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Spatiotemporal Patterns and Changes in Missouri River Fishes

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Abstract.—The longest river in North America, the Missouri, trends southeast from Montana across the mid continent of the United States, 3,768 km to its confluence with the Mississippi River near St. Louis, Missouri. Frequent flooding, a shifting, braided channel, and high turbidity characterized the precontrol "Big Muddy." Major alterations occurred over the past century primarily for flood protection, navigation, irrigation, and power production. Today, the middle one-third of its length is impounded into the largest volume reservoir complex in the United States and the lower one-third is channelized, leveed, and its banks stabilized.

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Spatial and temporal patterns of Missouri River fishes are reviewed for the main channel, floodplain, and major reservoirs. Twenty-five families, containing 136 species, compose its ichthyofauna. Seven families represent 76% of total species richness, with Cyprinidae (47 species), Catostomidae (13), Centrarchidae (12), and Salmonidae (10), the five most specious. Native fishes compose 79% of the river's ichthyofauna with representatives of four archaic families extant: Acipenseridae, Polyodontidae, Lepisosteidae, and Hiodontidae. Fifty-four percent of Missouri River fishes are classified as "big river" species, residing primarily in the main channel, and 93% of these are fluvial dependent or fluvial specialists. Significant floodplain use occurs for 60 species. Many of its big river fishes are well adapted for life in turbid, swift waters with unstable sand-silt bottoms.

Populations of 17 species are increasing and 53% of these are introduced, primarily salmonids, forage fishes, and Asian carps. Ninety-six percent of the 24 species whose populations are decreasing are native. Fishes listed as globally critically imperiled and federally endangered (G1) or globally vulnerable (G3) include pallid sturgeon *Scaphirhynchus albus* (G1), lake sturgeon *Acipenser fulvescens*, Alabama shad *Alosa alabamae*, sturgeon chub *Macrhybopsis gelida*, and sicklefin chub *M. meeki* (G3). Eleven fishes are listed by two of more of the seven main-stem states as imperiled; all are big river species.

Richness increases going downriver from 64 species in Montana to 110 species in Missouri with 36% of widely distributed taxa absent below one or more reservoir. Long-term fish collections from several states show declines in sauger *Sander canadensis* throughout the river and decreases in the lower river of several big river fishes (e.g., sturgeons, chubs, *Hybognathus* spp.). Spatiotemporal changes in Missouri River fishes reflect interactions between natural (climate, physiography, hydrology, and zoogeography) and anthropogenic (impoundment, geomorphic, flow, and temperature alterations, and introduced species) factors. Recurrent droughts and floods and persistent stakeholder conflicts over beneficial uses have recently directed national attention to Missouri River issues. Acquisition of floodplain lands and channel and floodplain rehabilitation programs are underway to improve habitat in the lower river. Unfortunately, many are site specific and few have included explicit ecological objectives and performance evaluations. Several proposals for flow normalization are being considered, but remain controversial.

Introduction

Great rivers, defined as having basins greater than 3,200 km^2 (Simon and Emery 1995), are the most profound flowing-water features of the continental landscape. Human societies developed and flourished along the banks of many of the world's great rivers, sustained by their plentiful resources and fertile floodplains. Rivers also provided efficient highways for transport of people and their products, facilitating exchange among diverse cultures. Expansion of human populations and alterations of their environments have affected aquatic resources of many of the world's great rivers, particularly in the north-temperate zone (Dynesius and Nilsson 1994). The Missouri River exemplifies such a system, and its fishes serve as indicators to assess natural and anthropogenic change.

Ideal indicators that provide a defensible ecological assessment for rivers should meet several guidelines: (1) characterize current river health (status), (2) track changes in river health at multiple spatial and temporal scales (trends), (3) identify and respond to major stressors and rehabilitation programs, and (4) interact across ecological, economic, and social realms. Additionally, they should show conceptual relevance, be logistically feasible to implement, differentiate natural from anthropogenic variability, and produce results that are clearly understood and accepted by scientists, policy makers, and the public (Jackson et al. 2000). Fishes meet all of these requirements (Fausch et al. 1990; Simon and Lyons 1995). Fish and fishing are socially relevant. They provide valuable goods and services to the public, and fish have a long tradition as bellwethers of water quality (Bayley and Li 1996; Schmutz et al. 2000). Fishes are particularly useful ecological indicators for large rivers because their various guilds integrate a wide range of riverine conditions, ranging from properties of bed sediments for egg development at the micro-scale to longitudinal integrity for spawning migrations at the landscape scale (Copp 1989; Scheimer 2000). As migratory organisms, fishes are ideal indicators of longitudinal and lateral connectivity across the riverscape (Jungwirth 1998; Fausch et al. 2002). At the habitat scale, fishes use clearly defined, life stage specific habitats. Their longevity helps fishes "register" environmental alterations across time. Fishes are often top predators in rivers and thereby subsume trophic conditions across the food chain (Schmutz et al. 2000). Additionally, cost-effective and standardized collection methods exist to characterize fishes at multiple spatiotemporal levels (Murphy and Willis 1996).

Our goal is to employ fishes as indicators of spatiotemporal patterns and change for the Missouri River. We first provide a brief background of the system's physiography and review its approximately 200 years of Euro-American occupation. Zoogeography of the basin's fishes is then summarized along with an abbreviated history of fish introductions.

Our primary objectives are to review

1. composition, distribution, relative abundance, general habitat use, conservation status, and relative population status of fishes in the Mis souri River channel, its floodplain, and mainstem reservoirs;
2. spatial and temporal patterns in relation to natural (i.e., zoogeographic) and anthropogenic (e.g., impoundment, channelization, and flow regulation) factors; and
3. activities underway to conserve and restore the Missouri River and its native fishes.

Study Area

The 3,768-km-long Missouri River is the longest river in North America from its named origin at the confluence of the Madison, Jefferson, and Gallatin rivers near Three Forks, Montana, to its confluence with the Mississippi River, near St. Louis, Missouri. Its basin is second in size (1,371,017 km^2) in the United States only to the Mississippi River. Elevation of the named river extends over 1,000 m from about 1,226 m above sea level (asl) at Three Forks, Montana, to about 122 m asl at the mouth, and its main channel covers nearly 10° latitude (48.17°N to 38.53°N); (Galat et al., in press). The southern limit of continental glaciations largely defines the Missouri's modern course. Its channel flows from northwest to southeast across the mid-continent, bisecting or contiguous to seven states (Figure 1).

Metcalf (1966) recognized three major preglacial (Pliocene) components in the evolution of the contemporary Missouri River basin: the southward-flowing Teays-Mississippi, an Arctic ("Hudson Bay") component to the northwest, and a preglacial plains stream system that flowed southward, but independent of the preglacial Mississippi. Metcalf (1966), Pflieger (1971), and Cross et al. (1986) summarize Missouri River drainage history and zoogeography of its fishes in greater detail.

The Missouri River begins in the Northern Rocky Mountain physiographic province, flows through highly erodible soils of the glaciated Great Plains and Central Lowlands provinces and then through the unglaciated, limestone-dolomite Ozark Plateaus. Its main channel traverses 6 of 13 terrestrial ecoregions within the basin, beginning in the North Central Rockies forests, passing through four grassland ecoregions, and then the Central Forest/Grassland Transition Zone (Ricketts et al. 1999). Convergence of four major air masses and its mid-continent location produce extreme seasonal and daily fluctuations in climate (Galat et al., in press). About 70% of the river's basin lies within the semi-arid Great Plains. Thus, the Missouri River is largely a dryland river with about one-half of its basin receiving less than 41 cm/year of precipitation, coming largely as rainfall during the growing season. Precipitation in the remainder of the basin averages

