Connectivity Influences Temporal Variation of Limnological Conditions in Missouri River Scour Lakes

Matthew F. Knowlton and John R. Jones
Department of Fisheries and Wildlife Sciences
302 Anheuser-Busch Natural Resources Building
University of Missouri, Columbia MO 65211-7240

ABSTRACT

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Two scour lakes in the Missouri River floodplain were sampled 20 months (April 1996 – December 1997) to examine effects of river inflow on mixing, seston, and nutrient dynamics. Lake NC-11 ($\approx$4 ha) is deep ($\approx$16 m), sheltered, dimictic, and connected to the river only during floods. Lake S-19 ($\approx$20 ha) comprises two sub-basins, a deep ($\approx$12 m) riverine forewater perennially connected to the river and a shallow ($\approx$4 m), polymictic backwater of variable connectivity. Stratification in NC-11 affected, and was affected by, river inputs – cool inflows mixed completely and sometimes destratified the lake, warmer inflows were partly or completely confined to the epilimnion. Mixing between basins at S-19 was incomplete except during floods. During floods, concentrations of seston and particulate N and P were similar in the two basins of S-19, but conditions in the two basins diverged substantially during inter-flood periods as lower water levels reduced lateral exchange. Seston concentrations in NC-11 during floods were much less ($\approx$90% less) than in S-19 or the river. In NC-11, algal blooms (chlorophyll 50-90 µg·L⁻¹) occurred in summer post-flood periods, but larger blooms (chlorophyll 50-256 µg L⁻¹) occurred in the S-19 backwater during periods of low connectivity in all seasons. Nitrate-N peaked at >2 mg·L⁻¹ during floods but was exhausted during algal blooms along with up to $\approx$90% of dissolved phosphorus. Silica declined sharply (up to 93%) in many, but not all blooms, but remained >0.5 mg·L⁻¹ in all observations. Connectivity influenced many lake features and enhanced nutrient availability, but other floodplain lakes lacking river connections have similar algal biomass.

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

Floodplain lakes and their associated wetlands play several vital roles in the function of river/floodplain ecosystems. These waterbodies comprise a range of physical and chemical environments that complement conditions in the parent river thus extending the range and diversity of habitats available to plant and animal communities (Junk et al. 1989, Ward and Stanford 1995). Floodplain waterbodies act as sinks and transformers for river-borne nutrients and organic matter and storage reservoirs for floodwaters. Lentic backwaters, oxbows, swamps and marshes provide critical nursery habitat for many riverine fish, reptiles and amphibians and food and other needed resources for hundreds of invertebrates, birds and mammal species (Welcomme 1985, Galat et al. 1996). Together with the rivers that create and maintain them, floodplain lakes and wetlands comprise integrated and dynamic ecosystems of enormous productivity.

Knowledge of the ecological significance of floodplain waterbodies has grown as their numbers have shrunk. In many river systems world-wide, floodplain waterbodies have been replaced by agricultural fields protected by flood control levees. The processes of erosional overbank flow and channel wandering that produce and maintain lake basins in floodplains have been severely reduced, and "connectivity" – the regular exchange of water, materials and organisms between river and floodplain – has been all but eliminated for the few floodplain waterbodies that remain (Ward and Stanford 1995).

The artificial levees instrumental in the elimination of so many natural floodplain waterbodies have, paradoxically, been involved in the creation of a new type of floodplain lake – the "scour basin" or "blew hole." Scour basins are created when levees are breached during major floods and are often sufficiently deep to remain as semi-permanent pools after flood waters recede. Scour basins have recently been the focus of

extensive research in the Missouri River floodplain in Missouri (Galat et al. 1998). The great midwest flood of 1993 created hundreds of new scour basin lakes (Galat et al. 1997) which, along with scour lakes created by previous and more recent floods, are the most numerous perennial waterbodies in some portions of the floodplain.

It is hypothesized that scour basins may function as semi-natural analogs of the natural floodplain waterbodies they have replaced (Galat et al. 1997). Testing this hypothesis has been a fundamental goal of an extensive research effort, the Missouri River Post-flood Evaluation (MRPE) project, conducted in the aftermath of the 1993 flood. The MRPE project examined over several years a variety of features of scour basins (e.g., morphology, limnology, invertebrates, fish, amphibians, reptiles, birds and mammals), in comparison with other types of floodplain waterbodies (Galat et al. 1998). This paper presents limnological data collected as one part of the MRPE project involving close-interval sampling of fish, zooplankton and water quality from two scour basin lakes distinguished by differing morphology and hydrology.

A survey of 12 floodplain lakes conducted in 1994-1998 as another part of the MRPE project (Knowlton and Jones 1997) examined differences among lakes of distinct basin-type and connectivity – remnant oxbows and scour lakes isolated hydrologically from the river (i.e., zero connectivity) and scour lakes connected permanently or seasonally to the river. The latter group was distinguished by extreme variability in response to the initiation or cessation of river inputs. Sampling in the 12-lake survey was conducted monthly and could not clearly resolve the temporal dynamics of lake response to connection events. The present study was undertaken to acquire a more detailed understanding of responses of scour lakes to river inputs during connection events by use of close-interval (usually weekly during summer) sampling of limnological conditions. We present here major findings of this work including the effect of connectivity on thermal regime, seston and nutrient dynamics.

Study Sites

The scour basins, designated NC-11 and S-19 in the MRPE project, are located adjacent to the Missouri River, respectively, 421 km and 387 km upstream (River Kilometers) from Missouri-Mississippi confluence. Both basins were formed as "entrance scours" (Galat et al 1997) in the flood of 1993 by river water flowing through levee breaks. Site NC-11 (Fig. 1) is 150-200 m from the riverbank with a surface area of 3.8 ha

when bank-full (surface elevation ≈ 194 m MSL) but not connected to the river. The flood control levee that broke during the formation of the scour was rebuilt landward from the pool and now forms over half the basin margin and substantially reduces wind from the north, south and east. The riverward margin of the basin and land between the basin and the river are occupied by dense stands of cottonwood (*Populus deltoides*) and willow (*Salix* spp.) that developed after the 1993 flood. The scour basin itself is ovoid and steep-sided, especially riverward, with mean and maximum depths of 5.7 and 16 m, respectively, when bank-full.

