

# Flooding to Restore Connectivity of Regulated, Large-River Wetlands

*Natural and controlled flooding as complementary processes along the lower Missouri River*

David L. Galat, Leigh H. Fredrickson, Dale D. Humburg, Karen J. Bataille, J. Russell Bodie, John Dohrenwend, Greg T. Gelwicks, John E. Havel, Douglas L. Helmers, John B. Hooker, John R. Jones, Matthew F. Knowlton, John Kubisiak, Joyce Mazourek, Amanda C. McColpin, Rochelle B. Renken, and Raymond D. Semlitsch

You can always count on finding the Mississippi just where you left it last year. But the Missouri is a tawny, restless, brawling flood. It cuts corners, runs around at night, fills itself with snags and traveling sandbars, lunches on levees, and swallows islands and small villages for dessert. Its perpetual dissatisfaction with its bed is the greatest peculiarity of the Missouri.... It makes farming as fascinating as gambling. You never know whether you are going to harvest corn or catfish (Fitch 1907, p. 637).

Annual "natural" flooding no longer occurs along the lower one-third of the Missouri River from Sioux City, Iowa, to St. Louis, Missouri, hereafter referred to as the lower Missouri River (Figure 1). Between 1937 and 1955, the middle one-third of the Missouri River was impounded behind six

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## Coupling passive management and natural flooding with intensive management and controlled flooding will ensure the viability of regulated river wetlands

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mainstem reservoirs, and the lower Missouri River was channelized and leveed and its banks stabilized (Hesse 1987, Galat et al. 1996). Reservoir storage and releases are managed for navigation, hydropower generation, and flood control, while downstream

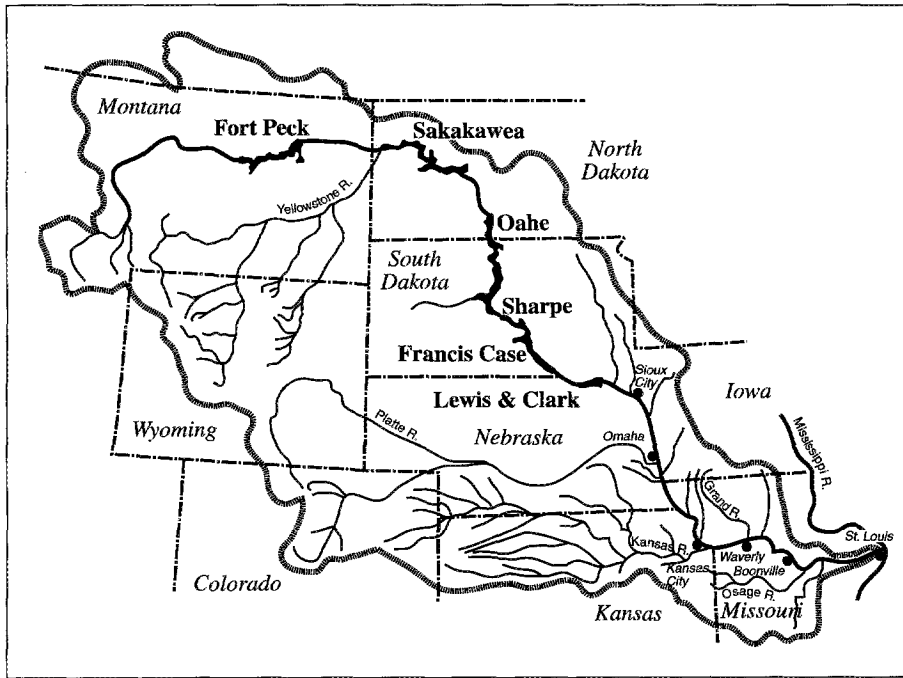
levees largely disconnect the lower Missouri River from its floodplain. Despite upstream flow regulation, contemporary "unmanaged" floods persist along the this part of the Missouri River. Levees in Missouri were overtopped in 5 of the 15 years between 1982 and 1996, reconnecting the river with part or, in the case of the "Great Midwest Flood of 1993," most of its floodplain.

In addition to these extensive but irregular natural floods, managed, or controlled, flooding is actively practiced along the lower Missouri River. Controlled flooding is, however, restricted to small parcels of intensively managed public lands and largely benefits migrant waterbirds. In this article, we provide a historical perspective on the development of controlled flooding and intensive wetland management as natural flooding disappeared along the lower Missouri River. We describe how the flood of '93 and subsequent contemporary, unmanaged flood events have provided an opportunity for restoring riverine wetlands. We also propose a two-pronged strategy for restoring the integrity of regulated, large river-floodplain ecosystems that entails passive management through contemporary unmanaged flooding as a complement to intensive wetland management through controlled flooding.

### The historical setting

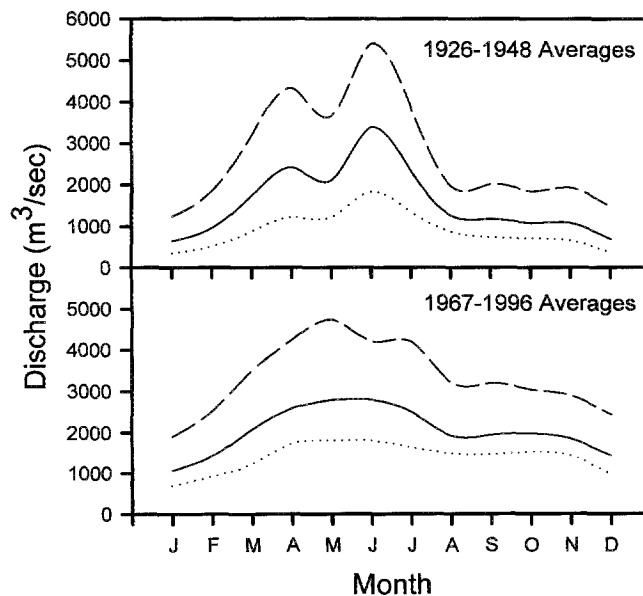
March and June flood pulses on the precontrol lower Missouri River typified the bimodal pattern produced

David L. Galat (e-mail: david\_galat@muccmail.missouri.edu) is assistant unit leader for fisheries of the US Geological Survey, Biological Resources Division, Cooperative Fish and Wildlife Research Unit, and associate professor at the School of Natural Resources, University of Missouri, Columbia, MO 65211. Leigh H. Fredrickson is Rucker Professor of Fisheries and Wildlife and director of the Gaylord Memorial Laboratory, University of Missouri, Puxico, MO 63960. Dale D. Humburg is a wildlife research biologist, Karen J. Bataille is a wildlife staff biologist, and Rochelle B. Renken is a wildlife research biologist at the Missouri Department of Conservation, Fish and Wildlife Research Center, Columbia, MO 65201. John R. Jones is a professor of limnology, Matthew F. Knowlton is a postdoctoral fellow in limnology, Greg T. Gelwicks is a research associate in fisheries, and John B. Hooker, John Kubisiak, Amanda McColpin, and Joyce Mazourek are graduate research assistants in the School of Natural Resources, University of Missouri, Columbia, MO 65211. John Dohrenwend is a consulting geologist, 5755 E. River Road, Tucson, AZ 85750. Douglas L. Helmers is a research biologist who holds joint appointments with the Missouri Department of Conservation and the US Department of Agriculture, Natural Resource Conservation Service, Columbia, MO 65203. Raymond D. Semlitsch is an associate professor of biology and J. Russell Bodie is a graduate research assistant in the Division of Biological Sciences, University of Missouri, Columbia, MO 65211. John E. Havel is an associate professor of biology, Southwest Missouri State University, Springfield, MO 65804.



**Figure 1.** The 3768 km Missouri River is the longest river in the United States. Its basin (thick broken line), including major tributaries and mainstem reservoirs (names in bold type), encompasses  $1.36 \times 10^6$  km<sup>2</sup>, or about one-sixth of the continental United States. This drainage basin contains four physiographic provinces: the Rocky Mountains in the northwest (10.7% of total area, 80 cm annual precipitation, primarily as snow), the Great Plains in the center (70.2% of total area, 45 cm annual precipitation), the Central Lowlands in the northeast (17.2% of total area, 75 cm annual precipitation), and the Interior Highlands in the southeast (1.9% of total area, 105 cm annual precipitation). The lower Missouri River extends downstream from Sioux City, Iowa (km 1178), to near St. Louis, Missouri, where it meets the Mississippi River.

