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Effects of Hydrologic Connection on Physicochemical Conditions and Algal Properties in Backwaters of the Lower Mississippi River

Orathai Pongruktham

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EFFECTS OF HYDROLOGIC CONNECTION ON PHYSICOCHEMICAL
CONDITIONS AND ALGAL PROPERTIES IN BACKWATERS OF THE LOWER
MISSISSIPPI RIVER

A dissertation
presented in partial fulfillment of requirements
for the degree of Doctor of Philosophy
in the Department of Biology
The University of Mississippi

by
ORATHAI PONGRUKTHAM

May 2012
ABSTRACT

In the last 50-100 years, the Mississippi River has been extensively engineered for flood control and navigation purposes. These modifications have substantially decreased the frequency of flooding and degree of contact of the river with its historical floodplain. However, in many areas within the current levee system there remain numerous secondary channels and other backwater sites with which the river is hydrologically connected on a seasonal basis.

In this study, the relationships of surface hydrologic connection with the main channel of the Lower Mississippi River to limnological properties and development of phytoplankton biomass in three backwater sites having different patterns of connection to the river were examined. Between November 2007 and September 2009, the depth of the river varied by up to 15 meters. At high river stage, the backwater sites and the main channel were hydrologically connected. As river water flowed into or through these backwater sites, they experienced elevated turbidity, elevated NO$_3$-N and PO$_4$-P concentrations, and had relatively low chlorophyll concentrations. As the river elevation declined, the backwaters became partly or fully disconnected from the river, resulting in an increase in light as suspended sediments settled out of the water column. Following this decline in turbidity, there was a rapid increase in phytoplankton biomass, and a corresponding decrease in NO$_3$-N and PO$_4$-P concentrations. Comparisons of photosynthetic parameters of algal communities in the Lower Mississippi River floodplain did not suggest photo-acclimation. However, there were differences in phytoplankton community composition between the main channel and backwater sites that depended on the
degree of connection. Diatoms dominated in the main channel and backwater sites during connection while cryptomonads dominated in backwater sites during disconnection.

Results indicate the importance of these backwater sites for production of phytoplankton organic matter, some of which may be transported into the main channel and contribute to the river food web, and possibly for nutrient immobilization, contributing to a reduction in the flux of nutrients downriver.
I would like to dedicate my dissertation to my family in Thailand for their faith and support.

To Bounthanom Munxayaphom who has assisted me throughout the program.

To my adoptive family, the Noonans, for pushing me to complete this goal.

To Dr. David Reed who believed in me and was always there for me.
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<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tbody>
<tr>
<td>$\alpha$</td>
<td>alpha, photosynthesis efficiency</td>
</tr>
<tr>
<td>$\alpha^b$</td>
<td>chlorophyll-specific photosynthetic efficiency</td>
</tr>
<tr>
<td>C.C.</td>
<td>colonial centric diatom</td>
</tr>
<tr>
<td>Coc</td>
<td>coccoid cyanobacteria</td>
</tr>
<tr>
<td>C.P.</td>
<td>colonial pennate diatom</td>
</tr>
<tr>
<td>CPOM</td>
<td>coarse particulate organic matter</td>
</tr>
<tr>
<td>Cryp</td>
<td>cryptomonads</td>
</tr>
<tr>
<td>Cyano</td>
<td>cyanobacteria</td>
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<tr>
<td>Des</td>
<td>desmids</td>
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<tr>
<td>Diato</td>
<td>diatoms</td>
</tr>
<tr>
<td>DIC</td>
<td>dissolved inorganic carbon</td>
</tr>
<tr>
<td>DI$^{12}$C</td>
<td>unlabeled dissolved inorganic carbon</td>
</tr>
<tr>
<td>DI$^{14}$C</td>
<td>radiolabeled dissolved inorganic carbon</td>
</tr>
<tr>
<td>DOC</td>
<td>dissolved organic carbon</td>
</tr>
<tr>
<td>Eugl</td>
<td>Euglenoid</td>
</tr>
<tr>
<td>Fla</td>
<td>flagellated phytoplankton</td>
</tr>
<tr>
<td>FPC</td>
<td>Flood Pulse Concept</td>
</tr>
<tr>
<td>FPOM</td>
<td>fine particulate organic matter</td>
</tr>
<tr>
<td>FPZ</td>
<td>functional process zones</td>
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<td>GPP</td>
<td>gross primary production</td>
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Green    green algae
I     irradiance, light intensity
Io     surface irradiance corrected for albedo loss
I_avg    averaged light intensities
k     light extinction coefficients
LMR     Lower Mississippi River
MRB     Mississippi River Basin
NTU    Nephelometric Turbidity Units
P     photosynthesis
P_max     maximum photosynthetic capacity
P_{max}^{b}     chlorophyll-specific maximum capacity of photosynthesis
P-I     photosynthesis-irradiance
Pa     *Pseudoanabaena*
PAR     photosynthetic active radiation (400-700 nm)
RCC     River Continuum Concept
RES     Riverine Ecosystem Synthesis
rkm     river kilometer
RPM     Riverine Productivity Model
S.C.     single cell centric diatom
S.P.     single cell pennate diatom
SURFRAD    Surface Radiation Network
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<tr>
<td>TDP</td>
<td>total dissolved phosphorus</td>
</tr>
<tr>
<td>TKN</td>
<td>Kjeldahl nitrogen</td>
</tr>
<tr>
<td>z</td>
<td>depth</td>
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CHAPTER 1

OVERVIEW OF LARGE RIVER ECOSYSTEM MODELS

Large river-floodplain ecosystems are important as habitats, food sources and transportation routes for many different kinds of organisms, including a large number of threatened and endangered species (Eckblad et al. 1984; Randall et al. 1995; Gutreuter et al. 1999; Dettmers et al. 2001; Sommer et al. 2001; Schultz et al. 2007). However, studies of large river-floodplain ecosystems are limited compared to those of lakes and streams because of the practical difficulties in adequate sampling (Johnson et al. 1995; Dettmers et al. 2001; Sommer et al. 2001). These difficulties arise from their longitudinal complexity (Basu and Pick 1995), temporal and spatial dynamics in hydrology and biological activity (Ochs and Capello 2008), and variable interactions with the floodplain (Ward 1997; Baranyi et al. 2002; Hein et al. 2003), not to mention their unpredictable and sometimes dangerous currents and turbulence.

In accord with their geophysical and hydrological variability, multiple conceptual models, such as the River Continuum Concept (RCC) (Vannote et al. 1980), the Flood Pulse Concept (FPC) (Junk et al. 1989) and the Riverine Productivity Model (RPM) (Thorp and Delong 1994), have been developed to explain the operation of large river ecosystems.

The RCC was developed for streams and rivers originating in a forested basin. It views the river network as a longitudinal structure that has continuous gradients of physical properties (depth, current, light, exposure to a riparian zone) which change predictably from headwaters to mouth. These physical gradients control biological properties along the river. According to the
RCC, patterns of ecological processes differ along the river according to its location in the river network and its size. In forested headwaters (order 1-3), the major source of carbon is considered to be allochthonous input from the terrestrial ecosystem. Autotrophic production within the stream is limited by shading of the dense forests. Dominant benthic macroinvertebrates are shredders which utilize coarse particulate organic matter (CPOM) and collectors which filter fine particulate organic matter (FPOM). Ecosystem respiration exceeds primary production in headwater streams. In medium-sized streams (order 3-6), the major carbon input is FPOM from upstream (allochthonous) and autochthonous production by algae and vascular plants. Autochthonous production in these larger order systems is considered to be more important than upstream because of lesser shading of the water surface by riparian vegetation. Benthic animals with feeding modes defined as collectors and grazers are dominant. In this portion of the system, primary production exceeds respiration. In larger rivers (order>6), the allochthonous FPOM transported from upstream is the principal source of organic carbon. Terrestrial input and in-stream primary production are insignificant because of the large size of the river relative to its border with the terrestrial floodplain, its turbidity, and its depth. In large rivers, ecosystem respiration exceeds primary production (Vannote et al. 1980).

Although the RCC has been applied to explain river dynamics in small to medium size constricted channels, some serious limitations have been pointed out. First of all, the RCC was based primarily on studies of small to medium temperate rivers with forested headwaters, but has been extended to explain rivers in general. Secondly, not all rivers begin within a dense forest. Thirdly, there is not a smooth and continuous gradient in physical or biological properties of rivers from the headwater to the mouth. Rivers may be better viewed as spatially and temporally patchy with respect to their hydrological and geomorphological, and correspondingly ecological,
characteristics (Thorp et al. 2006). Fourthly, the composition of biological assemblages may not be as closely related to stream size or order as the RCC suggests. Lastly, the importance of the lateral floodplain to river processes is not taken into account by the RCC (Junk et al. 1989; Johnson et al. 1995).

The FPC adds a lateral dimension to river systems. The FPC views a river and its connected floodplain as one unit where the flood pulse is the major force for ecological processes. During flood periods, the river and floodplain are well connected, and organic matter is exchanged between the river main channel and the floodplain. A river introduces dissolved and particulate nutrients to the floodplain which will be available to promote algal production within floodplain backwaters, even after the river and floodplain disconnect and light limitation becomes relaxed in backwaters. At the same time, organic matter from the terrestrial component of the floodplain, as well as algae in backwaters, can be washed into the river as the flood pulse stabilizes and later recedes. Junk et al. (1989) considered these carbon inputs from the floodplain as autochthonous because they are produced within the river-floodplain systems. Following flooding, backwaters may be rich in nutrients and algal production, but with prolonged disconnection the floodplain can become nutrient limited for primary production. Primary production in the river is normally lower than the floodplain because of light limitation in the river (Cole et al. 1992). The FPC considers the FPOM transported from upstream as an insignificant source of organic carbon (Junk et al. 1989). The FPC has been applied to many floodplain river systems. However, it is limited to rivers that have an extended floodplain and flood pulse.

The RPM was proposed as an alternative to the RCC and the FPC. The RPM argues for the importance of autochthonous algal production in river channels to the river food web. The
RPM points out that the carbon transported from upstream or the floodplain is too refractory for consumers to assimilate. In contrast, autochthonous inputs from algae are more labile, more easily assimilated and thus disproportionately more important for consumer growth than their percentage of the total organic pool might suggest. The limitation of the RPM is that it is restricted to river systems that have enough light to support in-river autotrophic production (Thorp and Delong. 1994).

The different points of views of these three conceptual models have stimulated a great deal of research of large and small rivers around the world that has improved understanding of material flows in river ecosystems. Apparently, no single model can be applied to all river systems. For example, the RCC best describes forested headwaters to (constricted) medium sized rivers, the RPM can be applied to less turbid medium sized rivers without an extended floodplain, whereas the FPC best applies to large river floodplains that regularly flood.

Recently, Thorp et al. (2006) proposed the Riverine Ecosystem Synthesis (RES). The RES is an integrated model explaining how river systems function. The RES views the river network as having a four dimensional organization including lateral, longitudinal, vertical and temporal dimensions. Parts of the RES incorporate and modify the three river models discussed above (the RCC, the FPC and the RPM) to explain how lotic systems function. One of the major points of the RES is that rivers function not as a continuum, as in the RCC, but are better viewed as nested, discontinuous hydrogeomorphic patches, which are associated with distinct functional process zones (FPZ). According to the RES, there are different FPZs along the longitudinal length of the rivers. Examples of FPZs are unconstrained channels, constrained channels, and floodplains. Each FPZ has a different physiochemical condition which influences biotic factors
within the FPZ. Therefore, the distribution of organisms from headwater to mouth depends on the types and order of FPZs, rather than the stream order.

As for the carbon sources to river systems, the RES proposes that the principal organic carbon input supporting the river animal food web is autochthonous from autotrophs. In addition, the RES also states that allochthonous organic carbon input is occasionally important to headwater streams (similar to what the RCC predicts for headwaters). In contrast to the FPC, the primary carbon sources in the floodplain lakes are derived from algal production, rather than from macrophytes or terrestrial riparian vegetation. Lastly, the RES agrees with the FPC in the aspect of hydrological connection as a major factor controlling the dynamics of river floodplain systems. Probably the major contributions of the RES is that it recognizes the problems of viewing a river system as a single longitudinal or lateral continuum, it highlights the spatial and hydrological complexity of river systems, and points out the importance of understanding the patch dynamics of functional process zones for analysis of ecological processes in rivers.

These conceptual models of rivers have contributed to a greater understanding of energy and matter flow in large river ecosystems, but clearly no single model applies to all large rivers (Johnson et al. 1995; Dettmers et al. 2001). A contemporary model of energy and materials flux in rivers must account for the fact that most of the world’s large rivers have been substantially altered by human activities in their watersheds (Turner and Rabalais 2003; Barko et al. 2006). In addition, humans directly alter river physical conditions by modification of the river channel for navigation and/or flood control (Baker et al. 1991; Hein et al. 2001; Day et al. 2003).