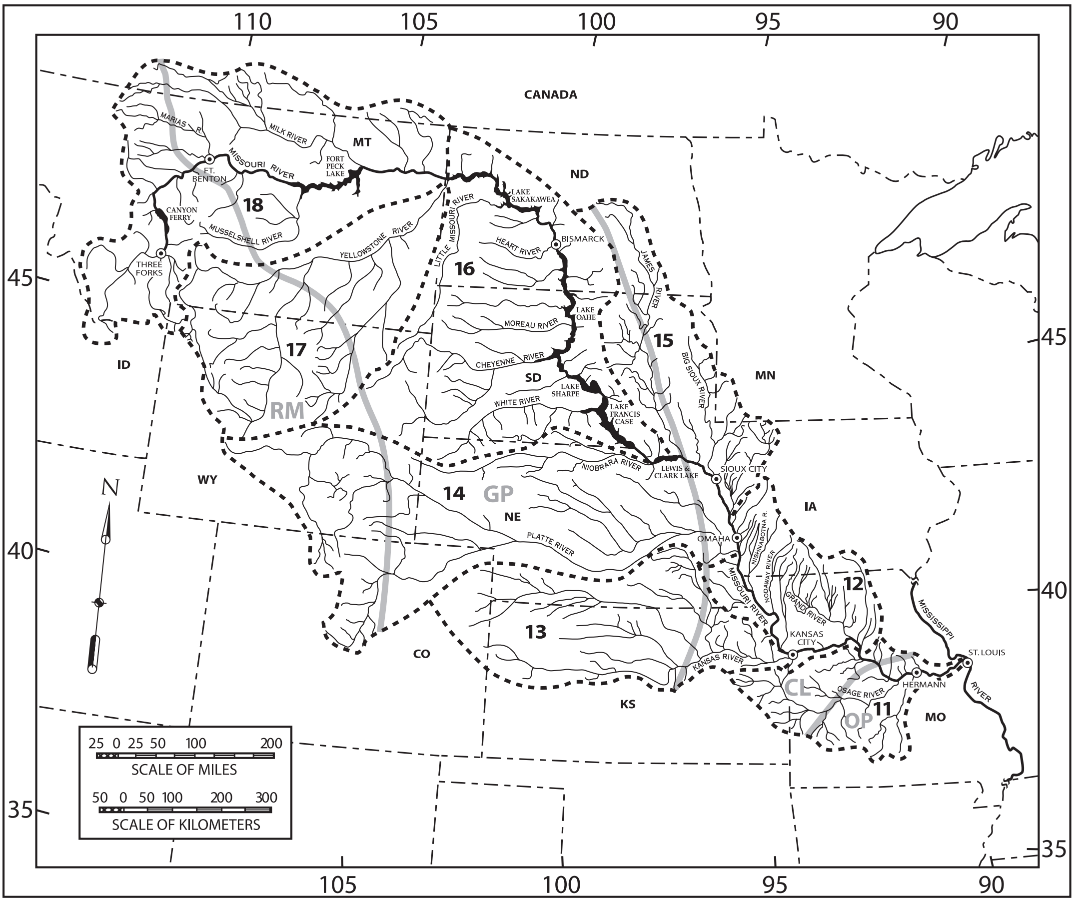

Figure 1.—Map of Missouri River basin showing physiographic provinces and inclusive drainage units (adapted from Cross et al. 1986), selected major tributaries, main-stem dams and reservoirs, and locations mentioned in text. Physiographic provinces: RM = Rocky Mountains, GP = Great Plains, CL = Central Lowlands, OP = Ozark Plateaus. Drainage units: 18, upper Missouri; 17, Yellowstone; 16, Little Missouri–White; 15, James-Sioux; 14, Niobrara-Platte (15 and 14 combined herein); 13, Kansas; 12, Nishnabotna-Chariton; 11, lower Missouri. Drainage units 17 and 13 were not analyzed as neither contains the Missouri River main channel.

more than 80 cm/year in the Rocky Mountains (~11% of basin total area), ranges from about 40–102 cm/year in the Central lowlands (~17%), and exceeds 100 cm/year in the Ozark plateaus (~2%). Land uses in the floodplain are primarily cropland (37%) or grassland (30%), with about 9% of the area developed (Revenga et al. 1998).

Three freshwater ecoregions (Upper Missouri, Middle Missouri, and Central Prairie; Abell et al. 2000) and 47 tributaries with drainage basins greater than 1,000 km^2 contribute to the Missouri River. Cross et al. (1986) divided the basin into eight drainage units based on tributary groupings (Figure 1), and we organized our treatment of fishes around a subset of these, as well as freshwater ecoregions and physiographic provinces. Largest tributaries to the Missouri River include the Platte, Yellowstone, and Kansas rivers, which are ranked from 13th to 15th in descending order, respectively, of drainage area in the United States (van der Leeden 1990). Selected tributaries are described in Galat et al. (in press).

Spatiotemporal patterns in runoff and hydrology reflect climatic and physiographic diversity of the basin (Galat et al., in press). The historical annual hydrograph was bimodal with the first peak or "spring rise" in March–April, corresponding to ice-out in the mid and upper basins and prairie snowmelt. The second, larger flow pulse or "June rise" occurred as a result of Rocky Mountain snowmelt and precipitation in the lower basin. Flows declined in July and were generally low until the following spring rise. Runoff to the Missouri River originates primarily at the upper and lower ends of the river in the Rocky Mountains (8.6 cm/year from basin above Fort Benton, Montana), and the Central lowlands and Ozark plateaus (29.9 cm/year between Kansas City and Hermann, Missouri; Galat et al., in press). Over 1,200 reservoirs have been constructed within the basin, with the six U.S. Army Corps of Engineers (Corps) main-stem reservoirs being the most significant (Table 1). These six reservoirs account for 69% of the basin's total water storage and collectively are the largest volume water storage project in the United States (~90.5 km^3). Their most significant effect on downriver seasonal flow patterns has been to dampen flood pulses, create artificially high summer–autumn flows (Galat and Lipkin 2000), and reduce flow variability (Pegg et al. 2003). Galat and Lipkin (2000) detail pre- and post-impoundment magnitude, timing, frequency, duration, and rate of change of the Missouri River hydrograph at multiple locations. Pegg and Pierce (2002a) classified the river into six hydrologically

Table 1.—Features of Missouri River main-stem reservoirs. Canyon Ferry is a Bureau of Reclamation reservoir, whereas the remaining reservoirs were constructed and are maintained by the Corps of Engineers. Location of dam is kilometers upriver from Missouri River mouth. Sources: U.S. Army Corps of Engineers (1994a), Galat and Frazier (1996).

	Reservoir						
Feature	Canyon Ferry	Fort Peck	Sakakawea	Oahe	Sharpe	Francis Case	Lewis & Clark
Name of dam	Canyon Ferry	Fort Peck	Garrison	Oahe	Big Bend	Fort Randall	Gavins Point
Location of dam (km)	3,688	2,850	2,236	1,725	1,589	1,416	1,305
Year dam closed	1953	1937	1953	1958	1963	1952	1955
Total drainage area (10^3 km^2)	41.2	148.9	469.8	630.6	645.8	682.4	723.9
Water surface elevation (m above sea level)	1,157	680.9	560.2	490.1	432.8	411.5	366.1
Surface area (km^2)	142.5	858.0	1,242	1,263	230.7	319.7	101.2
Length (km)	40	216	286	372	129	172	40
Mean width (km)	4.0	3.2	5.3	3.9	1.9	2.1	3.2
Shoreline length[a] (km)	122.3	2,446	2,156	3,620	321.8	868.9	144.8
Gross volume (km^3)	2.5	23.1	29.4	28.5	2.3	6.8	0.61
Mean depth (m)	17.7	24.1	18.9	19.2	9.4	15.2	4.9
Maximum depth (m)	50.0	65.8	53.9	61.9	22.9	41.5	17.1
~Mean annual water level change (m)	3.7	3.0	3.0	1.5	0.6	10.7	1.2
Mean annual summer surface water temperature (°C)		19.2	18.9	22.2		24.4	24.2
Exchange rate (years)	0.38	2.8	1.4	1.6	0.12	0.50	0.04

[a] At top of carryover multiple use level; base of flood control level.

distinct units based on flow characteristics, and Pegg et al. (2003) statistically showed that flows were most highly altered in the middle portion of the river. Galat et al. (in press) provide more detail on the river's physiography, climate, land use, geomorphology, hydrology, chemistry, and ecology.

The predevelopment Missouri River exhibited a braided, sandbar, and island filled channel that had continually shifting banks due to sediment erosion and deposition. Overbank floods were common, turbidity was high, and enormous quantities of sediment were transported to the Mississippi River. Lewis and Clark (1804–1806) were the first to formally document the Missouri River's ichthyofauna, describing specimens that later would be identified as goldeye *Hiodon alosoides*, blue catfish *Ictalurus furcatus*, channel catfish *I. punctatus*, interior cutthroat trout *Oncorhynchus clarkii lewis*, sauger *Sander canadensis*, and possibly golden shiner *Notemigonus crysoleucas* (Moring 1996). They remarked on a catch of blue catfish, "Two of our men last night caught nine catfish that would together weigh three hundred pounds" (Cutright 1969). The river became the first great highway for settlement and development of the West once steamboat travel began in 1819 (Thorson 1994). Societal interests to improve navigation, irrigate the arid Great Plains, control devastating floods, and generate hydropower began in earnest in the early 1900s and are well described elsewhere (Ferrell 1993, 1996;Thorson 1994; Schneiders 1999).

The contemporary Missouri River can be divided into three riverine zones plus an additional reservoir zone based on anthropogenic influences. The *upper unchannelized zone* extends 739 km from Three Forks to the first of the six major main-stem impoundments, Fort Peck Lake, Montana. Portions of this section are the most free-flowing remnants of the Missouri River and retain many of its historical features. Several small Bureau of Reclamation impoundments occur here (Canyon Ferry being the largest, Table 1), but their impact is small relative to the Corps reservoirs (Scott et al. 1997). The middle section is about 1,850 km long, and we recognize two zones: the six Corps reservoirs (*reservoir zone*) and an "*inter-reservoir*" riverine zone between the impoundments. We will include in the inter-reservoir zone a short, highly flow-altered reach extending 127 km below the lowermost impoundment, Lewis and Clark Lake, to Sioux City, Iowa, where channelization begins (Figure 1). Some authors (e.g., Hesse et al. 1993) consider this flow-regulated but unchannelized reach to be a unique zone and refer to it as the *lower unchannelized zone* or segment. The remaining 1,178 km of river below Sioux City to the Mississippi is referred to as the *channelized zone*. Here the main stem is altered by flow regulation from upriver main-stem reservoirs, numerous sub-basin reservoirs (e.g., on the Platte and Kansas rivers; Galat et al., in press), channelization, bank stabilization, and floodplain levees.

Most of the Missouri River is a warmwater river with average July–October water temperatures increasing from about 21.5°C to 27°C between the upper unchannelized and channelized zones. However, water temperatures in the river below the stratifying, large volume reservoirs (Table 1) are depressed due to hypolimnetic water releases (Galat et al. 2001).