**Figure 2.** Maximum (dashed line), mean (solid line), and minimum (dotted line) monthly average discharge of the Missouri River at Boonville, Missouri (km 317). Before impoundment (1926–1948; upper panel), the hydrograph was characterized by two seasonal flood pulses. The first, or March “rise,” was caused by snowmelt in the Great Plains and breakup of ice in the main channel and tributaries. The second, or June rise, was produced by runoff from Rocky Mountain snowmelt and rainfall in the Great Plains and lower basin. River regulation (1967–1996; lower panel) has altered the natural hydrograph by truncating the flood pulses and increasing summer–autumn flows. The resulting more flattened hydrograph from April through November is designed to facilitate navigation. Data are from USGS (1926–1997).



by basin physiography and seasonal precipitation (Figure 2). Approximately 60% of the river's discharge to the Mississippi originated within the lower Missouri River basin (Hedman and Jorgenson 1990). This region of the precontrol Missouri River was characterized by braided, shifting channels, innumerable snags, and countless migrating sand islands and bars. Channel migrations were a product of the Missouri River's course through highly erodible glacial soils in the arid Great Plains and recurrent flooding in the lower basin. The “Big Muddy's” sediment load to the Mississippi was so great prior to impoundment that it increased average turbidity below the two rivers' confluence sixfold (Platner 1946). Channel width varied between 610 and 1830 m (Slizeski et al. 1982), and river wanderings carved a floodplain averaging 8.1 km wide (Hesse et al. 1989). Annual flooding maintained this system in a state of dynamic equilibrium (NRC 1992) in which individual channels or islands came and went but the overall pattern of braiding, meandering, and island density remained relatively constant.

Before the lower river was constrained by levees, inundation of the floodplain during rising water levels typically began from the downstream end of meander bends, or “bottoms.” River water backed up through low elevations within the bottom, depositing fine sediments due to the river's low velocity (Schmudde 1963). When the upstream end of the bottom was overtopped, much of it was already inundated from this “backflooding.” Active overflow from the upstream end had higher velocities and retained more sediment than backflooding, thus eroding floodplain depressions and rejuvenating important wetland habitats.

Extensive bottomland forests with occasional prairies, oxbow lakes, and shallow, temporary wetlands dominated the ridge and swale topography of this active floodplain. Development of forest successional stages was driven by natural erosion and deposition processes as the free-flowing river meandered (Johnson et al. 1976). Forests on outside bends were eroded, while cottonwood (*Populus deltoides*) and willow (*Salix* spp.)

colonized newly deposited alluvium on the inside of bends. These pioneer forests were maintained on lower terraces adjacent to the channel, where erosion and deposition rates were high (Johnson et al. 1976, Bragg and Tatschl 1977). If channel migration bypassed pioneer forests, they were replaced by a transitional community of box elder (*Acer negundo*), silver maple (*Acer saccharinum*), red mulberry (*Morus rubra*), and American elm (*Ulmus americana*). Succession to a more mature forest community of hackberry (*Celtis occidentalis*), American elm, green ash (*Fraxinus pennsylvanica*), black walnut (*Juglans nigra*), and sycamore (*Platanus occidentalis*) occurred on higher terraces, where erosion rates were low but aggradation from overbank flow persisted (Bragg and Tatschl 1977).

### Disconnecting the river from its floodplain

Public demands to improve navigation, control floods, irrigate the arid Great Plains, and generate hydro-power ultimately led to regulation of the Missouri. In 1912, river channelization and bank stabilization began in earnest, and by 1945 a 2.7 m deep by 91.4 m wide navigation channel was engineered within the main-river channel, extending upstream 1178 km to Sioux City. By 1967, the cascade of mainstem dams operated as a system to support lower river navigation (Ferrell 1993). Flow regulation to maintain sufficient channel depth for April–November navigation depressed the March and June flood pulses while augmenting late summer–autumn low flows (Figure 2). Bankfull discharges occurred in 15 of the 24 years from 1929 through 1952 at Omaha, Nebraska, located at river kilometer 991 (Figure 1) but in only 2 of the 33 years from 1954 through 1986 (Hesse and Mestl 1993). Now, only approximately 10% of the original floodplain is inundated during the average annual flood pulse because levees confine the lower Missouri River to a width of 183–335 m (Hesse et al. 1989).

The impact on biota of the regulation of the lower Missouri River is not well documented, but information on vegetation and commercial

