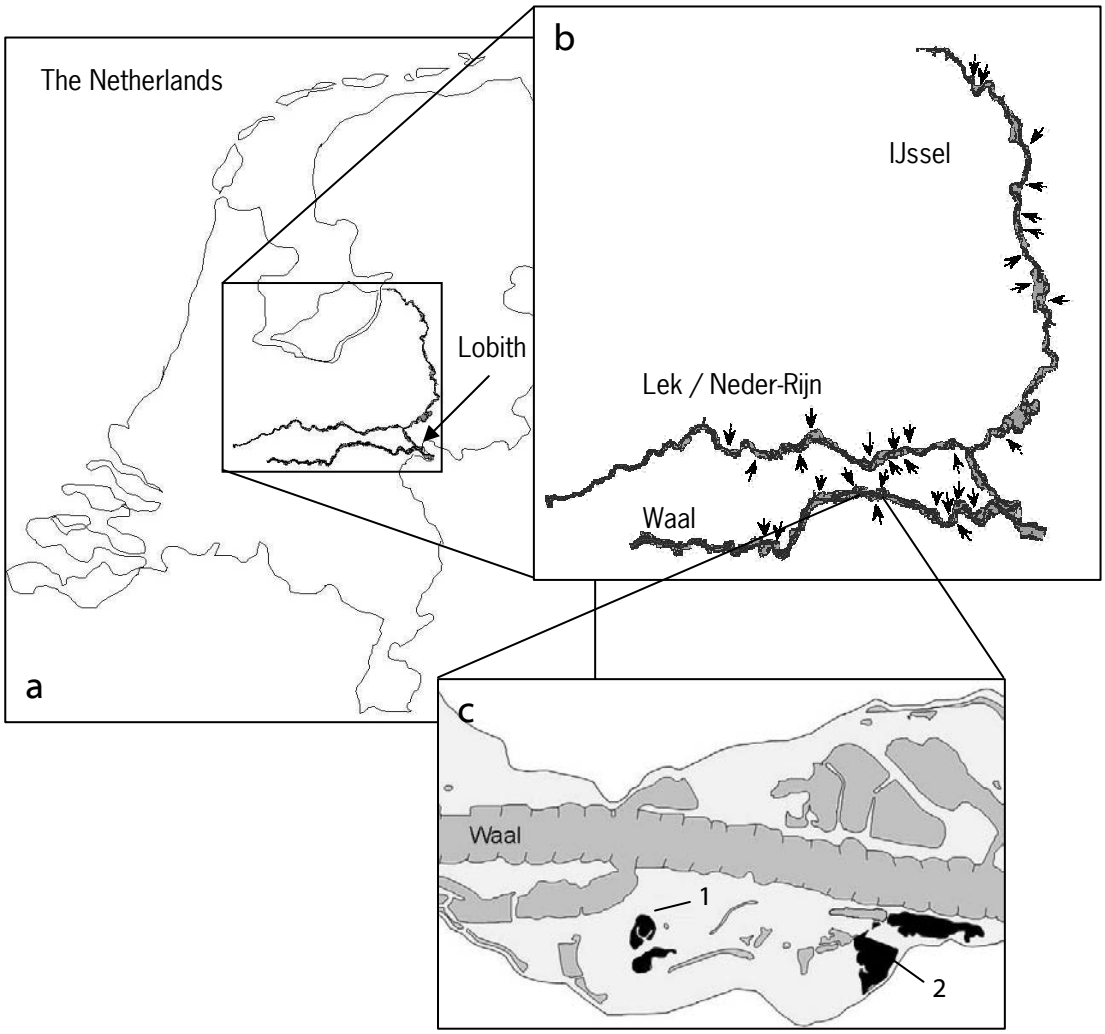

Figure 6.1. Map of The Netherlands (a, top-left) with the locations of floodplains (arrows) along the main branches of the river Rhine (b, top-right) where the 93 lakes sampled in the current study are situated. Also presented are the locations of the floodplain of Deest (c, bottom-right, lightly shaded areas) at the south bank along the river Waal and the lakes of the enclosure experiment (1) and sediment samples (2).

Field and laboratory procedures

In each lake, water was sampled using a transparent plastic tube (length 2 m, diameter 10 cm). The lakes were sampled from a boat, taking five to seven samples in a transect from the middle of the lake to the shore. The samples were mixed in a 30-L tank, from which sub-samples were

taken for further analyses. Five liters were taken for determination of chlorophyll-*a* and inorganic suspended materials. One-liter samples were taken and fixed in 3% (v/v) Lugol's solution (final concentration) for phytoplankton analysis. After one week of sedimentation the top 905-ml was carefully removed, and to the remaining 95 ml five ml formol (40%) was added. Phytoplankton abundance and composition were analyzed on an inverted microscope (Reichert) at a magnification of 500× in a sub-sample of 4 ml. Chlorophyll-a was determined following the ethanol extraction method with phaeopigments correction described by Moed and Hallegraeff (1978). Inorganic suspended solids were determined using the Dutch standard method (NEN-6484; for further details see below, section enclosure experiment).

6.2.2 Enclosure experiment

Study area

The enclosure experiment was carried out from 28 April till 8 May 2000 in a lake, at the south side of the river Waal, the main branch of the River Rhine, in the Netherlands (*Figure 6.1c, nr 1*). The lake was created in 1997 by excavating the first two meters of the floodplain surface, and is situated in the winter bed (floodplain area between minor and major embankments) about 200 meters from the main channel. The sediment is mainly sand with a thin top layer of clay, deposited during various inundations with an average duration of 2 – 20 days per year. The lake shore has a gentle slope, and its mean depth during the experiment was 1 meter. Aquatic vegetation and helophytes were absent, and during the experiment the lake was clear. The fish population of this lake has not been assessed.

Field and laboratory procedures

Twelve tube-like transparent Perspex enclosures 1.3 m in length and 1.05 m in diameter were installed in the lake in an almost straight line, at a water depth of about 0.9 m, on 26 April 2000. During installation each enclosure was lowered carefully to the lake bottom to minimize disturbance of the lake sediment. The enclosures were pushed about 10 cm in the sediment, and emerged about 30 cm above the water surface, resulting in a volume of ~780 L in each enclosure. Both top and bottom of the enclosures were open. The top of the enclosures was covered with a gauze (1 cm mesh size) to prevent bird predation on the fish and to prevent fish from jumping in or out the enclosures during the experiments. Light measurements indicated no negative effects of the gauze on irradiance.

On 28 April all enclosures were stocked with 10 sticklebacks (*Gasterosteus aculeatus*) that consume zooplankton, thereby suppressing the grazing impact on phytoplankton. Additionally, benthivorous fish may switch to planktivory when zooplankton is abundant (Lammens *et al.*, 1985) and stocking with planktivorous sticklebacks was chosen to prevent different cascading trophic effects among the various treatments. Eight enclosures also received one carp (*Cyprinus carpio*) each with an average length of 23 (± 3) cm and a biomass of 255 (± 58) g. Four of the enclosures with carp had nets installed, 10 cm above the sediment, to prevent carp reaching the sediment. Four enclosures did not receive carp and functioned as controls. The treatments were randomly assigned to the enclosures by means of lottery.

The enclosures were sampled on 28 April (t =0), 1, 3, 5 and 8 May. The vertical light attenuation coefficient (K_d), temperature and oxygen were recorded directly in the enclosures and the lake. K_d was measured with two Bottemanne light-sensors positioned at two different depths in the water column; one sensor slightly beneath the water surface and the other sensor 30-cm lower than the first. Both sensors were connected to a GRANT 1202 Squirrel Data-logger, reading signals every 5 seconds during one minute. The K_d was calculated as the mean of the readings during the measurement.

Oxygen and temperature were measured using a WTW OXI-191 oxygen meter, with the electrode connected to an EOT 196 stirrer. Water samples were taken from all enclosures and the lake using a transparent plastic tube (length 1-m, diameter of 10 cm). Water samples were depth-integrated from the water surface to about 10 cm above the sediment. In total, for each enclosure 30 L were sampled randomly and collected and mixed in a vessel. The pH was measured from the 30-L vessels using a WTW pH 320 meter. For zooplankton analysis 24 L of the 30-L sample was filtered over a zooplankton net (30 μm mesh size). The 24 L filtered water was returned to the corresponding enclosure, whereas the retained zooplankton samples were collected in 250-ml Polyethylene bottles and stored in 4% (v/v) formol (final concentration) until analysis in the laboratory. The remaining 5-L sample was used for analysis of phytoplankton abundance and composition, chlorophyll-*a*, nutrients, and suspended solids. Phytoplankton abundance and composition was analyzed microscopically using an inverted light microscope (Reichert, at 500x magnification) and zooplankton was analyzed quantitatively to the species level also with an inverted microscope (NIKON at 200x magnification).

Chlorophyll-*a* was determined as before. Nutrients were determined in the laboratory using an auto analyzer (SKALAR, SA40). Samples for NH_4-N, NO_2/NO_3-N and PO_4-P were filtered

through a 0.45 µm pore size membrane filter (NC45, Schleicher & Schuell, Dassel, Germany), within 5 hours after sampling. N-total and P-total were analyzed in water that had been passed through a 30 µm net. Inorganic and organic suspended solids (resp ISS and OSS) were analyzed from a known volume (v), collected on pre-weighed (m_0) filters (Whatmann GF/F), dried and stored for 24 hours at 105 °C, weighed (m_d), combusted for 3 hours at 510 °C and weighed again (m_c). Control filters (c) were processed similarly for each series.

The chemical and physical data as well as the vertical light attenuation and ISS, OSS and chlorophyll-a concentrations between the treatments are compared using General Linear Model, Repeated Measures analyses followed by Bonferroni post-hoc test. Phytoplankton and zooplankton abundances between treatments are compared using One-way ANOVA followed by Tuckey's post-hoc test. All these comparisons are performed in the statistical tool pack SPSS version 10.1.