Collectively, basin and channel-floodplain development have transformed nearly one-third of the Missouri River's lotic habitat into lentic reservoirs. Longitudinal and lateral connectivity has been fragmented, sediment transport and turbidity below reservoirs drastically reduced, and channel geomorphology altered through bed and bank degradation. Sediment aggradation occurs in reservoirs at the mouths of inflowing tributaries (e.g., Niobrara River into Lewis and Clark Lake) and produces shallow deltas at the upstream ends of reservoirs. The complex of delta sandbars and braided, shallow channels encourages riparian flooding and fosters growth of emergent and submergent vegetation. These delta wetland complexes attract waterfowl and influence fish assemblage structure. Summer water temperatures are depressed below large reservoirs, and contaminants, nutrients, and nonnative biota have been introduced. Much of the channelized river's in-channel habitat complexity and floodplain native vegetation are gone and inter-reservoir and channelized river flow patterns are highly altered. These changes in the river's structure, function, and processes and their effects on river health are further described elsewhere (Funk and Robinson 1974; Hesse et al. 1989; Schmulbach et al. 1992; Galat et al. 2001;

National Research Council 2002; Galat et al., in press).

Methods

A list of fishes documented in the Missouri River basin was revised and expanded from Cross et al. (1986). We abbreviated the Cross et al. (1986) list by including only those species reported from the main-stem Missouri River channel, floodplain, and reservoirs (Figure 1), excluding the remainder of the drainage basin (i.e., tributaries and non-main-stem reservoirs). Occurrence, distribution, and relative abundance were summarized spatially for each species within three geographic strata: drainage unit, freshwater ecoregion, and physiographic province. Boundaries and spatial cross-referencing for these geographic categories are summarized in Table 2. Common names of fishes will be used hereafter; scientific names are listed in Appendix A.

Species were grouped into five "sections" of the main stem that were contained within, or contiguous to, the eight Missouri River subbasin drainage units identified by Cross et al. (1986), (Figure 1, units 11–18). We follow the standard convention for the Missouri River of proceeding from upstream to downstream when referencing locations along the river (e.g., drainage units, river kilometer). For example, the White–Little Missouri drainage unit listed in Cross et al. (1986) was changed to Little Missouri–White. Yellowstone (17) and Kansas (13) drainage units were excluded, as they do not contain any of the main-stem Missouri River. We also combined the Sioux–James (15) and Platte Niobrara (14) drainage units from Cross et al. (1986) into a single unit: James–Sioux–Niobrara–Platte (15 + 14), since they overlap and are contiguous to the main channel. The five drainage units were also grouped into approximate freshwater ecoregions (Abell et al. 2000; Table 2). The status of each species within a drainage unit/ecoregion section of the river was classified as N = native; I = introduced, but could be native to another drainage unit/ecoregion section; U = uncertain if native or introduced; D = diadromous, migrates to or from ocean (not reservoir).

Relative abundance for each species included in the Missouri River for the four physiographic provinces through which it flows was summarized as P = prevalent or abundant; M = marginal or uncommon; S = sporadic or rare; X = present, but relative abundance unknown; E = extinct or an introduced species that is no longer stocked or collected. Species for which there is questionable validity of its presence or identification from the Missouri River at a single location were excluded (e.g., Sacramento perch *Archoplites interruptus*). Occurrence, distribution, and relative abundance data were updated from Cross et al. (1986) using more recent publications (e.g., Hesse et al. 1989, 1993; Galat and Frazier 1996; Patrick 1998; National Research Council 2002; Berry et al. 2004; Berry and Young, 2004); books about fishes from Missouri River states (e.g., Bailey and Allum 1962; Holton and Johnson 1996; Pflieger 1997); agency reports (e.g., Riis et al. 1988; Johnson et al. 1992; U.S. Army Corps of Engineers 1994a, 1994b, 2001; Power and Ryckman 1998; Hendrickson and Lee 2000; U.S. Fish and Wildlife Service 2001); data files of Montana Fish, Wildlife, and Parks; North Dakota Game and Fish Department; South Dakota Department of Game, Fish and Parks; Nebraska Game and Parks Commission; Rivers Corporation (Hesse 2001); Missouri Department of Conservation; and personal knowledge of authors and reviewers (see Acknowledgments). We deleted fishes in the Cross et al. (1986) species list that have not been reported from the main-stem Missouri River by any of the above sources since 1970 and are presumed extinct. Other species were deleted from various drainage units (e.g., striped bass *Morone saxatilis* from drainage unit between James and Platte rivers) for the same reasons. Species deleted were historically rare in the Missouri River, introduced, or reported only from tributaries.

Fishes were assigned to one of three general habitat-use guilds developed by Kinsolving and Bain (1993) to assess their relative dependence on riverine or floodplain habitats (see also Travnichek et al. 1995 and Galat and Zweimüller 2001). *Fluvial specialists* are fishes that are almost always found only in streams and rivers or are described as using flowing water habitats throughout life. These species may be occasionally found in a reservoir or lake, but most information on them pertains to lotic systems. *Fluvial dependent* fishes are found in a variety of habitats, but require flowing water at some point in their life

Table 2.—Cross references among physiographic provinces (Cross et al. 1986), freshwater ecoregions (Abell et al. 2000, upper Missouri, *middle Missouri*, Central Prairie), and drainage units (Cross et al. 1986) for main-stem Missouri River. Boundaries between physiographic provinces are approximate locations along main stem. Tributaries and main-stem reservoirs (**bold**) are listed in order from upriver to downriver. Drainage units (unit number 18–11 from Cross et al. 1986) apply to antecedent tributaries from unit number in parentheses. Distances (km) begin with 0 at confluence with Mississippi River.

Physiographic province	Approximate boundaries	Inclusive tributary confluences and freshwater ecoregion (normal, *italic* or underlined font)	Drainage unit
Northern Rocky Mountains km 3,734–3,386	Three Forks, MT, to between Ft. Benton and Great Falls, MT (Belt Creek is most downriver tributary in province)	Madison, Jefferson, Gallatin, **Canyon Ferry**, Sun, Smith	Upper Missouri (18)
Great Plains km 3,386–1,283	between Great Falls, MT, and Ft. Benton, MT, (below Belt Ck., includes Highwood Ck.)to and including confluence of James R., SD	Teton, Marias, Judith, Musselshell, **Ft. Peck**, Milk (18), Yellowstone (17) L. Missouri, **Sakakawea**, Knife, Heart, Cannonball, Grand, Moreau, Cheyenne, **Oahe**, Bad, **Sharpe**, White **Francis Case**, (16) *Niobrara, **Lewis & Clark*** (14), *James*	Upper Missouri (18) km 3,734-–2,545 Little Missouri–White (16), km 2,545–1,357
Central Lowland km 1,283–274	from below James R., SD, to and including Chariton R., MO, (~Perche Ck, MO)	*Vermillion*, *B. Sioux*, *Floyd*, *L. Sioux*, (15)*Platte*, (14) *Nishnobotna*, *L. Nemaha*, *Nodaway*, *Platte (MO)* (12), *Kansas (*13),Grand, Chariton (12), Lamine	James–Sioux (15)-Niobrara–Platte (14) km 1,357–957 Nishnabotna–Chariton (12) km 957–384
Ozark Plateaus km 274–0	from below Perche Ck., MO, to Mississippi R. confluence.	Osage, Gasconade (11)	Lower Missouri (11), km 384–0

cycle. These species may have significant lake, reservoir, or estuary populations, but use tributary streams or rivers for some life history trait, typically reproduction. *Macrohabitat generalists* include species that are commonly found in lakes, reservoirs, floodplain water bodies, and flowing waters, but are capable of completing their life cycle in lentic systems. Species were placed into habitat-use guilds based on literature (e.g., Pflieger 1971, 1997; Lee et al. 1980; Theiling et al. 2000; National Research Council 2002; Berry et al. 2004) and the authors' experience.

Habitat distribution of Missouri River fishes was further summarized by placing each species into one or more of five categories: main channel, main channel margin, floodplain, reservoir, and waif. The three channel-use categories include *main channel* = C, including "big river" fishes (defined in Pflieger 1971; Cross et al. 1986; Simon and Emery 1995), "sandbar," and "main channel" fishes (National Research Council 2002); *channel margin* (edge, border) = B, found in main channel, but generally along the edge out of current; and *waif* = W, not a large river fish, although records exist, the species is seldom collected from the main stem and specimens are likely washed out of a tributary or reservoir. *Floodplain* fishes are species found in off-channel habitats, including marshes, backwaters, backups, oxbows, scours, and so forth. Velocity is low or absent in floodplain habitats, and the waterbody may infrequently connect to the main channel. *Reservoir* fishes include those species reported within a reservoir and tailwater areas below dams.

Conservation status of fishes is reported as Global Heritage Status (NatureServe 2003) and listings under the U.S. Endangered Species Act (ESA, as reported in NatureServe 2003). Global Heritage ranks we include are critically imperiled (G1), imperiled (G2), vulnerable (G3), apparently secure (G4), secure (G5), or numeric range rank (G#G#), where uncertainty exists about the exact status of a species (e.g., G2G3). Similar state rankings (S) are also summarized. Species are listed under the ESA as endangered, threatened, or a candidate for listing.

We report relative temporal trends in population status over the main-stem Missouri River as increasing (+), stable (0), or decreasing (–). Species too uncommon in catches to rank are identified as U, and blanks indicate a species population status was unknown. Population information does not exist for many fishes, particularly small species (e.g., minnows, chubs, shiners) and species difficult to identify (e.g., *Hybognathus* spp.). Population trends are also difficult to assess across the entire Missouri River since a species may be increasing in one section and decreasing in another (see subsequent section on temporal trends for selected states). We report intermediate or differing intra-river trends as pairwise combinations of +, 0, and – to account for these patterns. Criteria for assigning population status were based on literature (e.g., National Research Council 2002) and file sources previously listed for relative abundance, as well as the author's collective professional judgment. Consequently, population trends reported here should be viewed as qualitative and approximate because consistent and riverwide benchmark fish sampling was absent prior to major changes in flow and habitat.

