

TROPHIC STATUS OF MISSOURI RIVER FLOODPLAIN LAKES IN RELATION TO BASIN TYPE AND CONNECTIVITY

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Abstract: Limnological data were collected over a two-year period from 12 lakes in the Missouri River floodplain in order to evaluate lake trophic status and the influence of basin type and connectivity on nutrient, seston, and phytoplankton dynamics. The lakes were located in west-central Missouri and included eight scour basins formed by levee breaks during a 1993 flood and four older oxbow lakes. The Missouri River was also sampled. Five of the scour basins (connected scours) were inundated by the Missouri River for varying periods during the study. The other lakes (protected scours) were hydrologically isolated from the river by levees. On the basis of mean total phosphorus (TP—61–282 $\mu\text{g/L}$), mean total nitrogen (TN—0.7–2.1 mg/L), mean chlorophyll (CHL—22–67 $\mu\text{g/L}$), and mean suspended solids (TSS—16–93 mg/L), all 12 sites were highly eutrophic compared to other lakes in Missouri. Nutrient fractions and seston composition indicated dominance of inorganic nutrients and abiotic seston in the riverine lakes. Maximum concentrations of nutrients and TSS occurred in oxbow lakes during periods of sediment resuspension and in connected scours during floods in spring 1995 and 1996 when connected sites were inundated by the Missouri River. Algal blooms with peak CHL >200 $\mu\text{g/L}$ occurred sporadically in the oxbow lakes. Similarly large blooms (peak CHL 81–689 $\mu\text{g/L}$) occurred in connected scours when low river levels reduced exchange with the river. Reduced connectivity was accompanied by rapid loss of dissolved N and P fractions, especially nitrate. Protected scours had lower average TP, TN, and TSS than the other sites and were less temporally variable.

Key Words: Missouri River, floodplain lakes, oxbows, scour basins, limnology, nutrients, chlorophyll, suspended solids, connectivity, 1993 flood

INTRODUCTION

The breaching of artificial levees in the Missouri River valley during a record flood in 1993 created hundreds of scour basins or “blew holes” (Galat et al. 1996). Scour basins not drained or filled during post-flood reconstruction remain as floodplain lakes, a rarity in this heavily agriculturalized river valley. Because of the potential significance of these new lakes as fish and wildlife habitat, several basins, together with a number of older, oxbow lakes, have become the subject of a multidisciplinary habitat evaluation study sponsored by the Missouri Department of Conservation and U.S. Environmental Protection Agency. Eight new scour basins and four older oxbow lakes located along a 250-km segment of the river valley in west-central Missouri have been intensively studied over the past few years.

Limnological investigation of these 12 lakes has focused on variation in trophic state variables such as nutrient concentrations, phytoplankton standing crops, and organic matter content. Such information provides a scale for gauging lake productivity but is not as

widely available for lakes in the Missouri River floodplain as for other subregions in Missouri (Jones and Knowlton 1993). This lack of comparative information limits our ability to assess the value of floodplain lakes relative to other aquatic habitats in the region. In this paper, we provide baseline information amenable to the comparison of floodplain lakes with other, better-documented lakes in the region. We also examine the roles of basin type and connectivity between lakes and the Missouri River in contributing to limnological differences among floodplain lakes.

STUDY SITES AND HYDROLOGIC CONDITIONS

The 12 lakes we studied are located in the Missouri River floodplain between Overton, Missouri and Missouri City, Missouri. Four sites, Cooley Lake, Sunshine Lake, Teteseau Lake, and Dalton Lake, are remnant oxbows that preexisted the 1993 flood and occupy abandoned segments of the Missouri River channel. The oxbows range from 17 to 323 ha in surface area and have mean depths <1 m at usual pool elevations.