6.3 Results

6.3.1 Multi-lake survey

The sampling of 93 floodplain lakes along the Rhine in The Netherlands in the summer of 1999 yielded a positive correlation (Pearson $r = 0.508$, $P < 0.0005$) between inorganic suspended solids concentration (ISS) and the phytoplankton biomass (*Figure 6.2a*). The ratio motile *vs.* non-motile algae showed a tendency to decrease with increasing ISS concentrations (*Figure 6.2b*).

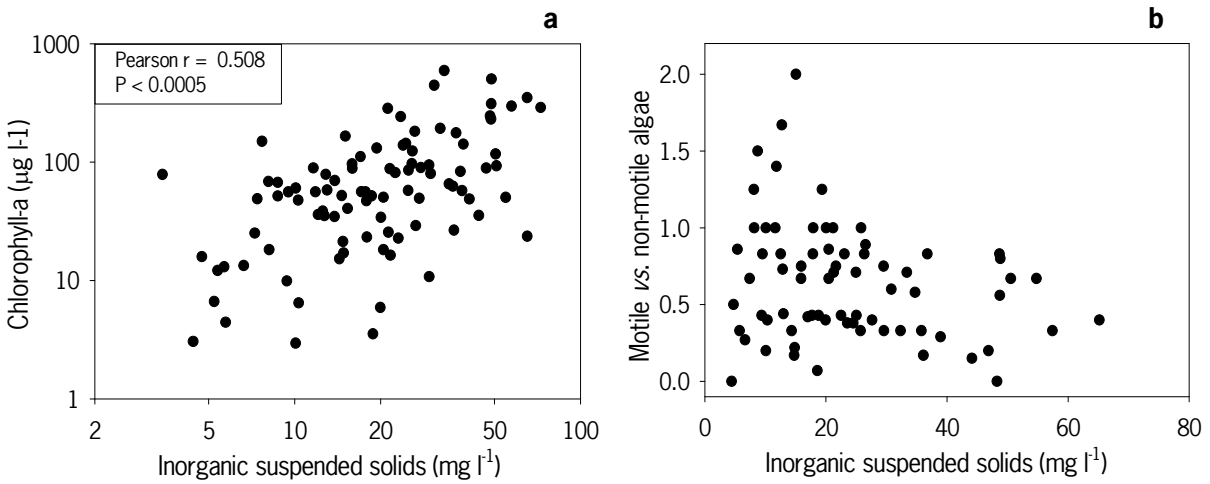

Figure 6.2. Inorganic suspended solids concentrations (mg L^{-1}) of 93 floodplain lakes in the lower River Rhine delta in The Netherlands, versus: a) the chlorophyll-a concentrations (µg L^{-1}) and b) the ratio of motile and non-motile.

Table 6.1. The temperature (ºC), pH, oxygen (mg L^{-1}) and nutrient concentrations (N and P in mg L^{-1}) in enclosures without carp (Control), or with carp with (Carp) or without access to the sediment (carp + net), and in the lake at the five sampling dates in 2000 (values are means ± one standard error; N = 4, except for the lake: N = 1). Similar symbols a,b,c within a column for each variable indicate homogeneous groups that are not significantly different among enclosure treatments at the 95% level (GLM, Repeated Measures analyses, Bonferroni test).

	28 April	01 May	3 May	5 May	8 May
Temperature (˚C)					
Control	19.8 (0.08) [a)]	16.3 (0.03) [a)]	15.2 (0.00) [a)]	16.4 (0.00) [a)]	20.5 (0.10) [a)]
Carp	19.7 (0.10) [a)]	16.3 (0.02) [a)]	15.2 (0.04) [a)]	16.9 (0.09) [b)]	20.6 (0.06) [a)]
Carp + net	19.8 (0.19) [a)]	16.3 (0.03) [a)]	15.2 (0.02) [a)]	16.4 (0.03) [a)]	20.3 (0.03) [a)]
Lake	18.9 (-)	16.4 (-)	15.3 (-)	16.3 (-)	20.5 (-)
pH (-)					
Control	8.7 (0.08) [a)]	8.5 (0.07) [c)]	8.6 (0.05) [c)]	8.8 (0.04) [b)]	8.9 (0.04) [b)]
Carp	8.7 (0.07) [a)]	7.8 (0.04) [a)]	7.7 (0.01) [a)]	8.0 (0.21) [a)]	7.9 (0.11) [a)]
Carp + net	8.7 (0.04) [a)]	8.0 (0.04) [b)]	8.1 (0.04) [b)]	8.5 (0.06) [b)]	8.6 (0.10) [b)]
Lake	8.9 (-)	8.7 (-)	8.7 (-)	8.8 (-)	8.8 (-)
Oxygen (mg L^{-1})					
Control	10.5 (0.43) [a)]	8.0 (0.23) [b)]	8.7 (0.17) [c)]	10.5 (0.40) [b)]	14.3 (0.84) [b)]
Carp	10.2 (0.61) [a)]	4.8 (0.49) [a)]	3.9 (0.30) [a)]	6.4 (1.23) [a)]	8.0 (1.07) [a)]
Carp + net	10.5 (0.29) [a)]	5.4 (0.21) [a)]	5.7 (0.27) [b)]	8.5 (0.43) [ab)]	10.9 (0.92) [ab)]
Lake	11.9 (-)	9.0 (-)	9.1 (-)	10.4 (-)	10.6 (-)
NO_2 +NO_3 (mg L^{-1})					
Control	0.07 (0.01) [a)]	0.07 (0.01) [a)]	0.05 (0.01) [a)]	0.05 (0.01) [a)]	0.04 (0.01) [a)]
Carp	0.19 (0.13) [a)]	0.09 (0.03) [a)]	0.10 (0.03) [a)]	0.08 (0.02) [a)]	0.14 (0.03) [b)]
Carp + net	0.06 (0.02) [a)]	0.05 (0.01) [a)]	0.05 (0.01) [a)]	0.05 (0.01) [a)]	0.06 (0.02) [ac)]
Lake	0.06 (-)	0.04 (-)	0.05 (-)	0.03 (-)	0.05 (-)
NH_4 (mg L^{-1})					
Control	0.04 (0.01) [a)]	0.09 (0.02) [a)]	0.07 (0.01) [a)]	0.04 (0.01) [a)]	0.13 (0.10) [a)]
Carp	0.15 (0.07) [a)]	0.31 (0.07) [b)]	0.40 (0.07) [b)]	0.27 (0.09) [b)]	0.08 (0.03) [a)]
Carp + net	0.05 (0.01) [a)]	0.18 (0.01) [a)]	0.17 (0.02) [a)]	0.07 (0.01) [a)]	0.09 (0.04) [a)]
Lake	0.05 (-)	0.04 (-)	0.06 (-)	0.08 (-)	0.02 (-)
N-total (mg L^{-1})					
Control	0.31 (0.01) [a)]	0.77 (0.19) [a)]	0.43 (0.09) [a)]	0.49 (0.10) [a)]	0.67 (0.08) [a)]
Carp	0.34 (0.07) [a)]	1.03 (0.24) [a)]	0.80 (0.05) [b)]	0.79 (0.17) [a)]	0.65 (0.05) [a)]
Carp + net	0.40 (0.04) [a)]	0.67 (0.14) [a)]	0.61 (0.16) [ab)]	0.90 (0.22) [a)]	0.67 (0.08) [a)]
Lake	0.32 (-)	0.86 (-)	0.91 (-)	0.60 (-)	0.79 (-)
P-total (mg L^{-1})					
Control	0.12 (0.02) [a)]	0.18 (0.02) [a)]	0.13 (0.01) [a)]	0.12 (0.02) [a)]	0.13 (0.04) [a)]
Carp	0.14 (0.04) [a)]	0.16 (0.06) [a)]	0.13 (0.02) [a)]	0.13 (0.02) [a)]	0.12 (0.01) [a)]
Carp + net	0.12 (0.01) [a)]	0.18 (0.05) [a)]	0.11 (0.02) [a)]	0.17 (0.03) [a)]	0.12 (0.02) [a)]
Lake	0.11 (-)	0.16 (-)	0.19 (-)	0.08 (-)	0.07 (-)

6.3.2 Enclosure experiment

The results of the physical and chemical analysis of lake water and water from the different enclosures (Control, Carp, Carp + Net) are presented in *Table 6.1*. Ortho-P is not presented, for the concentrations were all below the detection limit of 0.004 mg L^{-1}. The temperature of the water was comparable among the different enclosures and the lake, whereas the pH appeared significantly lower for the Carp enclosures compared with the Control and Carp + Net enclosures and the lake (*Table 6.1*).