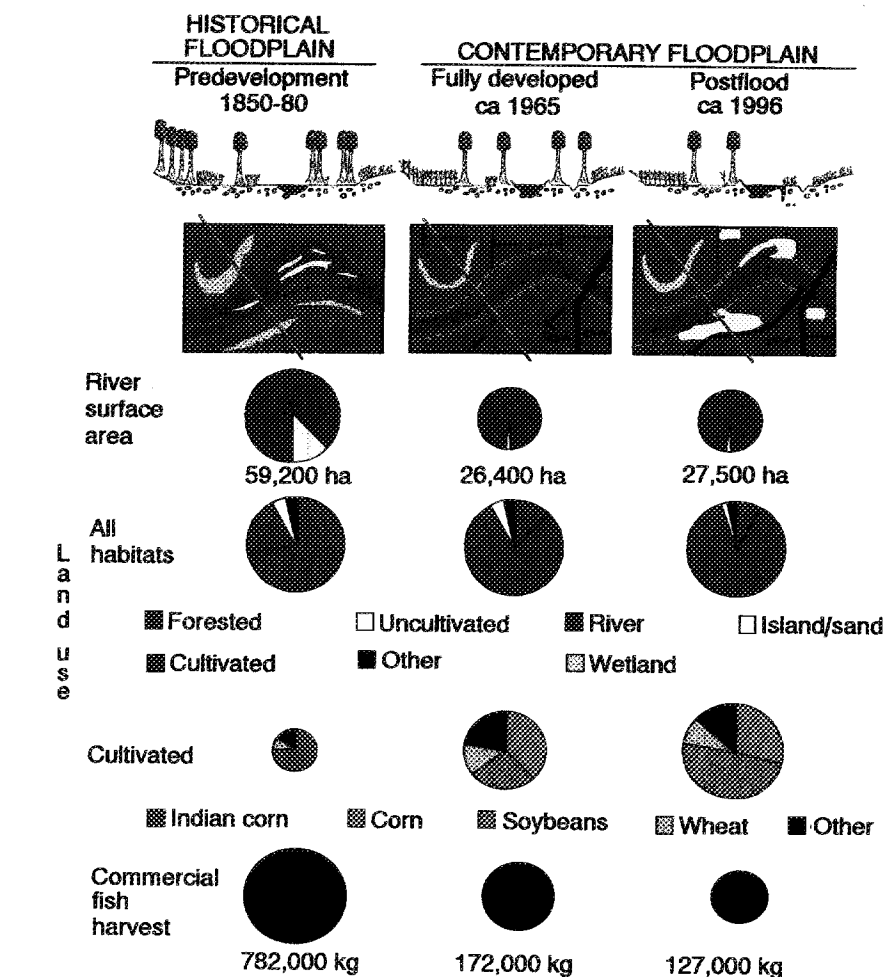


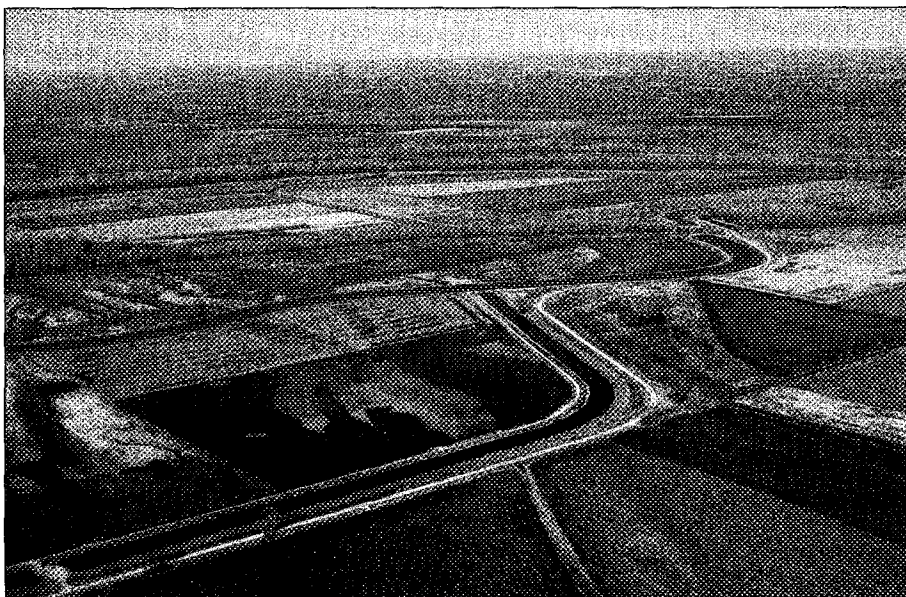
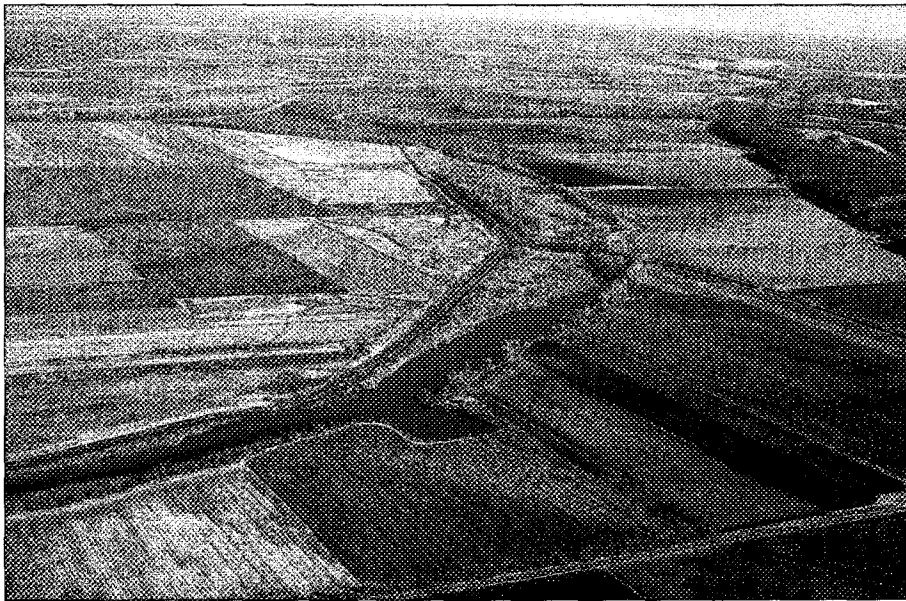
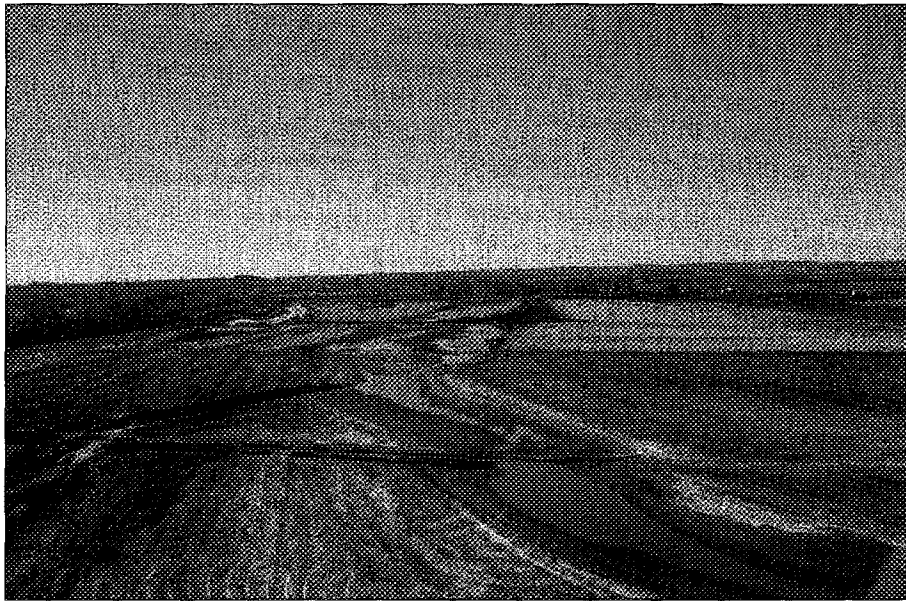
Figure 3. Changes in river channel and island characteristics, floodplain forest, cultivated field size, crops cultivated, and natural wetland distribution within the lower Missouri River floodplain. The schematic cross-section (top row) and plan view (second row) represent typical changes throughout the floodplain. Dashed lines and red lines in plan view indicate lateral levees and locations of cross sections, respectively. Channelization reduced surface area of the Missouri River in Missouri by 50% between 1879 and 1972 and shortened its length by 73 km; over the same period, the number of sand islands and their total area declined by 97% (Funk and Robinson 1974). Riparian forest declined by 63% from the 1870s to 1979, as cultivated land along the lower Missouri River increased by 65% (Bragg and Tatschl 1977). Total annual Missouri River commercial fish catch in Missouri declined by over 80% from the late 1800s to 1996 (Funk and Robinson 1974; J. Robinson, Missouri Department of Conservation, personal communication). Cultivated land uses were adapted from US Census Office (1853), Bay and Nelson (1975), and Bellinghausen and Schlegel (1996).

fish harvests illustrates the magnitude of change (Figure 3). By 1990, 16 species of fish, 7 of plants, 6 of insects, 2 of mussels, 4 of reptiles, 14 of birds, and 3 of mammals within the Missouri River floodplain complex were classified as endangered, threatened, or rare by state or federal agencies (SAST 1994). These declines are a collective response to loss of channel–floodplain habitat and disruption of the periodic river–floodplain connection, and they

prompted the organization American Rivers to list the Missouri River as North America's most endangered river in 1997 (American Rivers 1997).

### Controlled flooding along the lower Missouri River

By 1930, the lower Missouri River and its floodplain were almost totally disconnected. Native habitats were further degraded by drought in the 1930s, and conservationists re-



**Figure 4.** Lower Missouri River floodplain wetlands present before the Great Flood of 1993. (top) Habitat provided by temporary wetlands depends on the timing of inundation and drying as well as on agricultural disturbance. These shallow depressions have often been altered to enhance drainage. (middle) Remnant basins are more permanent wetland habitat, where perennial aquatic and woody vegetation typically prevail. Most remnant basins are at least partially altered by levees, ditching, roads, and agriculture. (bottom) State and federal efforts to enhance wetlands include a limited number of intensively managed areas. Here, controlled flooding using river water pumped into distribution channels and delivered to wetland cells ensures seasonal availability of food and cover, primarily for waterbirds.

sponded in earnest to protect habitat for waterbirds. Concern over declining duck populations was the impetus for legislation funding refuges for nesting and migrating waterfowl. A primitive management infrastructure also began in which controlled flooding was carried out on remnant wetlands (Figure 4). Fish and wildlife conservation efforts were strengthened in many states, supported with funds provided by the Federal Aid in Wildlife Restoration Act. However, these early conservation efforts were insignificant on a landscape scale compared to agricultural development. Only about 2800 ha of floodplain habitat, or approximately 0.7% of the Missouri River floodplain in Missouri, were protected through acquisition before 1965 (Table 1).