The eight scour lakes have surface areas of ≈ 3 –19 ha and mean depths of ≈ 1 –4 m at typical pool levels. In the text, scour basins are designated by their distance in “river kilometers” (RK) upstream from the Missouri-Mississippi confluence at St. Louis. The four oxbows and three scour basins are separated from the Missouri River by mainstem levees that have prevented incursion of river water since the 1993 flood. We refer to these 7 lakes collectively as “protected” sites. The other scour basins are located between levees and the river (“connected” scours) and receive varying amounts of inflow from the river. Connected basins have been extensively modified by levee and dike reconstruction and river incursion since 1993 (Galat et al. 1996). Basin depth, in particular, has been greatly reduced by sedimentation during subsequent floods in 1995 and 1996 (Natural Resources Conservation Service, unpublished data).

Rainfall and river water levels during 1994 were near or below average. The Missouri River at Boonville, Missouri remained below flood stage from the beginning of data collection in June 1994 until the start of near-record floods in May 1995 (United States Geological Survey, unpublished data). Between 8 May and 12 July 1995, the river was above flood stage almost continuously and reached a maximum stage (19 May) exceeded in this century only during the record flood in 1993. During this 1995 flood, water levels in connected sites rose ≈ 5 –6 m as the river inundated the adjacent floodplain. In the protected lakes, local runoff increased water levels ≈ 1 –3 m. River and lake levels fell rapidly after the flood and remained near 1994 levels until renewed flooding in spring 1996. During May and June 1996, the Missouri River exceeded flood stage four times for periods of 3–13 days. Maximum crests were about a meter less than in 1995. Water levels in protected lakes were also less than during the 1995 flood.

METHODS

The 12 lakes and one or more sites on the Missouri River were sampled year around between 13 June 1994 and 18 June 1996, usually at monthly intervals. Some monthly samples were missed due to equipment failure or road closures during floods. Selected sites (especially seasonally connected sites RK 304 and RK 398) were sampled more frequently during or after floods to document effects of changing connectivity.

Water samples (2 L) and temperature and dissolved oxygen profiles were collected at a single, mid-lake site and occasionally at 1–3 additional sites. Only data from perennially flooded sites are considered here. Samples were collected from the surface layer as grab samples during the open water period. When ice was

present, samples from ≈ 10 cm below the ice were collected by pump. River samples were collected from shore or by boat and were always taken in areas with strong current. Unfiltered water samples were analyzed for chlorophyll (CHL—Knowlton 1984, Sartory and Grobbelaar 1984), total phosphorus (TP—Prepas and Rigler 1983), total nitrogen (TN—Crumpton et al. 1992), suspended solids (A.P.H.A. 1985), nephelometric turbidity, and specific conductance (A.P.H.A. 1985). Suspended solids were measured gravimetrically from the residue retained by glass-fiber filters (Whatman 934-AH). Total, volatile (550°C), and non-volatile fractions of suspended solids (TSS, VSS, and NVSS, respectively) were determined. Filtrates from suspended solids determinations were analyzed for “filtrate” TP and TN (fTP, fTN), nitrate-nitrite-N ($\text{NO}_3\text{-N}$ —A.P.H.A. 1985), ammonium-N ($\text{NH}_4\text{-N}$ —Stainton et al. 1977), and nephelometric turbidity. Concentrations of particulate TP (pTP) and TN (pTN) were estimated by difference. All analyses except conductivity and turbidity were performed in duplicate. The Whatman glass-fiber filters used for suspended solids analysis and filtrate preparation removed, on average, only 83% of the turbidity in unfiltered samples. Thus, suspended solids, pTP, and pTN measurements are somewhat underestimated (Knowlton and Jones 1995).

Data from individual sites showed log-normal distributions and were converted to base 10 logarithms prior to analysis. $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ values were increased by 1 $\mu\text{g/L}$ before log transformation because the data include nominal values of zero. Except where noted in the text, average conditions are represented by grand means of \log_{10} values back-transformed to the original units (geometric means).

RESULTS

In terms of average concentrations of nutrients and algal CHL, all 12 lakes were highly productive. Mean TP ranged from 61 to 282 $\mu\text{g/L}$, mean TN from 0.7 to 2.1 mg/L, and mean CHL from 20 to 67 $\mu\text{g/L}$ (Table 1). Among the three types of floodplain lakes, oxbows had consistently greater algal biomass (mean CHL 37–67 $\mu\text{g/L}$) than either the protected or connected scour lakes, for which mean CHL values overlapped (mean CHL 20–31 $\mu\text{g/L}$). In comparison to protected scours, however, connected scours had uniformly greater mean concentrations of total nutrients and TSS. Among connected lakes and oxbows, total nutrients and TSS had similar average concentrations but differed consistently in composition.