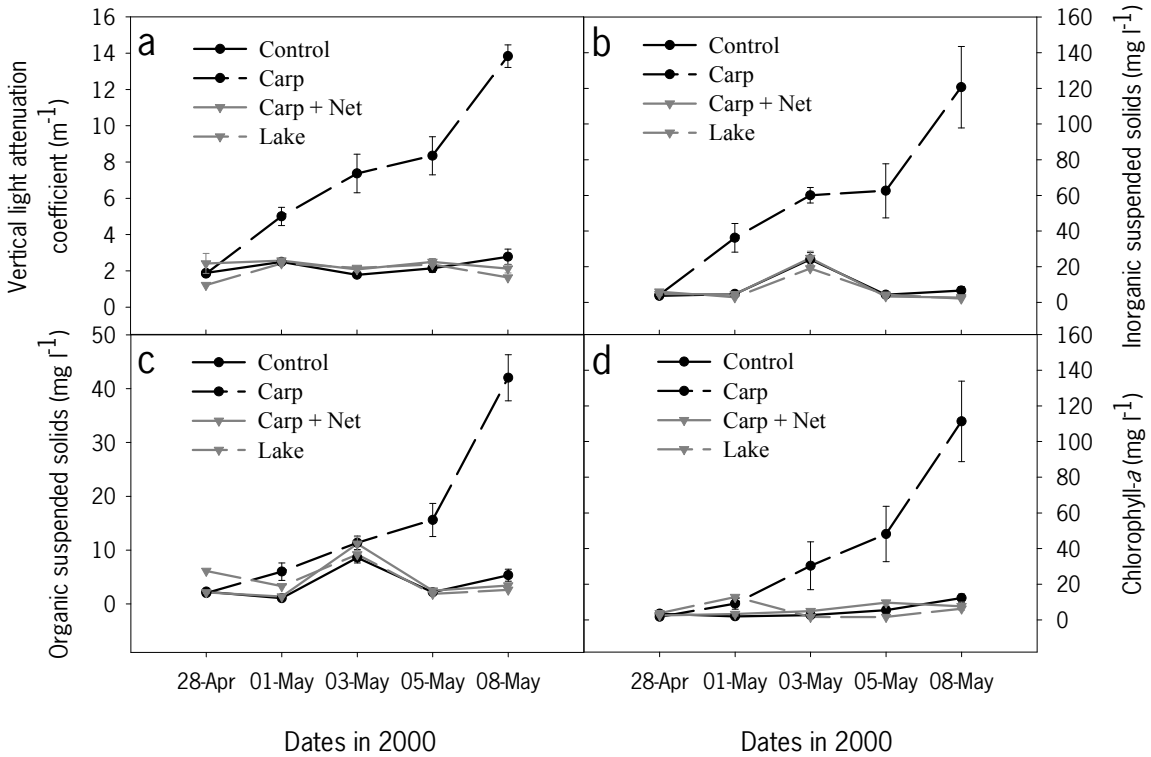

Figure 6.3. Course of the vertical light attenuation coefficient (m-1; Panel a), the inorganic suspended solids concentration (mg L-1; Panel b), the organic suspended solids concentration (mg L-1; Panel c), and the chlorophyll-a concentration (µg L-1; Panel d) in enclosures without carp, with carp with access to the sediment, with carp without access to the sediment and in the Lake. Error bars indicate one standard error (N = 4).

Oxygen concentration showed a brief decrease for all treatments and the lake in the first three days followed by a gradual increase. The Carp and Carp + Net enclosures had the lowest oxygen concentrations throughout the whole experiment. No major differences in the nutrients in water from the different enclosures and the lake were found, with exception of ammonium (NH_4^+) which showed an initial significant increase in the Carp and Carp + net treatments (*Table 6.1*).

The light attenuation (vertical light attenuation coefficient, K_d) did not differ significantly between the lake, the Control and Carp + Net enclosures during the period employed in this study and values remained fairly constant around 2 m^{-1}. By contrast, in the enclosures where Carp

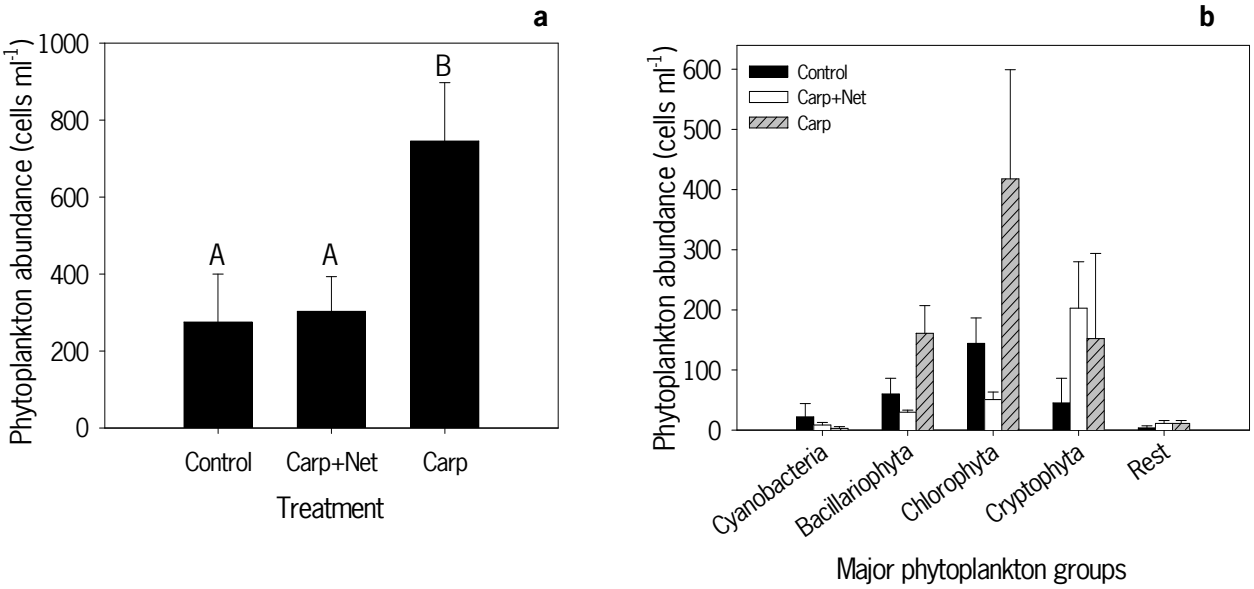

Figure 6.4. Phytoplankton abundance (cells ml^{1}) in enclosures without benthivorous fish (Control), with benthivorous fish with (Carp: Cyprinus carpio*) and without access to the sediment (Carp+Net) on May 8th. Panels a) presents total phytoplankton abundance, with symbols A, B indicating homogenous groups that are not significantly different at the 10% level (Tukey's post-hoc comparison; one way ANOVA F2,9 = 4.46; P = 0.045) and panel b) presents abundances of 5 different algal groups. Error bars represent one standard error (N = 4).*

had access to the sediment, light attenuation increased significantly up to 14 m^{-1} (*Figure 6.3a*). Also, the organic (OSS) and inorganic suspended solids (ISS) were similar among the lake and the Control and Carp + Net enclosures during the whole experiment, while in the Carp enclosures without a net significant higher values were found (*Figure 6.3b* & *c*). A similar pattern was observed for chlorophyll-*a* with a significant increase only in the Carp treatments (*Figure 6.3d*). Phytoplankton abundance also increased significantly in the enclosures where Carp had access to the sediment (*Figure 6.4a*) (one-way ANOVA: $F_{2,9}$ = 4.46; P = 0.045).

Comparison between the abundance of the major zooplankton groups between the Control enclosures and the Carp enclosures at the start of the experiment (P ≥ 0.4) and at the end (P ≥ 0.2) yielded no significant differences (*Figure 6.5*).

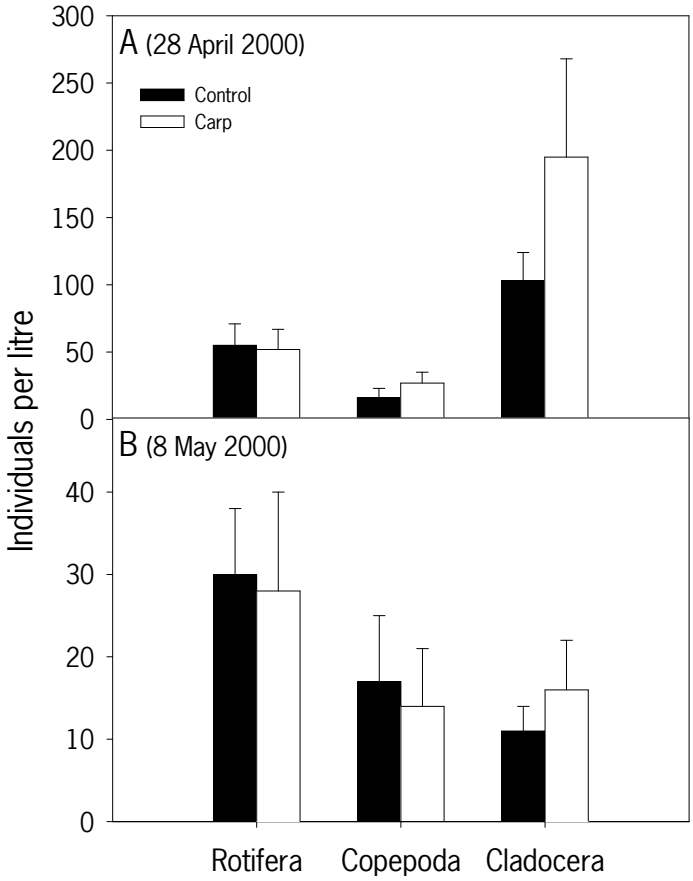

Figure 6.5. Abundance of major zooplankton groups at the start (panel A) and at the end (Panel B) of the enclosure experiment in enclosures without (Control) and with carp (Carp). Error bars indicate one standard error (N = 4).

Phytoplankton community composition was significantly different among the various treatments (*Figure 6.4b*). Especially diatoms ($F_{2,9}$ = 5.08; P = 0.033) and green algae ($F_{2,9}$ = 3.13; P = 0.093) differed among treatments and were significantly (α = 0.10) higher in the enclosures where carp had access to the sediment (*Figure 6.4b*). No differences in abundance of cyanobacteria ($F_{2,9}$ = 0.57; P = 0.586), cryptophyta ($F_{2,9}$ = 0.70; P = 0.520) and chrysophyta ($F_{2,9}$ = 0.96; P = 0.419) were found. The proportion of motile species in the phytoplankton community was significantly different among the enclosures (one way ANOVA: $F_{2,9}$ = 4.63; P = 0.042). Tukey's post hoc test indicated that in enclosures with carp that had no access to the sediment the percentage of motile

species (63%) was significantly larger than in the other treatments with 10% and 23% for control and carp treatments, respectively.