Spatial Changes

We review longitudinal distribution of fishes from research that evaluated distribution, habitat use, and population structure of benthic fishes over 3,217 km of the warmwater, unimpounded Missouri River (Berry et al. 2004; Berry and Young 2004). This study (hereafter referred to as the benthic fishes study) employed five standardized collection gears (drifting trammel net, benthic trawl, bag seine, stationary gill net, and electrofishing) to collect a diversity of fishes using all major main-channel habitat types. Gears were deployed using standardized effort in replicates of six macrohabitats (outside bend, inside bend, channel cross-over, tributary mouth, nonconnected secondary channel, and connected secondary channel) to target both small and large benthic fishes (Sappington et al. 1998). Sampling occurred from about mid-July to early October over 3 years (1996–1998) within macrohabitats from 15 representative segments of the 27 segments identified. Longitudinal distribution information is illustrated for taxa with greater than or equal to 100 individuals collected during the 3-year study or from information reported in Pegg and Pierce (2002b).

Temporal Changes

No standardized, long-term fish-monitoring program currently exists on the Missouri River as it does for the nearby upper Mississippi River (e.g., Theiling et al. 2000). Consequently, our treatment of temporal changes to its ichthyofauna is uneven. Trends for selected species and reservoirs or river reaches within several Missouri River states are summarized from published papers, Federal Aid in Sport Fish Restoration reports, and unpublished data from agency files.

Reservoir fishes.—Comprehensive, multi-year assessments of impoundment and postimpoundment activities on Missouri River fishes were conducted in the Corps reservoirs by the North Central Reservoir Investigations. Technical reports describe long-term changes in fish populations for Lake Oahe (1965–1974, Beckman and Elrod 1971), Lake Francis Case (1954–1975, Walburg 1977), Lewis and Clark Lake (1956–1974, Walburg 1976), and multiple reservoirs (e.g., Benson 1980). We illustrate differences in temporal trends for selected species within the six main-stem reservoirs by summarizing patterns from two morphologically very different impoundments: Lake Sakakawea and Lewis and Clark Lake (Table 1). Lake Sakakawea has a low exchange rate, it having the second largest surface area and largest volume of the six main-stem reservoirs. Lewis and Clark Lake has the smallest area and volume and the highest exchange rate (Table 1). Lake Sakakawea is managed as a cold, cool, and warmwater fishery, whereas Lewis and Clark Lake is managed as a cool and warmwater fishery (U.S. Army Corps of Engineers 1994a; see Wehrly et al. 2003 for a review of thermal terms relevant to stream fish assemblages). Temporal changes in Lewis and Clark Lake fishes were evaluated from the period following dam closure in 1956–2001 (45 years) by summarizing CPUE (mean catch per overnight gill net set) from Walburg (1976) (1965 missing) and annual surveys of Missouri River reservoirs conducted by the South Dakota Department of Game, Fish and Parks for 1983–1987 (Riis et al. 1988), 1988–1991 (Johnson et al. 1992), 1992–1996 (Wickstrom 1997), and 1997–2001 (Wickstrom 2002). Trends for nearly the same species in Lake Sakakawea were adapted from Hendrickson and Power's (1999) synthesis of changes in species abundance between 1956, 3 years after filling began, and 1998 (42 years). Linear regression was used following Hendrickson and Power's (1999) example with year as the independent variable and CPUE as the dependent variable to test for slopes significantly different from 0.0.

Riverine fishes.—Temporal changes in fish abundance and distribution in the main-stem Missouri River are best documented in Montana, South Dakota–Iowa–Nebraska, and Missouri, as these are the states where main-stem reservoirs are few or absent and reasonable historical databases exist.

Montana.—The few remaining largely free-flowing portions of the Missouri River are above Ft. Peck Lake, 240 km of which is a designated National Wild and Scenic River. The segment below Ft. Peck Lake and between the confluence of the Yellowstone River and the North Dakota border is also somewhat natural with minimal geomorphic alteration. Effects of Ft. Peck Lake flow regulation are dampened by discharge from the Yellowstone River, which is about 1.2 times that of the Missouri River above its confluence (U.S. Geological Survey 2002). The fish assemblage contains many coolwater species from about the origin of the named Missouri River at Three Forks to between Great Falls and Fort Benton, the approximate boundary between the Rocky Mountain and Great Plains physiographic provinces. The Missouri is considered a warmwater river below the Rocky Mountain province.

We contrasted catch per unit effort (CPUE) and percent composition of the total catch for selected fishes along a Wild and Scenic River segment above Fort Peck Lake (km 3,363–3,097) during two time intervals (1976–1979 and 1997–2002). Fishes were collected from five locations within this reach during the first period by Berg (1981) using boat electrofishing in autumn. Gardner (1998, 1999, 2001, 2003) repeated this sampling from the same sites using similar techniques about 20 years later. Potential differences between the two time periods were compared among sites for each species using a students paired t-test.

South Dakota–Iowa–Nebraska.—Three distinct segments occur in this section of the Missouri River (see Figure 1 in Hesse et al. 1993). There is a 58-km *upper unchannelized* riverine segment that is flow regulated between Ft. Randall Dam (Lake Francis Case) and Lewis and Clark Lake (South Dakota–Nebraska). This segment is a designated National Recreational River and the Niobrara River is the major tributary. A 127-km *lower unchannelized* and flow regulated segment extends from Gavins Point Dam to Sioux City, Iowa (South Dakota–Iowa–Nebraska); 93 km of this section below Lewis and Clark Lake is also a National Recreational River. The James and Big Sioux rivers are major tributaries entering the Missouri River within this reach (Figure 1). The last segment in Nebraska and Iowa is both *channelized* and flow regulated and extends about 288 km between Sioux City, Iowa, and the Missouri border. Hesse (1993a) and Hesse et al. (1993) summarized status of selected fishes from the Missouri River in these reaches. More specific trend information was synthesized in a series of articles on individual species or groups of species, including paddlefish (Hesse and Mestl 1993), burbot (Hesse 1993b), channel catfish (Hesse 1994a), flathead and blue catfish (Hesse 1994b), chubs and minnows (Hesse 1994c), and sauger (Hesse 1994d). We summarize spatial and temporal changes for several of these groups. We specifically analyzed data for slopes different from 0.0 as described above on Hesse's (1994d) data of temporal changes in experimental gill netting CPUE from unchannelized Missouri River segments in South Dakota, Iowa, and Nebraska.

Missouri.—Pflieger and Grace (1987) summarized changes in fishes of the Missouri River, Missouri, at multiple locations (usually 13) over three time periods 1940–1945 (Fisher 1962), 1962–1972, and 1978–1983. Bag seines were the major gear used to collect fishes, primarily from July to October. Gelwicks et al. (1996) and Grady and Milligan (1998) resampled most of the same sites in 1994 and 1997 using similar bag seines. Their primary interest was to update the status of five minnow species of concern: sicklefin chub, sturgeon chub, flathead chub, plains minnow, and western silvery minnow. Gelwicks et al.'s (1996) collections were made in November and Grady and Milligan's (1998) in July and August.

Lack of sampling effort data for early collections prevented statistical evaluation of changes in catch rate over time. However, Grady and Milligan (1998) used logistic regression to examine trends in fish distribution over time and among sites. They tested the probability of presence or absence of the five target species and six additional minnows over time and among sites for all collections.

Commercial harvest.—Trends in commercial catch provide another perspective to illustrate temporal changes in Missouri River fishes. We summarize trends in number of licensed commercial fishers and composition and weight of reported catches for the Missouri River, Missouri (V. Travnichek, Missouri Department of Conservation, personal communication).

Results

Our list of fishes includes 136 species from 25 families that presently occur in the Missouri River main stem, its floodplain, and reservoirs (Appendix A). This constitutes 79% of the 173 species listed by Cross et al. (1986) for the entire Missouri River basin. Seven families are represented by at least 5 species: Cyprinidae (47 species), Catostomidae (13), Centrarchidae (12), Salmonidae (10), Ictaluridae (9), Percidae (7), and Clupeidae (5). These families compose 76% of total species richness. Ten families are represented by only one species: Polyodontidae, Amiidae, Anguillidae, Percopsidae, Osmeridae, Gadidae, Poeciliidae, Gasterosteidae, Sciaenidae, and Cottidae. Native species of four archaic families are extant in the river: Acipenseridae, Polyodontidae, Lepisosteidae, and Hiodontidae.

We added seven species (four nonnative: alewife, cisco, big head carp, and silver carp; three rare natives: spotted gar, channel shiner, and Mississippi silvery minnow) for which we have reliable records for the main stem that were not reported in Cross et al. (1986) for any Missouri River drainage unit (Appendix A). Forty-four species were deleted that Cross et al. (1986) included (Table 3). The majority of these fishes (34 species) are presumed tributary species, and we have no records for them from the main-stem Missouri River, its floodplain, or reservoirs. Coho salmon were stocked into the Missouri River above Lake Sakakawea and main-stem reservoirs in North and South Dakota in the 1970s, but are no longer captured and presumed extirpated.

Native and Introduced Fishes

Native fishes comprise 78% of the Missouri River's main-stem fauna (106 species) in comparison with 80% (138 species) for the basin (Cross et al. 1986). Two diadromous fishes are present below the reservoirs, American eel and Alabama shad. The native status of some fishes to portions of the Missouri River is uncertain for several reasons: (1) the edge of their range occurs along the river, (2) their preEuro-American distribution is unclear, or (3) unrecorded stockings in the 1800s may have transferred sport and forage fishes before the native fauna was well catalogued.