Scour S-19 (Fig. 2) formed when the river cut across a meander bend (the Little Missouri Bend) forming a side channel (insert in Fig. 2). The levees breached in 1993 have not been repaired and flow through the side channel resumes during large floods. Site S-19 consists of the eroded zone at the upstream end of the side channel. The scour basin is >1 km long and occupies >20 ha (Fig. 2). S-19 comprises several smaller basins that form separate pools at low water. The two largest sub-basins are located adjacent to the river and along the northeastern edge of the scour. The riverward ("forewater") basin is separated from the river by rock-faced dikes maintained for navigation channel control by the U.S. Army Corps of Engineers. The dikes are notched to permit flow-through and were heavily eroded during floods in 1995 and 1996; thus there is considerable flow through the forewater at most river stages (Fig. 2). The forewater and the eastern basin of S-19 are separated by a shallower sill exposed at low river stages. The eastern basin functions as a backwater (no unidirectional flow) except during large floods when flow resumes across the meander bend. Bank-full (elevation ≈ 189 m MSL), the forewater basin has a mean depth of ≈4.4 m (maximum depth ≈12 m) and the backwater (including the entire scour inland from the sill) has mean depth of ≈1.3 m (maximum depth ≈4 m). Mean depth of the backwater declines to ≈0.7 m when the pool is disconnected from the forewater. Scouring and deposition continually alter the morphology of S-19. During the study, the elevation of the sill between the forewater and backwater increased ≈0.3 m, reducing connectivity of the backwater.

Materials and Methods

Limnological measurements were made during sampling of larval and adult fish and zooplankton between 26 April 1996 and 16 December 1997. Surface water samples (2 L) and temperature and dissolved
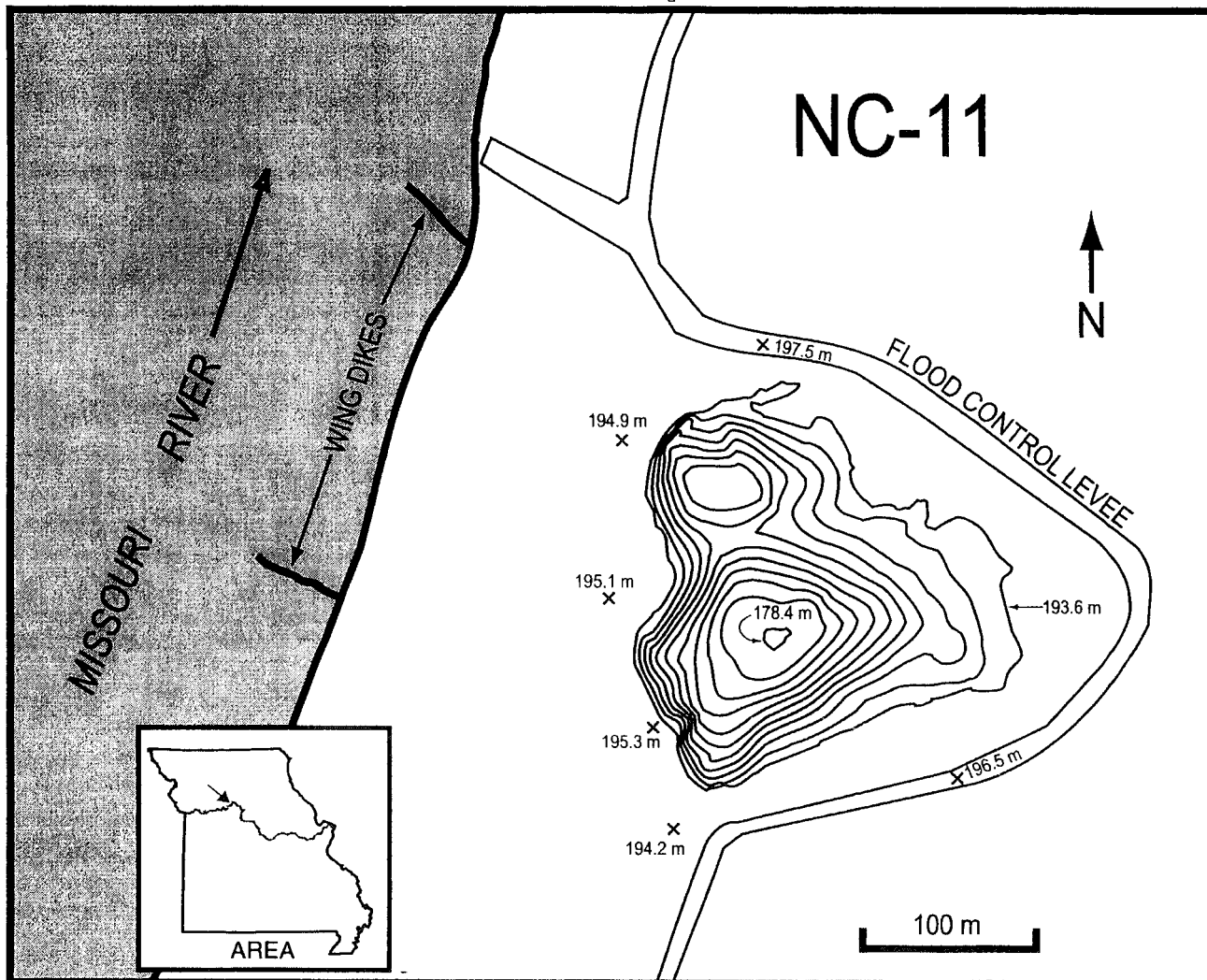
Figure 1.-Site map of NC-11. Bathymetric contours are at 1.52 m (5 ft) intervals. Elevations are in meters above mean sea level. Bathymetric and point elevation data are from a November 1996 survey by the Natural Resources Conservation Service (NRCS, unpubl. data). Point elevations west of the basin mark the highest land between the basin and the river. The Missouri River is approximately 260 m wide at the study site. Insert shows study site location in Missouri.

oxygen profiles were taken at NC-11 (Fig. 1) and the backwater basin of S-19 (Fig. 2) weekly during March-August and usually biweekly in February and September-November. The sites were sampled only once per month during ice cover in December 1996 and January 1997. Temperature and oxygen data were collected on the same schedule from the S-19 forewater (Fig. 2) and beginning in March 1997, water samples were also taken in the forewater. During May 1996 through February 1997 water samples collected in a separate study were taken monthly from the S-19 forewater (see Knowlton and Jones 1997) and bi-weekly from the Missouri River at S-19 or at other sites between River Kilometers 283 and 398. Because conditions in the forewater were essentially riverine, data from Missouri River samples for 7 and 20 May, 4 June, 28 October, 19 November and 2 December

1996 and 3 March 1997 are used in the results to represent the forewater during gaps in the time series. All water samples were collected from the surface (<15 cm depth) as grab samples from near the deepest point in each basin (Figs. 1-2). During ice cover (n=7 samples), holes were cut or drilled in the ice and samples taken as grabs or by pumping from just below the surface. Visual observations of currents and flow direction were made during sample collection but current velocities were not measured. Except for temperature and oxygen profiles, no measurements were made of subsurface strata. Spatial variation within basins and short-term (day-to-day or diurnal) temporal variation were not quantified.