The parallel but competing courses of agriculture and navigation, and fish and wildlife conservation, have continued throughout the century. Periods of drought in the 1960s and 1980s were interspersed with destructive floods that further justified efforts to control the river. Losses of wetlands continued; by the 1980s, over 80% of the estimated wetland acreage existing in the 1780s in Iowa, Missouri, and Illinois was lost (Dahl 1990). Initially, the management of acquired wetlands was driven by a perceived need to capture and store water for waterfowl wintering and migrating, rather than by an understanding of waterbird life-history requirements and wetland processes (Johnson and Loucks 1932, Fredrick-

son 1996) or as a way to enhance biodiversity. Controlled flooding and intensive wetland management were a response to programs that nearly eliminated periodic natural flooding along the lower Missouri River (Figure 4). In addition, controlled flooding on state wetlands was often done to accommodate a hunting public that found fewer opportunities for waterfowl hunting on private lands (Wilson 1938). Although hunting has always been an essential source of support for wetland conservation efforts, achieving a balance among wildlife, fishes, and public-use benefits is an ongoing challenge.

Water levels were at first managed to benefit fishes along with waterfowl. But as populations of common carp (*Cyprinus carpio*) exploded in the early 1900s, following their introduction to the United States from Europe, they destroyed wetland plants and increased water turbidity. Consequently, intensive management strategies increasingly excluded fishes, including floodplain-dependent native species (e.g., buffalos, *Ictiobus*; and carpsuckers, *Carpionodes*).

Intensive management of wetlands to emulate natural hydrology began

**Table 1.** Pre- and postflood management strategies for those portions of the approximately 390,000 ha of Missouri River floodplain, Missouri, that are publicly owned or are in federal programs.

Management Strategy	Preflood		Postflood	Total area as of 1997 (ha)
	Area before 1965 (ha)	Area added between 1965 and 1993 (ha)	Area added between 1993 and 1997 (ha)	
Intensive <sup>a</sup>	2800	5900	400	9100
Passive <sup>b</sup>		3500	19,800	23,300
Total	2800	9400	20,200	32,400

<sup>a</sup>Intensive denotes lands in which controlled flooding is practiced through construction of levees, water control structures, and water delivery systems.

<sup>b</sup>Passive denotes lands in which flood protection levees may or may not be present, a water delivery system is not present, and flooding is not controlled.

by adapting the predictable crop production approaches employed by agriculture. Controlled, seasonal flooding became the primary tool to stimulate seed production of moist-soil plants that thrive in mudflats (Fredrickson and Taylor 1982, Fredrickson 1996). These plant communities attracted and held a greater density of wetland wildlife than unmanaged sites, but ironically they reduced the potential of wetlands to produce submergent aquatic plants and provide native fishes with nursery areas. Controlled flooding strategies became more diverse through the 1980s to emulate a variety of

natural flooding regimes with varying benefits and costs to a wider range of plant and animal communities (Table 2).

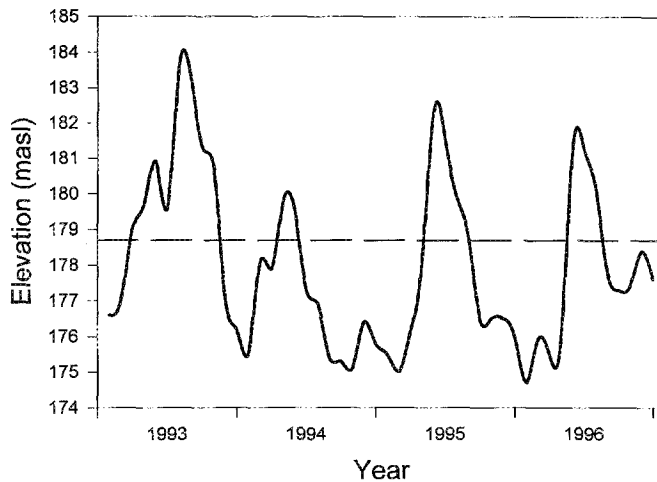
### Contemporary uncontrolled flooding: The Flood of 1993

Storms deluged the upper Midwest for six months preceding the catastrophic flood of 1993; most states in the region received 150–200% of the 1961–1990 January–June average rainfall (Parrett et al. 1993). Peak flood discharges in 1993 equaled or exceeded the 100-year recurrence interval (i.e., an equal or greater dis-

**Table 2.** Benefits and management challenges of various controlled flooding strategies on the lower Missouri River floodplain. Costs for levees, water control structures, and water pumping are high under all strategies.

Strategy	Emulates	Benefits	Challenges
Slow drawdown in early spring–summer	Natural water levels in seasonal floodplain wetlands during growing season	Promotes ideal conditions for germination of wetland forbs, cottonwoods, and willows; provides optimum foraging depths for waterbirds	Drawdown schedule must be varied within and among years; hydrologic connections with river or other wetland units restricts management potential; reduces fish spawning and nursery habitat
Maintain water level during summer	Natural water levels in semi-permanent floodplain wetlands	Provides foraging habitat for waders, spawning/nursery habitat for fishes, and breeding habitat for turtles and amphibians	Stable water levels reduce diversity and productivity and promote plant monocultures; hydrologic connection with groundwater increases pumping costs during summer drought
Slow drawdown during mid- to late summer–early fall	Natural drying of semipermanent wetlands in mid- to late summer	Provides foraging habitat for waders and shorebirds and early fall export of fishes to river; concentrates fishes for aquatic and avian predators	High soil moisture during growing season promotes invasion and development of perennial monocultures; midsummer export of fishes before they realize maximum growth; water quality deteriorates and may cause fish kills
Slow flooding of food-producing plants in late fall	Fall flooding from increasing precipitation	Provides foraging habitat for rails, shorebirds, and early migrant waterfowl, and access and egress for migrating fishes	Dynamic chronology of flooding is necessary to avoid perennial monocultures and low diversity
Slow flooding of food-producing plants from late fall into winter	Fall flooding from increasing precipitation	Provides foraging habitats for waterfowl and overwintering habitats for fishes and turtles	Dynamic chronology of flooding is necessary to avoid perennial monocultures and low diversity