Bailey and Allum (1962) indicated that largemouth bass, bluegill, and pumpkinseed were not native to South Dakota and that the status of black and white crappie was uncertain. Cross et al. (1986) list largemouth bass and both crappies as native to the James and Sioux rivers of South Dakota and bluegill and pumpkinseed as uncertain. We combined the James, Sioux, Niobrara, and Platte drainages where they were contiguous to the Missouri River channel and list these species as native to the main stem if Cross et al. (1986) classified them as native to any of these drainages. We follow Bailey and Allum (1962) and list pumpkinseed as introduced, since Cross et al. (1986) are uncertain for the James and Sioux rivers, but considered it introduced elsewhere in the Missouri River basin.

Table 3.—Fishes reported by Cross et al. (1986) in drainage units of the Missouri River basin that are not considered present in the Missouri River. Reasons for exclusion: T = presumed tributary species; E = introduced, presumed extirpated; U = originally listed as uncertain in Sioux–James drainage unit.

Species name	Common name	Reason
Ichthyomyzon fossor	northern brook lamprey	T
I. gagei	southern brook lamprey	T
Oncorhynchus mykiss aguabonita	golden trout	T
O. kisutch	coho salmon	E
Thymallus arcticus	arctic grayling	E
Umbra limi	central mudminnow	E
Luxilus zonatus	bleeding shiner	T
Nocomis biguttatus	hornyhead chub	T
Notropis anogenus	pugnose shiner	U
N. greenei	wedgespot shiner	T
N. heterodon	blackchin shiner	U
N. heterolepis	blacknose shiner	T
N. nubilus	Ozark minnow	T
N. topeka	Topeka shiner	T
Richardsonius balteatus	redside shiner	T
Minytrema melanops	spotted sucker	T
Moxostoma anisurum	silver redhorse	T
M.carinatum	river redhorse	T
M.duquesnei	black redhorse	T
Ameiurus nebulosus	brown bullhead	E
Typhlichthys subterraneus	southern cavefish	T
Fundulus catenatus	northern studfish	T
F. olivaceus	blackspotted topminnow	T
Poecilia mexicana	shortfin molly	E
Xiphophorus hellerii	green swordtail	E
X. variatus	variable platyfish	E
Ambloplites constellatus	Ozark bass	T
Lepomis gulosus	warmouth	E
Crystallaria asprella	crystal darter	T
Etheostoma blennioides	greenside darter	T
E. caeruleum	rainbow darter	T
E. chlorosoma	bluntnose darter	T
E. flabellare	fantail darter	T
E. gracile	slough darter	T
E. microperca	least darter	T
E. nianguae	Niangua darter	T
E. punctulatum	stippled darter	T
E. spectabile	orangethroat darter	T
E. tetrazonum	Missouri saddled darter	T
E. zonale	banded darter	T
Percina cymatotaenia	bluestripe darter	T
P. evides	gilt darter	T
P. maculata	blackside darter	T
Cottus carolinae	banded sculpin	T

Uncertainty exists over the native status of walleye within drainages of the middle Missouri River and the main stem (Tyus 2002). North Dakota considers it as native to the state (Power and Ryckman 1998), but (Tyus 2002) questions walleye's native status to the Missouri River based on its lacustrine habits, widespread stocking before its native range was fully documented, and misidentifications with sauger of early records. Bailey and Allum (1962) list walleye as native to eastern South Dakota, including the Missouri River. Cross et al. (1986) list it as native to the White–Little Missouri (16) and James–Sioux drainage units (15, exclusive of the Missouri River main stem) and as uncertain within the Niobrara-Platte drainage unit (14, including the Missouri River main stem). However, Bailey (R. M. Bailey, University of Michigan, personal communication) now considers walleye to be introduced to the main- stem Missouri River within the White-Little Missouri drainage and its status as uncertain in the James River. Our designation reflects the walleye's now uncertain status throughout most of the Missouri River (Appendix A). We have also listed yellow perch as uncertain for the same reasons.

The presence of fossil walleye from the Illinoian glacial cycle in Kansas where they are now listed as uncertain (Cross et al. 1986) raises the question of what temporal criteria should be used to designate a species as native or nonnative to a drainage basin?

Northern pike is another problematic species. Cross et al. (1986) list northern pike as native to the James–Sioux (15) and Niobrara–Platte (14) drainages, but as introduced to the Little Missouri–White drainage unit (16). However, North Dakota Game and Fish consider it a native species as records indicate its presence at the time Bismarck was settled (1882–1883, Barrett 1895). Rail service arrived in central North Dakota in the 1860s and U.S. Bureau of Fisheries records beginning in 1880 do not indicate northern pike stockings until 1899. We therefore list its status to the Little Missouri–White drainage unit drainage as native.

General Habitat Use

Fifty-four percent of Missouri River fishes reside primarily in the main channel (73 species) and are thereby categorized as big river fishes. We classified an additional 18 fishes as more common along the main-channel border (e.g., *Esox* spp., *Ameiurus* spp., *Lepomis* spp., *Pomoxis* spp.; Appendix A). Another 38 species are included in our list, but are considered waifs to the main channel from tributaries or reservoirs (Appendix A). Combining channel and channel border fishes yields a total of 91 species classified as main channel Missouri River fishes.

Significant use of floodplain habitats occurs for 60 species, including many that also frequent the channel border. Genera that include numerous floodplain representatives are *Lepisosteus* spp., *Esox* spp., *Carpiodes* spp., *Fundulus* spp., and *Lepomis* spp. (Appendix A). Use of reservoirs occurs for 72 species with 20 of them largely restricted to reservoirs or waifs from reservoirs to the main channel (16 of the 20 species). The majority of these (11 species) are fishes introduced into reservoirs for sport fishing (e.g., 7 species of salmonids) or forage for sport fishes (e.g., rainbow smelt and spottail shiner).

Roughly one-half of Missouri River fishes (68 species) require flowing water for some life-stage activity (i.e., fluvial specialist or fluvial dependent) and 21% (28 species) are categorized as fluvial specialists (Appendix A). Representative fluvial dependent native genera are *Acipenser, Polyodon, Alosa*, *Hiodon, Hybognathus*, *Moxostoma*, and *Morone*. Fluvial specialist fishes are predominately from the genera *Scaphirhynchus, Macrhybopsis*, *Notropis*, and *Noturus*. The 69 species of macrohabitat generalists contain numerous representatives from the families Clupeidae, Esocidae, Cyprinidae, Catostomidae (*Ictiobus*), Ictaluridae, Fundulidae, and Centrarchidae.

As their name implies, macrohabitat generalists show the widest distribution among drainage units, physiographic regions, and river habitats. However, proportion of macrohabitat generalists was higher in the Upper Missouri–Little Missouri–White drainage units (60.8%) than in remaining drainages (range: 49.1–54.8) with a corresponding decline in fluvial specialists. One-half of main channel fishes are macrohabitat generalists (44% of waifs) and 23% of the remaining species are fluvial specialists (23% of waifs). Macrohabitat generalists also dominate floodplains (78%) and reservoirs (65%). All fluvial specialists in the Missouri River are native fishes, whereas 54% of macrohabitat generalists and 46% of fluvial dependent species are nonnatives.

Population and Conservation Status

Populations of 33% of the 95 fishes we were able to classify are considered either stable to increasing or increasing (0, + or +, Appendix A), whereas 45% (43 species) of fishes are either stable to decreasing or decreasing (0, – or –, Appendix A). More specifically, we list populations of 17 species as increasing (+, Appendix A), 13 species as stable to increasing (0, +), 19 species as stable (0), 19 species as stable or decreasing (0, –), 24 species as decreasing (–), and 3 species as increasing in some reaches and decreasing in others (+, –). Forty-one species were too uncommon to rank or their status is unknown (Appendix A). Fifty-three percent of the species whose populations are increasing (+) were introduced into the river or reservoirs, and 18% are not present in the main channel except as waifs. Ninety-six percent of species with decreasing populations (–) are native or diadromous fishes, 72% of these reside predominately in the main channel (C) and 63% are fluvial specialist or fluvial dependent fishes.

Populations of some fishes we identify as declining include species whose conservation need is reported by others. Pallid sturgeon is federally listed as endangered and Alabama shad is a candidate for federal listing. The U.S. Fish and Wildlife Service recently concluded listing of sicklefin and sturgeon chubs as endangered was not warranted, despite a 56% reduction in their distribution along the Missouri River main stem (Department of Interior 2001).

Conservation status is judged globally secure (G5) for 120 native and nonnative Missouri River fishes included in Appendix A (NatureServe 2003). We identified populations of 13 native fishes (12% of native and diadromous species) as less than secure (Appendix A) using NatureServe's global rankings in comparison with our site-specific classification of 23% as declining (–). Pallid sturgeon is ranked as globally critically imperiled (G1) and no Missouri River fishes are classified as globally imperiled (G2). Lake sturgeon, Alabama shad, sturgeon chub, and sicklefin chub are ranked as globally vulnerable (G3). Speckled chub and blue sucker are classified as globally vulnerable to apparently secure (G3G4), and six native, main-channel fishes are apparently globally secure (G4): chestnut lamprey, silver lamprey, shovelnose sturgeon, paddlefish, western silvery minnow, and plains minnow. Highfin carpsucker is considered uncertain between apparently globally secure and secure (G4G5). Eleven fishes are listed by two or more main-stem states as imperiled (S1, S2): lake sturgeon, pallid sturgeon, paddlefish, western silvery minnow, plains minnow, sturgeon chub, sicklefin chub, silver chub, flathead chub, quillback, and highfin carpsucker. All are big river fishes, 45% are fluvial specialists, and another 36% are fluvial dependent species.