This dissertation work focused on the relationships of the Lower Mississippi River main channel and its connected floodplain lakes with respect to physicochemical properties and phytoplankton community dynamics. The primary research question was: What role does
hydrological connectivity to the main river play in temporal patterns of physicochemical and biological properties of backwater sites? This question was directly influenced by the view of the importance of river-floodplain interactions to riverine ecosystems as presented most clearly by the FPC. However, whereas Junk et al. (1989) addressed primarily the effects of floodplain connection on the river, this study focused primarily on the effects of floodplain connection on backwater sites. To examine the relationships of the river and backwater systems, data were collected on three backwater systems that varied in their degree of hydrologic connection to the main channel. Data were collected over a 22-month period so that all degrees of connection were represented, from strong connection with the river to full surface water disconnection. It was predicted that during low hydrologic connection, floodplain backwater sites have high algal biomass but lower nutrient concentrations relative to the main river. When the river stage increases, these floodplain lakes become connected to the main river flow. During this period, algae in the floodplain lakes can be washed out to the main channel. At the same time, river water contributes to high turbidity and high nutrient concentrations in the floodplain lakes. This low light condition limits algal growth in the lakes. When the river and lakes are disconnected again, the suspended solids (in the lakes) settle out from the water column. As the photic zone of the backwater system deepens, algal production and biomass will increase, drawing nutrients from the water and reducing dissolved nutrient concentrations. Thus, temporal variation in physicochemical and biological properties of the floodplain backwaters are directly linked to their degree of connection, and time since last connection, with the main channel of the river.
CHAPTER 2

EFFECTS OF HYDROLOGIC CONNECTION ON PHYSICOCHEMICAL CONDITIONS AND PHYTOPLANKTON BIOMASS IN BACKWATERS OF THE LOWER MISSISSIPPI RIVER FLOODPLAIN

Introduction

The degree and timing of hydrologic connection between a river and its floodplain influence the morphology (Bayley 1995; Amoros and Bornette 2002), water chemistry, biotic community structure (Descy 1993; Bayley 1995; Tockner et al. 1999; Amoros and Bornette 2002), and energy pathways (Tockner and Schiemer 1997) of backwater aquatic habitats. For example, nutrients transported from a light-limited main river channel may support high primary production in less turbid connected backwaters (Cloern 2007), with cascading effects on productivity of both the microbial (Borsheim et al. 2005) and grazing food webs (Baranyi et al. 2002). Conversely, primary production in a backwater site can be transported via hydrologic connection to the river (Junk et al. 1989; Preiner et al. 2008), potentially intensifying secondary production of invertebrates, fishes, and other organisms in the main channel (Eckblad et al. 1984; Walks and Cyr 2004; Cloern 2007). In addition to serving as an conduit for movement of native species between the river and backwater sites, hydrologic connection can facilitate the spread of pollutants or invasive aquatic organisms through a river system (Bayley 1995; Pringle 2001). Clearly, hydrologic dynamics are a key factor controlling ecological and biogeochemical processes in river floodplain ecosystems (Junk et al. 1989; Tockner and Schiemer 1997; Hein et al. 2001; Pringle 2003).
The Mississippi River Basin (MRB) encompasses approximately 41% of the contiguous United States, and includes many of the largest rivers of North America, including the Mississippi River, the Ohio River, and the Missouri River. The Lower Mississippi River (LMR) is at the lower end of the MRB network, and therefore receives water and suspended materials from the entire Basin. The LMR extends nearly 1000 river kilometers (rkm) from its confluence with the Ohio River to the Gulf of Mexico.

In the last 50-100 years, the morphologies of all of the large rivers of the MRB have been extensively engineered in ways that have substantially altered their physical and chemical properties, and their influence on the Lower Mississippi River and the Gulf of Mexico. With the exception of the Lower Mississippi, each major river has been serially impounded, allowing some control over water flow, but resulting since the early 20th century in a substantial decline in transport and possible downstream deposition of suspended sediments. Along the Lower Mississippi, reinforcement of river banks with concrete revetments has prevented creation of new meanders. Engineered cutoffs across river meanders to straighten the river channel have increased water velocity, leading to a deepening of the channel, but also contributed to a reduction in lateral interaction with the floodplain. For millions of years prior to engineering modification, the Mississippi River would flood annually, resulting in the deep, rich agricultural soils of the Lower Mississippi alluvial valley. Development of an extensive levee system after large-scale flooding in 1927 separated the river main channel from all but a fraction of the historical floodplain. The net results of these anthropogenic alterations to channel morphology of the LMR are a substantial reduction in the degree of contact of the river with the terrestrial floodplain, floodplain lakes, and other backwater sites, with conversion of much of the historical floodplain to agriculture, urban development, or other uses (Baker et al. 1991).
However, despite a much lesser spatial extent of floodplain compared to the pre-engineering past, in many areas within the current levee system of the Lower Mississippi there remain numerous secondary channels and backwater sites, including hundreds of sloughs, lakes and other wetlands, with which the river is hydrologically connected on a seasonal basis (Baker et al. 1991). The LMR is a highly dynamic system responding to major precipitation inputs from across the entire Basin. Typically, river depth and discharge is greatest with snowmelt in the spring months, and at a minimum in late summer and fall. Therefore, springtime is the period of strongest and most prolonged hydrologic connection between backwater sites and the river main channel. The strength of the connection, and the direction of water flow, depends on the presence of connecting channels, the topography of the intervening landscape, and the relative surface elevations of the river and floodplain sites (Jones 2010). During the high-water period, river water is likely to flow into and through backwater sites. During the low-water period, in contrast, the elevational gradient favors a flux of water from the floodplain into the river.

River management must satisfy competing interests, including for river transport, flood control, ecosystem protection, and recreation. Given changes that have already occurred due to river engineering in the hydrologic interactions of the river and the floodplain, and the possibility of additional alterations for various purposes, and particularly because of the relative scarcity of floodplain aquatic sites on the LMR, it is critical to evaluate the roles that hydrologic connection plays for diversity, productivity and other ecological processes in these backwater sites, as well as for the Lower Mississippi River itself.

The purpose of this study was to investigate temporal patterns in phytoplankton biomass, water chemistry, and seston chemistry, in several backwater sites of the LMR varying in the strength and timing of their hydrologic relationships to the main channel. There were two related
hypotheses regarding the relationship of connectivity to backwater conditions: 1) During the period of hydrologic connection with the river, the backwater conditions will be similar to river conditions; 2) Following disconnection, the backwaters will decline in turbidity, and increase in phytoplankton biomass relative to the main river. Associated with the increase in phytoplankton biomass, there will be a decline in concentrations of growth-promoting nutrients such as NO$_3$-N and PO$_4$-P.

Methods and Materials

Study Sites

One LMR main channel location and three backwater sites varying in degree and timing of hydrologic connection to the main river were chosen for this study (Figure 2.1). The three backwater sites are Quapaw Chute, Modoc Lower Lake, and Mellwood Lake. The section of the river which connects these three backwater sites is approximately 20 rkm long. All river stage heights referred to are from the gauging station at Helena, Arkansas, which is about 50 rkm north of our study area, and operated by the U.S. Army Corps of Engineers.

Quapaw is a secondary river channel with both upstream and downstream ends connecting to the LMR main river at high river stage. It is about 9 km in length. For many years, the upper end of Quapaw was blocked from connection with the river by a dike constructed in 1961. In an effort to improve fish habitat, shortly before this study began, in 2006, the dike was reduced in size to increase water flow through the chute. Presently, when the river stage is higher than 2 m, river water flows directly through Quapaw from the northern to the southern end. At a lower river stage, the upstream end becomes disconnected to the main channel abruptly reducing input of river water and current within the chute. The LMR can
intermittently drop below a Helena river stage of 2 m in late summer through early winter. The sample site in Quapaw Chute was located approximately 1.5 km from the southern connection of the chute with the river, at 34°15'49.98" N, 90°44'36.54" W.

Modoc Lower Lake is an abandoned chute on the Arkansas side of the river, and about 4 km in length. Although separated from the river by a high revetment on the river west bank, at river stages above 7.5 m there is an extensive lateral surface connection of the southern portion of the lake with the LMR main channel. At lower river stages, the river drops below the top of the revetment, nearly eliminating surface connection of the lake and river main channel. The sample site at Modoc Lower Lake was located approximately 0.5 km from the southern end of the lake at 34°17'0.30" N, 90°49'48.00" W.

Mellwood Lake is slightly south of Modoc Lower Lake, also in Arkansas, and is about 10 km in length. It was formed in the 1930s by an artificial cut-off of the Mississippi River that was intended to aid river transport by reducing meanders. At Helena river stages above 10 m, river water from the western edge of the LMR enters at the northern end of Mellwood Lake and exits at its southern end. At lower river stages, the upstream end of Mellwood Lake becomes disconnected from the river, but the downstream end remains permanently connected to the main channel through a 0.5 km long, narrow channel. The flow of water between the river and the southern end of the lake appears to switch from river-to-lake to lake-to-river on a short-term basis depending on their relative surface elevations. The sample site at Mellwood Lake was located approximately 1 km from the southern end of the lake at 34°11'30.22" N, 90°54'26.46" W.

In summary, of the three backwaters, Quapaw has the most extensive and prolonged hydrologic connection to the main channel. The other two backwater sites mix substantially with
river water when the river elevation is high, but switch to either nearly complete surface water disconnection (Modoc Lower), or highly reduced connection (Mellwood), as the river drops in elevation between spring and late summer.

The LMR main channel sample site (34°16’32.27” N and 90°47’28.32” W) was located in the reach of the river between Quapaw Chute and Modoc Lower Lake. Samples were collected and measurements made near the center of the river channel.

![Map of study sites](image)

**Figure 2.1: Study sites; the LMR main channel, Quapaw Chute, Modoc Lower Lake, and Mellwood Lake. The stars indicate sampling locations.**
Hydrologic Connection

Hydrologic connection at times of sample collections was categorized based on the river stage at Helena, Arkansas, combined with direct observations of surface hydrologic connection between the river and backwater sites. River stage readings during this study were provided by the United States Army Corps of Engineers, Memphis District. Connectivity was defined with respect to the influence of the river on the backwater site. The river and lake were considered to be hydrologically connected when river water flows freely into or through the backwater sites. Connection was considered absent (“disconnection”) when the flow of river water into or through these sites was halted, although flow of water from Quapaw Chute or the two lakes into the river may still have occurred. Patterns of hydrologic connection in Quapaw and Modoc Lower Lake were relatively easy to monitor due to the influence of a prominent physical barrier on degree of connection. The height of the dike at the upper end of Quapaw, and the height of the river bank at the lower end of Modoc Lower Lake, determines whether or not there is surface connection between the river and these two backwater sites. Based on the height of these barriers, and the river stage, we could estimate when these two backwater sites last connected to the main channel. Day post-connection of these sites to the river was calculated from the number of days from the last connection to the sampling date. It was more difficult to determine day post connection for Mellwood Lake due to the lack of a physical barrier completely separating surface river water from lake water. On the sample days, we could surmise river influence at the southern end by visual observation of the direction of water flow between the river and lake. On other days, however, direction of water flow could not be confidently determined, as data on surface elevation for Mellwood were not available, and we were therefore unable to evaluate relative surface elevation compared to the river.
**Water Collection**

Samples and basic limnological data were collected on a bi-monthly to monthly basis at all four locations on 21 dates from November 2007–September 2009. Lake water and mid-channel river water were collected at 0.5 meter below the surface using 2-L Nalgene bottles. Additional water samples were collocated at the same location in BOD bottles for pH measurements. At each sample site three replicate water samples were collected, and kept cool and dark during transport to the laboratory (2-4 hours).

**Physical and Chemical Conditions**

Dissolved oxygen and temperature were measured using an YSI 57 meter. Depth was measured using a Hawkeye Handheld Sonar System PX (H22PX). In the laboratory, turbidity was measured using a Hach 2100A turbidometer.

Whatman GF/F filtered water was used for analysis of dissolved organic carbon (DOC), dissolved nitrogen (NO₃-N), and dissolved phosphorus (PO₄-P). Dissolved organic carbon was analyzed using a Teledyne-Tekmar Apollo 9000, NO₃-N using a Dionex ion chromatograph, and soluble orthophosphate (PO₄-P) by colorimetry according to Wetzel and Likens (2000). An Accumet Excel XL60 pH meter was used to measure pH.

Phosphorus, nitrogen and carbon were measured in seston retained on Whatman GF/F filters. Particulate phosphorus (P) was measured by the method of Solorzano and Sharp (1980). Particulate carbon (C) and nitrogen (N) were analyzed using a CE Elantech CHN analyzer.