In general, the connected sites tended toward the dominance of abiotic seston and inorganic nutrients typical of the Missouri River, and the protected sites

Table 1. Geometric means and ranges of selected variables.

	TP ($\mu\text{g/L}$)	TN (mg/L)	CHL ($\mu\text{g/L}$)	TSS (mg/L)	$\text{NO}_3\text{-N}$ ($\mu\text{g/L}$)
Oxbows					
Cooley	239 71–2175	2.0 0.7–14.5	48 3–847	45 4–633	11 0–545
Dalton	235 69–438	1.6 0.9–3.2	37 8–224	46 7–288	40 0–979
Sunshine	282 137–887	1.7 1.0–3.2	67 25–256	81 7–556	17 0–551
Teteseau	190 86–480	1.2 0.5–2.9	64 4–277	32 7–89	6 0–1567
Protected Scours					
RK 512	61 28–122	0.7 0.4–1.2	25 8–61	16 6–57	10 0–338
RK 528	64 34–110	0.7 0.5–1.1	25 12–55	16 5–60	2 0–80
RK 330	94 44–230	0.8 0.5–1.1	29 10–60	22 8–74	15 0–277
Connected Scours					
RK 304	120 50–465	1.3 0.4–3.2	22 4–81	37 5–380	146 0–1677
RK 398	129 44–867	1.2 0.7–3.2	31 4–177	34 5–816	49 0–1434
RK 346	197 90–1249	2.1 1.1–4.2	21 7–689	56 9–1470	908 0–2885
RK 351	241 127–804	2.0 1.1–3.6	20 8–139	93 9–696	1164 349–2810
RK 386	225 64–1603	1.9 1.1–3.8	23 6–126	78 11–2018	1098 399–2947
Missouri River					
	374 145–1808	2.2 1.1–4.2	20 6–45	236 27–2340	1210 542–2953

tended toward organic dominance. Dissolved inorganic N ($\text{DIN} = \text{NO}_3\text{-N} + \text{NH}_4\text{-N}$) usually comprised <10% of filtrate N (dissolved and fine particulate N) in the protected sites. The small concentrations of DIN typically measured (e.g., Table 1) were not consistently dominated by either $\text{NO}_3\text{-N}$ or $\text{NH}_4\text{-N}$ (Table 2). However, in the connected scours and the river, $\text{NO}_3\text{-N}$ comprised >95% of DIN in the majority of samples, and DIN was usually >60% of fTN (Table 2). Ratios of pTP:TP and pTN:TN were usually greater in the protected lakes than in the connected scours and river (Table 2), as were ratios of pTP, pTN, VSS, and CHL to TSS (Table 2). Ratios of pTN:TSS and CHL:TSS were usually 2–3 times greater in protected lakes than in the connected scours and were often >10 times greater than in the river (Table 2). Assuming CHL represented 2% of algal biomass (Reynolds 1984), phytoplankton usually comprised >5% of TSS in the protected lakes, <2.5% of TSS in connected scours, and <1% of TSS in the river. Algal biomass seldom com-

prised more than 20% of TSS or 50% of VSS (<5% of all observations) in any of the lakes despite the wide range of CHL. Thus, the organic seston in all sites was probably dominated by detritus, even during algal blooms.

Conditions were temporally variable at all the sites but less so in the protected scours than in other lakes. Ranges of CHL and TSS exceeded 10-fold in all the oxbows and connected scours and exceeded 100-fold at some sites but were usually <10-fold in the protected scours (Table 1).