Longitudinal Spatial Patterns

There is a general trend of increasing species richness going downriver. Total numbers of native/introduced species by drainage unit section are as follows: Upper Missouri 37/27 (64), Little Missouri–White 53/22 (79), James–Sioux–Niobrara–Platte 73/16 (94), Nishnabotna–Chariton 68/15 (87), and lower Missouri 89/18 (110). Species totals do not always equal the sum of native plus introduced due to status uncertainties and exclusion of diadromous fishes. The proportion of native big river fishes varies little among drainage units, ranging from 48% in the upper Missouri and Little Missouri–White units, where the river is both least altered and the six main-stem reservoirs are located, to 51% in the remaining units. The number of introduced fishes is highest in the Upper Missouri ecoregion (28 species) where the main-stem reservoirs are located. Forty-one and 24% of introduced fishes use reservoirs in the upper Missouri and Little Missouri–White drainage units, respectively. Most introductions are sport fishes from four families: Salmonidae, Esocidae, Centrarchidae, and Percidae, or forage species (e.g., cisco, rainbow smelt, spottail shiner, golden shiner). Fewer introduced fishes occur in the Middle Missouri (19 species) and Central Prairie (18 species) ecoregions, and a much lower percentage of these fishes use reservoirs (9–13%) compared with upper river drainage units. Predominant species include the same sport and forage fishes stocked into upriver reservoirs as well as Asian carps (grass, silver, and bighead). Gavins Point Dam appears to be a barrier to upriver migration of introduced Asian carps at the time of this writing.

Salmonids decrease going downriver as a proportion of total species richness within each drainage unit (unit number): 19% (18), 11% (16), 3% (15 + 14), 0% (12), and 1% (11). Ictalurids make up a slightly higher proportion of species (11.3–12.9%) in the lower two drainage units than the upper three (9.6–9.9%) and clupeids compose between 4.2% and 5.0% of species richness in drainage units below the reservoirs (15–11) compared with 0.0–1.6% in the Little Missouri–White and Upper Missouri units (16 and 18). No clear longitudinal trends occur for species richness among the other major families.

The benthic fishes study collected approximately 114,000 fishes of 106 species from the mainstem Missouri River (Berry et al. 2004). Longitudinal distributions for the 50 taxa with greater than or equal to 100 individuals collected during this study also show an increase in species richness from the upper unchannelized to lower channelized river (Figure 2). Twenty-seven taxa were collected above Ft. Peck Lake, 39 taxa in the inter-reservoir segments below Ft. Peck Lake to Lewis and Clark Lake, and 44 taxa were sampled below Lewis and Clark Lake. Four coolwater fishes, longnose dace, longnose sucker, white sucker, and burbot were only collected above approximately km 1,200. Twenty-one taxa were absent above about km 3,000, and three species (speckled chub, blue catfish, and mosquitofish) were collected only downriver from approximately km 1,100. Thirty-six percent of widely distributed taxa were absent in one or more river segments below a reservoir.

Structure, morphology, functional composition, and life history features of the river's benthic fish assemblage have been evaluated in relation to differences in flow regime among six distinct longitudinal flow units (Pegg and Pierce 2002a, 2002b). Pegg and Pierce (2002b) showed that gizzard shad, emerald shiner, red shiner, river shiner, plains minnow, flathead catfish, and freshwater drum were most associated with the lower channelized river (they defined this as from Kansas City to the mouth), whereas longnose suckers, white suckers, and sicklefin chubs were most associated with the upper unchannelized and inter-reservoir segments. Fish assemblages from the uppermost segments above Fort Peck Lake (km 3,217–3,029) had a Bray-Curtis similarity of less than 45% with fishes from the lower channelized river.

Fish trophic guilds above Ft. Peck Lake are composed largely of invertivores (e.g., flathead chubs and sturgeon chubs) and herbivorous species (e.g., *Hybognathus* spp.). These guilds decline precipitously and omnivores and benthic invertivores increase below Ft. Peck Lake and Lake Sakakawea. Planktivorous fishes, predominantly gizzard shad, are most abundant in the channelized river. Bergsted et al. (2004) further summarize feeding and reproductive guilds of benthic fishes throughout the warmwater Missouri River.

Riverine fishes above Lake Oahe are dominated by species exhibiting a more elongate body shape (e.g., flathead chubs, *Hybognathus* spp., and longnose suckers) than elsewhere, whereas prolonged swimmers like gizzard shad were most abundant in the channelized river (Pegg and Pierce 2002b). Water velocities where fishes are generally found based on the literature also varied among longitudinal flow units. Welker and Scarnecchia (2003) compared catostomid fishes in two upper reaches of the Missouri, North Dakota: a Yellowstone River confluence to Lake Sakakawea (YSS), a moderately altered reach, and the Missouri river between Garrison Dam and Lake Oahe (GOS), a highly altered segment. Differences in sucker species composition, prey density and composition, and sucker feeding ecology were associated with the major anthropogenic disturbances in the GOS reach.

Species associated with either fast (e.g., shovelnose sturgeon, blue sucker, and sicklefin and sturgeon chubs) or moderate (e.g., walleye, sauger, and emerald shiner) water velocities are most abundant above Fort Peck Lake. Fishes frequenting moderate and slow velocities (e.g., bigmouth buffalo, carpsuckers, and freshwater drum) are more prevalent in the channelized river. Fishes routinely collected over sand substrate predominated above Ft. Peck Lake and Lake Sakakawea (e.g., emerald shiners and *Hybognathus* spp.). Species use of gravel (e.g., blue suckers and shorthead redhorse) was greater than 40% below these two reservoirs, but well be-

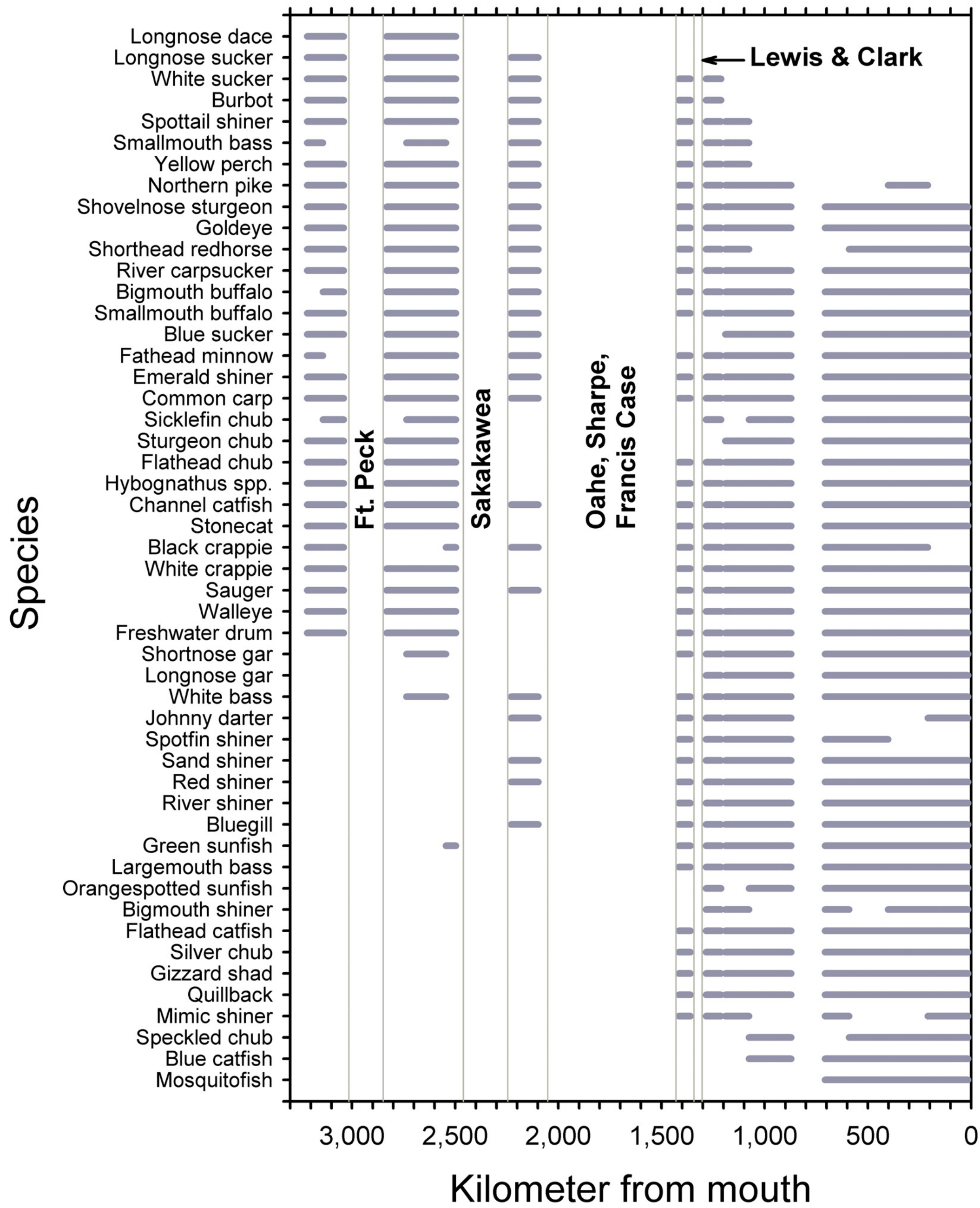

Figure 2.—Longitudinal distribution of major (3,100 collected) Missouri River fishes based on standardized sampling between July and October 1996–1998, from main-channel habitats exclusive of reservoirs. A taxon was presumed present in segments not sampled if it was collected from segments sampled above and below the missing reach. Vertical lines represent reservoir boundaries. *Hybognathus* spp. represents Western silvery, brassy, and plains minnows combined. Based on data from Berry et al. (2004).

low 20% elsewhere in the river. Fishes that use gravel (e.g., longnose and white suckers and shovelnose sturgeon), sand (e.g., *Notropis* spp. and river carpsucker), and structure for spawning predominate above the reservoirs; gravel spawners dominate in inter-reservoir segments; and a high percentage of general and pelagic spawners (e.g., gizzard shad and freshwater drum) occur in channelized segments. Pegg and Pierce (2002b) suggest that fishes from river segments with a high degree of flow alteration tend to be deeper bodied and not well suited for the more natural flow patterns that still exist in some portions of the river.