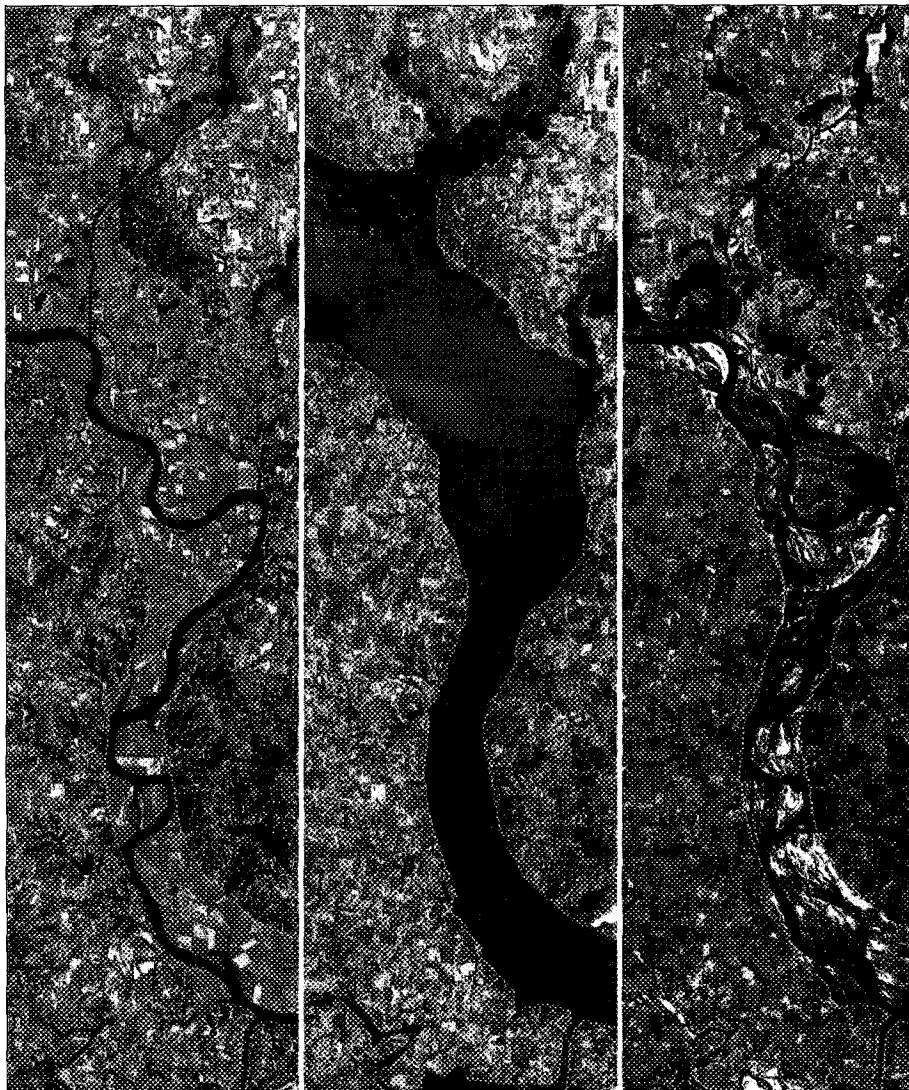


**Figure 5.** The “Great Flood of ’93” was the highest magnitude and longest duration flood on record for the Missouri River at Boonville, Missouri (km 317). Monthly maximum river elevations (meters above sea level, masl) from 1993 to 1996 are shown; the horizontal dashed line indicates the approximate flood stage (178.7 m). A more typical flood pulse was observed in 1994, and catastrophic flooding occurred again in 1995, with the second-highest flood of record for the 1990s, which was followed by a third unusually high flood event in 1996. In these post-1993 floods, some floodplain waterbodies scoured by the flood of 1993 were eroded further (see Figure 7), while others were partially filled with sediment (see Figure 8).

charge is expected, on average, only once in any 100-year period) at many streamflow stations within the region (Parrett et al. 1993). At Boonville, Missouri (km 317, Figure 1), maximum discharge (Parrett et al. 1993) and river stage (Figure 5) ex-

ceeded even the record flood of 1844. More than 500 levees were overtopped or breached along the lower Missouri River (SAST 1994), and for the first time since it had been “tamed” in the mid-twentieth century, this portion of the Missouri River occupied nearly its entire floodplain from Kansas City (km 589, Figure 1) to St. Louis (Figure 6, middle panel).

Levees and flood walls are reported to have prevented more than \$7 billion of damage during this flood; nevertheless, 81% of them were breached, overtopped, or otherwise failed (USGAO 1995), contributing to the \$12–16 billion in total flood damages (IFMRC 1994). Lateral levees (a flood-control levee located parallel to river flow) and cross levees (a flood-control levee perpendicular to river flow) typically failed at their upstream ends (Galat et al. 1997). Unlike natural



**Figure 6.** Color-enhanced Landsat Thematic Mapper satellite images of a portion of the Missouri River in central Missouri (km 389–323). (left) On 24 September 1992, nearly all of the floodplain (light blue line defines boundary) was under cultivation. The channelized mainstem appears as the blue-black ribbon of uniform width traversing north (top) to south (bottom). Three major tributaries and their floodplains also are evident (clockwise from top: Chariton, Little Chariton, and Lamine Rivers). (center) On 1 August 1993, just after the 29 July peak of the “Great Flood of ’93,” the entire floodplain and the lower ends of tributaries were inundated by floodwaters. The light green lines delineating the river channel are narrow strips of remnant riparian forest treetops that once dominated the floodplain. (right) Cropland was devastated in this 26 August 1993 scene on all but the highest floodplain terraces and where floodplain width was greatest (9.0 km wide at top left versus 4.5 km wide at lower right). White to grey areas are thick sand deposits, and blue-black streaks in the floodplain illustrate standing water in flood-scoured depressions and stripped zones. Much of the flood-damaged land in the “S”-shaped river meander in the lower half of the scene was acquired by a Natural Resources Conservation Service easement and then purchased for the US Fish and Wildlife Service’s Big Muddy National Fish and Wildlife Refuge. This land will be passively managed by not rebuilding flood-protection levees. Images prepared by Ron Risty, Hughes STX, USGS–EROS Data Center.

backflooding, heightened hydraulic pressure and concentrated flow through narrow openings at upstream breaks created zones of intense scour downstream (SAST 1994). Approximately 33,000 ha of lower Missouri River floodplain were scoured when levees failed (SCS 1993). This erosion left behind deep (over 10 m), steep-sided "scour holes" (Figure 7) that were skirted on their downstream sides by a stripped zone in which erosion was generally less than 1 m deep (Jacobson and Oberg 1997). Downstream of the stripped zone was a transition zone of sand deposition (Figures 7 and 8). Approximately  $4.3 \times 10^8$  m<sup>3</sup> of sediment, ranging in depth from 15 to over 61 cm, was deposited in the lower Missouri River floodplain (SCS 1993). More than 400 flood scours were created between Kansas City and St. Louis (Galat et al. 1997). We hypothesize that these flood-created scours function as early successional analogs to historical floodplain water bodies in the contemporary lower Missouri River, where few natural wetlands remain.

### 1990s floods: New opportunities and challenges

Record flooding occurred along the lower Missouri River again in 1995 and 1996 (Figures 5 and 7), once more devastating navigation, ground transportation, housing, and agriculture. Yet out of recurrent tragedy, a stimulus to rethink management options in large-river floodplains has arisen. Postflood acquisition of damaged lands from willing sellers provides unique opportunities to restore some semblance of the natural Missouri River–floodplain linkage. State and federal programs were established to purchase or protect lands through easements. These restoration programs have acquired or protected far more of the lower Missouri River floodplain area than all previous enhancement efforts (Table 1). Over 20,000 ha of floodplain habitat has been protected since the floods, and much of this area can potentially be rehabilitated into a complex of braided channels and wetlands through "passive" approaches. Passive management relies largely on nonstructural techniques

(i.e., those that involve little or no channel manipulation, mechanical habitat alteration, or building of structures). Examples include re-creation of the natural river–floodplain geometry by "letting the river do the work" (Hey 1994, Stanford et al. 1996, Poff et al. 1997). Where needed, we recommend implementing low-cost and low-maintenance structural approaches on flood-damaged lower Missouri River public lands (e.g., low-elevation gradient control structures in secondary channels or low-elevation levees set far back from the channel margin) to ensure adequate water depths for navigation in the main channel.

The knowledge required to implement passive management strategies on large rivers is, however, in its infancy. Complex hydrological modifications and land ownership patterns within the floodplain require solutions beyond simply removing levees. Foremost among the challenges is developing ways to maximize ecological benefits based on the size, distribution, juxtaposition, and quality of these new public holdings.

### Characterizing pre- and postflood wetlands

The floods of the 1990s also offered an unprecedented opportunity to evaluate the dynamics and recovery of a regulated, large-river–floodplain ecosystem following catastrophic disturbance. The Missouri River Postflood Evaluation (MRPE) project was organized as a collaboration of academic and agency researchers to investigate the structure, function, and successional patterns among wetland types and their plant and animal communities. Through this effort, MRPE scientists seek to provide managers with strategies to integrate contemporary flooding of passively managed lower Missouri River wetlands with controlled flooding of intensively managed sites.

Postflood ecological research is conducted within a 296 km segment (km 550–254) of the lower Missouri River that contains a representative diversity of pre- and postflood wetlands. The most pervasive variable among study basins is the influence of the river. Sites adjacent to the river are frequently flooded, whereas

sites that are more distant, or that are protected from the river by levees or forest patches, are more influenced by runoff, groundwater, and drying. To assess their postflood responses, wetland basins were grouped into pre- and postflood categories, and by water source, hydrology, and degree of connectivity to the river.

Four types of wetland basins were identified: "temporary," "remnant," "isolated scours," and "connected scours" (Table 3). Wetlands that are saturated or seasonally, temporarily, or intermittently flooded (Cowardin et al. 1979) were classified as temporary. These shallow basins are not connected to the river; they receive water largely from local precipitation runoff and, when near the river, from groundwater as the river rises (Table 3; Figure 4). Most temporary basins were present prior to the 1993 flood and were subject to farming and drainage. We classified as remnant basins (Figure 4) all pre-1993 flood wetlands that may or may not have a river connection and are characterized by semipermanent to permanently flooded water regimes, emergent vegetation, and open water (Cowardin et al. 1979). Remnant and nonfarmed temporary wetlands often exhibit mid- to late-successional plant communities because of their longevity. Disturbance from the 1993 flood reset succession in these basins.