Unfiltered water samples were analyzed for chlorophyll (CHL – Knowlton 1984, Sartory and Grobbelaar 1984), total phosphorus (TP – Prepas and Rigler 1982),
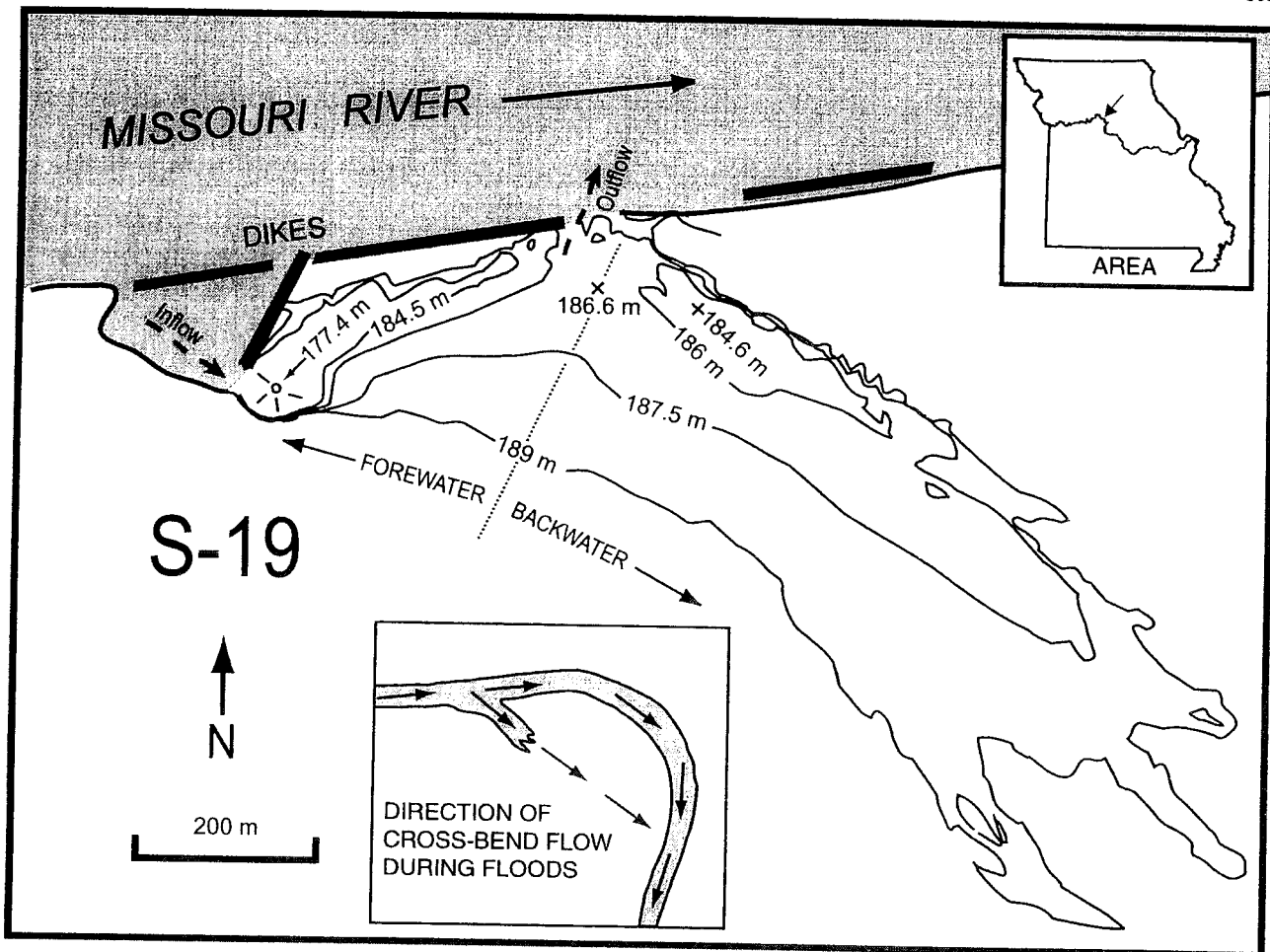
Figure 2.–Site map of S-19. Elevations are in meters above mean sea level. Bathymetric contours and point elevation data are from a November 1996 survey by the Natural Resources Conservation Service (NRCS, unpublished data). Except during floods, the boundary of the lake basin is defined approximately by the 189 m contour landward, and by the dikes riverward. Dashed lines labeled "inflow" and "outflow" indicate the major flow path of water through the forewater in non-flood periods. The Missouri River is approximately 300 m wide at the study site. Inserts shows general study site location in Missouri and the local site location on the Little Missouri Bend together with the direction of cross-bend flow during floods.

total nitrogen (TN – Crumpton et al. 1992), and suspended solids (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 "dissolved" TP and TN (dTP, dTN), nitrate-nitrite-N (NO$_3$-N - A.P.H.A. 1985), ammonia + ammonium-N (NH$_x$-N - Stainton et al. 1977), silica (A.P.H.A. 1985) and alkalinity (A.P.H.A. 1985). Concentrations of particulate TP (pTP) and TN (pTN) were estimated by difference. All analyses except alkalinity were performed in duplicate and means used in data analysis. Concentrations of NO$_3$-N and NH$_x$-N were often near zero. Limits of detection varied with background turbidity and other interferences but were always better than 0.02 mg·L^{-1}.

Measured (i.e., nominal) concentrations less than 0.02 were used as measured in determining site averages and plotting time series.