Braaten and Guy (2002) also used the benthic fishes' database to examine species-specific life history characteristics for two short-lived (emerald shiner and sicklefin chub) and three long-lived fishes (freshwater drum, river carpsucker, and sauger) across a large portion of the Missouri River's latitudinal (48°03'N to 38°47'N) and thermal gradients. Mean water temperature and number of days in the growing season averaged 1.3 times greater and growing-season degree-days were twice as high in southern than northern latitudes of the main stem. Longevity for all species, except freshwater drum, increased significantly from south to north. Other population variables like length at age, growth coefficients, and growth rates during the first year of life varied differently with latitude among the species studied. They demonstrated that latitudinal variations in thermal regime across the Missouri's broad spatial gradient greatly influence growth and other life history characteristics of fishes studied.

Pegg and Pierce (2001) conducted a similar latitudinal analysis as Braaten and Guy (2002) on channel catfish, emerald shiner, freshwater drum, river carpsucker, and sauger. They observed significant latitudinal trends in growth rate coefficients only for emerald shiners, while results were inconclusive for the other four species. Growth coefficients were higher for age 1+ emerald shiners at higher latitudes. They concluded that natural (e.g., differences in biological communities and variability in individual growth rates) and anthropogenic (e.g., flow alteration, impoundment, and channelization) factors may have been responsible for the few river-wide latitudinal trends observed in growth rates, despite large differences in growing season and cumulative degree-day gradients.

Bergsted et al. (2004) used the benthic fishes data to develop a preliminary index of biotic integrity for the warmwater Missouri River to evaluate changes related to channelization and impoundment. The least-altered zone served as the reference condition with all sites rated excellent to good. The inter-reservoir zone showed the greatest variability in ratings with 60% of sites rated fair to very poor. The regulated-unchannelized zone (Gavins Point Dam to Ponca, Nebraska) had 60% of sites rated "good," and the channelized zone had 89% of its sites rated between good and fair.

Hesse and Mestl (1993) and Hesse (1994a, 1994b, 1994c, and 1994d) reported trends for several Missouri River fishes at a smaller spatial scale within the upper unchannelized, lower unchannelized, and channelized segments previously described. Drift net collections for larval fishes between 1983 and 1991 yielded the highest mean total CPUE (number/1,000 m^3) in the channelized section (539), followed by the lower unchannelized section (316), with much lower CPUE from the upper unchannelized section between Lake Francis Case and Lewis and Clark Lake (49.4, Hesse 1994d). Although reservoir fragmentation was associated with reduced density of larval fishes in the upper unchannelized section of the lower river, the pattern of lowest larval CPUE in the inter-reservoir reach was not necessarily similar for individual species. For example, mean larval paddlefish CPUE was highest in the upper unchannelized reach (0.30), lower in the channelized reach (0.10), and larvae were generally absent from the lower unchannelized river in Nebraska (CPUE = 0.005, Hesse and Mestl 1993). The spatial trend observed for larval sauger was different with highest CPUEs in the lower unchannelized section (2.3), and nearly similar catches from the channelized (1.1) and upper unchannelized segments (0.9, Hesse 1994d).

Hesse (1994b) compared CPUE from electrofishing collections of flathead catfish from the same three river segments in South Dakota, Iowa, and Nebraska. Mean CPUE (number/min) between 1981 and 1991 was 1.1 for the channelized reach, 0.6 for the lower unchannelized reach, 0.0 for the upper unchannelized reach upstream from the Niobrara River, and 0.1 downstream from the Niobrara River.

Standardized seine collections of small fishes from years with comparable data (1986–1993) showed a different pattern with highest mean CPUEs (number/seine haul) in the lower unchannelized section (67.4) and the other two sections about the same (upper unchannelized: 37.7, channelized: 35.0, Hesse 1994c). Sicklefin, sturgeon, flathead, and speckled chubs were absent from small fish collections from the unchannelized Missouri River above and below Lewis and Clark Lake in 1976 and between 1983 and 1993. Average composition of total seine catches was also very low from the lower unchannelized and upper unchannelized segments for silver chubs: 0.03% and 0.14%, respectively, and for plains/silvery minnows: 0.04% and 0.07%. These chubs and minnows were collected from the channelized reach as well, with sicklefin, sturgeon, and flathead chubs composing less than 0.06% of catch. Silver chub (6.6%), plains/western silvery minnow (2.1%), and speckled chub (0.21%) were slightly more abundant in the channelized reach. Despite its being channelized, highest CPUEs or percent composition for total larval and small fishes and flathead catfish were observed in the channelized river section, the reach farthest from the influence of reservoirs.

Temporal Changes

Reservoir fishes.—Mean yearly CPUE for goldeye, common carp, black and white crappie combined, and yellow perch significantly declined in Lake Sakakawea over the 42 years examined, whereas catches of spottail shiner, white bass, and johnny darter increased (Hendrickson and Power 1999). No significant differences in CPUE were observed over time for 10 other taxa, 6 of which we compared with Lewis and Clark Lake (Table 4). Mean yearly CPUE significantly declined over the 45 years examined for six taxa from Lewis and Clark Lake, and increased for four taxa (Table 4). Goldeye and common carp CPUE significantly declined, whereas only walleye CPUE significantly increased in both reservoirs.

Trends in walleye were similar for Lake Sakakawea (Figure 3 in Hendrickson and Power 1999) and Lewis and Clark Lake (Figure 3) with a gradual increase in CPUE occurring from the mid-1950s to mid-1970s and then the increase becoming more variable thereafter. Sauger showed a simi-

Table 4.—Regression statistics showing temporal trends in mean yearly catch per unit effort CPUE (number/standard gill-net set) for Missouri River fishes in Lake Sakakawea (1956–1998; various years missing; N =16 to 22 years; source: Hendrickson and Power [1999]) and Lewis & Clark Lake (1956–2001; 1965, 1973–1983 missing; N = 35 years; see text for sources). Bigmouth and smallmouth buffalos compose "buffalos" and black and white crappies compose "crappies." Gizzard shad are absent from Lake Sakakawea. See text for collection methods. Only slopes significantly different from 0.0 at P less than 0.05 are shown.

	Lake Sakakawea			Lewis & Clark Lake		
Species	r^2	P	slope	r^2	P	slope
gizzard shad				0.16	0.019	+0.277
goldeye	0.22	0.027	–0.031	0.44	<0.001	–0.027
common carp	0.33	0.005	–0.012	0.58	<0.001	–0.412
river carpsucker	0.19	0.090		0.32	<0.001	–0.099
buffalos	0.02	0.635		0.60	<0.001	–0.049
shorthead redhorse	0.04	0.387		0.42	<0.001	–0.017
channel catfish	0.12	0.111		0.28	0.001	–0.061
white bass	0.65	<0.001	+0.001	0.03	0.295	
crappies	0.35	0.004	–0.006	0.02	0.411	
yellow perch	0.34	0.004	–0.027	0.00	0.903	
sauger	0.13	0.096		0.43	<0.001	+0.167
walleye	0.77	<0.001	+0.028	0.38	<0.001	+0.139
freshwater drum	0.05	0.334		0.48	<0.001	+0.211

lar temporal pattern in Lewis and Clark Lake, but CPUE declined in the Missouri River below this reservoir (see *Riverine fishes*).

Catch per unit effort for goldeye, common carp, river carpsucker, and buffalos in Lewis and Clark Lake showed a precipitous decline in the 16 years following impoundment, then became more stable thereafter. This pattern is illustrated by a regression of buffalo CPUE against year for the 1956–1972 period yielding a highly significant decrease in CPUE (Figure 3, compare with buffalos in Table 4). However, CPUE did not change significantly with time thereafter. The decline was more gradual for shorthead redhorse (Figure 3) and channel catfish. We were not able to determine if the pattern

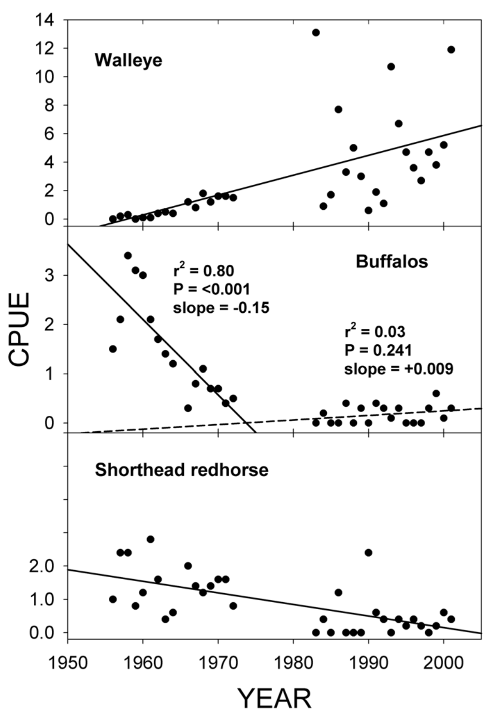

Figure 3.—Changes in mean yearly catch per unit effort (CPUE, number/standard gill-net set) for walleye, bigmouth and smallmouth buffalos combined, and shorthead redhorse from Lewis and Clark Lake, 1956–2001. Year-CPUE regressions for buffalos were divided into two periods, 1956–1972 and 1983–2001, to illustrate their rapid decline following impoundment followed by fairly stable catches. See Table 5 for regression statistics for the three taxa over the entire 1956–2001 interval. See text for data sources.

was similar in Lake Sakakawea because fish sampling did not begin immediately following impoundment.