Inflow events contributed noticeably to variation in the protected lakes, especially in Dalton and Sunshine lakes and site RK 330, all of which have relatively large catchments (17–150 km^2) and occasionally received turbid, nutrient-rich inflows. Fluvial inputs were most important, however, to the connected scour lakes. Conditions in these waterbodies were dominated by the temporal extent and intensity of inputs from the Missouri River. During floods, all the connected scours

Table 2. Geometric mean ratios of dissolved inorganic nitrogen (DIN) to filterable total nitrogen (fTN), nitrate-nitrite nitrogen (NO₃-N) to DIN, particulate total phosphorus (pTP) to total phosphorus (TP), particulate total nitrogen (pTN) to total nitrogen (TN), volatile suspended solids (VSS) to total suspended solids (TSS), chlorophyll (CHL) to TSS, pTN to TSS and pTP to TSS for the three lake types and the Missouri River.

		Connect-			
		Protected	ed	Missouri	
		Oxbows	Scours	Scours	River
DIN:fTN ¹	(%)	4.9	4.8	31.4	71.1
NO ₃ -N:DIN ²	(%)	40.2	39.1	79.5	96.4
pTP:TP	(%)	63.6	62.4	53.3	61.7
pTN:TN	(%)	40.3	36.3	16.6	16.6
VSS:TSS	(%)	24.5	26.8	16.6	9.6
CHL:TSS	(%)	0.11	0.15	0.05	0.009
pTP:TSS	(%)	0.31	0.26	0.17	0.10
pTN:TSS	(%)	1.33	1.54	0.53	0.15

¹ Data from the connected scours were highly skewed. Median DIN:fTN was 64.4%.

² Data from lake sites were highly skewed. Median NO₃-N:DIN was 66.9%, 52.7%, and 97.7%, respectively, for the oxbows, protected scours, and connected scours.

were incorporated into side channels with strong currents throughout their basins. During inter-flood periods, these basins functioned as backwaters or became disconnected from the river. Site RK 304, which is located several hundred meters from the river, had no surface connection to the river except during floods. Site RK 398 is adjacent to the river, but at normal river stages, the main pool of the scour was separated from the river by a shallower pool that sometimes dewatered when the river was low. The other sites usually circulated freely with the river but became disconnected during periods of low water, especially in winter when ice damming of lake inlets may have contributed to reduced connectivity.

River water typically contained 3–10 times the TSS, TP, and TN found in protected scour lakes and >100 as much NO₃-N (Table 1). Suspended solids and particulate nutrients in the river typically increased by >10-fold during floods, and total dissolved solids (indicated by specific conductance) decreased by half or more. Thus, water quality conditions in connected sites depended directly on river stage because of its effect on inflow to scours and the composition of those inflows.

Near the peak of flooding in 1995, currents flowing through sites RK 304, RK 351, and RK 386 were so strong that TSS in these scours (380–2018 mg/L) was >86% of TSS in the main river channel a few hundred meters away. At lesser river stages, when scours were functioning as backwaters rather than side channels,

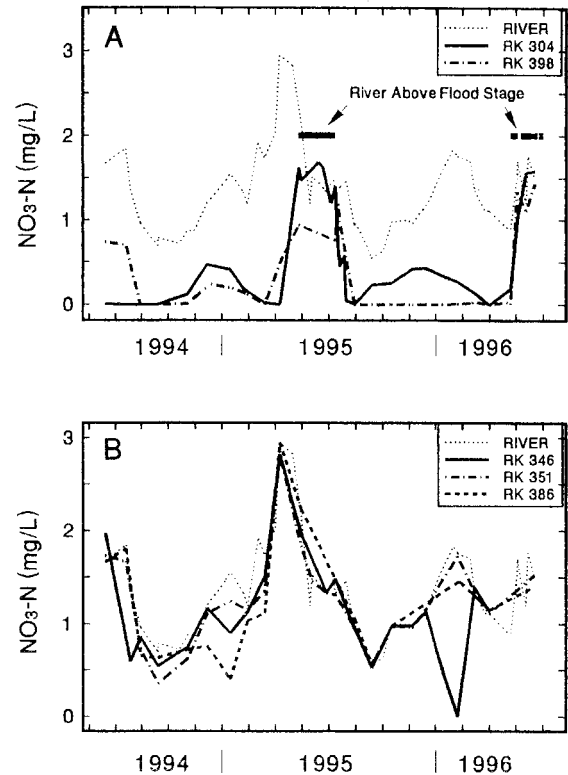


Figure 1. Time series of NO₃-N concentrations in the Missouri River and connected scours A) RK 304 and RK 398 and B) RK 346, RK 351, and RK 386. Horizontal bars in A indicate periods when the Missouri River was above flood stage at Boonville, Missouri (RK 316).