The actual presence of algal cells in the sediments of these lakes is illustrated by examination of algae released in the laboratory from the top layer of the sediments (taken with a core-sampler) from a floodplain lake in the near vicinity of the lake in which our enclosure experiment was performed (*see Figure 6.1*). *Scenedesmus* was among the dominant algae released from it (*see Table 6.2*). *Scenedesmus* was also one of the most dominant green algal genera in the enclosures where carp had access to the sediment.

Table 6.2. Phytoplankton species recruited from floodplain lake sediment after six days incubation in the laboratory.

Cyanobacteria	Bacillariophyta	Chlorophyta
Phormidium spp.	*Achnantes spp.*	*Monoraphidium contortum*
	Cymbella spp.	*Oocystis spp.*
	Gomphonema spp.	*Scenedesmus cf bijugatus*
	Nitzschia sigmoidea	*Scenedesmus obliquus*
	Nitzschia spp.	*Scenedesmus quadricauda*
		Scenedesmus tenuispina

6.4 Discussion

Taken together the results from our multi-lake survey and enclosure study provide cumulative support to the idea that fish-induced resuspension of algal cells not only boosts overall phytoplankton biomass, but also alters the phytoplankton community structure.

6.4.1 Resuspension of sediments

The starting point is the multi-lake survey which showed a significant correlation between ISS concentration and chlorophyll-*a*. High ISS concentrations in the water column are indicative for resuspension of sediments and have a clear effect on water turbidity (Roozen *et al.*, 2003; Scheffer, 1998). In shallow lakes, two important mechanisms contribute to resuspension of sediment; wind and benthivorous fish (e.g. Aalderink *et al.*, 1984; Lürling *et al.*, 1995). The relative small size of these lakes, and the fact that the smallest lakes tend to have the highest ISS concentrations excludes wind resuspension as a major factor (*see Chapter 2* for a quantitative backup of this statement). This leaves the foraging behavior of benthivorous fish which are often abundant in these lakes (Grift, 2001) as the main potential cause for resuspension (Roozen *et al.*,

2003). The winnowing process of the fish separates food and sediment particles during benthic feeding and thereby causes resuspension of sediments to the water column, resulting in a strong relationship between fish biomass and suspended solids (Breukelaar *et al.*, 1994). Importantly, the high concentrations of inorganic suspended solids (ISS) by themselves should have a negative effect on photosynthetic organisms like phytoplankton (Hellström, 1991). The positive relation between ISS concentrations and the concentration chlorophyll-*a* in our data thus implies that there are benefits associated with resuspension of sediments which are considerable, as they outweigh the costs resulting from increased shading.

6.4.2 Resuspension related mechanisms increasing chlorophyll-a

Resuspension by benthivorous fish is likely the major factor causing increased inorganic turbidity (ISS) and chlorophyll-a in our studied lakes during summer. Several underlying mechanisms have been proposed as causal factors for this type of observations, where algal biomass increases with inorganic turbidity, due to the presence of (benthivorous) fish. The first is that benthic feeding transports nutrients from the sediments to the water column to the benefit of phytoplankton (e.g. Breukelaar *et al.*, 1994; Shormann & Cotner, 1997). The second explanation is that nutrient recycling by the fish itself could lead to increased algal biomass (Qin & Threlkeld, 1990; Attayde & Hansson, 1999). The third is that abundant fish reduce larger zooplankton resulting through cascading, top-down effects in a higher algal biomass (Carpenter *et al.*, 1985). A fourth mechanism is the resuspension of settled algal cells by fish (Scheffer, 1998).

Our enclosure experiment was performed to examine the impact of benthivorous fish (carp) with or without access to the sediment on water transparency and algal community composition, and to determine which of the four aforementioned mechanisms contributes most strongly to the results.

<u>Nutrient release from the sediment / excretion of nutrients by fish</u>

Enhanced nutrient availability for the phytoplankton may be an important factor associated with benthic feeding of fish. The nutrient transport from the sediment to the water column might occur indirectly, trough excretion by the fish (Attayde & Hansson, 1999; Qin & Threlkeld, 1990) or by direct release of nutrients from the sediment (Cline *et al.*, 1994; Ogilvie & Mitchell, 1994). Therefore, feeding on benthos results in the transport of nutrients from the benthic to the pelagic zone of the lake (Andersson *et al.*, 1978; Breukelaar *et al.*, 1994). Nonetheless, in the

current study no major differences in nutrient concentration in the different enclosures and the lake were found, with exception of ammonium (NH_4) that showed an initial significant increase in the Carp and Carp + Net treatments (*see Table 6.1*). The initial molar N:P ratio in the lake at the start of the experiment based on the total N and total P concentrations was about 7:1, suggesting strong N-limitation. Enhanced availability of ammonium could therefore have caused the phytoplankton growth in the Carp enclosures. However, if this would have been the case, then the increase in ammonium in the Carp + Net enclosures would have resulted in a similar increase in phytoplankton biomass as in the Carp without net enclosures - which was not observed.

Top-down control

A trophic cascade (Carpenter *et al.*, 1985) as the main cause of the significant differences in chlorophyll-*a* between the carp enclosures and the other treatments could be excluded, because the abundance of the major zooplankton groups between the control and carp enclosures were similar (*see Figure 6.5*). All enclosures had been stocked with sticklebacks to avoid differential grazing among the various treatments.

Physical resuspension

Resuspension may bring back viable algal cells which have been lost through sedimentation, one of the major loss processes operating in phytoplankton (Reynolds & Wiseman, 1982; Reynolds *et al.*, 1982). Recurrent resuspension may especially augment the pelagic biomass of large species with a relatively large sedimentation velocity. Most of the resuspended material originates from a thin film of newly deposited material (Bengtsson & Hellström, 1992). The observation that access to the sediment for the carp was essential for most of the observed effects provides support to the hypothesis that resuspension of algal cells was the main mechanism causing differences between the enclosures. This is corroborated by the observation that the increase in phytoplankton biomass - in the enclosures where carp had access to the sediment - was largely caused by an increase in green algae and diatoms. These algae are known for their relatively high sedimentation rates (Reynolds, 1984) and will settle from the water during periods of low turbulence. An increased density of diatoms and green algae in the presence of benthivorous fish has been reported in several other studies (e.g. Andersson *et al.*, 1978; Havens, 1991; Meijer *et al.*, 1990b; Jeppesen *et al.,* 1999). Also, their presence in shallow water has been shown to increase with wind speed (Gons, 1991; Schelske *et al.*, 1995; 2000) and artificial mixing (Ogilvie & Mitchell, 1998).

6.4.3 Community composition

Overall, the results of the enclosure experiment, as well as those from the multi-lake survey, seem in favor of the hypothesis that resuspension results in less motile algae but more benthic/meroplanktonic species. Another line of evidence in favor of the hypothesis that fish-induced resuspension of settled algal cells might alter the phytoplankton community composition is derived from studies on the structuring role of macrophytes in shallow lakes. Flagellates, such as *Cryptomonas* and *Chlamydomonas*, dominated in the presence of macrophytes, but were replaced by diatoms and green algae, such as *Scenedesmus*, in the absence of plants (Schriver *et al.*, 1995). Also Hasler & Jones (1949) found *Scenedesmus* among the most abundant algae in the absence of plants, but virtually lacking in the presence of macrophytes. The major steering factor for this is assumed to be reduced resuspension in plant beds (Søndergaard & Moss, 1998; Van den berg *et al.*, 1998).

6.4.4 Summarizing

While the different approaches in our study each have their limitations, the combined observations from the lake survey and enclosure experiments provide strong support for the hypothesis that fish-induced resuspension of settled algal cells asserts a strong effect on phytoplankton biomass and composition. Moreover, this idea is well in line with results from numerous other studies on effects of benthivorous fish and of wind driven resuspension. Therefore, we conclude that besides fish-mediated nutrient release and possible cascading trophic interactions, the fish-induced resuspension of algal cells from the sediment may be considered an important mechanism affecting phytoplankton biomass and community structure in shallow lakes.

6.5 Acknowledgements

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CHAPTER 7

Future Developments

Frank Roozen

F Future developments

As my results show the share of transparent floodplain lakes can be enhanced by regular (re)excavation, and an emphasis on the creation of small shallow lakes with abundant vegetation cover which lack high abundances of benthivorous fish. There are, however, two important developments that should be considered in the near future, a natural one and a political one: 1) the potential changes in the hydrological regime of the river due to climate change and 2) the European Water Framework Directive (WFD, 2000/60/EC). The next two sections provide some discussion of these developments.

7.1 Effects of Climate Change.

The fact that river restoration and, consequently, more knowledge about the functioning of aquatic systems in floodplains is needed, again became clear in 2003, when a winter with extremely high river discharges was followed by a very dry summer with extremely low river discharges. This pattern - wet winters followed by dry summers - is expected to become more general in the future due to the global climate change (Middelkoop & Van Haselen, 1999). As a result, floodplain lakes will be flooded more regularly in winter and many of these lakes will dry up during the warm and dry summer. This makes the hydrological rate of change in individual lakes more extreme, strongly influencing the aquatic ecosystem. Van Geest (2005) showed the importance of these events in summer to the chances in macrophyte-development, implying effects on water quality and plankton communities as well. So, when the expected increase in dry summers indeed happens in the future, the rate of desiccation of lakes will increase, resulting in an enhanced probability of obtaining clear, vegetation rich (shallow) lakes in floodplains.