Seston C:N ratios were used to evaluate sources of organic matter at different river stages. A C:N ratio less than 8 indicates that the organic matter is primarily from planktonic sources including autotrophic and/or heterotrophic microorganisms. A C:N ratio more than 8...
indicates non-planktonic derived materials comprising terrestrial soil or plants, and/or macrophytes (Kendall et al. 2001; Hein et al. 2003).

**Phytoplankton biomass**

Chlorophyll *a* concentration was used as an indicator of phytoplankton biomass. In the laboratory, 200-500 mL of water was filtered through a Whatman GF/C filter. Filters were extracted with 90% alkaline acetone overnight, and chlorophyll *a* measured using a calibrated Turner Designs TD-700 fluorometer (Wetzel and Likens 2000).

**Statistical Analysis**

For comparison and statistical analysis, all limnological data and chlorophyll *a* concentrations were classified into six different groups; river, Quapaw during connection, Quapaw during disconnection, Modoc Lower during connection, Modoc Lower during disconnection, Mellwood during connection and Mellwood during disconnection. One-way ANOVAs were used to access differences among groups. For ANOVA results indicating significantly differences, Tukey-Kramer HSD tests were applied to determine which means were different from one another. To meet the assumptions of ANOVA, values for turbidity, dissolved O₂, DOC, chlorophyll *a*, and particulate C, N and P were log₁₀ transformed, and pH values were square-root transformed. Pairwise correlations were used to explore the relationship of limnological parameters and chlorophyll *a* concentration.

**Results**

**Degrees and Patterns of Hydrologic Connection**

The river stage of the LMR fluctuated about 15 m during the study period (Figure 2.2), resulting in a high degree of temporal variation in hydrologic connection between each
backwater and the river. Peaks of river depth and elevation occurred in April 2008 and May 2009. The lowest river elevations occurred in November 2007, early in September 2008, and in late October 2008. Depth measurements at our sample locations in all three backwater sites were highly correlated to river stage; $r^2 = 0.92$, 0.83 and 0.91 in Quapaw, Modoc Lower and Mellwood, respectively (Figure 2.3).

![Figure 2.2: Lower Mississippi River stages at Helena, Arkansas, November 2007-September 2009. Squares indicate sampling dates. The river stages above horizontal lines were connection phases of each study site.](image-url)

**Figure 2.2:** Lower Mississippi River stages at Helena, Arkansas, November 2007-September 2009. Squares indicate sampling dates. The river stages above horizontal lines were connection phases of each study site.

![Figure 2.3: Relationship of river stage at Helena, Arkansas and depth measurements at sample locations of backwater sites.](image-url)

**Figure 2.3:** Relationship of river stage at Helena, Arkansas and depth measurements at sample locations of backwater sites.
Effects of Hydrologic Connection

Mean values of limnological parameters and chlorophyll $a$ concentration are shown in Table 2.1. Hydrologic connectivity affected turbidity levels in Quapaw and particulate N in Quapaw, Modoc Lower Lake and Mellwood Lake. It influenced phytoplankton biomass and dissolved nutrients (NO$_3$-N, PO$_4$-P) in all three backwater sites. On the other hand, averaged particulate C, particulate P, pH, dissolved O$_2$, temperature and DOC were not significantly different between connection and disconnection phases.
<table>
<thead>
<tr>
<th>Variables</th>
<th>River</th>
<th>Quapaw Connected</th>
<th>Quapaw Disconnected</th>
<th>Modoc Lower Connected</th>
<th>Modoc Lower Disconnected</th>
<th>Mellwood Connected</th>
<th>Mellwood Disconnected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turbidity (NTU)</td>
<td></td>
<td>50±4.1a (21)</td>
<td>51±4.8a (18)</td>
<td>16±3.2b,c (3)</td>
<td>19±3.8b (12)</td>
<td>10±1.5b,c (9)</td>
<td>13±3.7b,c (8)</td>
</tr>
<tr>
<td>pH</td>
<td></td>
<td>7.98±0.04 (21)</td>
<td>7.99±0.04 (18)</td>
<td>8.06±0.30 (3)</td>
<td>8.44±0.15 (12)</td>
<td>8.27±0.21 (9)</td>
<td>8.30±0.18 (8)</td>
</tr>
<tr>
<td>Temperature(°C)</td>
<td></td>
<td>20.3±1.8 (19)</td>
<td>20.2±2.0 (17)</td>
<td>22.5±5.0 (2)</td>
<td>19.1±2.4 (12)</td>
<td>26.2±1.5 (7)</td>
<td>17.1±2.4 (8)</td>
</tr>
<tr>
<td>O2 (mg L⁻¹)</td>
<td></td>
<td>7.6±0.5 (19)</td>
<td>7.5±0.6 (17)</td>
<td>9.9±1.2 (2)</td>
<td>10.3±0.6 (11)</td>
<td>10.5±1.8 (9)</td>
<td>10.6±0.9 (8)</td>
</tr>
<tr>
<td>DOC (mg L⁻¹)</td>
<td></td>
<td>4.4±0.1 (21)</td>
<td>4.3±0.1 (18)</td>
<td>3.1±0.5 (3)</td>
<td>4.5±0.2 (12)</td>
<td>5.6±0.3 (9)</td>
<td>4.0±0.1 (8)</td>
</tr>
<tr>
<td>NO3-N* (mg L⁻¹)</td>
<td></td>
<td>1.8±0.1a (21)</td>
<td>1.8±0.1a (18)</td>
<td>0.6±0.5b,c (3)</td>
<td>1.2±0.1b (12)</td>
<td>0.3±0.1b (9)</td>
<td>1.3±0.4b (8)</td>
</tr>
<tr>
<td>PO4-P* (mg L⁻¹)</td>
<td></td>
<td>0.029±0.003a (15)</td>
<td>0.029±0.003a (13)</td>
<td>0.002±0.002b (3)</td>
<td>0.011±0.004b (7)</td>
<td>0.002±0.006b (9)</td>
<td>0.011±0.004ab (5)</td>
</tr>
<tr>
<td>Particulate C (mg L⁻¹)</td>
<td></td>
<td>3.5±0.4 (21)</td>
<td>3.4±0.6 (18)</td>
<td>6.3±4.1 (3)</td>
<td>2.2±0.2 (12)</td>
<td>4.2±0.8 (9)</td>
<td>1.6±0.2 (8)</td>
</tr>
<tr>
<td>Particulate N* (mg L⁻¹)</td>
<td></td>
<td>0.35±0.03b (21)</td>
<td>0.33±0.05b (18)</td>
<td>0.90±0.55a (3)</td>
<td>0.35±0.05b (12)</td>
<td>0.69±0.13a (9)</td>
<td>0.27±0.05b (8)</td>
</tr>
<tr>
<td>Particulate P (mg L⁻¹)</td>
<td></td>
<td>0.15±0.02 (21)</td>
<td>16±0.02 (18)</td>
<td>0.18±0.04(3)</td>
<td>0.08±0.01(12)</td>
<td>0.12±0.02(9)</td>
<td>0.06±0.01(8)</td>
</tr>
<tr>
<td>Chlorophyll a* (µg L⁻¹)</td>
<td></td>
<td>6.3±0.7c,d (21)</td>
<td>5.6±0.6d (18)</td>
<td>150.4±122.7b,c (3)</td>
<td>31.9±7.1b (12)</td>
<td>107.9±29.9a (9)</td>
<td>21.3±7.1b,c (8)</td>
</tr>
</tbody>
</table>

Table 2.1: Mean values of limnological properties and chlorophyll a concentration according to hydrologic connection ± SE (number of observation). DOC = dissolved organic carbon.

* indicates parameters that are significantly different between connection and disconnection periods (p < 0.05). Letters in front of the mean values indicate test results from Tukey-Kramer HSD tests. Different letters indicate significant differences among means.
Temporal and spatial variation in turbidity is shown in Figure 2.4. Turbidity varied from 22-79 NTU in the main channel. It ranged from 12-81 NTU in Quapaw, 3-41 NTU in Modoc Lower Lake and 2-33 NTU in Mellwood Lake. In general, turbidity in the main channel and Quapaw were similar. However, when Quapaw disconnected from the main channel at low river stage, turbidity in Quapaw decreased drastically (Figure 2.4a). Modoc Lower and Mellwood lakes usually experienced relatively low turbidities (Figure 2.4b). Mean turbidities in Quapaw during the disconnection phase, and Modoc Lower and Mellwood during both connection and disconnection phases, were significant lower than in Quapaw during the connection phase and in the main channel ($F_{(6,77)} = 21.73$, $p < 0.0001$).

**Figure 2.4:** Spatial and temporal variation of river stage at Helena, Arkansas, and turbidity a) in the main channel and Quapaw and b) in the main channel, Modoc Lower and Mellwood.

Spatial and temporal variation in chlorophyll $a$ and river stage is shown in Figure 2.5. Overall, chlorophyll $a$ concentrations in the main channel were low (less than 13 $\mu$g L$^{-1}$). As for turbidity, Quapaw tended to track the main channel in chlorophyll $a$ concentration, except at very low river depth. Upon disconnection, a high chlorophyll $a$ concentration developed in Quapaw, between 24-396 $\mu$g L$^{-1}$ depending on the day (Figure 2.5a). At high river stage when Modoc
Lower and Mellwood were strongly connected with the river, chlorophyll $a$ concentration in the lakes dropped as low as in the main channel. As river depth declined, and the lakes separated, chlorophyll $a$ in Modoc Lower and Mellwood lakes increased correspondingly, often exceeding river values by an order of magnitude or more (Figure 2.5b). Mean chlorophyll $a$ concentrations in all three backwater sites were 3-30 times higher during disconnection than during connection. The difference was significant for all three sites ($F_{(6,77)} = 29.80$, $p < 0.0001$).

Dissolved NO$_3$-N and PO$_4$-P exhibited similar patterns, nearly identical to the river with hydrologic connection, diverging from river values following disconnection. For both nutrients, mean values in all three backwater sites (Table 2.1) during connection, and in the main channel, were significantly greater than during the disconnection period (for NO$_3$ –N, $F_{(6,77)} = 20.08$, $p < 0.0001$; for PO$_4$-P, $F_{(6,58)} = 19.95$, $p < 0.0001$).

**Figure 2.5:** Spatial and temporal variation of river stage at Helena, Arkansas, and chlorophyll $a$ a) in the main channel and Quapaw and b) in the main channel, Modoc Lower and Mellwood lakes.
Figure 2.6: Limnological properties and chlorophyll $a$ in the river and three backwater sites according to day post connection.

As mentioned above, only in Quapaw and Modoc Lower could number of day(s) post connection be estimated reliably. The duration of disconnection was very different between
these two sites, corresponding to the difference in the height of the boundaries separating them from the main channel. In Modoc Lower Lake, the period of disconnection lasted over 200 days, extending from May 2007 to December 2007. In Quapaw, the period of disconnection was much more transient, lasting only 20 days. At both sites, turbidity declined rapidly, and chlorophyll $a$ and particulate N increased rapidly, following disconnection. However, after about 50 days of disconnection, turbidity in Modoc Lower increased, and chlorophyll $a$ and particulate N declined from their peak values (Figures 2.6a, b and e). Dissolved nutrients decreased rapidly after disconnection at both sites, but after prolonged disconnection in Modoc Lower, dissolved nutrients slightly increased (Figures 2.6c and d).

Including data from all sites, chlorophyll $a$ concentration was negatively correlated ($p < 0.0001$) to turbidity, dissolved NO$_3$-N and PO$_4$-P ($r^2 = -0.45$, -0.60 and -0.63, respectively). Chlorophyll $a$ was positively correlated ($p < 0.0001$) to particulate N and particulate C ($r^2 = 0.85$ and 0.59, respectively), but not correlated to particulate P.

**Source of Organic Matter**

Seston C:N ratios were significantly higher in the main channel and in Quapaw during connection than in Quapaw during disconnection, and Modoc Lower and Mellwood during both disconnection and during connection ($F_{(6,77)} = 17.09$, $p < 0.0001$; Figure 2.7a). The majority (about 95% for both sites) of C:N ratios in the main channel and Quapaw were higher than 8. In contrast, only about 24% and 14% of the seston C:N ratios in Modoc Lower and Mellwood, respectively, were higher than 8 (Figure 2.7b). These data suggest that the main channel and Quapaw received organic matter primarily from terrestrial sources. On the other hand, the two floodplain lakes derived organic matter mostly from autochthonous sources, especially during the period of disconnection, but also during connection.
Figure 2.7: a) Mean values of C:N ratios in the river and three backwater sites. Capital letters over the bars indicate test results from Tukey HSD tests. Different letters indicate significant differences of the means and b) molar seston C:N ratios in the river and three backwater sites relative to river stage at Helena, Arkansas.