Postflood scours fall into two classes: those connected to the river (either continuously or periodically), and those isolated from it (Table 3; Figures 7 and 8). Connected scours formed when flood flows overtopped lateral levees. Following the 1993 flood, many connected scours were "ringed" on their landward margin with a new lateral levee to reestablish flood protection for adjacent cropland. Isolated scours were formed away from the river margin where a cross levee failed. They will not reconnect to the river unless levees are breached during another exceptional flood.

### Biotic response to floods in the 1990s

Connectivity to the river greatly influenced basin limnology (Knowlton and Jones 1997). Relatively deep, isolated scours exhibited much lower

**Table 3.** Physical characteristics of common pre- and post-1993 flood wetland types along the lower Missouri River.

Feature	Pre-1993 flood		1993 flood scoured	
	Temporary	Remnant	Isolated	Connected
Formation process	Exposed tertiary channels; deposition in drainage basins; late succession remnants	Abandoned channels, oxbows	Breached cross levee	Breached lateral levee
Water source (%)				
River connection	0-10	10-70	0	90-100
Local precipitation/runoff	80-100	10-80	10-20	0-10
Groundwater	0-10	0-20	70-80	0
Tributary	0	0-80	0-10	0
Frequency of surface connection to river within 10 years (%)	0-30	10-60	0-30	100
Turbidity	Moderate; autogenic, wind driven	Moderate; autogenic, wind driven	Low; autogenic, wind driven	High; allogenic, wind and river driven
Estimated longevity (yr)	Over 20	Over 50	Over 30	3-20
Relative hydraulic flushing rate	Very low	Low to moderate	Very low	High
Range of maximum depth over year (m)	1.0	1-5	5-15	1-15
Frequency of annual drying (%)	80-100	10-30	10-20	20-50
Percentage of basin that is in mud flats each year	80-100	25-75	10-50	25-100

and less variable turbidity, organic suspended matter, nutrients, and algal biomass than other wetland types (Table 3). Remnant basins and connected scours had higher and more variable turbidity, nutrients, and algal biomass, but for different reasons. High turbidity, nutrients, and algal blooms in remnant wetlands were often associated with periods of low inflow, shallow water, and resuspension of bottom sediments by wind or biota. By contrast, conditions in connected scours were most influenced by river connectivity. As connectivity changed, morphometry became an important factor controlling limnological conditions. Deeper sites resembled isolated basins, whereas shallow sites resembled remnant wetlands.

Plants and animals immediately exploited reconnection of the lower Missouri River with its floodplain, even though in-channel conditions remained largely unchanged. We briefly summarize patterns observed to date for the major biota being evaluated.

**Vegetation.** Perennial plant communities recovered quickly in remnant ba-

sins after the 1993 flood (Mazourek 1998). These communities were dominated by obligate emergent and floating-leaved species that rely on vegetative reproduction and are adapted to flooding (e.g., river bulrush, *Scirpus fluviatilis*; water smartweed, *Polygonum amphibium*; duckweed, *Lemna minor*). Scoured sites provided new habitats in which invasive species responded to exposed soils but submergent plants failed to colonize (Figures 7 and 8). Along with cottonwoods and willows, pigweed (*Amaranthus rudis*), eclipta (*Eclipta alba*), millet (*Echinochloa* spp.), foxtail (*Setaria* spp.), and nut-sedges (*Cyperus* spp.) were common along scour borders (Mazourek 1998).

The timing of flooding influences plant response because it affects seed dispersal and specific conditions required for germination (Figure 9; Fredrickson and Taylor 1982, Leck 1989). Flooding in 1995 and 1996 removed many cottonwoods and willows that had established on lower terraces following the 1993 event. Repetitive removal of cottonwood/willow stands by floods suggests that succession to an older and more diverse forest mosaic on the contem-

porary floodplain is unlikely unless large areas or entire river bottoms are reopened to channel migration and flooding.

**Zooplankton.** Colonization of new habitats by zooplankton was facilitated by flooding, as evidenced by higher cumulative species richness in connected scours than in isolated scours or remnant wetlands (Table 4). However, numbers within dominant taxa were reduced as richness increased. Total abundance of cladocerans and copepods in periodically connected sites was higher than in continuously connected sites, where both turbidity and hydraulic flushing rates were high. These numbers are consistent with the enhanced algal standing crop and reduced turbidity associated with periodically connected scours following their isolation after the spring flood pulse. A strong positive correlation between species richness and connectivity suggests that recurrent flooding helps to maintain a diverse zooplankton community and provides the force for both reducing dominant taxa and introducing colonists to wetlands created by the 1993 event.



**Table 4.** Cumulative species richness (family richness for benthic invertebrates) and number of unique species present (underlined) among pre- and post-1993 wetland types along the channelized Missouri River in central Missouri, 1994–1996.

Category (N <sup>a</sup> )	Plants	Zooplankton	Aquatic insects	Fishes	Amphibians	Reptiles	Birds
Preflood							
Remnant (4)	35	30	47	ns	11	10	89
	<u>5</u>	<u>3</u>	<u>3</u>		<u>2</u>	<u>2</u>	<u>16</u>
Temporary (4–10)	ns <sup>b</sup>	ns	39	ns (0) <sup>c</sup>	ns	4 <sup>d</sup>	45
			<u>1</u>				<u>1</u>
Postflood							
Connected (5–8)	38	41	51	61	9	7	70
	<u>5</u>	<u>6</u>	<u>5</u>	<u>17</u>		<u>1</u>	<u>4</u>
Isolated (3–5)	23	31	40	26	9	6	69
	<u>3</u>	<u>1</u>			<u>2</u>		<u>1</u>

<sup>a</sup>Number of sites sampled.

<sup>b</sup>Not sampled.

<sup>c</sup>Assumed 0.

<sup>d</sup>Only turtles were sampled.

**Insects.** Aquatic insect dynamics among wetland types appear linked to the direct and indirect influences of hydrology on plant communities. Organic matter input from aquatic and shoreline terrestrial vegetation probably accounts for much of the particulate food base required by insects in remnant wetlands, whereas shoreline terrestrial vegetation dominates in isolated scours. Deep flooding and repetitive, intense scouring reduce habitat and food for insects in connected scours. However, large amounts of fine particulate organic matter enter connected sites with river water. Recolonization of connected basins may come from downstream drift, upstream migration, and aerial movements by winged adults, whereas aerial movement is the primary means for colonization of isolated scours. Midges (Chironomidae) were the most abundant insect family in all wetland types, comprising 90% of the total number of insects taken in emergence traps. Flood pulses in 1995 and 1996 reduced insect numbers, but these rebounded quickly. Richness and density of insect assemblages in recurrently flooded, connected scours were lower than in less frequently flooded sites.

**Fishes.** The response of riverine poikilotherms (fishes and herpetofauna) to flooding depends on the timing and degree of connectivity and water temperature (Figure 9). Many lower Missouri River fishes benefit from floodplain connections that occur when water temperatures are appropriate for spawning (15–25 °C; Gelwicks 1995). Normally, these temperatures occur between late

April and late June, when overbank flow historically provided access to the floodplain for spawning. Timing and duration of postimpoundment floodplain inundation prior to the 1993–1996 floods were seldom optimal for floodplain-spawning fishes (Figure 10).

Access to floodplain wetlands was enhanced by flooding in 1995 and 1996 and enabled us to compare the effects on community structure of recurrent flooding of connected scours with those of no river connectivity in isolated scours. Over twice as many fish species were captured in connected scours as in isolated scours (Table 4). Although adult fish assemblages were similar among scour categories, the composition of larval and juvenile fishes was markedly different between isolated and connected basins. Sunfishes (Centrarchidae) dominated in isolated basins, whereas connected basins had a more diverse riverine assemblage dominated by goldeyes (Hiodontidae), minnows (Cyprinidae), suckers (Catostomidae), and drums (Sciaenidae). We found little evidence of reproduction by riverine species trapped in isolated scours, and we predict that succession in such basins will be toward a pondlike fish community dominated by bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and crappies (*Pomoxis* spp.).

**Herpetofauna.** Turtles, like fishes, have two prevalent life-history strategies in large rivers that take advantage of either river-connected habitats or pondlike habitats, which are less affected by fluvial processes.