7.2 The Water Framework Directive.

The European Water Framework Directive (WFD, 2000/60/EC) is a directive with a result-commitment. All aquatic systems in the countries of the European Union are to be in a certain defined ecological state by 2015. For implementation of the WFD floodplain lakes along the Dutch part of the River Rhine are all classified as heavily modified lakes of the type: 'shallow, line-shaped waters, connected to or inundated by the river' (type: M5; van den Berg, pers. comm.). The overall objective of the WFD is a 'good status' to be achieved for all waters by December 2015. For surface waters, 'good status' is determined by a 'good ecological' and a 'good chemical status'. The ecological status is determined by biological, hydro-morphological

(e.g. the habitat conditions) and physical-chemical quality elements. The point of reference is given by the biological variables of (nearly) undisturbed waters. These are waters with only 'very minor' human impacts.

Reference conditions are presented in a scale ('maatlat'), ranging from a high status (reference values) through different quality values to a bad status. The reference situation for phytoplankton species (indicators) for these water type is currently in development (Van den Berg, pers. comm). The scale for algal biomass (chlorophyll-a) has already been set (*Table 7.1*). This variable is measured as the summer average (from April 1st until September 30th), based on monthly measurement at representative places in the lake. The classification of the status of the lakes (water bodies) should at least be the 'good status' in a specified period (Moss *et al*, 2003).

Table 7.1 Scaling (lower class-limits) of chlorophyll-a (in $\mu g.l^{-1}$) for the Water Framework- type: 'shallow line-shaped waters, connected to or inundated by the river' (M5).

high	good	moderate	poor	bad
6.1	15.7	27.0	54.0	108.1

When we compare the summer averages of the ten lakes of the 3-year monitoring with this scale for chlorophyll-a, there are major patterns (*Figure 7.1*). First, lakes differ enough to cover all quality classes. Second, large differences between years exist. Interannual differences seem likely to be related to inundation (*Chapter 5*). The high chlorophyll-a levels in 1999 could well be related to the inundation in the spring of that year.

As mentioned in the first section, ageing of floodplain lakes eventually will result in a more turbid state of these lakes. In view of the WFD this in an undesired development resulting in a decreased ecological status. However, ageing of floodplain lakes is a natural and important process for lakes in fluvial (river) systems and differences in lake age result in a natural diversity in lakes, from clear, vegetation rich lakes with low phytoplankton biomass (Chlorophyll-a) to very turbid (high chlorophyll-a and inorganic sediments concentrations), vegetation poor lakes. When implementing the WFD in these dynamic systems (using only one lake type (M5)) this diversity in lakes would be lost (due to the commitment of obtaining good quality status lakes), and only the low chlorophyll-a lakes would remain, losing the phytoplankton dominated lakes, which are also part of a river-floodplain system.

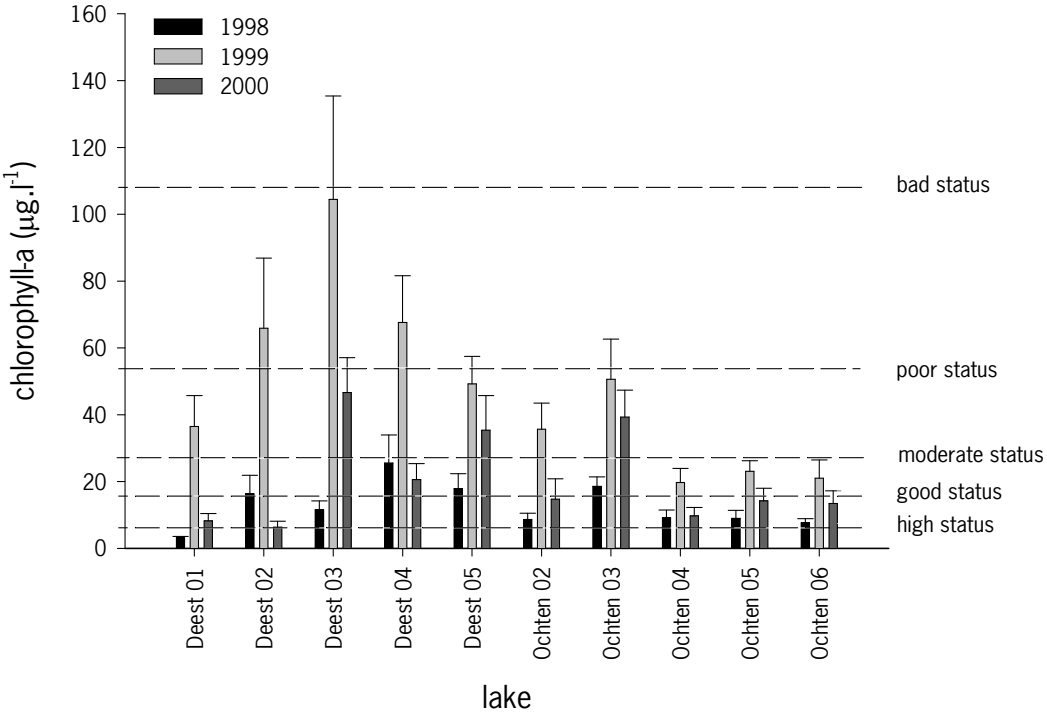

Figure 7.1 Summer average chlorophyll-a levels (monthly average from April until September, µg.l^{1}) of ten floodplain lakes along the river Waal for the years 1998, 1999 and 2000. The five quality status according to the Water Framework Directive are presented on the right of the graph. The lower class limits for each status are indicated by the horizontal lines. Whiskers on the bars indicate Standard error.

This illustrates that the (simple) classification by the WFD is not appropriate for these aquatic systems, and that the scale of phytoplankton biomass used in the scale (chlorophyll-a *see: Table 7.1*) is not realistic or, in my opinion, not even desirable. Rather than aiming at a low algal biomass for all lakes, one should perhaps aim at a certain natural frequency distribution of algal biomass. Since turbid lakes harbor a partly different set of species than clear lakes, the strategy to aim at a range of lake-status would also promote biodiversity on a landscape level.

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SUMMARY AND CONCLUSIONS

Frank Roozen

Summary and conclusions

Serious floods in 1993 and 1995 in the Netherlands resulted in a political awareness of the need for safety against possible future flooding ('Ruimte voor de Rivier' (Ministry of Transport, Public Works & Water Management, 2000)). It was decided that rivers must be given more space to be able to handle high(er) discharges in future, and (local) excavation of floodplains is one of the proposed measures for obtaining this goal. This measure implies perspectives for nature development in the floodplains as well. New (semi)permanent lakes will arise, and shape and position of these new lakes are well designable. However, the effect of these morphometric variables, in relation to the hydrology of the system (river and floodplain), on the future ecological state of these hydrological dynamic lakes was far from clear. Therefore the Dutch Institute for Inland Water Management and Waste Water Treatment (RIZA) started a research project to increase our understanding of the ecological functioning of floodplain lakes. This knowledge would then be used for the development of practical recommendations and guidelines for ecological rehabilitation of floodplains along the Lower Rhine and the river Meuse.

This thesis deals with plankton, chemistry and turbidity of temporarily isolated floodplain lakes and is based on four research questions:

1. *Is hydrological connectivity/isolation a major determinant of ecology and chemistry of floodplain lakes along the Lower Rhine?*
2. *Which are the major factors determining the ecological state of temporarily isolated floodplain lakes?*
3. *What determines plankton diversity in floodplain lakes?*
4. *How resistant are temporarily isolated floodplain lakes to inundations, and how rapid do they recover?*

Summary of the results

This thesis starts with an analysis of factors that determine turbidity of a large set of lakes (Chapter 2). In August 1999, 93 floodplain lakes situated in the floodplains of the Lower River Rhine have been sampled in search for morphometric and other factors that explain their variation in clarity. The results showed that lakes with a drop in summer water level were less turbid at the time of sampling, mainly due to a lower inorganic suspended solids concentration. Older lakes were more turbid than younger lakes and that this was largely due to an increase in phytoplankton biomass. Furthermore, the water clarity was positively related to lake depth and the presence of vegetation. Model calculations on the data indicated that the underwater light

climate was strongly affected by chlorophyll as well as inorganic suspended solids, the latter being the dominant factor affecting Secchi depth. Dissolved organic carbon seemed to be of less importance. The high inorganic suspended solids concentrations suggested that intensive resuspension occurs in most of the lakes, while resuspension is the main process for this settling material. Using a simple wave model, and assuming vegetation to protect sediments against resuspension, wind resuspension could be eliminated as an important process in 90% of the lakes, leaving resuspension by benthivorous fish as probably the most important factor determining transparency. While chlorophyll-a concentration showed a strong positive correlation to inorganic suspended solids concentration, resuspension was hypothesized to have a positive effect on phytoplankton biomass in these lakes as well. Overall, in-lake processes, rather than river dynamics, seemed to be driving the turbidity of floodplain lakes along the lower River Rhine.

Linked to the statistical study of turbidity in lakes is an analysis of the vegetation structure of 215 lakes in the floodplains (*Chapter 3*). The frequency distribution of the cover of submerged macrophytes was not normal, implying that submerged macrophytes in any one lake were either scarce or abundant. Clear water lakes with submerged macrophyte dominated over a wide range of total P concentration (0.020 to 0.40 mg total P L^{-1}); Multiple logistic regression indicated that the probability of dominance by submerged macrophytes decreased markedly with the surface area, depth and age of the lakes. The surface area effect occurred independently of the depth. Further, there was a negative relationship between submerged macrophyte dominance and the long-term annual duration of inundation by the river. Nymphaeid cover showed a distinct optimum with respect to mean lake depth, being almost absent in lakes shallower than 0.5 m. In contrast to what was found for submerged plants, the probability of occurrence of nymphaeids increased with lake age. The probability of helophyte occurrence increased with lake age, and decreased with the presence of trees, cattle grazing, surface area, use of manure and mean lake depth. In all cases the critical level of one factor (e.g. mean lake depth) depended on other factors (e.g. surface area or age of lake); small lakes tended to remain dominated by submerged macrophytes up to a greater depth than large lakes, and helophytes colonized smaller lakes in an earlier phase. The effect of inundation by the river on the vegetation structure of the lakes was modest, probably because most of the studied lakes are rarely inundated during the growing season and experience only moderate current velocities while flooded. The results imply that in

new water bodies, macrophyte domination will be promoted if many small shallow lakes, rather than few large deep ones, are excavated.