Discussion

Effects of Hydrologic Connection

With hydrologic connection, the backwater sites resembled the river channel, with high turbidity and nutrient concentrations, and low phytoplankton biomass and particulate N. Influx into backwater sites of suspended solids and associated turbidity from river water reduced light
availability for phytoplankton growth, as has been observed in other floodplain lake systems (Reynolds and Descy 1996; Amoros and Bornette 2002). Once the river level dropped, backwaters become disconnected from the main channel reducing advective water movement, and increasing settling of suspended solids, while dissolved nutrients in backwaters remained high. These conditions promoted high phytoplankton production (Pongruktham and Ochs, unpub. data) and accumulation of biomass in the backwater sites. With the increase in phytoplankton biomass, particulate N increased, while dissolved nutrients were depleted to below the detection limit following disconnection (Figure 2.8). The disappearance of these nutrients may be due partly to assimilation by phytoplankton (Tockner et al. 1999; Hein et al. 2004; 2005) and/or macrophytes (Bondar-Kunze et al.), and/or, for N, by denitrification (Richardson et al. 2004; Forshay and Staney 2005). Interestingly, rapidly accumulating chlorophyll $a$ was strongly inversely correlated with NO$_3$-N ($r^2 = -0.60$) and PO$_4$-P ($r^2 = -0.63$) concentrations, while chlorophyll $a$ concentration was significantly positively correlated to the increase in particulate N ($r^2 = 0.85$). These results suggest uptake and assimilation of the nutrients by a phytoplankton community that substantially increases in biomass with temporary cessation of river influence. The subsequent slight increase in dissolved nutrients in Modoc Lower after 50 days of post-connection might be due to collapse of the phytoplankton community (as indicated by chlorophyll $a$ levels, Fig.2.6b), or possibly to some mixing of surface water with bottom water as the depth of the lake declined.
The results can be compared with studies of river-floodplain connectivity in the Danube River ecosystem (Tockner et al. 1999; Hein et al. 2004) and the Missouri River (Knowlton and Jones 1997). During connection with the river, floodplain lakes of the Danube and the Missouri experienced higher turbidity and nutrient concentrations, but lower chlorophyll $a$ concentrations. With disconnection, water turbulence and turbidity in floodplain lakes decreased while nutrient levels initially remained high, resulting in an increase in phytoplankton concentration and a simultaneous decline in nutrient concentration. This is the same pattern of responses with changing degree of connection that we observed for the LMR floodplain. The magnitude of chlorophyll $a$ increase and the disappearance of nutrients found in the Missouri River’s floodplains were comparable to what we found in Quapaw and Modoc Lower following disconnection. However, the Danube River lakes did not exhibit the same degree of change as in these two LMR backwater sites. Backwaters of the Upper Mississippi River are also very effective at reducing nitrate load (James et al. 2008a, b)

Sources of Organic Matter

The data indicate that the main channel and Quapaw obtain particulate organic matter primarily from non-planktonic sources. This is in contrast to the cautious speculation of Kendall and others (2001) who suggested, based on the particulate isotope signature and C:N ratio, that phytoplankton are a major source of particulate organic matters in the Lower Mississippi River.
main channel. In contrast, organic matter in Modoc Lower and Mellwood Lake were primarily plankton-derived, even during most of the connection phase. Only at the very high-water elevations of spring (Helena river stages higher than 13 m) did C:N ratios higher than 8 occur at these sites (Figure 2.7). This suggests that except for at the highest degree of hydrologic connection, the residence time of river water in these long lakes during connection was long enough for suspended solids to drop out of the water column, allowing enhanced phytoplankton growth in the higher light, high nutrient and low turbulence systems. Hein et al. (2003) found a similar trend for the Danube River ecosystem, where the mean C:N ratio significantly increased from sites having lower connection to sites with higher river connection.

In summary, hydrologic connection with the LMR main channel appears to be an important factor influencing limnological properties and phytoplankton biomass of connected backwater systems. During connection, river water contributed to high turbidities and nutrient concentrations in the backwater sites. Low light availability suppressed phytoplankton development in the backwater sites. When the backwater sites disconnected from the main channel, turbidity levels decreased while chlorophyll $a$ concentrations increased. In addition, nutrient depletion was found during the disconnection phase. Accumulation of high phytoplankton biomass highlights the importance of these backwater sites in the food web of the entire river system. As sinks for nutrients these sites could be important in removing nutrients from further downstream transport, an ecosystem service of potential importance to water quality in the Gulf of Mexico.
CHAPTER 3
ALGAL PRODUCTION AND PHOTOSYNTHETIC PARAMETERS IN THE LOWER MISSISSIPPI RIVER AND ITS CONNECTED BACKWATERS

Introduction

Phytoplankton production in the main channel flow of large rivers is commonly limited by light availability (Descy and Gosselain 1994, Ochs et al. in review). Much of the phytoplankton biomass that occurs in a large river channel may be produced in less light-limited portions of the system including shallow lateral areas of the channel, or backwater sites to which the river is more-or-less strongly hydrologically connected depending on the time of year (Thorpe et al. 2006). Organic substrates derived from phytoplankton tend to be easier to assimilate and have higher energy content per unit mass than terrestrially-derived detritus (Thorpe and Delong 1994; 2002). For this reason, phytoplankton biomass in large rivers, whether produced in situ, or obtained by washing in from connected floodplain sites, may serve, compared to non-algal derived organic matter, as a disproportionately important food resource for secondary consumers.

In river floodplain ecosystems, hydrologic dynamics are a key factor controlling ecological and biogeochemical processes of backwater aquatic habitats (Junk et al. 1989; Tockner and Schiemer 1997; Hein et al. 2001; Pringle 2003). It is believed that, with a hydrologic link between river-floodplain systems, nutrients transported from the main channel may support high primary production in backwaters (Cloern 2007). Conversely, primary
production in a floodplain lake can be transported to the main channel (Preiner et al. 2008). This imported primary production may potentially promote secondary production in the main channel (Eckblad et al. 1984; Walks and Cyr 2004; Cloern 2007). Therefore, understanding the dynamics of phytoplankton production in relation to hydrologic connection is critical to explain how food webs of river-floodplain systems function (Power and Dietrich 2002).

In floodplain lakes, underwater light availability can vary dramatically with degree of hydrological connection to the river (Talling and Rzoska 1967; Tockner et al. 1999; Gabellone et al. 2001; Hein et al. 2001; Schemel et al. 2004). At high river stage, backwater sites connect to the main channels. During this time, river water flows into floodplain lakes bringing high suspended solids and associated turbidity into the backwaters resulting in low light condition in the water column. On the other hand, as the river height declines, the floodplain lakes and main channels may start to separate. As a result, water turbulence and turbidity in floodplain lakes decrease, leading to more light availability in underwater light in the backwater sites (Chapter 2). This leads to more light availability in underwater light in the backwater sites.

With changes in the light environment over a short period of time, algae may physiologically acclimate by altering: 1) the amount and ratio of photosynthetic pigments, 2) photosynthetic responses (photosynthetic efficiency or maximum photosynthetic capacity), 3) cell chemical composition, 4) cell volume, 5) dark respiration rate, or 6) enzyme activity associated with carbon fixation (Falkowski 1984; Hill 1996; Geider et al. 1997). Over a longer episode, when resident phytoplankton taxa cannot withstand changing environmental conditions, species succession may occur, as is common on a seasonal basis in many temperate lakes (Falkowski 1984; Wetzel and Likens 2000). In either case, under different light conditions, it is expected that the phytoplankton community will vary in their photophysiological responses.
either due to photo-acclimation of the original species, or community changes by species succession.

The photosynthesis-irradiance (P-I) relationship is one commonly used method for evaluating phytoplankton physiological responses to light variation (Falkowski 1984; Gallegos 1992; Descy and Gosselain 1994; Geider et al. 1996; Hill 1996). Two critical photosynthetic properties indicating physiological condition that can be acquired from a P-I curve (Figure 3.1) are $\alpha$ (alpha) and $P_{\text{max}}$. At low irradiances, photosynthesis rate increases linearly with increasing irradiance. This portion of the curve, the slope of which is $\alpha$, is a measure of phytoplankton photosynthetic efficiency at sub-saturating irradiances. The maximum capacity of photosynthesis by the community at saturating irradiance, or $P_{\text{max}}$, is indicated by the portion of the P-I curve at which photosynthetic rate levels off at high irradiances. In some cases, at increasing irradiance, there may be a decline in photosynthetic rate due to photo-inhibition of photosynthetic activity (Kirk 1994; Hill 1996).

![Figure 3.1: Relationship of photosynthetic rate and irradiance level (P-I curve) in Modoc Lower water in December 2007.](image)

In this study the temporal and spatial patterns in surface water phytoplankton gross primary production and photosynthetic parameters in a portion of the Lower Mississippi River (LMR) and its floodplain were examined. There were two objectives. The first was to compare
phytoplankton production in the river with several backwater ecosystems, as well as within each ecosystem over time, during periods of hydrologic connection with, and disconnection from, the river. It was hypothesized that phytoplankton production in backwaters would be similar to the river during connection, but diverge strongly from the river following disconnection. The relationships of phytoplankton production to variation in temperature, light levels, and nutrient levels were explored. The second objective was to determine if there was spatial or temporal variation in phytoplankton photosynthetic parameters either between ecosystems, or within a system, as degree of connection with the river changed. It was hypothesized that, in a light-limited environment, such as a river main channel or lakes highly influenced by the river due to a strong hydrological connection, there would be a higher biomass-specific $\alpha$ value but lower biomass-specific $P_{\text{max}}$ value than in a phytoplankton community from a high light environment. The basis of this hypothesis is that a phytoplankton community will often adapt to a low light environment by an increase in concentration of intra-cellular antenna pigments and a decrease in dark reaction enzymes (Hill 1996). In addition, we conducted three nutrient limitation experiments to investigate the potential for nutrient limitation of phytoplankton growth in the LMR floodplain ecosystem.

**Methods and Materials**

*Study sites*

Water samples were collected from a single location in the Lower Mississippi River main channel and from three backwater sites within a 20 river kilometers (rkm) section of the river reach. These backwater sites included a secondary river channel, Quapaw Chute, and two oxbow lakes, Modoc Lower and Mellwood lakes, which have different patterns of connection to
the main channel. All river stage heights to which we refer are from the gauging station at
Helena, Arkansas, which is about 50 rkm north of our study area, and operated by the U.S. Army
Corps of Engineers.

Quapaw chute is the most strongly and persistently connected site to the river main
channel. When connected, river water flows directly through the chute from the northern to the
southern end. When disconnected, river water is prevented from entering the chute at the upper
end by a low weir. While at the lower end the chute remains hydrologically in contact with the
river, exchange with river water is greatly reduced. The critical river stage depth at which the
chute switches between connection and disconnection is 2 m. Quapaw is approximately 9 km in
length. At a typical summer river velocity of 1 m sec⁻¹ (data provided by U.S. Army Corps of
Engineers), it would take only about 2.5 h for river water to flow from one end of the chute to the
other. The sampling location was about 1.5 km from the southern end of the chute.

Modoc Lower is a floodplain oxbow lake located on the west side of the river main
channel, and is approximately 4 km in length. It is separated from the main channel by a
revetment composed of concrete and rock riprap. Unlike Quapaw, river water does not flow
directly from the upper end to the lower end of this study site. Instead, at high river stage, it has
a strong lateral connection to the main channel for approximately 1 km along the southern end.
The critical river stage when the southern end of the lake switches from lateral connection to
disconnection is 7.5 m. The sampling site in Modoc Lower was about 0.5 km from the southern
end of the lake, in the region that strongly connects with the river during high water.

Mellwood Lake, an artificial cut-off of the Mississippi River, is about 10 km in length,
and has both upstream and downstream connections to the main channel when the river stage is
high. The critical river stage when river water flows from the northern end of this lake through
the southern end of the lake is about 10 m. At lower river stages, only the downstream end of the lake remains in contact to the main channel through a narrow (5 – 50 m, depending on river height) channel about 0.5 m in length. The direction of water flow through this channel between the river and lake at the southern end depends on their relative surface elevations, which can change rapidly, and during this study, water flowing in both directions was observed. The sample spot was located approximately 1 km from the southern end of the lake.

The LMR main channel was sampled in the center of the river channel, close to the thalweg. The reach of the river sampled was located approximately midway between Quapaw and Modoc Lower.

*Hydrologic connection*

Hydrologic connection of these backwater sites to the main channel was defined with respect to the influence of the river on the backwater sites at the sampling locations. The backwater sites were considered hydrologically connected to the river when river water flows through or into them. When the flow of river water into or through the backwaters ceased, they were considered hydrologically disconnected. Therefore, to categorize hydrologic connection, direct observations of flow direction and river stage at Helena, Arkansas were combined.