TSS in the scours averaged only 30% (range 9–69%, n = 9 transects) compared to the adjacent river.

In river water, particulate P and N were strongly related to TSS (n = 36, r = 0.99, and 0.87, respectively) and showed similar temporal and sedimentation patterns in the river and connected scours. Filtrate P and N and NO₃-N were more weakly correlated to TSS (n = 36, r = 0.63, 0.49, and 0.41, respectively). In transects, differences in fTP, fTN, and DIN between the scours and the adjacent river were seldom greater than analytical errors (≈±5%), except when sites were isolated from the river or weakly connected across an intervening shallow pool, submerged sand bar, or ice dam. The loss or reduction of connectivity under these circumstances led to rapid declines in dissolved nutrients, especially NO₃-N. For example, following the 1995 flood, NO₃-N in site RK 304 dropped from >1400 μg/L to <20 μg/L less than a month after the site disconnected from the river (Figure 1a). Nitrate declined similarly at site RK 398, although this lake remained connected to the river. At average river stages, there seems to be little exchange of water through the pool that separates the main body of the scour from the river. Thus this lake was at least par-

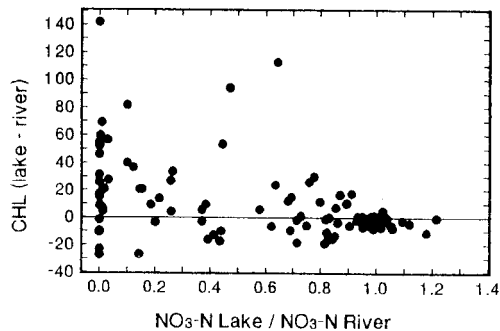


Figure 2. Chlorophyll ($\mu\text{g/L}$) versus $\text{NO}_3\text{-N}$ in the connected scours relative to contemporaneous concentrations in the Missouri River. River concentrations are from samples collected the same week the scour lakes were sampled. If the river was sampled more than once during that week, river values were averaged. One outlying observation (nitrate ratio = 0.43, CHL difference = $663 \mu\text{g/L}$) was omitted from the plot.

tially isolated from the river much of that year despite a surface connection between the two systems. Sites RK 346, RK 351, and RK 386 became partly, or completely, isolated from the river in summer 1994 and during winter in one or both years, and showed corresponding declines in $\text{NO}_3\text{-N}$ relative to the river (Figure 1b). During other periods, $\text{NO}_3\text{-N}$ at these three sites was indistinguishable from the adjacent river when both lake and river were sampled simultaneously.

Like $\text{NO}_3\text{-N}$, CHL in scour basins paralleled concentrations in the river except when sites became partly or completely isolated, after which CHL varied independently (Figure 2). In most instances, when lake:river $\text{NO}_3\text{-N}$ was >0.8 , the scours were freely circulating with the river and differed only slightly from the river in CHL. In 11 transects run under such conditions, CHL in the scours was an average of 21% less than in the adjacent river (range 2% to 46% less). Nitrate ratios less than 0.8 were usually indicative of hydrologic isolation of scours from the river (with some exceptions due to the effect of spatial or temporal variation of $\text{NO}_3\text{-N}$ in the river). Under condition of isolation, CHL diverged substantially, both positively and negatively, from ambient river concentrations.