Results

Water Levels and Connectivity

During the study, discharge of the Missouri River at Waverly, Missouri, averaged 185% of mean discharge for the period since mainstem reservoirs have regulated flow of the river (1958-present). At Waverly, which is ≈50 km upstream from NC-11, river surface elevation varied by 4.9 m during the study (Fig. 3). At Glascow, Missouri, 22 km downstream from S-19, river elevation
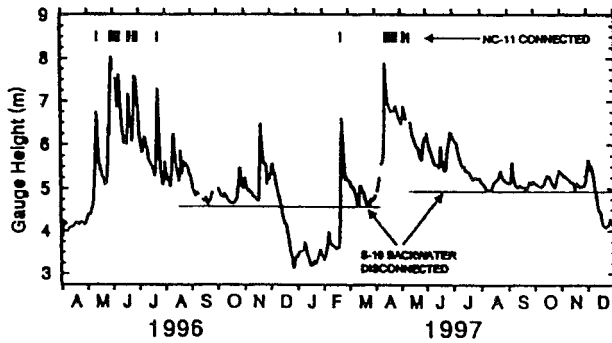
Figure 3.-Missouri River stage at Waverly, Missouri (River Kilometer 472), April 1997 to December 1997. Dates on which NC-11 was connected to the river are shown as bars above the plot. Gaps in the plotted line indicate missing data. The dashed line indicates the approximate river stage below which the S-19 backwater completely disconnected from the forewater.

varied by 6.5 m. River levels were not gauged at either scour site but track the sequence, if not the exact magnitude, of fluctuations at the gauges (e.g., Fig. 3). NC-11 was connected to the river for 57 days in 9 separate periods of 1 to 16 days each. During the largest floods, (May 1996, April 1997) the river crested about 2 m above the basin rim (elevation ≈194 m MSL - Fig. 1) that usually separated NC-11 from the river. NC-11 connected to the river when the gauge at Waverly was above about 6 m. Stage readings above 6 m at the Waverly gauge has occurred in about 5% of daily observations since 1958 (U.S. Geological Survey Water Year Records). Thus connection between the river and NC-11 during this study was about twice as frequent as expected from long-term records.

At S-19, the forewater remained confluent with the river throughout the study with strong current always noted except during periods of low water in December 1996 and January 1997 when the site may have disconnected from the river. Ice cover and river ice jams at that time prevented direct observation of flow at the inlet or outlet of the forewater (Fig. 2).

During floods cresting above ≈6.7 m at Waverly, the river at S-19 flowed through the scour, across the downstream meander bend (insert in Fig. 2). At other times, flow into the backwater was too weak to produce visible current except, perhaps, when the backwater was filling after a period of disconnection. Between spring floods of 1996 and 1997 the sill between backwater and forewater of S-19 was exposed at river stages (Waverly gauge) less than ≈ 4.6 m. After the 1997 floods, the backwater disconnected at stages below ≈4.9 m (Fig. 3). The backwater was completely disconnected >2 months in winter 1996-1997 and again in December 1997, but was often weakly connected during the summer and fall of both years. In subsequent time-series graphs we have used a river stage of ≤5.1 m as an

indication of little or no connectivity for the backwater. In the post-regulation period (after 1958) stages of 5.1 and 6.7 m at the Waverly gauge have been exceeded, respectively, in about 15% and 3% of daily observations. During this study these level were exceeded in 55% and 6% of observations.

Water levels in NC-11 were gauged on-site during 1997. When first measured in late January the pool surface was ≈3.5 m below the basin rim. The pool filled with river water during a February flood and subsequently tracked changes in river stage during the generally declining water levels in March and later in May-August. Water levels were not gauged in 1996, but followed a seasonal pattern similar to 1997, tracking changes in river levels. At the S-19 backwater, surface elevation during winter 1996-1997 remained just below the sill separating it from the forewater and was perched as much as 2 m above the elevation of forewater and river. At NC-11 the lake surface during lengthy periods of low water in winter 1996 and late summer 1997 was at or near the surface elevation of the river and probably retained some degree of groundwater connection with the river alluvium.

Temperature Regimes

In 1996, river water first entered the basin of NC-11 during 11-13 May weakening stratification, but not mixing completely with the hypolimnion (Fig. 4). A second, larger flood (27 May-6 June) also did not produce holomixus - surface to bottom temperature differences of 1.5-3.0° were measured at the peak of flooding. But a rapid 3-4° warming of the hypolimnion during this period indicates considerable exchange across the temperature gradient. Hypolimnetic temperature remained nearly constant at ≈18 degrees during three subsequent floods that seem to have affected only the epilimnion. Fall overturn occurred in late September and the site was ice-covered with inverse stratification from late December through January 1997.