During low water, Quapaw and Modoc Lower are separated from the main channel by a physical barrier. The dike at the upper end of Quapaw and the revetment at the lower end of Modoc Lower function as near “on-off switches” for hydrologic connection. Quapaw and Modoc Lower are connected to the main channel at river stages above the critical river stages. When the river stage is below the critical river stage, or falls below the barrier between the river and these two sites, then these two sites were considered disconnected from the main channel.
In Mellwood Lake, at river stages higher than the critical stage, river water flows through the lake, and the lake is connected with the river. At lower river stages, visual observation of the direction of water flow through the channel at the southern end of the lake was used to determine if there was connectivity or not. Mellwood Lake was characterized as hydrologically connected when river water flows into the lake. On the other hand, this lake is considered disconnected to the main channel when lake water flowed into the main channel.

During the period of connection between the river and backwaters, the degree of connection may vary from minimally connected to maximally connected. Minimal connection would be the case if there was only a small volume of water from the river entering the backwaters. At maximal connection there would be a relatively large volume of water flowing from the river into backwaters. In an attempt to quantitatively assess the “degree of connection” we evaluated the ratio (NO$_3$-N of each backwater site: NO$_3$-N in the main channel). At maximum connection this ratio should approach 1; at minimal connection the ratio should vary from 1, either smaller or larger. This determination was only made for times when the river was connected to some degree.

_Sample collection and water analysis_  

Samples were collected on a bimonthly to monthly basis for 17 sample days during November 2007-April 2009. Water was sampled from about 0.5 m below the surface in 2 L-bottles. Water samples for dissolved inorganic carbon (DIC) were collected in BOD bottles. All samples were stored in cool dark coolers during transport to the laboratory for estimation of phytoplankton production and photosynthetic parameters of the phytoplankton community. On site temperature was measured using an YSI Model 57 meter.
In the laboratory, 150-200 mL of water was filtered through Whatman GF/F filters for analysis of dissolved nitrogen (NO$_3$-N) and dissolved phosphorus (PO$_4$-P). A Dionex ion chromatograph was used to analyze NO$_3$-N. Soluble orthophosphate (PO$_4$-P) was evaluated by colorimetry according to Wetzel and Likens (2000).

**Phytoplankton production**

Phytoplankton production at the four sample sites was estimated based on light availability in the field combined with photosynthesis-irradiance (P-I) curves produced in the laboratory, using the $^{14}$C-method to measure production (Howarth and Michaels 2000; Wetzel and Likens 2000; Staehr and Sand-Jensen 2006).

**Light availability in the field**

Surface irradiance in the field was acquired from the Surface Radiation Network (SURFRAD) website (http://www.srrb.noaa.gov/surfrad/goodwin.html). Data from Goodwin Creek, Mississippi were used. To obtain a representative measure of surface light availability for the time period, photosynthetically active radiation (PAR: 400-700 nm) were averaged over 10-days starting from 9 days before the sampling date to the sampling date. A constant albedo of 10% to account for loss of light due to surface-water reflectance was used.

Light extinction coefficients (k) were derived from an empirically derived relationship of extinction coefficient and turbidity (NTU): $k = 1.81 \times 2.72^{(0.027\text{NTU})}$ ($r^2 = 0.94, n = 25$). Mean light intensities (I) per day in 1 m depth (z) were calculated as: $I = (I_0)(1-e^{-kz}) (kz)^{-1}$, where $I_0$ is surface irradiance corrected for albedo loss. Irradiances calculated for each 0.1 m depth interval for the upper 1 m of water column were used for estimating surface water phytoplankton production by Jassby and Platt (1976), as discussed further below. To assess the possibility of light limitation of production, mean irradiances in 1 m depth at mid-day (09:00-15:00) for each
sampling date/site were compared to the irradiance for \( P_{\text{max}} \) (see below). In addition, the photic zone depths (depth at 1% light level) were calculated and compared.

**Laboratory incubations**

Water samples were incubated in a laboratory photosynthetron (Lewis and Smith 1983; Babin et al. 1994) at 15-21 different light levels (from 0-700 \( \mu \text{mol photon m}^{-2} \text{s}^{-1} \)). Radiolabeled dissolved inorganic carbon (D\( ^{14}\text{C} \)), as NaH\( ^{14}\text{CO}_3 \), was added in water samples to a final concentration of 0.20 \( \mu \text{Ci mL}^{-1} \). Seven mL of D\( ^{14}\text{C} \) spiked sample water was pipetted into 20-mL glass scintillation vials. For killed controls, two of the vials were acidified with 700 \( \mu \text{L} \) of 1N HCl. The rest of the vials were incubated in the photosynthetron for 1-1.5 h at *in situ* temperature. To end the incubation, samples were acidified with 1N HCl and shaken in uncapped vials at 75 rpm for 24 h to remove unincorporated D\( ^{14}\text{C} \). For scintillation counting, 14 mL of Perkin Elmer Ultima Gold XR LSC-Cocktail was added to samples. A Beckman LS6500 Multi-Purpose Scintillation Counter was used to measure D\( ^{14}\text{C} \) incorporated into organic molecules (fixed organic \( ^{14}\text{C} \)). For all incubations, vouchers were taken for the measurement of initial D\( ^{14}\text{C} \) availability.

Available unlabeled dissolved inorganic carbon (D\( ^{12}\text{C} \)) in water samples was calculated from total alkalinity, pH and water temperature using the Gran titration method (Wetzel and Likens 2000). From the amount of fixed D\( ^{14}\text{C} \) per time, and the ratio of D\( ^{14}\text{C} \) to D\( ^{12}\text{C} \) present, the total amounts of inorganic D\( ^{12}\text{C} \) incorporated per time were calculated at each light level. It was assumed that total D\( ^{12}\text{C} \) incorporated in a photosynthetron incubation was gross primary production or GPP (Sakshaug et al. 1997).

The relationship of total C-incorporation at each particular light level in the photosynthetron and irradiance was used to construct P-I curves (Figure 3.1). A P-I curve was
constructed for every sample date for all four sample sites. Maximum photosynthetic rate ($P_{\text{max}}$) and $\alpha$ acquired from each P-I curve were used for calculating phytoplankton production. Photosynthetic efficiency ($\alpha$) was determined from the slope of the linear portion of the photosynthetic rate at low irradiance ($< 100 \mu\text{mol photon m}^{-2} \text{s}^{-1}$). Maximum photosynthetic rate ($P_{\text{max}}$) was calculated as the average photosynthesis at saturating light levels.

Chlorophyll $a$ concentrations were used for calculating the chlorophyll-specific maximum capacity of photosynthesis ($P_{\text{max}}^b$) and the chlorophyll-specific photosynthetic efficiency, $\alpha^b$. Chlorophyll $a$ was evaluated by fluorescence of acetone-extracted plankton samples retained on Whatman GF/C filters (Wetzel & Likens 2000).

Phytoplankton production at a particular irradiance ($I$) and normalized for chlorophyll $a$ concentration was derived from Jassby and Platt (1976), where phytoplankton production (mg C (mg chlorophyll $a$)$^{-1}$ h$^{-1}$) = $P_{\text{max}}^b$tanh[$\alpha^bI(P_{\text{max}}^b-1)$]). For comparison among sites, phytoplankton production was integrated over a 1 m depth interval from the surface. This was done by summing phytoplankton production measured at 0.1 m intervals over 1 m depth.

**Photosynthetic parameters**

Photosynthetic parameters acquired from the P-I relationship are commonly used to indicate photo-adaptation of phytoplankton to a particular environment (Falkowski 1984; Gallegos 1992; Descy and Gosselain 1994; Geider et al. 1996). In this study, $P_{\text{max}}^b$ and $\alpha^b$ were compared in order to investigate the physiological condition of the phytoplankton community at different locations and times of year.

**Nutrient Limitation Experiments**

Following the phytoplankton production study, three sets of nutrient limitation experiments were conducted to determine whether there was potential for development of
nutrient limitation in surface water of the river main channel and two of the backwater sites, Modoc Lower and Mellwood Lake. These experiments were performed in May, August and September 2009, spanning the period of high to low river water. Incubation water volumes were 300 mL in 500-mL Erlenmeyer flasks. Into each of two flasks nitrogen ((NH₄)₂SO₄), phosphorus (NaH₂PO₄·H₂O) or a combination of nitrogen and phosphorus were added. The addition accounted for a total of 93 µmol (1.30 mg L⁻¹) nitrogen and 17 µmol (0.53 mg L⁻¹) phosphorus. There were also a set of control flasks that did not receive a nutrient addition. Water samples were incubated for three days at a saturating light level (> 280 μEm⁻²s⁻¹) under a 14:10 hr light:dark cycle at ambient temperature. At the end of the incubation, samples were filtered onto GF/C filters for chlorophyll a analysis, as described above. Initial NO₃-N and PO₄-P concentrations in the water samples were analyzed following the same methods as explained above.

Statistical Analyses

Factorial ANOVA was used to explore differences in phytoplankton production among the three backwater sites and by connection (connected vs. disconnected). In case of significant results from the analysis, four planned contrast analyses were performed to test the following four null hypotheses: 1-3) phytoplankton production in each backwater site (Modoc Lower, Mellwood, Quapaw) was not significantly different between connection and disconnection phases and 4) phytoplankton production in all backwater sites was the same as in the main channel. For the fourth hypothesis, if the planned contrast indicated a significant difference, a Tukey-Kramer HSD was used to determine which mean(s) was/were significantly different. Phytoplankton production was log₁₀ transformed to meet the normality assumption of ANOVA. Pairwise correlation was used to explore relationships between phytoplankton production and
physical or chemical properties expected to influence production (temperature, light availability, NO$_3$-N and PO$_4$-P concentrations).

Factorial ANOVA, planned contrast analysis and Tukey-Kramer HSD were used to explore mean differences of $P_b^{\text{max}}$ and $\alpha^b$ in a similar manner as for production. Pairwise correlation was also used to examine relationships between $P_b^{\text{max}}$ and $\alpha^b$ and physical or chemical properties. In addition, it was used to investigate the relationship of $P_b^{\text{max}}$ and $\alpha^b$. Maximum photosynthetic rate ($P_b^{\text{max}}$) and $\alpha^b$ were square-root transformed to meet the normality assumption of ANOVA.

**Results**

*Degrees and patterns of hydrologic connection*

Hydrology of the LMR changed drastically during the study period. The river stage of the LMR varied approximately 15 m. It was highest in April 2008 and at a minimum in November 2007, early in September 2008, and in late October 2008 (Figure 3.2). Of the 17 sampling dates, Quapaw was connected to the main channel on 14 days. The three sampling dates when this site disconnected to the main channel were in November 2007, early in September 2008, and in late October 2008 when the river stage was lower than 2 m. Modoc Lower and Mellwood lakes were connected to the main channel 10 days and 7 days, respectively. Modoc Lower was connected to the main channel during high water in March-July 2008 and March-April 2009. Mellwood Lake was connected to the main channel when the river stage was higher than 10 m during March-May 2008 and April 2009. This backwater site also experienced river influences in late June 2008 when the river stage was 8.5 m.
According to the site NO₃-N ratio, at stage heights above 2 m, the degree of hydrologic connection between Quapaw and the river was consistently high. The NO₃-N ratio of Quapaw: main channel during connection ranged from 0.9-1.1. For Modoc Lower and Mellwood lakes, the NO₃-N ratio indicated variation in the degree of connection, with ratios near 1 during the high water period of spring, and lower ratios as the river elevation dropped (Figure 3.3).

**Light**

The temporal and spatial variations of mean light level in 1 m depth fluctuated greatly. It ranged from 48-265 and 46-331µmol photons m⁻² s⁻¹ in the main channel and Quapaw,
respectively. It varied from 103-547 and 121-307 umol photons m\(^{-2}\) s\(^{-1}\) in Modoc Lower and Mellwood lakes, respectively. Comparison of average light over a 1 m depth interval at mid-day (Figure 3.4) and the light at which maximum phytoplankton production occurred in laboratory incubations (at least 200 umol photons m\(^{-2}\) s\(^{-1}\) on most days), indicates that phytoplankton production in the main channel and Quapaw during connection, even in only the top 1 m depth, was not always, but on average, limited by light. In contrast, phytoplankton production over the 1 m depth interval was not usually light-limited in either Modoc Lower or Mellwood lakes during either the connection or disconnection periods, or in Quapaw during disconnection.

Figure 3.4: Light availability (mean and SE) in the field (1 m interval, from 09:00-15:00) of the four study sites during connection and disconnection phases.

Temporal and spatial variations in photic zone depth are shown in Figure 3.5. Photic zone depth in the main channel varied from 0.3-1.4 m. Photic zone depth in Quapaw during connection followed the main channel closely. However, during disconnection in November 2007, early September 2008 and October 2008, the photic zone depth in Quapaw was slightly higher than in the main channel (Figure 3.5a). In Modoc Lower and Mellwood lakes, the photic zone depth was consistently deeper than in the main channel, ranging from 0.8-2.4 m and 1.0-2.4
m, respectively (Figure 3.5b). During periods of hydrologic connection, the photic zone depths in these lakes was most similar to the main channel, but still slightly deeper.