Temporally, hydrologic isolation was usually followed by large algal blooms. CHL peaked at 55 and $178 \mu\text{g/L}$, respectively in sites RK 304 and RK 398 shortly after they disconnected from the river following the 1995 floods. CHL peaked at $126 \mu\text{g/L}$ at site RK 386 when it disconnected in late winter 1995 and peaked at $62 \mu\text{g/L}$ at site RK 346 under similar circumstances in winter 1996 (Figure 3). At the latter site, CHL reached an exceptional concentration of $689 \mu\text{g/L}$ in a period of low water in summer 1994. These

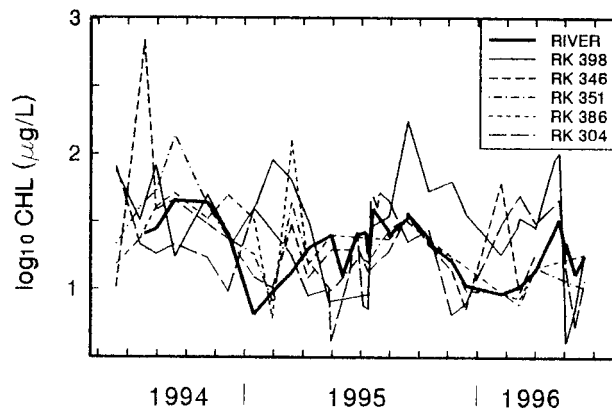


Figure 3. Time series of CHL in the Missouri River and connected scours.

blooms no doubt contributed to the rapid decline in dissolved nutrients under such conditions (e.g., Figure 1). Post-isolation blooms are largely responsible for the greater temporal variation of CHL in connected scours versus their permanently isolated counterparts (Table 1).

Peaks in CHL following isolation of connected scours were the most consistent temporal patterns shown by phytoplankton in the study. Temporal variation in CHL in protected lakes was only weakly related to other variables measured. CHL was not strongly seasonal. Annual minima sometimes coincided with periods of ice cover, but this association was not consistent among sites or years. Peak CHL was usually associated with above average concentrations of TP and TN, but this trend was also inconsistent. Among unaveraged observations from individual sites, CHL was not consistently correlated with TP or TN. Among sites, however, mean CHL from protected lakes was positively correlated with mean TP and TN (Figure 4). Grand means from the connected sites do not follow this relationship, but when the data are separated into periods of high and low connectivity, means from periods with little or no river influence follow the same positive trend with nutrients as the protected lakes (Figure 4). During periods of high connectivity, connected scours had much lower mean ratios of CHL:TP and CHL:TN than other sites.

DISCUSSION

Floodplains of the Missouri and Mississippi rivers, together with portions of the lower Grand and Des Moines rivers, comprise a distinct zoo-physiographic region named the Big Rivers province by Thom and Wilson (1980). Previous limnological studies in Missouri (e.g., Jones 1977, Hoyer and Jones 1983, Jones and Knowlton 1993) have not included waterbodies from this province, in part because few lakes now exist

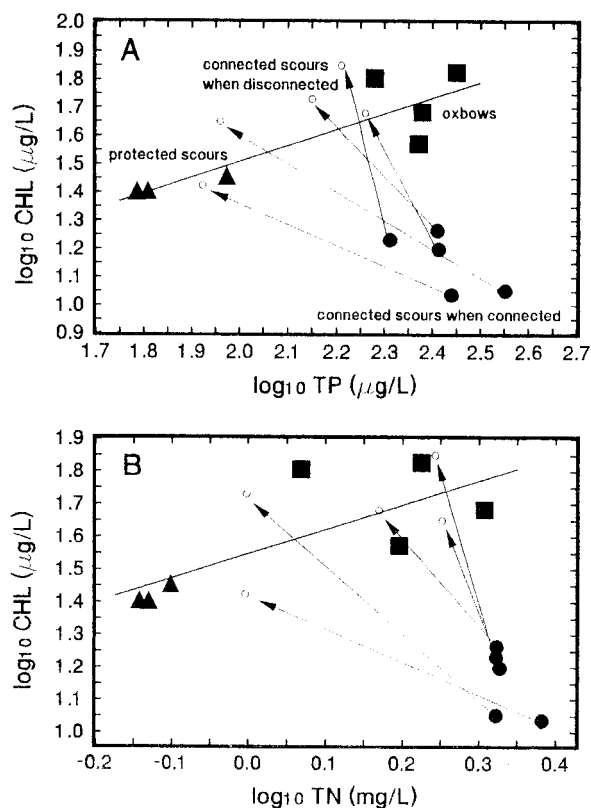


Figure 4. Logarithmic plots of mean CHL versus (A) mean TP and (B) mean TN for lakes in this study. Data from connected scours were averaged separately for periods of low and high connectivity as determined by visual observation and difference in $\text{NO}_3\text{-N}$ between the site and the Missouri River. Regression lines shown are based on data from the protected lakes only.