Flooding helped produce a markedly different temperature regime in 1997. River and lake water were of similar temperature during a brief (1 day) connection in February. In a larger flood (16 days) in April, incoming river water was initially about 5° but warmed to 14° during the period of connection. Initial inflows destratified NC-11 and reduced bottom water temperature by 4°. Subsequent, warmer inflows replaced the surface layer but did not substantially mix with the deeper water which warmed <1° during the flood and remained <11° until overturn in early November. Thus stratification in 1997 seems to have been established by sequential inflow of increasingly warm river water
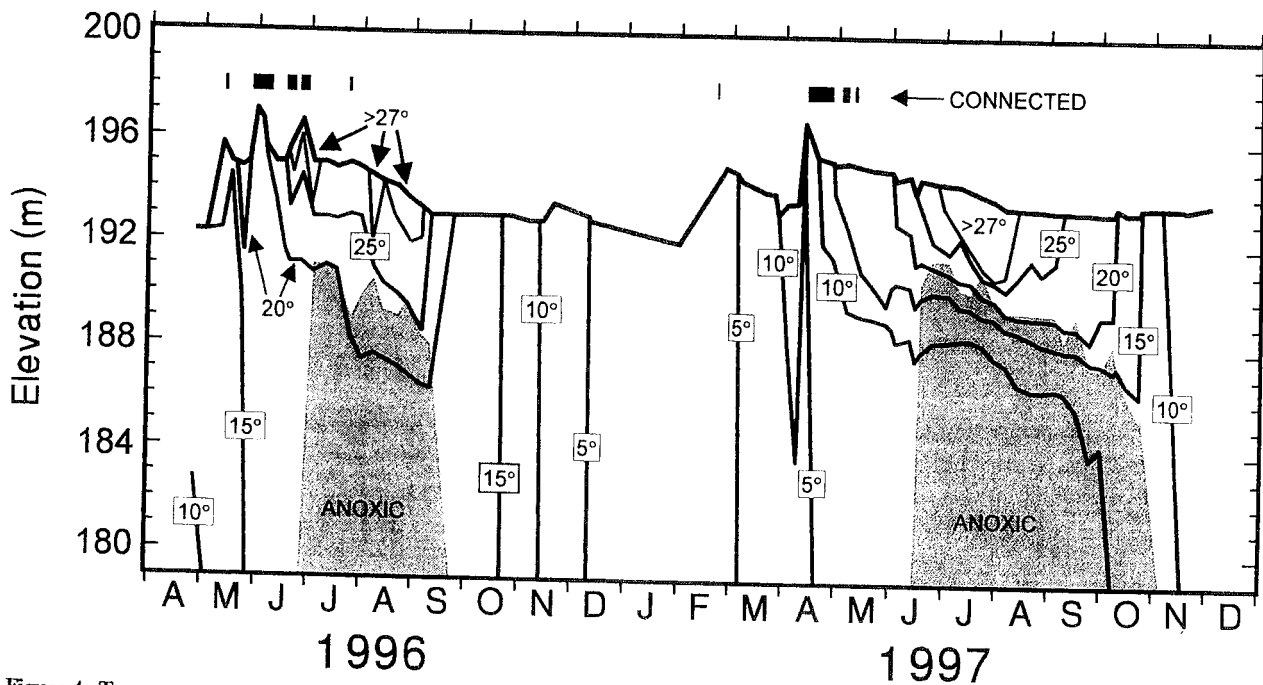
Figure 4.–Temperature regime of scour NC-11, April 1996 – December 1997. Surface elevations (meters above mean sea level) for March–December 1997 are based on gauge heights measured on site. Earlier surface elevations are estimated from river stage (Fig. 3) as extrapolated from a regression of river stage and pool elevation for the 1997 data. Elevations are plotted only for sampling dates and do not show details of river stage variation during periods of connection. The shaded area represents water with dissolved oxygen <0.5 mg·L⁻¹. Summer surface temperatures ranged up to 29.5° in both years.

rather than by the usual processes of *in situ* solar heating and wind mixing.

Temperature regimes in S-19 differed between the two sub-basins. In the lotic forewater, vertical temperature differences (surface to bottom) were never greater than measurement error ($\approx0.2°$). In the backwater, stratification developed intermittently in summer with vertical temperature differences (surface to bottom) of 1-8° (Fig. 5). In about 70% of the observations, surface

Figure 5.–Spatial temperature variation at site S-19. Surface to bottom temperature differences at the backwater sampling site (Fig. 2) are plotted as a heavy dashed line. The solid line represents surface temperature of the forewater minus that of the backwater. Observations marked by solid circles occurred when the stage of the Missouri River at Waverly, Missouri, was <5.1 m. Open circles represent a river stage >6.7 m.

temperatures differed by >0.5° between the forewater and backwater sites and were usually higher in the backwater (Fig. 5). When water levels at the Waverly gauge exceeded 6.7 m (open circles in Fig. 5), neither vertical nor site-to-site temperature gradients >0.5° were measured, but at lower river stages, water circulation in the site was insufficient to prevent vertical and lateral temperature gradients from developing. Physical disconnection between the basins (noted approximately by solid circles in Fig. 5) was not necessary for temperature differences to develop. The greatest temperature variations occurred when the forewater and backwater were connected.

Suspended Solids

Suspended materials, including particulate N and P, differed greatly among the three sites following inter-site differences in connectivity. Average concentrations of TSS, pTP, and pTN were ≈2-10 times greater in the S-19 fore-water than in NC-11 with the S-19 backwater intermediate (Table 1).

Temporal dynamics of seston were also greatly influenced by connectivity. As exemplified by TSS data (Fig. 6), seston in the S-19 backwater peaked during large floods, reaching concentrations similar to those in the forewater. TSS in NC-11 also peaked during
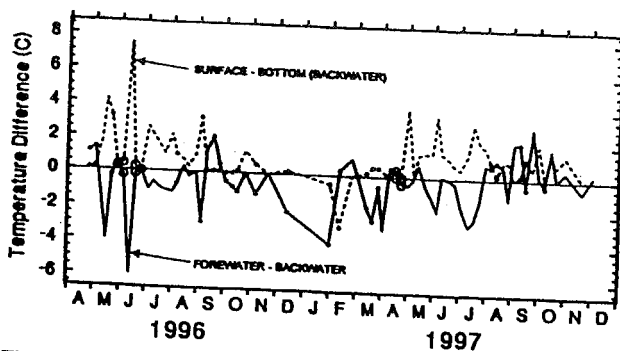
Table 1.-Means, medians, minima and maxima of selected variables. Concentrations are in mg·L⁻¹ except CHL (µg·L⁻¹). Data for the S-19 forewater (S-19-F) include seven observations based on samples from the Missouri River here used to fill gaps in the time series (see text).

		TSS	VSS	pTP	dTP	pTN	dTN	NO₃-N	NHₓ-N	SiO₂	CHL
NC-11	mean	32	5.5	0.050	0.046	0.24	0.95	0.497	0.050	5.8	26
(n=64)	median	26	5.3	0.046	0.033	0.22	0.83	0.323	0.024	5.8	22
	min.	5.0	1.1	0.009	0.013	<0.05	0.31	<0.02	<0.02	0.7	2.9
	max.	198	19	0.196	0.161	0.75	2.38	1.920	0.200	12.0	91
S-19-B	mean	179	19	0.177	0.094	0.51	1.41	0.959	0.038	9.3	45
(n=68)	median	81	14	0.130	0.094	0.41	1.47	1.001	0.025	9.6	27
	min.	12	1.8	0.021	0.018	<0.05	0.32	<0.02	<0.02	1.1	1.4
	max.	3015	190	1.400	0.193	2.04	3.78	2.960	0.230	15.4	256
S-19-F	mean	336	27	0.273	0.102	0.45	1.53	1.107	0.040	10.3	25
(n=53)	median	213	19	0.194	0.093	0.37	1.61	1.171	0.023	10.2	24
	min.	12	1.7	0.051	0.065	<0.05	0.48	0.250	<0.02	7.1	4.6
	max.	1643	133	1.130	0.209	1.53	3.74	3.060	0.280	16.8	63

floods, but remained about an order of magnitude less than in S-19. TSS in NC-11 and the S-19 backwater usually declined sharply after floods. An exception occurred after the last flood in May 1997, when TSS in NC-11 increased 16 mg·L⁻¹ after disconnection due to calcite precipitation during a post-flood algal bloom that reduced alkalinity by 35 mg·L⁻¹ (as CaCO₃). TSS at all 3 sites were minimal under ice in the winter. TSS in NC-11 increased during fall overturn in both years.