Phytoplankton primary production

Phytoplankton production (GPP) in the upper 1 m of the LMR main channel and all three backwater sites varied greatly during the study period. In the main channel, it ranged from 10-573 mg C m$^{-3}$ day$^{-1}$. Production in the main channel was highest at low river stage, i.e. when the river was most shallow (Figure 3.6a). In Quapaw, GPP ranged from 10-390 mg C m$^{-3}$day$^{-1}$. With connection, production in Quapaw followed the values in the main channel closely. However, at river stages lower than the critical depth, the magnitude of production in the upper 1 m was twice to almost 30 times higher than in the main channel on the same day (Figure 3.6b). Phytoplankton production in Modoc Lower and Mellwood lakes varied from 37-9,110 and 55-3,435 mg C m$^{-3}$day$^{-1}$, respectively. In general, surface water production in these two lakes was double to about 40 times or to about 70 times (in Modoc Lower and Mellwood, respectively) greater than in the main channel on the same day (Figure 3.6c). There was a significant effect of connection ($F_{(5,45)} = 32.52$, $p < 0.0001$) on phytoplankton production. There was also a significant interaction effect ($F_{(5,45)} = 3.56$, $p = 0.037$) indicating that production in the three
ecosystems responded differently to changes in connection. Planned contrast analysis supports the observation that phytoplankton production in Quapaw during disconnection (mean = 4,195 mg C m\(^{-3}\) day\(^{-1}\), SE = 1,935) was higher than during connection (mean = 103 mg C m\(^{-3}\) day\(^{-1}\), SE = 27; \(F_{(1,15)} = 21, p = 0.0004\)).

Figure 3.6: Patterns of phytoplankton production in 1 m depth; a) in the main channel b) in the main channel and Quapaw, c) in the main channel, Modoc Lower and Mellwood, and river stage at Helena, Arkansas.
Similar results for GPP were found for Modoc Lower Lake (disconnection mean = 2,798 mg C m\(^{-3}\) day\(^{-1}\), SE = 1,182; connection mean = 814 mg C m\(^{-3}\) day\(^{-1}\), SE = 257; \(F_{(1,15)} = 5.10, p = 0.039\)) and Mellwood Lake (disconnection mean = 1,534 mg C m\(^{-3}\) day\(^{-1}\), SE = 443; connection mean = 627 mg C m\(^{-3}\) day\(^{-1}\), SE = 280; \(F_{(1,15)} = 7.28, p = 0.017\). The planned contrast analysis revealed that even during connection surface water phytoplankton production in the main channel and Quapaw were lower on average than in Modoc Lower and Mellwood lakes (\(F_{(3,44)} = 9.36, p = <0.0001\)).

Data from all four sites and both connection and disconnection phases were pooled to examine the relationship of phytoplankton production and environmental variables (temperature, dissolved NO\(_3\)-N, dissolved PO\(_4\)-P and mean light) using pairwise correlations. Phytoplankton production was positively correlated to temperature (\(p = 0.002, r^2 = 0.37\)) and light (\(p < 0.0001, r^2 = 0.89\)). On the other hand, production was negatively correlated to NO\(_3\)-N (\(p < 0.0001, r^2 = -0.74\)) and PO\(_4\)-P (\(p < 0.0001, r^2 = -0.71\)). The values for these physical and chemical parameters are shown in table 3.1.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Temperature (°C)</th>
<th>Light (µmol photons m(^{-2}) s(^{-1}))</th>
<th>Dissolved NO(_3)-N (mg L(^{-1}))</th>
<th>Dissolved PO(_4)-P (mg L(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main channel</td>
<td>18.2 (4.6-29.0)</td>
<td>150 (48-265)</td>
<td>1.80 (0.74-3.26)</td>
<td>0.029 (0.015-0.046)</td>
</tr>
<tr>
<td>Quapaw</td>
<td>18.3 (5.0-29.5)</td>
<td>169 (46-331)</td>
<td>1.62 (0.29-3.93)</td>
<td>0.024 (0-0.042)</td>
</tr>
<tr>
<td>Modoc Lower</td>
<td>19.4 (6.0-31.0)</td>
<td>352 (103-547)</td>
<td>0.83 (0-1.56)</td>
<td>0.006 (0-0.025)</td>
</tr>
<tr>
<td>Mellwood</td>
<td>19.7 (8.4-31.0)</td>
<td>224 (121-307)</td>
<td>0.72 (0-1.69)</td>
<td>0.006 (0-0.025)</td>
</tr>
</tbody>
</table>

Table 3.1: Average (range) of physical parameters in all study sites. The light value is the mean for the upper 1 m of the water column.
**Nutrient limitation experiments**

Results from the nutrient limitation experiments are displayed in Figure 3.7. Based on the three set of experiments, surface water phytoplankton in the river main channel were limited by nitrogen in September 2009, while there was no evidence of nutrient limitation on the other dates. Phytoplankton collected from Modoc Lower responded to the addition of N in August and September, but not in May. The results also suggested co-limitation of N and P in August. Phytoplankton from Mellwood appeared to be co-limited by N and P in August, and by N alone in September.

**Figure 3.7:** Results from nutrient limitation experiments conducted in May, August and September 2009. The diagrams represent data from the main channel, Modoc Lower and Mellwood.

Initial concentrations of nutrients in the water column are shown in Figure 3.8. Both NO$_3$-N and PO$_4$-P in the main channel were generally high on all three dates, despite the positive
response of phytoplankton growth in river water samples in September 2009. In May when the river stage was high and the two lakes were strongly connected to the main channel, nutrient concentrations in the backwater sites were similar to the river. Both nutrients decreased drastically in the lakes in August and September, in accordance with the temporal pattern in nutrient limitation of both sites.

**Figure 3.8:** a) NO$_3$-N and b) PO$_4$-P concentrations in the water of the main channel, Modoc Lower and Mellwood on dates of nutrient limitation experiments.

**Photosynthetic parameters**

For all study sites, $P^b_{\text{max}}$ and $\alpha^b$ varied greatly, and overlapped among the four sites (Figure 3.9). $P^b_{\text{max}}$ ranged from 1.35-13.57 mg C (mg chlorophyll $a$)$^{-1}$ h$^{-1}$, and $\alpha^b$ varied from 0.005-0.045 mg C (mg chlorophyll $a$)$^{-1}$ h$^{-1}$ (umol photons m$^{-2}$ s$^{-1}$)$^{-1}$. However, the peak of these photosynthetic parameters occurred at different times in the sites. In the main channel, $P^b_{\text{max}}$ and $\alpha^b$ peaked in March and April 2009. In Quapaw, both photosynthetic parameters peaked in March 2009, but were reduced in April. In Modoc Lower, $P^b_{\text{max}}$ and $\alpha^b$ were highest in June 2008 and November 2007, respectively. As for Mellwood, $P^b_{\text{max}}$ and $\alpha^b$ did not display a clear peak. An analysis of variance (ANOVA) suggested no significant differences in $P^b_{\text{max}}$ and $\alpha^b$ among the four sites. Moreover, there were no significant differences among the three backwater sites, regardless of connectivity, in $P^b_{\text{max}}$ and $\alpha^b$ (Figure 3.10).
Figure 3.9: Spatial and temporal variation of photosynthetic parameters; $P_b^{\text{max}}$ and $\alpha_b$ of the four study sites. Units for $P_b^{\text{max}}$ and $\alpha_b$ were mg C (mg chlorophyll a)$^{-1}$ h$^{-1}$ and mg C (mg chlorophyll a)$^{-1}$ h$^{-1}$ ($\mu$mol photons m$^{-2}$ s$^{-1}$)$^{-1}$, respectively.

Figure 3.10: Photosynthetic parameters (mean and SE) at the four study sites according to connectivity; a) $P_b^{\text{max}}$, b) $\alpha_b$. 
Maximum photosynthetic rate ($P_{\text{max}}^b$) was significantly correlated to PO$_4$-P ($r = 0.40$, $p = 0.008$) and turbidity ($r = 0.31$, $p = 0.035$), and $\alpha^b$ was negatively correlated with temperature ($r = -0.038$, $p = 0.005$). Moreover, $P_{\text{max}}^b$ was positively correlated with $\alpha^b$($r = 0.74$, $p < 0.0001$) (Table 3.2).

<table>
<thead>
<tr>
<th></th>
<th>$P_{\text{max}}^b$</th>
<th>$\alpha^b$</th>
<th>Temperature</th>
<th>NO$_3$-N</th>
<th>PO$_4$-P</th>
<th>Turbidity</th>
</tr>
</thead>
<tbody>
<tr>
<td>data</td>
<td>mg C/(mg chlorophyll a)$^{-1}$h$^{-1}$</td>
<td>mg C/(mg chlorophyll a)$^{-1}$h$^{-1}$ (umol photons m$^{-2}$s$^{-1}$)$^{-1}$</td>
<td>°C</td>
<td>mg L$^{-1}$</td>
<td>mg L$^{-1}$</td>
<td>NTU</td>
</tr>
<tr>
<td>$P_{\text{max}}^b$</td>
<td>0.74</td>
<td>0.04</td>
<td>0.25</td>
<td>0.40</td>
<td>0.31</td>
<td></td>
</tr>
<tr>
<td>$\alpha^b$</td>
<td>-0.38</td>
<td>0.29</td>
<td>0.18</td>
<td>0.20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.41</td>
<td>0.13</td>
<td>-0.24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NO$_3$-N</td>
<td>0.43</td>
<td>0.51</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>PO$_4$-P</td>
<td>0.78</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turbidity</td>
<td></td>
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</table>

Table 3.2: Correlation matrix. Correlation coefficients ($r$) are based on 68 samples for $P_{\text{max}}^b$, $\alpha^b$, temperature, NO$_3$-N and turbidity, and 43 samples for PO$_4$-P. Bold values are significant.

Discussion

Phytoplankton primary production

At lower river stage, phytoplankton GPP to 1 m depth in the main channel and Quapaw were greater than at higher river stage. Temporal variation in surface water GPP on a seasonal basis is a consequence of lower turbidity, and development of a higher phytoplankton biomass (Chapter 2), during the low water period of summer to late fall. As well, spatial variation in turbidity across the four sites explains why the floodplain lakes were substantially more productive than the river or Quapaw while it remained connected. Phytoplankton in the main
channel and Quapaw during connection consistently experienced a lower light condition than in Modoc Lower and Mellwood lakes (both during connection and disconnection). Upon disconnection from the river, the current slowed, and suspended solids fell out of suspension. This resulted in a prolonged enhanced light condition in both lakes, and more transientsly in Quapaw, which promoted phytoplankton production (Reynolds and Descy 1996; Amoros and Bornette 2002).

Elevated production in side channels and other backwater aquatic systems may contribute to the phytoplankton community of the river channel. For example, Cole et al. (1992) hypothesized that the annual spring and summer bloom phenomenon of the tidal Hudson River is a result of elevated production in more shallow and possibly less turbid lateral portions of the river system. A similar phenomenon may be occurring in the Lower Mississippi River where, due to severe light-limitation, and after accounting for respiratory losses, positive net phytoplankton growth is not possible (Ochs et al. in review). It is also possible that phytoplankton production in the backwater sites can be transported to the main channel. However, the role of backwater sites as sources of phytoplankton production to the LMR main channel is unknown and remains an open question.

Phytoplankton production was positively correlated with light and negatively correlated with nutrient concentrations. It was hypothesized that at high suspended solids and high nutrients, phytoplankton production was limited by low light availability. Once light limitation was removed, phytoplankton production increased. At the same time, nutrients in the water column were used to support phytoplankton production, perhaps contributing to a depression of nutrient levels to growth-limiting concentrations.
Photosynthetic parameters

In a light-limited environment, such as a river main channel or lakes highly influenced by the river due to a strong hydrological connection, it has been reported that algae tend to have a higher $\alpha^b$ but lower $P^b_{\text{max}}$ than algae from a high light environment (Talling and Rzoska 1967; Gabellone et al. 2001; Schemel et al. 2004). This is hypothesized to be due to adaptation of the phytoplankton community to the low light environment by an increase in concentration of intracellular antenna pigments and a decrease in dark reaction enzymes (Hill 1996). In this study, there was no evidence of photoacclimation of the phytoplankton community by alteration of photosynthetic parameters. Despite substantial variation in the values of $\alpha^b$ and $P^b_{\text{max}}$, there were no significant differences in photosynthetic parameters among sites or between periods of connection and disconnection.