there. Most of the hundreds of sloughs and oxbow ponds that dotted these floodplains in the last century have been drained for agricultural purposes. Channelization or impoundment of the rivers has largely eliminated the processes of channel braiding, meandering, and natural levee-building that create new lakes. Reservoirs, which are numerous in most areas of the state, are also rare in the floodplain because the level topography (and great economic value of the land) are not favorable for reservoir construction. The hundreds of scour-hole lakes created during the 1993 flood (Galat et al. 1996), plus numerous other such lakes created in floods before or after 1993, are now among the most numerous standing waterbodies in the floodplain.

On the basis of trophic state indicators like nutrients and algal biomass, lakes in this study expand the upper range observed for lakes in Missouri. From averages of these variables, each of the lakes would be classified as eutrophic based on the criteria of Jones and Knowlton (1993—TP >25 $\mu\text{g/L}$, TN >0.5 mg/L, CHL >7 $\mu\text{g/L}$). On the basis of average TN and TP, the oxbows

Table 3. May–September arithmetic means of TP, TN, CHL, and TSS for lakes in this study (Big Rivers region) and those from other regions in Missouri compared by Jones and Knowlton (1993). Values are grand means averaged by lake-year, by lake, and then by region. TP and CHL are in $\mu\text{g/L}$, TN and TSS are in mg/L.

Region	TP	TN	CHL	TSS
Ozark Highlands	25	0.4	12	5
Ozark Border	41	0.6	20	11
Glaciated Plains	47	0.7	15	10
Osage Plains	67	0.8	23	20
Big Rivers	283	1.8	65	142
Oxbows	371	2.3	113	103
Protected Scours	87	0.7	29	24
Connected Scours	330	2.0	47	243

and connected scours would be further categorized as hypereutrophic (TP >100 $\mu\text{g/L}$, TN > 1.2 mg/L) and rank in the upper 10% of lakes in the state of Missouri (Jones and Knowlton 1993). If we consider these waterbodies as a sample of lakes in the Big Rivers province, then lakes in this region have much higher average values of TP, TN, CHL, and TSS (Table 3) than lakes in the other major zoo-physiographic provinces compared by Jones and Knowlton (1993) on the basis of growing season (May–September) means.

Among the lakes considered in this study, physical and hydrologic features probably contribute to the wide range of average conditions and temporal variability (Table 1, 2), especially among different site-types. As noted above, variation in connected scours was closely tied to connectivity and riverine inputs (Figure 1, 2, 3, 4). Conditions in the protected sites, however, seem more influenced by lake morphology than fluvial inputs. The fact that nutrients, CHL, TSS and overall temporal variability were less in the protected scours than in the oxbows is probably related to the smaller size (3–19 ha) and greater depth (1.5–4 m) of protected scours. Average depth in each of the oxbows was usually <1 m. Locations sampled in Cooley, Sunshine, and Dalton lakes had maximum depths <0.5 m during much of the sampling period. Peak concentrations of TSS and total nutrients in the oxbows were typically observed on windy days and probably resulted from sediment resuspension (Carper and Bachmann 1984, Hamilton and Lewis 1990). This effect was most important in Dalton and Sunshine lakes, which are large (323 ha and 216 ha, respectively) and windswept. Inflows did contribute occasionally to temporal variation in the protected sites but fluvial influences were minor compared to the connected scours.