Surprisingly, differences in TSS between the forewater and backwater of S-19 were minimal during periods of low connectivity in late summer. But this similarity of concentrations was coincidental rather than an indication of lateral exchange. The composition of seston differed greatly between the sites during such periods. For example, in August-October 1997, seston in the backwater contained, on average, 2.2 times as
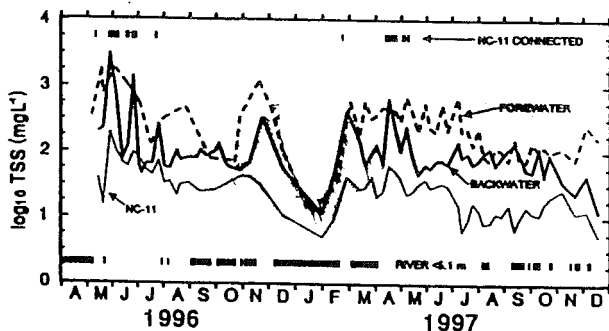

Figure 6.-Temporal variation in total suspended solids (TSS) at NC-11 and S-19. Bars above the plot indicate days on which NC-11 was connected to the Missouri River. Bars below the plot show days when the stage of the Missouri River was <5.1 m at Waverly, Missouri, indicating little or no connection between the forewater and backwater of S-19.

much VSS (n=12, range 1.3-4.4) and 3.3 times as much pTN (n=12, range 0.2 to 5.8) as seston in the forewater.

Algal Biomass and Dissolved Nutrients

Algal CHL averaged 25-26 µg·L⁻¹ in NC-11 and the S-19 forewater compared to 45 µg·L⁻¹ in the S-19 backwater (Table 1). Temporally, CHL was related to connectivity (Fig. 7). In NC-11, CHL was greatest during inter-flood or post-flood periods with maximum CHL (91 µg·L⁻¹) between the last two connection events in 1997. Mixing depths in summer were seldom >2 m and were often less, thus summer light conditions were favorable for algal growth despite relatively high turbidity. In the S-19 backwater, CHL was highest during low-water periods when the site was partly or completely disconnected from the forewater and mixing depths were restricted by the shallow basin and intermittent stratification. CHL in the forewater followed the seasonal pattern typical of the Missouri River (Knowlton and Jones 2000) with CHL minima in winter and maxima in the spring or fall. CHL at NC-11 was also minimal in winter, but in the S-19 backwater phytoplankton bloomed under the ice in January-February 1997 yielding maximum CHL of 110 µg·L⁻¹.

Connectivity and algal dynamics were closely coupled to variation in dissolved nitrate and silica. Nitrate-N in the S-19 forewater varied between highs of 1.8-3.1 mg·L⁻¹ in spring to lows of 0.25-0.45 mg L⁻¹ in late summer-fall (Fig. 8). When strongly connected to the river, NO₃-N in NC-11 and the S-19 backwater were comparable to that in the forewater. But reduced
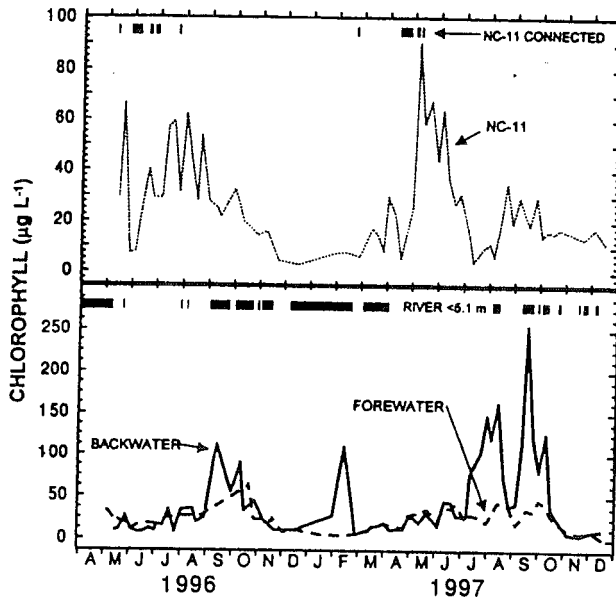
Figure 7.-Temporal variation in chlorophyll at NC-11 and S-19. Bars above the plot in the upper panel indicate days on which NC-11 was connected to the Missouri River. Bars above the plot in the lower panel show days when the stage of the Missouri River was <5.1 m at Waverly, Missouri, indicating little or no connection between the forewater and backwater of S-19.

connectivity produced sharp reductions in NO_3-N. Nitrate-N in NC-11 in 1996 dropped from 1.1 mg L^1 to <0.02 mg L^1 in five weeks during the algal blooms that followed the last connection event in late July (Fig. 8). Nitrate-N disappeared with similar rapidity in May-June 1997. In both years, NO_3-N remained undetectable until fall overturn. Nitrate-N was also quickly depleted in the S-19 backwater during blooms in September and October 1996 and in January and July-August 1997. In the backwater, NO_3-N inputs during transient connection events prevented the extended
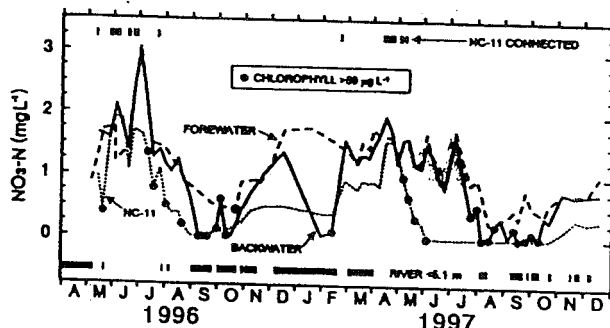
periods of NO_3-N deficiency seen in NC-11.