Even though it is expected that $P^b_{\text{max}}$ values are strongly correlated with temperature due to the temperature effect on enzymatic rate (Côté and Platt 1983; Pennock and Sharp 1986; Macedo et al. 2001), the results from this study displayed no significant correlation between these two variables. The lack of a significant relationship between $P^b_{\text{max}}$ and temperature was also reported in Mono Lake, CA. (Jellison and Melack 1993) and in the Atlantic Ocean (Marañón and Holligan 1999). Their explanation for this was that the temperature effect was obscured by stronger effects of physical variation or biotic factors which were plankton composition and irradiance in Mono Lake; and nutrient supply in the Atlantic Ocean.

In this study $P^b_{\text{max}}$ was weakly correlated with PO$_4$-P. The results are consistent with the study by (Knoll et al. 2003) from 12 reservoirs in Ohio that higher phosphorus was associated with higher $P^b_{\text{max}}$. As for the positive correlation between $P^b_{\text{max}}$ and turbidity in the current study,
it is contradicted by the theory that $P_{\text{max}}^b$ should decrease with increasing light (Marañón and Holligan 1999). The reasons for this are left to be determined.

Alpha is a function of the photochemical processes in photosynthesis and depends on the quantum yield and on the ability of cells to trap incident light. There is little organized information available on environmental control of $\alpha$ (Côté and Platt 1983), or the potential effects of light quality (Wallen and Green 1971, or nutrient availability. Marañón and Holligan (1999) found that $\alpha$ increased with depth (less light). However, the results from this study do not show a relationship of $\alpha$ and light. There are some other studies that do not demonstrate this relationship (Côté and Platt 1983, Pennock and Sharp 1986, Knoll et al. 2003). We only found that $\alpha$ was negatively correlated with temperature which is opposite to the study by Côté and Platt (1983).

$P_{\text{max}}^b$ and alpha were strongly correlated to each other according to the present study. This relationship was also found in studies of marine phytoplankton (Côté and Platt 1983), and of phytoplankton production in the Lower Mississippi River (Ochs et al. in review). One explanation for the coupled $\alpha$ and $P_{\text{max}}^b$ is that the entire photosynthesis unit in the thylakoid membrane for photosynthesis is uncoupled/coupled by circadian ion fluxes across the membrane. Therefore, both the quantum yield and the photosynthetic capacity of the cells vary in similar way (Prezelin and Sweeney 1977).

This is interesting in that it reveals that despite obvious variation among environments in the light regime, the degree of turbulence, the degree of productivity, and even phytoplankton community composition (Chapter 4), the phytoplankton communities were not detectably dissimilar in their photosynthetic properties. This result should not be interpreted as an inability of the phytoplankton community to vary in their photosynthetic properties by acclimation or
changes in composition, as it is clear that variation in both parameters did occur, if not predictably or consistently (Figure 3.9). However, exactly how these properties are controlled in these mixed phytoplankton communities remains to be determined.

Nutrient limitation

The decline over summer in nutrient concentrations in the water columns of the two lakes (Chapter 2) suggests that nutrients transported to the backwater lakes during high water connection are utilized in support of new phytoplankton production in these backwater sites (Cloern 2007). The nutrient limitation experiment indicated that in May, when nutrient levels were still high in the river and in the backwater lakes, nutrient limitation by N or P was not a factor affecting phytoplankton growth, even at saturating light levels. However, by early August, after the lakes had been separated from the river for a prolonged period, dissolved N or N+P were sufficiently depleted (Chapter 2), to result in limitation of surface water phytoplankton growth, a situation that persisted until at least mid-September. Thus, across the river-backwaters system, surface-water phytoplankton biomass appears to become increasingly nutrient limited by N or N+P availability during the low water period, with the more productive lakes becoming nutrient limited by mid-summer. It was evidenced from laboratory experiments that nutrient limitation inhibited phytoplankton growth in Lake Barkley on the Cumberland River (P-limited) and Kentucky Lake on the Tennessee River (co-limited by N and P) where there was more light available for phytoplankton (Köch et al. 2004). Moreover, a review by Reynolds and Descy (1996) suggested that some rivers in Europe became nutrient-limited during low water. These findings are consistent with our results.
Conclusions

This study is the first attempt to quantify and compare phytoplankton gross primary production in the surface waters of the LMR main channel and its connected backwaters. A secondary channel, (Quapaw chute), although usually indistinguishable from the river in production, was a major site of phytoplankton growth during the occasional and brief periods when it became disconnected. Backwaters disconnected to the main channel for a longer period (Modoc Lower and Mellwood) supported orders of magnitude more primary production than the river itself. This study also showed that in these backwater lakes, phytoplankton production was significantly higher soon after disconnection compared to later in the disconnection phase. With disconnection from the river, light availability in backwater sites increased, resulting in higher average light in surface water, a deeper photic zone depth, and greater GPP. With prolonged disconnection, surface water GPP became nutrient limited, but remained much higher than in the main channel. These results suggest that connectivity is a major factor affecting phytoplankton production in some backwaters of the LMR floodplain, and indicate the potential for these backwater systems to act as sources of phytoplankton organic matter to the food web of both the floodplain system and the main river channel.
CHAPTER 4

EFFECTS OF HYDROLOGIC CONNECTION ON PHYTOPLANKTON COMMUNITY COMPOSITION IN BACKWATER SITES OF THE LOWER MISSISSIPPI RIVER

Introduction

Understanding why organisms are found where they are, and how they respond to environmental changes, are principal objectives of ecological research. This knowledge is necessary for predictions of responses in community dynamics to environmental variation (Green et al. 2008). In the floodplain of the Lower Mississippi River (LMR) there are numerous lakes and other backwater wetlands. These sites experience substantial changes in physicochemical and biological properties with changes in hydrologic connection with the main river. During spring high water, river water flows into the backwaters carrying with it a suspended sediment load, corresponding high turbidity, and high concentrations of nutrients. Despite elevated available nutrients, this low light condition suppresses algal biomass and algal production in backwater sites. When the connection is reduced during low water, as typically occurs beginning in mid-summer, suspended solids settle out of the water column creating higher light availability. This high light and nutrient environment in backwaters, promote algal biomass and production (Chapters 2 and 3).

Although the phytoplankton communities of large river systems are less well studied than of lakes, there have been a number of studies of phytoplankton community composition in large rivers and floodplain lakes around the world. Although, phytoplankton composition in large
rivers differed to some extent, most of these studies found diatoms (Division Chrysophycophyta) to be the most dominant group of phytoplankton in the main channels. This was reported in the Upper Mississippi River (Baker and Baker 1981), the Rhine River (Ietswaart et al. 1999), the Lower Mississippi River (Duan and Bianchi 2006), the Middle Paranà River (Zalocar de Domitrovic et al. 2007), the Lower Paranà River (Unrein 2002), and 31 rivers in Ontario and western Quebec (Chetelat et al. 2006). The sub-dominant phytoplankton groups in these river systems were different but within these three categories: green algae (Division Chlorophycophyta, cryptomonads (Division Cryptophycophyta), and the prokaryotic cyanobacteria. Nevertheless, a long term study (1993-1994 and 2000-2007) of phytoplankton community in the three rivers of the Upper Paranà River floodplain (the Upper Paranà, the Ivinhema and the Baía) reported that cyanobacteria were co-dominant with diatoms in 1993-1994, and cryptomonads and cyanobacteria dominated in 2000-2007 (Rodrigues et al. 2009). In the Middle Paranà River, Devercelli (2006) reported an unusual development of small unicellular flagellated (cryptomonads) followed by small diatoms during a dry season.

Development of phytoplankton in connected backwaters of large rivers also varied widely depending on the river systems. For examples, in a connected lake of the Paranà River floodplain, at high flow, flagellated chlorophytes and cryptophytes dominated. When the lake was separated from the main channel, dinoflagellates and filamentous cyanobacteria became dominant (Garcìa de Emiliani 1993). In a connected pond of the Salado River (Argentina), coccoid green algae and diatoms dominated during clear water, while cyanobacteria dominated during the flood season (Gabellone et al. 2001). A gradual change in phytoplankton composition in Batata Lake, a connected lake of the Trombetas River in the Amazonian floodplain, was reported. The lake was dominated by small phytoplankton (cryptomonads and diatoms) during
high water and high flashing. When the water flow was low, desmids and diatoms became dominant. When the river dropped, the lake became shallow, and cyanobacteria were dominant (Huszar and Reynolds 1997).

In this chapter, temporal changes in the composition of the phytoplankton community were studied in the main channel of the Lower Mississippi River and in two backwaters with different degrees of connection to the river. It was hypothesized that in the turbulent main river channel, and in the backwater sites during strong connection, diatoms, which have a high efficiency for light capture, would be dominant (Gallegos 1992; Reynolds 1994; Reynolds and Descy 1996; Diehl et al. 2002). With a reduction in connection, heavy cells such as large diatoms would sink out of the water-column (Reynolds 1994; Reynolds and Descy 1996; Ghosal et al. 2000). Additionally, it was expected that in the quiet floodplain backwaters during disconnection there would be dominance by phytoplankton expected to be able to persist longer in a stratified water column such as filamentous cyanobacteria, unicellular green algae, and other motile or buoyant phytoplankton (Reynolds 1994; Diehl 2002; Diehl et al. 2002).

**Methods**

Water samples were collected from two backwater sites (Modoc Lower and Quapaw) and the LMR main channel at different river stages from high connection to several days after the last date of connection with the main river (see chapters 2 and 3 for site descriptions). Integrated samples (from 3 replications of water samples on each date and site) for plankton counts were collected on 26 April, 18 May, 17 August, 7 September, 28 September, 26 October 2008, and 19 May 2009. Of these seven dates, Quapaw was disconnected from the main channel on 7 September and 26 October 2008 when the river stage was lower than 2 m. Modoc Lower was
disconnected from the main channel on 17 August, 7 September, 28 September, and 26 October 2008 when the river stage was lower than 7.5 m. Mellwood Lake was not included in this study because due to a permanent channel between the lake and the LMR, it is difficult to estimate a temporal pattern in the degree of river influence on the lake (See chapters 2 and 3 for explanation). Water samples (500 mL) were collected from mid-channel and in the backwaters about 0.5 m below the surface using 2-L Nalgene bottles. Samples were preserved in 1% Lugol’s solution for microscope analysis.

In the laboratory, 3-5 mL of preserved samples was settled in a counting chamber for at least 24 hours. Phytoplankton were identified and counted under an Olympus IMT-2 inverted microscope at 600X. At least 400 counting units were counted per sample. The unit for phytoplankton counts is units mL⁻¹ (cells, filaments or colonies). Phytoplankton were classified into five major groups; cryptomonads, cyanobacteria, diatoms, euglenoid forms, and green algae. When possible, cyanobacteria, euglenoid forms, and green algae were identified to genera according to Wehr and Sheath (2003). Most cryptomonads and diatoms could not be identified to genus with an inverted microscope in this study. Cryptomonads were classified according to size (<10, 10-20 and >20 µm). Diatoms were grouped according to their morphology (centric/pennate or single cell/colonial). Phytoplankton smaller than 5 µm were not enumerated and therefore are not included in this analysis.

To examine succession of the phytoplankton communities in Quapaw and Modoc, the phytoplankton community compositions were compared on dates varying in time from the last connection with the river. For Quapaw, this included both dates following last connection with the river in 2008. For Modoc Lower, this included four of seven sample dates after connection, varying from 0 to 53 days post-connection.
Statistical Analysis

To access the effects of hydrologic connection on phytoplankton composition, phytoplankton groups were compared among a) the main channel, b) backwater during connection period (both from Quapaw and Modoc Lower) and c) backwater during disconnection phase (both from Quapaw and Modoc Lower). Multivariate analysis of variance (MANOVA) was used to examine the differences of phytoplankton community composition among the three hydrologic conditions above. Total counts of each algal group were log$_{10}$ transformed to meet the normality assumption of MANOVA.

Results

Total phytoplankton counts ranged from about 600-2800 units mL$^{-1}$ in the main channel (Figure 4.1a). For all sampling dates, the phytoplankton composition in the main channel was dominated by diatoms, which accounted for 29-64% of total unit number (Figure 4.1b). About 20-60% of the diatoms were single-cell centric diatoms; Cyclotella and Stephanodiscus.

The second most common group in the main channel were cryptomonads which composed 13-31% of the total number (Figure 4.1a,b). For all sampling dates, small cryptomonads (<10 µm) accounted for the majority (54-100%) of total cryptomonad densities. Cyanobacteria, green algae and euglenoid phytoplankton were found at all sampling dates in relatively low proportions; 5-21%, 5-13% and 2-13%, respectively. On 17 August 08, 7 September 08 and 26 October 08, which were the three days that experienced the lowest water, cyanobacteria were more abundant than other sampling dates (Figure 4.1a), accounting for more than 15% of total algae (Figure 4.1b). Common diatoms, organized by morphology, and
cyanobacterial groups in the main river on dates that they were more than 15% of total phytoplankton units are shown in Figure 4.2.