In *Chapter 4* I focus on the factors that determine the diversity of phyto- and zooplankton in the studied floodplain lakes. Diversity of plankton in natural floodplain lakes is shown to be related to the hydrological connectivity with the river. For the Lower Rhine, diversity is supposed to increase with decreasing connectivity, while in the Danube an optimum has been found at intermediate levels of connectivity. Numerous studies (in non-floodplain lakes) have shown that diversity is related to lake productivity, with highest diversity occurring at intermediate productivity and disturbance levels. However, almost all analyses focus on one trophic level only. It has been suggested however, that optimum taxonomic diversity should tend to occur at higher productivity levels for herbivores than for carnivores, as energy is lost from one trophic level to the next and therefore animals require higher levels of primary productivity to maintain population sizes to recover from stochastic fluctuations. Here I address the connectivity-diversity relation in the temporarily flooded lakes of the Lower Rhine river floodplains, as well as the productivity-diversity relation at different trophic levels, using 71 shallow (<1,5 m depth) floodplain lakes. Diversity of zooplankton and phytoplankton in the studied floodplain lakes appeared inversely correlated. No relation of phyto- and zooplankton diversity with connectivity, nor with morphometric variables was found. Using chlorophyll as a proxy for productivity, taxonomic richness of both phytoplankton and zooplankton showed a humped relationship to productivity, but unlike predicted the hump occurs at lower productivity levels for zooplankton than for phytoplankton. Phytoplankton taxonomic richness was low at low chlorophyll levels where submerged plants tended to dominate the lakes, but on the other end of the range in very turbid lakes phytoplankton diversity also dropped. By contrast zooplankton taxonomic richness showed an overall negative relationship to chlorophyll, and a positive relationship to submerged vegetation cover, even though taxonomic diversity dropped of at the lowest chlorophyll levels. The patterns found may be explained from the phenomenon that in shallow lakes intensity of top-down control (a form of 'disturbance') of zooplankton tends to increase steeply with productivity for zooplankton. This may overrule the classic interpretation of the diversity productivity gradient in the sense that the decrease of zooplankton taxonomic richness at high chlorophyll-a levels which I found may occur despite (rather than due to) high productivity, and is caused by strong top-down control rather than competitive exclusion.

The focus of *Chapter 5* is on the response of floodplain lakes to inundations. Key variables in ecosystems tend to operate on widely different time scales. These time scales become relevant when a disturbance (*e.g.* inundation) rocks the ecosystem. In this chapter I try to explain the fast dynamics of plankton and nutrients in the water column of floodplain lakes after disturbances (inundations) in relation to slow components such as vegetation and fish. I took advantage of natural experiments, i.e. occasional massive overflow of the floodplain lakes with river water. Ten lakes in two floodplains along the Dutch river Waal have been sampled monthly for three years, capturing the impact of three inundation events. The inundations reset the plankton and chemical composition of most lakes to largely the same state. While the biologically inert macro-ion data reflected a large and long lasting impact of the river water, dynamics of nutrients, phytoplankton and zooplankton communities between lakes diverged in a few weeks to regimes characteristic for the different lakes. While one spring inundation synchronized plankton dynamics to let the subsequent clear water phase occur at the same moment in different lakes, winter inundations did not have the same effect and apparently dynamics quickly diverged. The results in this chapter showed that effects of inundations and other processes that affect the state of the ecosystem, should be studied considering the level of the slow components such as the sediment nutrient pool, fish stock and macrophyte communities. Plankton communities and lake water nutrient status represent are a practically instantaneous reflection of the condition of these slow components.

In *Chapter 6* I test the hypothesized relation between resuspension by benthivorous fish and high concentrations of inorganic suspended solids and algal biomass (from *Chapter 2*). Positive effects of fish on algal biomass have been explained from cascading top-down effects and fish-mediated nutrient enrichment. Here I used a combination of approaches to test the hypothesis that the physical resuspension of settled algal cells by fish enhances algal biomass and alters community composition. A multi-lake survey showed an increase of phytoplankton biomass, and of the fraction of motile algae with the concentration of inorganic suspended solids. This correlation could not be explained by wind induced resuspension. In an enclosure experiment, chlorophyll-a concentrations, phytoplankton abundance and inorganic suspended solid concentrations increased significantly in the presence of Carp, but only if the fish had access to the sediment. Nutrient effects and zooplankton grazing appeared unimportant in explaining these effects, suggesting that fish-induced resuspension of settled algae from the surface film of deposited material was the major mechanism. An increase in diatoms and green algae (organisms with a

relatively large sedimentation velocity) only in enclosures where Carp could reach the sediment supported this view. I concluded that - indicated by several lines of evidence - fish-induced resuspension of algal cells from the sediment should be considered to be an important mechanism that affects phytoplankton biomass and community structure in shallow floodplain lakes.

Finally, in *Chapter 7* I reflect briefly on two future developments that will be important in the management of these lakes. I suggest that increased climatic variability will enhance the chance that floodplain lakes are in transparent state. On the other hand I stress that management goals motivated by the EU Water Framework Directive would lead to impoverished biodiversity on the landscape level, as the natural situation in these floodplains would probably be one characterized by lakes in states varying from clear to very turbid, depending on their age, morphometry and degree of isolation from the river. This situation with the resulting high biodiversity on the landscape level would disappear if all lakes would become clear, as is the aim in the European Water Framework Directive.

Conclusions

In conclusion, the influence of connectivity on various ecological variables in the temporarily flooded lakes is not as strong as was demonstrated in the broad study of Van den Brink (1994). Flow pulse appear to have a stronger influence on the state of the ecosystems than the flood pulse, mainly through the effects of water level fluctuations, with desiccation as an extreme (*research question 1*). Water quality variables seemed mainly determined by biotic interactions, through slow ecosystem variables like fish and vegetation (which are subject to stronger influence by hydrology, creating a cascading effect of the hydrology on the water quality, via the slow ecosystem variables), and by the morphometric characteristics of the lakes (*research question 2*). Similarly, diversity of plankton seems largely driven by the presence or absence of aquatic vegetation and fish, through the effect of vegetation structure, competition and predation. These factors vary over the gradient of productivity. Again, in contrast to the study by Van den Brink (1991), no relations with hydrology were found (*research question 3*). The weak relationship between plankton community characteristics and hydrology does not imply that flooding has little impact. Plankton and nutrients are radically altered by a flood events. However, after the water retreats plankton communities in the lakes rapidly develop to their idiosyncratic state, which depend largely on slow ecosystem components such as the sediment nutrient pool, fish stock and

macrophyte community, which are also important factors in shallow lakes outside the floodplain (*research question 4*).

SAMENVATTING EN CONCLUSIES

Samenvatting en conclusies

Serieuze overstromingen in 1993 en 1995 in Nederland hadden tot gevolg dat de politiek de noodzaak inzag om Nederland voor de toekomst beter te beschermen tegen overstromingen door de rivieren ('Ruimte voor de Rivier', Ministerie van Verkeer en Waterstaat, 2000). Er werd besloten de rivieren meer ruimte te geven, zodat deze in de toekomst in staat zijn grotere hoeveelheden rivierwater te kunnen afvoeren, waardoor het risico op overstromingen verminderd wordt. Het lokaal afgraven van uiterwaarden is hierbij één van de voorgestelde maatregelen, waarmee tevens kansen voor natuurontwikkelingen ontstaan. Zo kunnen nieuwe (semi)permanente plassen ontstaan, waarvan de vorm en positie vooraf goed te ontwerpen zijn. Er bestaat echter nog veel onduidelijkheid over het effect van deze 'stuurbare' morfometrische kenmerken, in relatie met de hydrologie van het rivier-uiterwaardsysteem, op de toekomstige ecologische staat van deze hydrologisch-dynamische plassen. Om die reden is het Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterzuivering (RIZA) een project gestart om de kennis over het ecologisch functioneren van uiterwaardplassen te vergroten. Deze kennis kan vervolgens worden gebruikt om praktische aanbevelingen te doen en een handleiding op te stellen voor het ecologisch herstel van uiterwaarden langs de Rijn en de Maas in Nederland.