Connected scours were dominated by false map turtles (*Graptemys pseudogeographica*) and softshells (*Trionyx* spp.), whereas remnant wetlands were dominated by sliders (*Trachemys scripta*), painted turtles (*Chrysemys picta*), and snapping turtles (*Chelydraserpentina*). Isolated scours and temporary basins had unique turtle assemblages that depended on characteristics of nearby aquatic habitats. Turtle species richness was highest in connected scours, suggesting that these new habitats and their interaction with the river may contribute key processes that are important to overall turtle biodiversity. However, remnant wetlands supported the highest abundance of turtles, indicating that late successional wetlands promote higher population growth rates of a few species. Herpetofauna other than turtles were more diverse in remnant wetlands than in connected or isolated basins. All wetland types had a core of seven anuran species, but salamanders and snakes had more representatives in remnant wetlands.

Contemporary river-flow management may place turtle nests and juveniles occupying habitats adjacent to the river in jeopardy. Turtle embryos can suffer high mortality late in development when their nests are inundated by late-summer water levels that are higher than those that existed before river-flow regulation (Tucker et al. 1997). Also, juvenile turtles overwintering in shallow basins show high mortality because they hibernate in early fall during artificially high river levels; reductions in water levels at the end of the navigation season in late November (Figure

2) may expose juveniles to desiccation and freezing.

**Birds.** Use of wetlands by birds is determined more by food availability and suitable habitat conditions than by river connections, although connectivity influences the type of vegetation and food produced. Remnant basins had the highest avian species richness and the greatest number of unique species, probably because of their large size and greater structural diversity. Avian species richness in newly created scours was initially intermediate between that in remnant and temporary basins but has increased over time as habitat structure developed. Migrating birds, which dominate central Missouri's wetland bird communities, travel in flocks and readily locate required resources because of their mobility. Thus, the availability of preferred habitats dictates the distribution of different taxa. For example, about half of the unique species found on remnant sites (e.g., bitterns) are typically associated with emergent marsh vegetation. By contrast, shorebirds require more open habitats and readily exploited newly formed connected scours, which were devoid of vegetation and provided extensive mudflats. Because water-bird distribution is determined by changing habitat conditions over time (e.g., variable water depth and vegetation structure), site type is less important than the required conditions for foraging, which our studies indicate are dynamic among seasons and years for different wetland types.

### Community dynamics and river–floodplain integrity

These collective responses of plants and animals provide initial insights into the ecological potential of the newly restructured lower Missouri River floodplain. The presence or absence of a surface connection between wetland basins and the river greatly influences species assemblages. Factors such as the frequency, timing, magnitude, and duration of connectivity and floodplain habitat structure determine the magnitude of biotic responses. The occurrence of unique species in each wetland type (Table 4) and their differential

use depending on location, water level, season, and habitat structure indicate that a mosaic of wetland types and successional stages is necessary to restore and maximize floodplain biodiversity.

Controlled, temporary flooding of wetlands protected by levees is a successful management strategy within the disrupted lower Missouri River floodplain to benefit mobile species, especially waterbirds. By contrast, fishes and turtles that require direct access to the floodplain to complete life-cycle events are at a great disadvantage within the fragmented and disconnected lower Missouri River floodplain. The 1990s floods have enhanced habitat for these groups in particular.

Unfortunately, some of the most imperiled Missouri River vertebrates did not benefit directly from the 1990s floods because a wide, braided channel interlaced with sand islands is no longer a feature of the lower Missouri River landscape. The lack of this channel–island complex has contributed to federal listing, or petitioning for listing, of birds that nest on exposed sand islands, such as the least tern (*Sterna antillarum*) and piping plover (*Charadrius melodus*), and obligate large-river fishes, such as the pallid sturgeon (*Scaphirhynchus albus*), sicklefin chub (*Macrhybopsis meeki*), and sturgeon chub (*M. gelida*). Restoring the biological integrity of the lower Missouri River necessitates a natural flow regime (Poff et al. 1997) and segments of unconstrained channels and floodplains to enable high and low flows to create, modify, and connect in- and off-channel habitats.

### Integrating controlled and contemporary flooding

Recurrent floods of the 1990s demonstrated that the lower Missouri river–floodplain complex can be a self-renewing system. Flood-scoured river bottoms are the archetypal “beads” or “patches” of prime riverine wetland habitat envisioned in the “string of beads” restoration concept (Rasmussen 1994, Church et al. 1995). The essence of this concept is that not all of a large river's floodplain needs to be reopened to riverine flooding to revitalize ecosystem

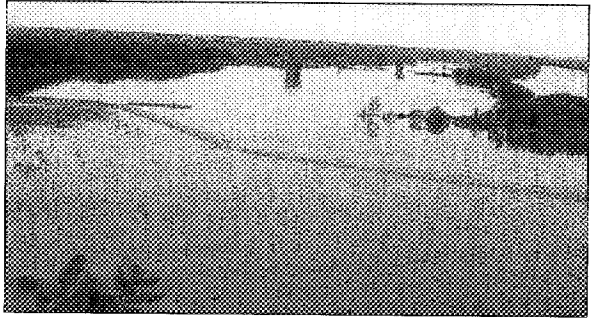
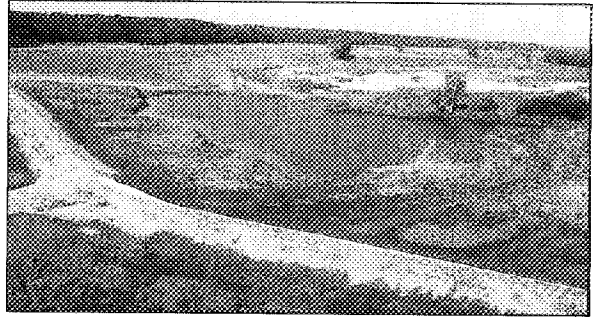
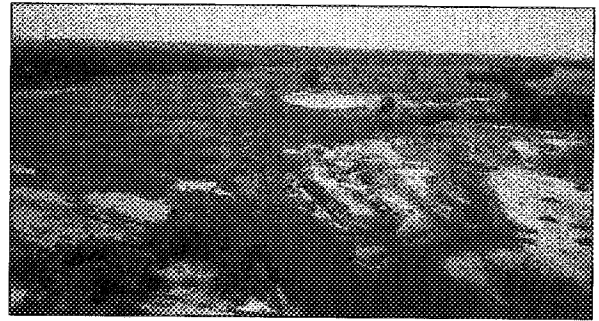
integrity. Rather, rehabilitation of essential components of river–floodplain structure and function can be achieved through the acquisition of a series of key floodplain habitat patches. These “beads” include low-lying lands that are vulnerable to periodic flooding, flood-prone areas adjacent to tributary confluences, remnant oxbows and backwaters, and flood-scoured agricultural lands.

Once acquired, such sites are amenable to restoration and passive maintenance by natural or regulated hydraulic forces. One meander bend in central Missouri, Lisbon Bottom, sustained flood-breached levees 12 times between 1943 and 1986 (SAST 1994) before the flood of 1993 damaged its infrastructure beyond repair (Figure 6). It was eventually purchased by the US Fish and Wildlife Service as part of the Big Muddy National Fish and Wildlife Refuge and will provide an experiment in passive floodplain wetland restoration along the lower Missouri River.

Our early postflood experience has demonstrated the resiliency of floodplain communities, given diverse habitats and recurrent flooding. However, flood scours may be short-lived features within the leveed lower Missouri River landscape because of sedimentation (Figure 8). Wetland dynamics are unbalanced unless erosion through periodic overbank flooding creates new basins as existing ones fill. Continued public acquisition of areas with a history of flood damage and high potential flood risk provides the most cost-effective solution to reducing future flood destruction while maximizing ecological benefits.