Figure 4.1: Total phytoplankton (bars) in the main channel; a) density, b) relative abundance.
The lines indicate the river stage at Helena, Arkansas.
Figure 4.2: Proportion of each diatom group: single cell centric (S.C.), colonial centric (C.C.), single cell pennate (S.P.) and colonial pennate (C.P.) diatoms; and dominant cyanobacteria: *Pseudoanabaena* (Pa), *Anabaenopsis* (An), *Raphidiopsis* (Ra), *Eucapsis* (Eu), other coccoid (Coc); and other flagellate (Fla) algae in the main channel.
In Quapaw chute, phytoplankton abundance ranged from 1,000–125,000 units mL$^{-1}$ (Figure 4.3a1 and 4.3a2). The magnitudes of total counts in the chute were usually greater than in the main channel, most notably during times of disconnection. For most of the sampling dates, diatoms (*Cyclotella* and *Stephanodiscus*) and small cryptomonads were the dominant phytoplankton, as was observed for the main channel. There was an exception on 7 September 2008 when diatoms were a low proportion of the phytoplankton community and cryptomonads accounted for almost 100% of total phytoplankton (Figure 4.3b). It is also interesting to note that, on this date, the density of green algae, euglenoid algae and cyanobacteria were higher than on other dates (Figure 4.3a1). Diatoms varied in proportion from less than 1-65% of all cells. Cryptomonads ranged from 9-96%. Cyanobacteria, euglenoid algae, and green algae varied between 2-32%, 1-13% and 2-12%, respectively (Figure 4.3b). Common diatoms and cyanobacteria groups in Quapaw when they accounted for more than 15% of total phytoplankton units are shown in Figure 4.4.
Figure 4.3 Total phytoplankton (bars) in Quapaw; a) density, b) relative abundance. The lines indicate the river stage at Helena, Arkansas. The total densities of phytoplankton are shown in two separate plots; a1) density of green algae, euglenoid forms, diatoms and cyanobacteria, and a2) density of cryptomonads.
In Modoc Lower, total phytoplankton counts ranged from 1,400-30,500 units mL$^{-1}$ (Figure 4.5a1 and a2). Dominant phytoplankton, depending on the sample date, were cryptomonads (22-94%) and diatoms (less than 1-61%). About 3-22% of total phytoplankton
were green algae. Cyanobacteria and euglenoid algae contributed to a small proportion of total algae; 1-12% and 1-2%, respectively. The proportion of cryptomonads were higher than diatoms when this lake disconnected from the main channel (river stage < 8 m). On the other hand, during high water, the proportions of diatoms were at least the same or higher than cryptomonads (Figure 4.5b). Common diatoms, green algae and cyanobacteria groups when they were more than 15% in Modoc Lower are shown in Figure 4.6.

Figure 4.5: Total phytoplankton (bars) in Quapaw; a) density, b) relative abundance. The lines indicate the river stage at Helena, Arkansas. The total densities of phytoplankton are shown in two separate plots; a1) density of green algae, euglenoid forms, diatoms and cyanobacteria, and a2) density of cryptomonads.
Figure 4.6: Proportion of each diatoms group: single cell centric (S.C.), colonial centric (C.C.), single cell pennate (S.P.) and colonial pennate (C.P.) diatoms; dominant cyanobacteria: *Pseudoanabaena* (Pa), *Anabaenopsis* (An), *Raphidiopsis* (Ra), *Eucapsis* (Eu), other unidentified coccoid (Coc) and other flagellate (Fla); and green algae: *Scenedesmus* (Scen), *Crucigenia* (Cru) and desmids (Des) in Modoc Lower.

During connection Quapaw and Modoc Lower were similar in phytoplankton density to the LMR main channel. During disconnection, the phytoplankton densities in the main channel were lower than in the backwater sites. There was an exception on 7 September 2008 in Modoc
when this site was disconnected to the main channel, phytoplankton counts were not much different from in the main channel.

The relative abundance of the dominant phytoplankton groups, diatoms and cryptomonads, in Quapaw and Modoc Lower were plotted against day(s) post connection with the main river. Diatoms represented a high proportion of total algae when the floodplains connected to the river (0 day post connection). The diatom proportion decreased the longer the backwaters were disconnected from the main channel. The opposite trend was found for cryptomonads. Cryptomonads were found in a lower proportion when the backwaters were connected to the river. As the disconnection progressed, the proportion of cryptomonads increased (Figure 4.7). In terms of abundance, diatom densities started to increase after the backwater sites disconnected from the main channel. In Modoc Lower, with prolonged disconnection, diatom density declined (Figure 4.8a). A similar trend was found for cryptomonads densities in both backwater sites (Figure 4.8b).

Figure 4.7: Relationship between dominant percent phytoplankton groups (diatoms and cryptomonads) and day(s) post connection in Quapaw and Modoc Lower.
Figure 4.8: Densities of dominant phytoplankton; a) diatoms and b) cryptomonads according to date and day(s) post connection (in parentheses after date) in Quapaw and Modoc Lower.

A Wilks’ Lambda test indicated that phytoplankton compositions from the three conditions; the main channel, and the backwaters when connected and disconnected, were significantly different ($F_{(10, 28)} = 2.95, p = 0.012$). Post MANOVA tests were conducted to compare the similarity of phytoplankton composition during connection and disconnection to the
phytoplankton composition in the main channel. Phytoplankton during connection in both
backwater sites were not significantly different from phytoplankton in the main channel. During
the disconnection phase, however, phytoplankton significantly differed from the main channel
\( F(5, 7) = 4.15, p = 0.045 \).

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Table 4.1 MANOVA Table

**Discussion**

Phytoplankton composition in the main channel and backwaters during connection were
different from the backwaters during disconnection. At high river stage, backwaters strongly
connected to the main channel experienced an increase in turbulence, and turbidity due to river
inflow. In the main channel and the backwater during connection, single-cell centric diatoms
represented the majority of phytoplankton. This result is similar to results for phytoplankton
composition in other lake-river systems, such as in the floodplains of the Danube River (Schagerl
et al. 2009), the Upper Mississippi River (Duan and Bianchi 2006), the Lower Paranà River
(Unrein 2002), the Rhine River (Ietswaart et al. 1999), and the River Spree (Köhler 1994). Other
studies have specified that small centric diatoms, such as *Cyclotella* and *Stephanodiscus*,
dominated in turbulent and low light environments; the Upper Mississippi River (Baker and
Baker 1981); the Middle Paranà River (Devercelli 2006; Zalocar de Domitrovic et al. 2007) and
31 rivers in Ontario and western Quebec (Chetelat et al. 2006). The second most dominant
group of phytoplankton found in our study during high water were the cryptomonads, which also
presented in large number (at least on some sampling dates) in the Upper Mississippi River (Baker and Baker 1981) and the Middle Parana River (Devercelli 2006).

River conditions select phytoplankton that are small and fast growing (Reynolds and Descy 1996; Chetelat et al. 2006), tolerant to low light (Reynolds and Descy 1996), and can cope with turbulence (Schagerl et al. 2009). These algae are diatoms (Reynolds et al. 2002; Gallegos 1992) and cryptomonads (Kugrens and Clay 2000; Reynolds et al. 2002).

In backwater sites, during the disconnection, the most dominant phytoplankton (diatoms and cryptomonads) in the main channel remained in the water column and increased in abundance and proportion of the community as disconnection progressed (Figure 4.8). Cryptomonads represented a major proportion of the phytoplankton community in backwaters even though there was nutrient depletion (Chapter 2). There were cryptomonads blooms in both backwater sites. Cryptomonads increased in number and proportion as the disconnection progressed while other groups of algae remained minor. Similarly, it was reported that cryptomonads were dominant with prolonged disconnection in a floodplain of the Danube River (Schagerl et al. 2009) and the Lower Paraná River (Unrein 2002). This result is dissimilar to results from some other river-floodplains which with prolonged disconnection there were a succession of cyanobacteria (the River Spree: Kohler 1994; the Trombetas River: Huszar and Reynolds 1997), dinoflagellates and cyanobacteria (the Paraná river: García de Emiliani 1993), and green algae and diatoms (the Salado River: Gabellone et al. 2001).

The results suggested that cryptomonads have the capacity to develop and adjust to broad ranges of environmental conditions (both in the low-light environment main channel and low-nutrient availability backwater sites). A high concentration of cryptomonads was also found in the Middle Paraná River in varied physicochemical conditions (Devercelli 2006). These
competitive advantages of cryptomonads over other phytoplankton in these systems could be explained by 1) their high reproductive rate that allows them to counteract the rapid changes of the environments and survive high flows (Huszar and Reynolds 1997; Zalocar de Domitrovic et al. 2007); 2) their high area/volume ratio which contributes to decreased losses by sedimentation in slack water (Devercelli 2006; Zalocar de Domitrovic et al. 2007); 3) their alternative nutritional strategy that permit them to use various resources (Kugrens and Clay 2003; Zalocar de Domitrovic 2007); and 4) their high metabolic activities that allow nutrient uptake in low nutrient conditions and light-harvesting in depleted light environments (Devercelli 2006). Moreover, it is also hypothesized that cryptomonads in nutrient depleted system could migrate to deeper water where more nutrients are available and return to the surface where there is more light (Gervais 1997).
CHAPTER 5
IMPORTANCE OF HYDROLOGIC CONNECTION

Hydrologic connection with the LMR is a key factor controlling limnological and phytoplankton properties in connected backwaters. Conversely, these systems can be sources of organic matter to the main channel (Tockner et al. 1999; Hein et al. 2003, 2004). Specifically, development of high phytoplankton biomass in backwater sites is important for animal production in the backwater itself (Baker et al. 1991), and possibly in the main channel at times of lake water discharge into the river (Cloern 2007). As the river elevation drops, and backwaters flow into the main channel, they may carry large amounts of phytoplankton derived in less turbulent lakes or other floodplain sites. Another important source of phytoplankton to the main channel could be lateral areas where the water is sufficiently slow-moving and shallow to support positive production, as Cole et al. (1992) suggested for the Hudson River. Further research quantifying fluxes of materials across the river system, including its backwater sites, is needed to determine the relative importance of lateral channel areas, and backwater sites, as sources of inputs of phytoplankton biomass to the main channel. Another potentially fruitful area of research would be to investigate the potential of natural or created backwater sites for nutrient sequestration. As discussed above, connected backwaters can also be a potential sink for nutrients and sedimentation, and therefore, in the case of the LMR system, contribute to reducing nutrient loading into the Gulf of Mexico.
This study demonstrates the importance of large river backwaters for production of phytoplankton biomass, and presumably biological production in general, as well as in nutrient immobilization, and the role of connectivity in these processes. Strong and rapid responses to disconnection in turbidity, chemical concentrations, and phytoplankton biomass indicate that the degree of hydrologic connection to the main channel is a major factor controlling ecological processes across the aquatic floodscape. The role of hydrologic connection must be considered for informed conservation and management of large river ecosystems to maintain habitat diversity and biocomplexity (Amore and Bornette 2002), and as a possible mechanism for removal of nutrients that would otherwise flow downstream to the coastal zone (Tockner et al. 1999). For example, management of the river-backwater connection through targeted removal or lowering of dams or revetments, with re-watering of former backwater sites, might be a useful ecotechnology (Mitsch et al. 2001; Day et al. 2003) to address water quality and wetland loss issues in the LMR basin, and perhaps even the Gulf of Mexico.
BIBLIOGRAPHY
BIBLIOGRAPHY


wetland habitat loss problems in the Mississippi basin: a hierarchical approach.

*Biotechnology Advances*, **22**, 135-159.


# APPENDIX

## Phytoplankton Genera List

<table>
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Contracts, grants and scholarships

- Spring 2012 Dissertation Fellowship from the Graduate School, the University of Mississippi
- 2009-2011: Research Assistantship from the U.S. Army Engineer Research and Development Center, Waterways Experiment Station in Vicksburg
- 2006-2009: Teaching Assistantship from the Department of Biology, the University of Mississippi
- Summer 2008: Summer Graduate Research Assistantship from the Graduate School, the University of Mississippi
- Spring 2007: Graduate School Council Research Grant Award

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• Ochs C.A., Pongruktham O and Zimba P. Darkness at the break of noon: Phytoplankton production in the Lower Mississippi River. *In review.*

• **Pongruktham O.** Ochs C.A. Effects of hydrological connectivity on physicochemical conditions and algal biomass in backwaters of the Lower Mississippi River. *In preparation.*

• **Pongruktham O.** C.A. Ochs and Hoover J.J. Feeding and digestion selectivity of silver carp (*Hypophthalmichthys molitrix*). *In preparation.*

**Presentations**