Dit proefschrift handelt over het plankton, de chemie en de troebelheid van tijdelijk geïsoleerde (of tijdelijk geïnundeerde) uiterwaardplassen. De studie is gebaseerd op vier onderzoeksvragen:

1. *Is de hydrologie (connectiviteit/isolatie) een dominante factor voor de ecologie en chemie van uiterwaardplassen langs de Rijntakken in Nederland?*
2. *Wat zijn de belangrijkste factoren die de ecologische toestand van tijdelijk geïnundeerde plassen langs de Rijntakken bepalen?*
3. *Waardoor wordt de diversiteit van plankton in de uiterwaardplassen langs de Rijntakken bepaald?*
4. *Hoe sterk worden tijdelijk geïnundeerde plassen beïnvloed door inundaties en hoe snel herstellen ze na een inundatie?*

Samenvatting van de resultaten

Dit proefschrift begint met een analyse van de factoren die de troebelheid van een groot aantal geïsoleerde uiterwaardplassen langs de Rijntakken beïnvloeden (*Hoofdstuk 2*). In augustus 1999 zijn 93 uiterwaardplassen bemonsterd. Er werd gezocht naar factoren, waaronder morfometrische, die mogelijk de variatie in troebelheid tussen de plassen verklaren. Plassen met

een sterke daling van het waterpeil in de zomer waren minder troebel op het moment van bemonstering. Dit is met name het gevolg van lagere concentraties anorganisch zwevend materiaal (slib). Oudere plassen waren troebeler dan jongere plassen. Dit werd voornamelijk veroorzaakt door hogere algen biomassa in de oudere plassen. Verder bleken diepere plassen helderder te zijn dan ondiepere plassen. De aanwezigheid van vegetatie bleek een positief effect te hebben op de helderheid van plassen. Modelberekeningen met de data lieten zien dat het onderwater lichtklimaat sterk werd beïnvloed door zowel het chlorofyl-a gehalte (algen) als het zwevend slib. Met name het slib was van invloed op de Secchi-diepte (visuele doorzicht, gemeten met de ronde schijf afgebeeld op de titelpagina). Opgelost organisch koolstof bleek van weinig invloed te zijn op het lichtklimaat. Gezien in veel plassen grote hoeveelheden slib in het water werden gemeten werd het vermoeden gewekt dat de waterbodem veelvuldig wordt opgewerveld. Door gebruik te maken van een simpel golf-model, waarbij werd aangenomen dat waterplanten het sediment beschermt tegen opwerveling, bleek opwerveling veroorzaakt door wind in 90% van de plassen te kunnen worden uitgesloten als belangrijk proces. Hiermee bleef het proces van opwerveling veroorzaakt door benthivore (bodemwoelende) vissen als de meest waarschijnlijke factor over die de troebelheid van de plassen beïnvloedt. Aangezien er een sterke positieve correlatie werd gevonden tussen de concentraties algen en slib (een toename van algen ging gepaard met een toename van slib), ontstond de hypothese dat resuspensie ook een positief effect heeft op de biomassa van de algen in de plassen. Over h*et al*gemeen lijkt de troebelheid in uiterwaardplassen langs de Rijntakken met name te worden bepaald door autogene (plas-eigen) processen in plaats van de hydrologische dynamiek gestuurd door de rivier.

Naast de studie naar de troebelheid is ook een analyse van de vegetatiestructuur in 215 uiterwaardplassen uitgevoerd (*Hoofdstuk 3*). De frequentieverdeling van de bedekking met ondergedoken waterplanten was niet normaal verdeeld, maar liet zien dat plassen werden gedomineerd door deze planten dan wel dat de planten nauwelijks aanwezig waren. Heldere plassen met ondergedoken waterplanten domineerden in een brede range van totaal-fosfaat concentraties (0.020 tot 0.40 mg totaal P L^{-1}). Uit multipele logistische regressie analyses bleek dat de kans op dominantie met ondergedoken waterplanten kleiner is in grotere, diepere en oudere plassen. Bij het bovengenoemde effect is er geen relatie tussen plasoppervlak en plasdiepte gevonden. Verder bleek de kans op dominantie met ondergedoken waterplanten in een plas kleiner, naarmate een plas langer door de rivier overstroomd wordt. Nymphaeiden vegetatie liet een duidelijke optimum bedekking zien. In plassen ondieper dan 0.5 meter waren ze vrijwel

afwezig. In tegenstelling tot wat gevonden was voor de ondergedoken waterplanten, neemt de kans op nympaeiden vegetatie en helofyten juist toe wanneer de plassen ouder worden. Helofyten kwamen juist minder voor in de grotere en diepere plassen en wanneer de directe omgeving van de plassen werden begraast of bemest, of in de aanwezigheid van bomen. Bij iedere analyse was het kritische niveau van de ene factor (zoals de gemiddelde diepte) afhankelijk van andere factoren; ondergedoken waterplanten vestigen zich tot op grotere diepte in kleinere plassen dan in grotere plassen. Tevens koloniseren helofyten kleinere plassen in een vroeger stadium (leeftijd) van successie. Het effect van overstroming op de vegetatiestructuur in de plassen was slechts matig, waarschijnlijk doordat de meeste plassen nauwelijks gedurende het groeiseizoen overstroomd raken en tijdens overstroming slechts geringe stroomsnelheden ondervinden. De resultaten in dit hoofdstuk laten zien dat wanneer waterplantenrijke plassen gewenst zijn, het kansrijker is dit te behalen door het aanleggen van veel nieuwe kleine plassen dan het aanleggen van slechts enkele nieuwe grote plassen.

Hoofdstuk 4 zoemt in op de factoren die de diversiteit (soortenrijkdom) van het fyto- en zoöplankton in de bestudeerde plassen bepalen. Van de diversiteit van plankton in natuurlijke uiterwaardplassen is aangetoond dat het is gerelateerd aan de hydrologische connectiviteit met de rivier. Voor de Rijntakken in Nederland wordt de diversiteit van planktongemeenschappen verondersteld toe te nemen naarmate de connectiviteit afneemt, terwijl in de Donau een optimum diversiteit gevonden is bij intermediaire waarden van connectiviteit. Talloze studies (in niet-uiterwaardplassen) hebben laten zien dat de diversiteit van de plassen ook is gerelateerd aan de productiviteit, met de hoogste diversiteit bij intermediaire waarden van productiviteit en niveaus van verstoring. Echter, bijna al deze studies zijn gericht op een enkel trofisch niveau. Er wordt verondersteld dat het optimum in taxonomische diversiteit voor herbivoren bij een hoger niveau van productiviteit zou optreden dan voor carnivoren. Vanwege het verlies aan energie van het ene trofische niveau naar het andere, zouden organismen van hogere trofische niveaus een hoger niveau van primaire productiviteit nodig hebben om bij willekeurige milieufluctuaties de populatiegrootte in stand te houden. In *Hoofdstuk 4* benader ik de connectiviteit-diversiteit relatie alsmede de productiviteit-diversiteit relatie in 73 tijdelijk geïnundeerde uiterwaardplassen (diepte <1.5 m) langs de Nederlandse Rijntakken. De diversiteit van het zoöplankton en fytoplankton in de bestudeerde uiterwaardplassen bleken negatief gecorreleerd te zijn. Er werden geen relaties gevonden tussen de diversiteit van zoöplankton en fytoplankton met enerzijds connectiviteit en anderzijds met diverse morfometrische variabelen. Wanneer chlorofyl-a werd gebruikt als maat

voor productiviteit, lieten zowel fytoplankton als zoöplankton een optimum zien in de relatie tot productiviteit. Echter in tegenstelling tot wat voorspeld was, bevond het optimum voor zoöplankton zich bij een lagere productiviteit dan voor fytoplankton. De soortenrijkdom van fytoplankton was gering bij lage chlorofyl-a waarden in plassen waar ondergedoken waterplanten domineren, maar ook aan de andere kant van het chlorofyl-a gradiënt, in de zeer troebel plassen, daalde het aantal fytoplankton taxa. In tegenstelling tot het fytoplankton bestond er een negatieve relatie tussen het aantal zoöplankton taxa en de chlorofyl-a concentratie. Echter bij de laagste chlorofyl-a concentraties nam de diversiteit af bij afnemende productiviteit. Het aantal zoöplankton taxa nam toe wanneer er meer ondergedoken waterplanten in de plassen aanwezig waren. De gevonden patronen in deze studie kunnen wellicht worden verklaard door het fenomeen dat de top-down intensiteit van zoöplankton in ondiepe plassen (een vorm van verstoring) sterk nijgt toe te nemen met de productiviteit van het zoöplankton. Dit fenomeen zou de klassieke interpretatie van het diversteit-productiviteit gradiënt kunnen weerleggen. De afname in het aantal zoöplankton taxa bij hoge chlorofyl-a waarden zoals ik deze in mijn studie gevonden heb, bestaat ondanks (in plaats van dankzij) de hoge productiviteit. Daarnaast zou deze afname in meerdere mate wordt veroorzaakt door een sterke top-down controle (predatie door vis) dan door competitieve uitsluiting (competitie tussen diverse zoöplankton soorten).

In *hoofdstuk 5* ga ik in op de reactie (weerstand en herstel) van uiterwaardplassen op overstromingen. Belangrijke ecosysteemvariabelen reageren op veranderingen in hun omgeving binnen sterk verschillende tijdschalen. Het belang van deze verschillen in tijdschalen wordt zichtbaar wanneer verstoringen zoals overstromingen het ecosysteem overhoop gooien.
In dit hoofdstuk heb ik geprobeerd de snelle dynamiek van het plankton en de nutriënten in het water van de uiterwaardplassen tijdens en na een overstroming met rivierwater te verklaren in relatie tot de langzamere dynamiek van de vegetatie en marco-ionen. Hierbij maakte ik gebruik van een natuurlijk 'experiment' in de vorm van volledige overstromingen met rivierwater van tien uiterwaardplassen langs de Waal. Drie jaar lang zijn de tien plassen, gelegen in twee verschillende uiterwaarden, maandelijks bemonsterd. In deze periode zijn beide uiterwaarden drie keer volledig door het rivierwater overstroomd, waarbij de samenstelling van het plankton en de chemische parameters in de plassen grotendeels vergelijkbaar werden. Al binnen een paar weken na isolatie, lieten de zoö- en fytoplanktongemeenschappen van iedere uiterwaardplas een individuele ontwikkeling zien, die min of meer kenmerkend was voor de verschillende plassen. Hetzelfde gebeurde met de nutriënten in de plassen. De biologisch-inerte macro-ionen lieten daarentegen

juist een sterk en langdurig effect van de inundaties met het rivierwater zien. De resultaten uit dit hoofdstuk laten zien dat de effecten van verstoringen, zoals inundaties, welke de ecologische gesteldheid van het aquatische systeem beïnvloeden, moeten worden beschouwd vanuit het niveau van de langzame componenten van het ecosysteem, zoals opgeslagen nutriënten, vis- en vegetatiegemeenschappen. De aanwezige planktongemeenschappen en nutriënten laten een vrijwel onmiddelijke weerspiegeling zien van de langzame componenten van het ecosysteem.