Controlled flooding needs to remain a component of natural resource management within the regulated lower Missouri River. We estimate that less than 20% of the river's vast floodplain in Missouri is amenable to restoration and passive management, given the existing infrastructure and importance of agriculture. Consequently, to propose natural flooding on the scale experienced by early explorers would be irresponsible. Controlled flooding and intensive management across large areas of newly acquired floodplain are also impractical. These prac-

**Figure 7.** Time series of a flood-scoured lower Missouri River wetland basin. These basins were created when 1993 floodwaters breached levees designed to protect floodplain agricultural lands and eroded deep "scours" (top; May 1994). The Missouri River channel, bordered by a remnant riparian forest strip, is visible in the upper right corner, and a breached levee is the nearly horizontal line across the upper one-third of the panel (middle; September 1994). The levee was reconstructed within one year of the 1993 flood and can be seen "ringing" the scour landward of the river. Cottonwood and willow growth is evident in undisturbed areas adjacent to the basin. At this time, the scour was isolated from a surface water connection to the river. Severe flooding recurred in 1995 (bottom; June 1995), inundating the entire floodplain; the reconstructed levee is exposed above the floodwaters and was breached to the left of this scene.



tices are expensive and currently have limited benefits for many species. High development and operational costs restrict intensive management to a few high-visibility locations.

Instead, wetland managers need to adopt a broader ecosystem perspective and provide more flexible manipulation of habitats at some intensively managed areas or selected basins within them. This approach will enhance floodplain biodiversity and make a wider variety of natural resource recreation opportunities reliably available to the public. In the string of beads analogy, intensively managed lower Missouri River wetlands can be the "gems" to comple-

ment the many dynamic, but comparatively low-cost, passively managed beads. Knowledge developed from controlled flooding on intensively managed sites can be integrated with emerging knowledge from studies like that of the MRPE project to amend river-floodplain restoration and management. Coupling complementary practices from contemporary and controlled flooding is essential to assure the long-term viability of regulated,

large-river-floodplain systems in the US Midwest.

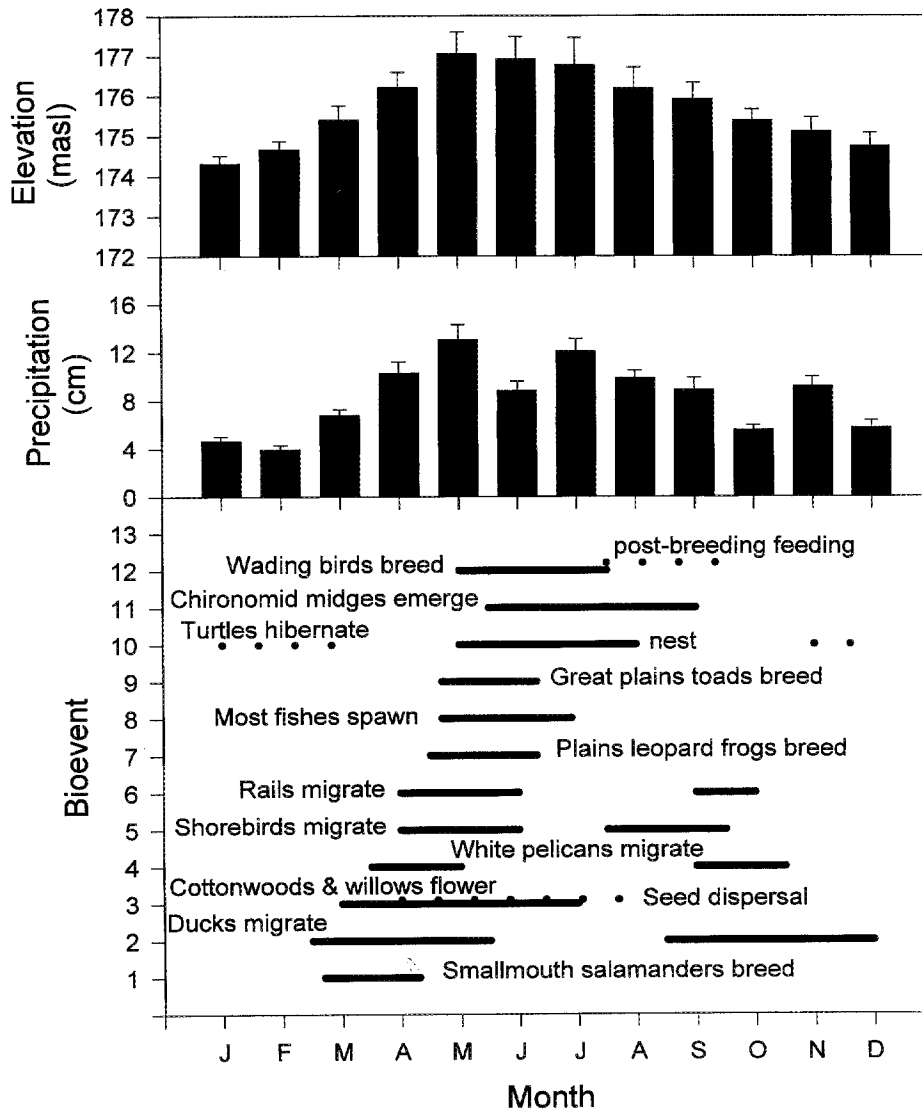
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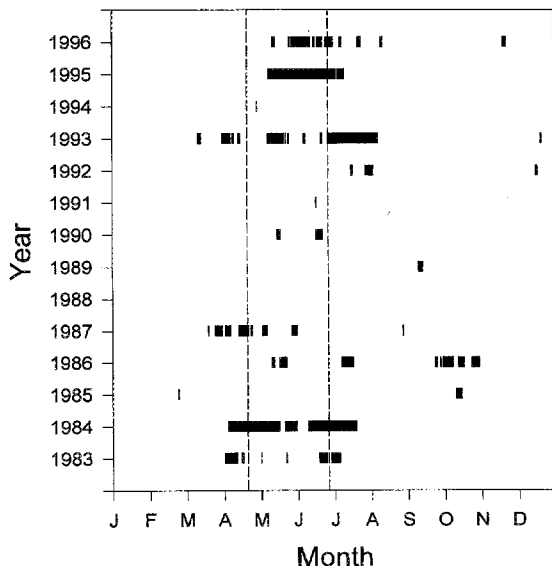


**Figure 8.** Succession of a flood-created wetland scour connected to the Missouri River. Connected scours (top; April 1994) were eroded during the 1993 flood, when levees parallel to the Missouri River were breached. Water and aquatic biota are exchanged between connected scours and river channel continuously or periodically, depending on temporal patterns of site connectivity. Approximately 40% of basin volume had been lost from this site by September 1996 (bottom) due to sedimentation. A reconstructed rock wall, or revetment, with notches for fish passage is visible as a broken line across the opening to the river. Such structures are constructed by the US Army Corps of Engineers to facilitate navigation by reducing bank erosion and stabilizing the channel's position; they may also accelerate sedimentation within the scour.



**Figure 9.** Relation of seasonally important bioevents to river stage and precipitation in lower Missouri River wetlands. (top) 1987–1996 monthly mean water surface elevation  $\pm 1$  SE in Boonville, Missouri. Flooding of wetlands that depend on a surface or groundwater connection to the river generally occurs between March and July in years when river stages are high enough. (middle) 1987–1996 monthly mean precipitation  $\pm 1$  SE from five locations along the river in Missouri. Temporary wetlands dependent on precipitation and runoff also flood during this season. (bottom) Seed dispersal by pioneer forest species, spring waterbird migrations, and amphibian and fish reproduction all depend on this period of flooding. Fall waterfowl migration and turtles seeking deep water for winter hibernation coincide with the November precipitation pulse. Feeding of naive juvenile wading birds (e.g., great blue heron, *Ardea herodias*) occurs as floodplain wetlands dry in late summer, concentrating fish forage.

**Figure 10.** The coupling of water temperature that is within the proper spawning range, and accessibility to submerged floodplain vegetation, is essential for successful recruitment of floodplain-dependent fishes. The majority of lower Missouri



River fishes spawn between 15 and 25 °C (represented by dates within the vertical dashed lines). Horizontal bars indicate time intervals each year when river-water elevation exceeded flood stage at Waverly, Missouri (km 472; Figure 1), which allowed fishes access to the floodplain. Flood stage was exceeded at least once per year for 14 of the 15 years ending in 1996. However, inundation of the floodplain for ten or more consecutive days during the optimal spawning temperature range occurred in only four years (1984, 1993, 1995, and 1996).

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