Silica ranged from 7.1 to 16.8 mg L^1 in the S-19 forewater (Fig. 9). Silica concentrations in the three sites were comparable during flood events but sometimes diverged with reduced connectivity. In NC-11, SiO_2 declined 6.6 mg L^1 during post-flood algal blooms after the site disconnected in late June 1996 and declined again after the site briefly reconnected in July. In 1997, SiO_2 declined >6 mg L^1 during large blooms in the 4 weeks after the last flood reaching a minimum of 0.7 mg L^1 a week after NO_3-N became undetectable. The silica minimum occurred during a period of strong warming and shallow mixing (mixed depth < 1m) and concentrations recovered as mixing subsequently deepened. Silica increased through the rest of the stratified period despite additional algal blooms (CHL 30-35 µg L^1). Silica in the S-19 backwater also dropped sharply during blooms in September and October 1996 and in January-February and September-October 1997 but did not decline during large blooms in July-August 1997.

Dissolved phosphorus (dTP) in NC-11 was related to connectivity and algal biomass much the same as NO_3-N and SiO_2. Annual maximum dTP in NC-11 (0.1 to 0.16 mg L^1) occurred during connections and concentrations declined ≈90% during subsequent blooms (Fig. 10). But as with NO_3-N and SiO_2, high CHL was not always accompanied by declining dTP. Blooms in late-May and early June 1997 yielded no net loss of dTP. In the S-19 backwater dTP sometimes declined relative to the forewater during periods of low connectivity (e.g., September and October 1996, January-February, July and October 1997), but in September and October 1997, dTP in the backwater was greater than in the forewater despite little or no river inputs and intense algal blooms (CHL 256 and 126 µg L^1, respectively) during that period. Return of phosphorus from deeper strata or bottom sediments seems a likely explanation for these observations.
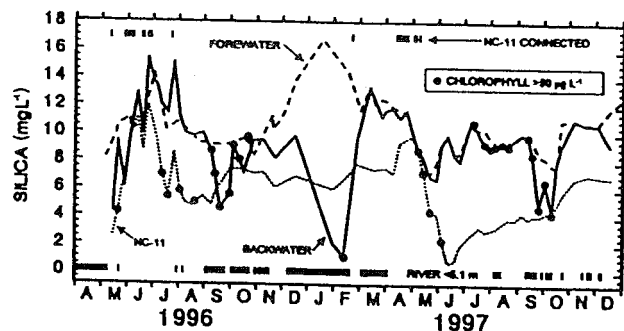
Unlike the other dissolved nutrients, ammonia +

Figure 8.-Temporal variation in nitrate-N (NO_3-N) at NC-11 and S-19. Horizontal bars on the graph are as in Fig. 6. Solid circles mark observations made when chlorophyll was >50 µg L^1. Note that CHL >50 µg L^1 occurred in NC-11 only in May-August 1996 and in May-June 1997. CHL >50 µg L^1 occurred in the S-19 forewater only in October 1996.

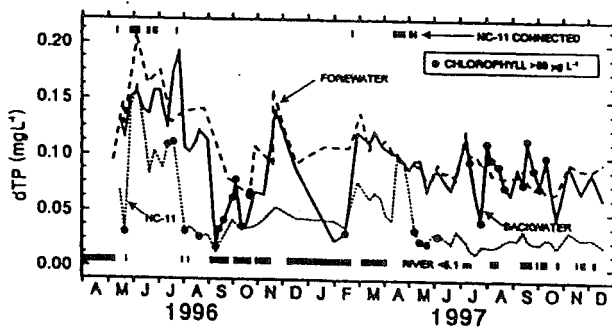Figure 9.-Temporal variation in dissolved silica at NC-11 and S-19. Symbols on the graph are as in Fig. 8.

Figure 10.–Temporal variation in dissolved total phosphorus (dTP) at NC-11 and S-19. Symbols on the graph are as in Fig. 8.

ammonium-N (NH_x-N) usually occurred in low concentrations in the river. Concentrations in the S-19 forewater were usually <0.05 mg·L^{-1} except during winter when NH_x-N peaked at 0.28 mg·L^{-1} (Fig. 11). NH_x-N in the S-19 backwater was also usually low. The largest differences (>0.1 mg·L^{-1}) between the forewater and backwater occurred during the long period of disconnection in winter 1996-1997 and in early April 1997 before the April flood. In the former instance, NH_x-N in the backwater fell below detection during the February algal bloom. In the latter case, concentrations in the backwater increased while NH_x-N in the forewater were declining from their winter maximum. NH_x-N in NC-11 was more dynamic than in S-19. In spring of both years NH_x-N rose to several times the concentration in the river between or immediately after con-
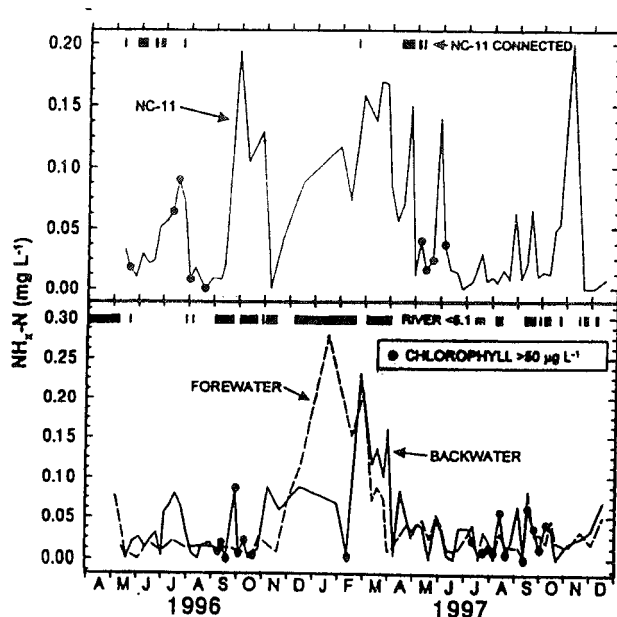

Figure 11. Temporal variation in ammonia + ammonium-N at NC-11 and S-19. Horizontal bars on the graph are as in Fig. 6. Solid circles mark observations made when chlorophyll was > 50 µg·L^{-1}.

nections then fell to undetectable levels. In several instances, especially in summer 1997, peaks in NH_x-N occurred during declines in CHL and vice versa. NH_x-N peaked at ≈0.2 m g·L^{-1} during fall overturn in both years then dropped to near zero. The decline of NH_x-N co-occurred with an approximately equimolar increase in NO_3-N (Fig. 8) suggesting the occurrence of nitrification. As NO_3-N concentrations stabilized (e.g., early November 1996), NH_x-N again increased. The brief, February 1996 flood increased NH_x-N, as it did the other nutrients, but otherwise, river inputs tended to reduce, rather than increase NH_x-N. It is possible, however, that the post-flood peaks in NH_x-N were due to ammonification of riverine organic materials introduced during connection events and are thus directly dependent on connectivity.