Factors regulating phytoplankton also varied among

site-types. The relatively clear water, low nutrient concentrations, and high CHL:nutrient ratios of the protected scours (Figure 4) indicate that phytoplankton were probably nutrient-limited, at least during bloom periods (Reynolds 1984, Knowlton and Jones 1995). It is likely that phytoplankton in the oxbows were also nutrient-limited during blooms because of the high CHL:nutrient ratios observed at such times (Figure 4), but phytoplankton in the connected scours were usually not nutrient-limited. The low CHL:nutrient ratios seen under riverine conditions in these sites (Figure 4) are typical of large rivers (Søballe and Kimmel 1987, Van Nieuwenhuysse and Jones 1996) and are probably due to light limitation (Knowlton and Jones 1996) and rapid flushing (Søballe and Threlkeld 1985, Søballe and Kimmel 1987) in these turbid basins. But turbidity declined by an average of $\approx 80\%$ during periods of reduced connectivity in the connected sites. The algal blooms often observed at such times (Figure 2, 3) probably resulted from relief of light limitation (Knowlton and Jones 1996). High CHL:nutrient ratios measured during such blooms suggest that nutrients may have been limiting (Figure 4).

In a natural setting, the characteristics of floodplain lakes are dominated by the annual cycle of flooding and the resulting periodic incursions of river water ("flood pulse" *sensu* Junk et al. 1989). Variation in frequency and duration of river inputs or "connectivity" is a major distinguishing factor among waterbodies (Hamilton and Lewis 1990, Amoros 1991, Ward and Stanford 1995). For lakes in this study, however, constructed levees have reduced or eliminated connectivity of protected lakes—river inputs occur only during rare, levee-breaking floods such as in 1993. Removing direct river influence means that floods can have only indirect effects caused by elevated water tables or accumulation of local runoff that otherwise would drain to the river. These permanently unconnected lakes share common climate and edaphic setting with nearby riverine lakes but must be functionally different in that the relative importance of external versus internal processes will certainly follow in some proportion to connectivity.

The connected sites in this study offer clear evidence for the supposition that riverine influence, or connectivity, dominated their limnological characteristics. The transition, back and forth, between a state of high connectivity (characterized by high turbidity, high concentrations of dissolved and particulate nutrients, and light limitation of algal growth) and low connectivity (characterized by low turbidity, low dissolved nutrients, and nutrient limitation of phytoplankton) was the largest and most obvious source of temporal variation in these enormously variable waterbodies (e.g., Figure 1, 3). For the protected lakes, however,

external influences were far less obvious, and internal processes, notably those related to sediment resuspension and thermal stratification, seemed of equal, if not greater, importance (Osgood 1988, Scheffer et al. 1993).

This work was undertaken to help evaluate floodplain waterbodies as habitat for fish and wildlife. These limnological data do not by themselves provide conclusive evidence of habitat suitability, but they do raise some points of discussion. The oxbows, while enormously productive, share with the protected scours the disadvantage of having no regular exchange with the river. These sites may be valuable habitat for birds and terrestrial animals and resident aquatic communities but, unlike natural floodplain lakes, cannot function as nursery areas and refugia for the Missouri River aquatic communities. Connected scours may serve these functions, but their long-term value as habitat may be limited by their rapid loss to sedimentation.

Neither category of scour basin approaches the high average concentrations of algal biomass (CHL) of the oxbows (Table 1), but plausible scenarios for the future of the connected scours may move them in that direction. These sites become shallower and less connected as their basins fill and thus acquire the optical advantages of shallow depth and reduced allochthonous turbidity coupled with the benefits of occasional flood pulses of nutrients and organic matter from the river. The substantial response of phytoplankton in connected sites to periodic loss of connectivity (e.g., Figure 3) supports the idea that some intermediate level of connectivity may be optimal for autochthonous primary productivity. If so, is increased internal production at the cost of lost connectivity to the advantage of consumer organisms? From the data examined here, we can make no direct inference about the relative importance of allochthonous organic matter to the food-webs in these lakes or its quantitative relation to connectivity. Ultimately, questions of food-web dynamics and related aspects of habitat quality in these sites must draw on observations of the higher trophic levels in these systems. Fortunately, studies of zooplankton, macroinvertebrates, fish, and other consumers in these lakes are currently underway and should eventually provide answers to some of these questions.

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