De hypothetische relatie tussen de opwerveling (resuspensie) van het sediment door benthivore (bodemwoelende) vis en de hoge concentraties anorganisch materiaal en algenbiomassa uit *hoofdstuk 2* wordt onderzocht in *hoofdstuk 6*. In één van de tien uiterwaardplassen uit *hoofdstuk 5* heb ik een enclosure experiment uitgevoerd waaruit bleek dat zowel de biomassa van algen (chlorofyl-a) als de concentratie aan anorganisch zwevend materiaal (slib) significant toenamen als gevolg van de aanwezigheid van karper. Dit was echter alleen het geval wanneer de vissen toegang hadden tot het sediment. Wanneer de vissen geen toegang tot het sediment hadden, werden er geen afwijkingen ten opzichte van de controle (geen vis) gevonden. De verschillen tussen de behandelingen konden niet worden veroorzaakt door verschillen in nutriëntenconcentraties of door top-down controle door zoöplankton. Dit doet vermoeden dat het foerageergedrag van de benthivore karper de belangrijkste oorzaak is van de opwerveling van gesedimenteerde algencellen uit de toplaag van het sediment. Dat juist de 'zwaardere' diatomeeën en groenalgen (soorten met een relatief hoge sedimentatiesnelheid) in de enclosures met aan karper geëxponeerd sediment in aantallen toenamen is een bevestiging van dit vermoeden. Opwerveling van algencellen door bodemwoelende vis als karper en brasem (de laatste is in grote mate aanwezig in uiterwaardplassen) moet, naast de algemeen erkende processen als top-down controle en excretie/opwerveling van nutriënten door vis, beschouwd worden als een belangrijk mechanisme welke zowel de biomassa als de samenstelling van het fytoplankton in ondiepe (uiterwaard)plassen sterk kan beïnvloeden.

In *hoofdstuk 7* ga ik kort in op twee (toekomstige) ontwikkelingen die van belang zijn voor het beheer van uiterwaardplassen. Veranderingen in het klimaat, resulterend in meer droogval in de zomer en meer overstromingen in de winter, zullen er naar verwachting toe leiden dat uiterwaardplassen een grotere kans hebben zich in een helderwater systeem te ontwikkelen, waarbij troebele plassen gedomineerd door algen in aantallen zullen afnemen. Daarnaast plaats ik kanttekeningen bij de implementatie van de Kaderrichtlijn Water. Deze Europese richtlijn kent

een resultaatsverplichting, waarbij de doelen die door de lidstaten zelf worden gesteld binnen een bepaalde termijn bereikt moeten worden. Nederland heeft aan tijdelijk geïsoleerde/geïnundeerde uiterwaardplassen slechts één type met bijhorende kenmerken toegekend. Dit zal ertoe leiden dat de grote diversiteit aan plassen in deze hoogdynamische systemen, gevormd door verschillen in leeftijd, morfologie en mate van isolatie van de rivier, op landschapsniveau sterk zal afnemen. Gezien er vanuit de Kaderrichtlijn Water wordt gestreefd naar een zo hoog mogelijke ecologische en chemische kwaliteit van het aquatische systeem (met daarbij onder andere zeer lage algenbiomassa's), zullen de troebele plassen die van nature in uiterwaardsystemen voorkomen, uit het landschapsbeeld verdwijnen.

Conclusie

De invloed van connectiviteit op diverse ecologische variabelen in de tijdelijk overstroomde uiterwaardplassen is niet zo groot is zoals deze was toegedicht in de uitgebreide studie van Van den Brink (1994). De 'flow-pulse' (connectiviteit via het grondwater) lijkt wel een sterkere invloed te hebben op het aquatische ecosysteem dan de 'flood-pulse' (overstromingen), voornamelijk vanwege de waterpeilfluctuaties met droogval als een belangrijk sturend proces (*onderzoeksvraag 1*). De waterkwaliteit (algen en nutriënten) van uiterwaardplassen lijkt direct te worden gestuurd door biologische interacties en de morfologie van plassen (met name diepte). Deze interacties worden sterk beïnvloed door de langzamere ecosysteemvariabelen zoals vis en vegetatie, die op hun beurt sterk worden beïnvloed door hydrologie en door morfologie. Hydrologie heeft dus indirect wel een sterk effect op de waterkwaliteit van de uiterwaardplassen (*onderzoeksvraag 2*). Ook de diversiteit van het plankton in de uiterwaardplassen wordt voor een belangrijk deel gestuurd door de aan- en afwezigheid van vis en vegetatie, via vegetatiestructuur, competitie en predatie. Het belang van deze factoren varieert over het productiviteitsgradiënt van de plassen. Een directe relatie tussen diversiteit en connectiviteit is niet gevonden (*onderzoeksvraag 3*). De zwakke relatie tussen de samenstelling van planktongemeenschappen en de hydrologie van het uiterwaardsysteem weerlegt niet het feit dat overstromingen geen of weinig impact heeft op deze planktongemeenschappen. Plankton en nutriënten worden sterk verstoord tijdens een overstroming, maar wanneer het rivierwater zich heeft teruggetrokken ontwikkelen de plassen zich weer snel naar hun eigen individuele patronen. Hierbij worden de plassen in sterke mate gestuurd door de langzame ecosysteemcomponenten, zoals vegetatie, vis en nutriëntenpool, die ook een belangrijke rol spelen in de ontwikkeling van plassen buiten de uiterwaarden (*onderzoeksvraag 4*).

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Roozen F.C.J.M., Lürling M., Vlek H., Ibelings B. & Scheffer M. Fish-mediated resuspension of algal cells boosts phytoplankton biomass and alters community structure in shallow lakes.

Roozen F.C.J.M., Peeters E.T.H.M., Bransen F, Ibelings B., Roijackers R., Buijse A.D. & Scheffer. Predation may reverse diversity-productivity patterns in lake plankton.

Roozen F.C.J.M., Peeters E.T.H.M., Roijackers R., Van der Wyngaert I., Wolters H., de Coninck H., Ibelings B.W., Buijse A.D. & Scheffer M. Fast response of lake plankton and nutrients to slow ecosystem components: effects of river inundations on floodplain lakes.

CURRICULUM VITAE

Curriculum vitae

Frank Roozen werd geboren op 18 december 1973 te Tilburg. Na het doorlopen van HAVO en VWO aan het Dr. Schaepmancollege te Dongen begon hij in 1993 aan de opleiding Milieuhygiëne (T32) bij de Landbouwuniversiteit te Wageningen. Binnen deze studie koos hij voor de specialisatie Aquatische Ecologie en Waterkwaliteitsbeheer (AEW) aan de gelijknamige leerstoelgroep van de universiteit. Tijdens de stage aan de Can Thó universiteit te Viet Nam bestudeerde hij het ecosysteem van een garnalen-mangrovesysteem in de Mekong Delta. Het afstudeervak werd uitgevoerd aan de leerstoel AEW binnen het inspirerende promotieonderzoek van Miquel Lürling en richtte zich op de chemische communicatie tussen zoö- en fytoplankton. De resultaten van dit afstudeervak zijn in 2001 gepubliceerd in *Journal of Plankton Research*.
Aansluitend aan de studie begon hij in 1998 als assistent in opleiding (AiO) aan onderzoek naar het ecologisch functioneren van uiterwaardplassen, het OER-project, dat eind 2002 afliep. Dit project was een samenwerking tussen de leerstoelgroep AEW van de Wageningen Universiteit en afdeling Watersystemen Ecologie (WSE) van het RIZA.
Vanaf 2003 heeft hij diverse functies uitgevoerd: medewerker waterkwaliteit bij Waterschap Rivierenland, junior onderzoeker bij de afdeling Zoetwaterecosystemen van Alterra en adviseur statistische verwerkingsmethoden van ecologische gegevens aan de Danube Delta National Institute te Tulcia, Roemenië. Sinds juli 2004 is hij werkzaam bij het Ministerie van Landbouw, Natuur en Voedselkwaliteit, waarvan het eerste half jaar als beleidsadviseur van het Expertisecentrum (nu Directie Kennis) en per januari 2005 als beleidsmedewerker Voedselkwaliteit bij de directie Visserij.

DANKWOORD

Dankwoord

Eindelijk is het dan zover, het boekje is af!

Het heeft, zeker de laatste jaren, aardig wat discipline geëist om dit promotietraject af te ronden met het proefschrift zoals het nu voor u ligt. Het werk en het gezinsleven, zorgden ervoor dat het schrijfwerk aan dit onderzoek op een lager pitje kwamen te staan. Het eindpunt, hoe onbekend dan ook, heb ik echter nooit uit het oog verloren. In de periode vanaf het begin van het promotietraject tot en met de verdediging in de Aula hebben velen een bijdrage geleverd aan het wel slagen van dit project. Al deze mensen verdienen een plaatsje te krijgen in dit dankwoord, waarvoor ik nu een poging zal doen.

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Een van de leuke facetten van het promotieonderzoek is het begeleiden van afstudeervakkers. Het OER-project was aardig in trek bij studenten, zodat er aardig wat personen een belangrijke bijdrage hebben geleverd aan het verkrijgen van de grote hoeveelheden data en de verwerking daarvan. Ivo Roessink, jij was mijn eerste 'afstudeervakker'. Beiden hebben we die eerste 'test' met veel plezier doorstaan. Bedankt voor de bijdrage aan het project. Bart Groeneveld en Susan Graas, jullie hebben een grote rol gespeeld in het verkrijgen van chemische en hydrologische data tijdens de Survey '99, bedankt daarvoor. Hanneke Vlek en Edwin van den Pouw Kraan, jullie wil ik bedanken voor de grote bijdrage aan de experimenten in het veld en in het lab. Jullie enthousiasme creëerde een erg plezierige samenwerking. Verder ben ik mijn dank verschuldigd aan Roel Geraeds en Harm de Coninck.

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Frank Roozen

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Photographs by *Frank Roozen*.