Discussion

Water in most large rivers is nutrient-rich, turbid and populated by light-limited algae (Reynolds et al. 1994). Movement of river water into comparatively shallow or quiescent backwaters or floodplain lakes is accompanied by a predictable sequence of events and transformations including loss of suspended load and increased transparency that stimulate algal growth with a consequent reduction of dissolved nutrients (Junk et al. 1989). Analogous processes operate in estuaries and in the transitional zones of reservoirs. It is no surprise that Missouri River scour lakes follow suite. Connectivity between small lakes and large rivers is profoundly consequential to the lakes. The frequency and duration of connection events and their timing with respect to seasonal cycles can control or influence fundamental limnological processes such as thermal stratification, algal dynamics and nutrient availability.

The major findings of this study were anticipated by Knowlton and Jones (1997) who observed the effects of connection events on suspended solids, nutrient concentrations and algal blooms in several scour basin lakes including S-19 (site RK 386 in that study). This work adds information about factors producing differences among sites and variation over time.

Of particular consequence is the orientation of the scour basin relative to the downstream flow of the river. During floods, suspended solids, including particulate N and P, in NC-11 remained ≈10 fold less than in the river (Fig. 6) because of the position of the site, ringed by the protective levee approximately perpendicular to the direction of flow and further protected by wing dikes designed to divert flow to the river channel (Fig. 1). Also, the dense stands of woody vegetation between the scour and the river undoubtedly

helped slow water movement and reduce sediment transport to the site. Similarly, TSS in the S-19 backwater during floods remained well below forewater concentrations except when the flow across the downstream meander bend was reestablished yielding lotic, unidirectional flow through the scour. At other times currents in the site were too weak to maintain suspended load or prevent thermal stratification (Fig. 5). Dissolved nutrients and CHL remained similar in the forewater and backwater until the depth of water over the sill fell below ≈1 m after which conditions in the two basins diverged sharply except when small rises in the river, such as in early September 1997 (Fig. 3) flushed the surface layer of the backwater.

The fact that NC-11 is substantially protected from direct flow means that prevailing temperature conditions have considerable influence on the degree of mixing between the lake and river. Water in the lake seems to have mixed completely with river water only when incoming river water was of equal or lower temperature than the lake as in the flood of February and April 1997. Other connection events did not produce complete vertical mixing and floods in June and July 1996 and May 1997 had little, if any, effect on stratification. But flooding did greatly influence the overall mixing regime. Warming of the hypolimnion during floods in May-June 1996 lead to early turnover in the fall, whereas cooling of the bottom waters by flood inflows in April 1997 resulted in stronger stratification that delayed turnover by over a month compared to the previous year.

Average CHL concentrations in NC-11 and the S-19 backwater was much higher than in the river and S-19 forewater (Table 1), presumably because of the difference in light availability. Mixing depths in NC-11 in summer are typically ≈1 m which also the case for the S-19 backwater year around. Such shallow mixing provides favorable light conditions for phytoplankton at all but the highest turbidities. Flushing during connection events always reduced CHL, though sometimes only slightly. Whether phytoplankton became nutrient-limited during inter-flood periods cannot be determined from our data, but there is some evidence of algal-nutrient interactions. In NC-11, CHL reached a minimum in July 1997 (Fig. 7) corresponding to the disappearance of NO_3-N and seasonal minima of SiO_2, dTP, and NH_x-N (Fig. 9-11). CHL subsequently increased, but without further depletion of SiO_2, possibly because of a shift from a diatom-dominated to non-diatom community. Similarly, the 1997 July-August CHL peak in the S-19 backwater (Fig. 7) was not accompanied by declining SiO_2 (Fig. 9), but silica declined sharply during a later bloom following a brief period of increased connectivity in early September (Fig. 9).

There is little reason to doubt that connectivity enhanced availability of inorganic nutrient in the lakes. Concentrations of NO_3-N, dTP, and SiO_2 in NC-11 were considerably greater in inter-flood or post-flood periods than during spring and fall mixing. Connections were too frequent to permit a similar comparison for the S-19 backwater, but the declines in nutrients that usually accompanied low water suggest that availability would be less if disconnection were long-lived or permanent. Nonetheless, it is not evident that inputs from the river substantially increased the primary productivity of these lakes compared to floodplain lakes of similar morphology without river connections. Growing season (May-September) mean CHL in NC-11 (34 µg·L⁻¹) was only slightly greater than the average for three similarly deep scours (29 µg·L⁻¹) isolated from the Missouri River by flood-control levees (Knowlton and Jones 1997). For the S-19 backwater, May-September CHL averaged 52 µg·L⁻¹ compared to 113 µg·L⁻¹ for four shallow, remnant oxbow lakes also protected by levees (Knowlton and Jones 1997). The protected scours and oxbows feature relatively low concentrations of dissolved inorganic nutrients. As reported by Knowlton and Jones (1997) NO_3-N averaged no more than 0.04 mg·L⁻¹ in the seven lakes. But the sites are highly productive despite lack of river inputs.

Most lakes in the Missouri River floodplain, irrespective of connectivity, fall into the upper range of trophic state variables of waterbodies surveyed in Missouri (Knowlton and Jones 1997). In such eutrophic systems, nutrient-limitation of primary production may be too infrequent for the pulse of nutrients from the river to greatly affect overall autochthonous productivity (Reynolds 1992), although the composition of the producer communities might differ greatly in response to the different physical and chemical environments embodied by connected and protected waterbodies (Reynolds 1997).

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