Riverine fishes. Montana.—Sufficient CPUE and percent composition data were available to contrast temporal changes for nine fish species between the 1976–1979 and 1997–2002 periods at five locations above and below Fort Benton (Table 5). Most species are fluvial dependent, big river fishes and two species (common carp and walleye) were introduced to the Upper Missouri drainage unit. Catch per unit effort over the 20-year interval decreased significantly ($P \leq 0.05$) only for longnose sucker and increased for river carpsucker, shorthead redhorse, walleye, and freshwater drum. No significant change in CPUE between the two periods was observed for goldeye, common carp, white sucker, and sauger. The proportion a species contributed to the total catch decreased significantly for goldeye and longnose sucker, increased for walleye, and freshwater drum, and did not change during the approximately 20 years for common carp, white sucker, and sauger.

Our analysis and that of McMahon and Gardner (2001) show that saugers have declined in the Missouri River main stem above Fort Benton, but not below. McMahon and Gardner (2001) also reported declines of sauger in Ft. Peck Lake, the Missouri River between Ft. Peck Dam and the North Dakota border, the Yellowstone River, and in spawning runs up important tributaries (Marias, Milk, and Tongue rivers). They estimated a 22% range reduction of sauger in the main-stem Missouri River and a 75% reduction in occupancy of tributaries. Sauger populations at the peripheries of their distributions (i.e., tributary streams, upper and lower ends of their distribution) appear to have been most altered. Factors attributed to sauger declines over the past 20 years in Montana include low reservoir levels and river flows, dams and water diversions, hybridization with introduced walleye, interactions with nonnative piscivorus walleye and smallmouth bass, and overfishing.

South Dakota–Iowa–Nebraska.—Declines in CPUE from 1983 to 1991 occurred for 6 of the 22 species Hesse (1993a), Hesse et al. (1993), and Hesse (1994d) reported from the unchannelized river, whereas increasing trends occurred for only three species, and the remainder showed no clear pattern

Table 5.—Change in catch per unit effort (CPUE, number fish electrofished per hour) and percent composition (%, percent composition of species relative to the entire catch for the year) of nine fishes from five locations along the Missouri River, Montana, between two time periods 1976–1979 (76–79) and 1997–2002 (97–02). Data for the 1976–1979 period are from Berg (1981), and data for the 1997–2002 period are from W. Gardner files. T = Trace, replaced with 0.05 for statistics. Comparisons significantly different at *P* less than 0.05 are in **bold**.

		Location and kilometers above St. Louis, Missouri							
Species	Statistic	Morony Dam 3,363	Fort Benton 3,339	Coal Banks 3,266	Judith Landing 3,189	Robinson Bridge 3,097	Mean	Paired *t*-statistic	*P* value
goldeye	CPUE 76–79	22.7	13.2	29.3	13.9	19.5	19.7		
	CPUE 97–02	25.4	27.2	22.9	13.3	16	21.0	–0.35	0.743
	% 76–79	27	20.7	38.2	27.9	59.8	34.7		
	% 97–02	16	17.6	18.1	13.1	20.6	17.1	2.91	**0.044**
common carp	CPUE 76–79	1.5	3.7	6.5	3.2	6.3	4.2		
	CPUE 97–02	9	7	6.8	6.3	3.6	6.5	–1.35	0.247
	% 76–79	1.8	5.8	8.5	6.4	19.3	8.4		
	% 97–02	6.4	7.2	7.3	7.3	5.3	6.7	0.52	0.634
longnose sucker	CPUE 76–79	17.9	11.9	8	4.3	0.1	8.4		
	CPUE 97–02	13.6	4.7	4	2	0.4	4.9	2.84	**0.047**
	% 76–79	21.3	18.7	10.4	8.6	T	11.8		
	% 97–02	9.5	3.3	3.3	1.6	0.5	3.6	3.06	**0.038**
river carpsucker	CPUE 76–79	0.3	0.9	2.2	3	0.9	1.5		
	CPUE 97–02	2.1	2.4	5.8	6.5	7.5	4.9	–3.75	**0.020**
	% 76–79	T	1.4	2.9	6	2.8	2.6		
	% 97–02	1.4	3.1	5.8	7.6	10.9	5.8	–2.46	0.069
shorthead redhorse	CPUE 76–79	7.8	22	21.4	16.5	2.1	14.0		
	CPUE 97–02	53.2	60.7	41.5	24.1	14.9	38.9	–3.39	**0.027**
	% 76–79	8.7	34.5	27.9	33.1	6.4	22.1		
	% 97–02	35.1	42.7	34.5	26.2	19	31.5	–1.75	0.155
white sucker	CPUE 76–79	1.8	1	0.3	0.5	0	0.7		
	CPUE 97–02	4.3	11.6	3.3	0.2	T	3.9	–1.61	0.183
	% 76–79	2.1	1.6	T	1	0	0.9		
	% 97–02	2.7	7	1.7	0.3	T	2.3	–1.31	0.261
sauger	CPUE 76–79	20.1	6.7	3.6	3.6	2.9	7.4		
	CPUE 97–02	1.9	3.6	6	7.7	9.6	5.8	0.36	0.734
	% 76–79	23.9	10.5	4.5	7.2	8.9	11.0		
	% 97–02	1.4	2.1	5.8	9	14.4	6.5	0.88	0.428
walleye	CPUE 76–79	0.3	0.1	T	T	T	0.1		
	CPUE 97–02	2.1	1.8	2.9	3.9	1.7	2.5	–5.50	**0.005**
	% 76–79	T	T	T	T	T	T		
	% 97–02	1.6	1.5	2.8	3.7	2.5	2.4	–5.83	**0.004**
freshwater drum	CPUE 76–79	2.6	0.6	0.2	0.2	0.1	0.7		
	CPUE 97–02	6.1	3.6	5.9	2.7	1.2	3.9	–4.21	**0.014**
	% 76–79	3.1	1	T	T	T	0.8		
	% 97–02	4.4	2.9	5.7	2.8	1.4	3.4	–3.20	**0.033**

(Table 6). Percent composition of total catch declined over the 9 years for 5 species and increased for 3 species. White sucker, white crappie, and sauger declined both in CPUE and percent composition. These data were collected 30 and 28 years, respectively, after Francis Case and Lewis and Clark reservoirs began filling, and it is likely many changes in fish composition and abundance had already taken place. There is evidence supporting this claim for sauger as Hesse (1994d) reported declining electrofishing catch rate in the unchannelized river between 1963 and 1991 (Figure 4). These data show the same precipitous decrease following dam closure (1963–1975) with a less steep decline thereafter (1983–1991), as was observed for several riverine fishes in Lewis and Clark Lake (Figure 3).

Density of larval sauger from the upper unchannelized segment also declined, from 10.6/1,000 m^3 in 1965 to an average of 0.9/1,000 m^3 between 1983 and 1991 (Hesse 1994d). Similarly, a 93% reduction in sauger larvae was observed between 1974 and 1985–1991 from the channelized segment. Sportfishing harvest of sauger from the Gavins Point Dam tailwater also decreased from 49% of total harvest in 1961 to 0.2% in 1992 (Hesse 1994d).

Small fishes were seined from the channelized reach of the Missouri River, Iowa–Nebraska, each year from 1970 to 1975 and again from 1986 to 1993 enabling comparison of these two periods separated by about a decade (Hesse 1994c). There was no significant difference in CPUE for all small fishes combined (*t*-test assuming unequal variances, $t = 0.74$, $P = 0.50$) between the 1970s (mean ± 1 SE = 46.5 ± 14.4) and the 1980–1990s (35.0 ± 6.1). However, fewer flathead chubs ($t = 2.83$, $P = 0.066$) and plains/western silvery minnows ($t = 3.29$, $P = 0.046$) were collected in the second period. Sicklefin and sturgeon chub numbers were so low by 1970 that they were collected in only 1 of the subsequent 11 years sampled (1988, 0.2 fish per standard haul). Some small fishes apparently did benefit from changes in the river as Hesse (1994c) reports emerald shiners increased from about 17% of the catch in 1971–1975 to 69% of catch in 1989.

Table 6.—Regression statistics showing temporal trends in catch per unit effort (CPUE) and percent composition of fishes from experimental gillnetting in the unchannelized Missouri River, Nebraska, 1983–1991. Only slopes significantly different from 0.0 at $P <$ 0.10 are shown. Source of data: Hesse (1994d).

	CPUE			Percent composition		
Species	r^2	P	slope	r^2	P	slope
shortnose gar	0.14	0.315		0.02	0.702	
gizzard shad	0.39	0.073	–0.187	0.32	0.114	
goldeye	0.06	0.538		0.19	0.237	
northern pike	0.61	0.014	0.117	0.53	0.026	1.232
common carp	0.43	0.056	–0.317	0.34	0.102	
river carpsucker	0.10	0.402		0.31	0.121	
white sucker	0.67	0.007	–0.015	0.54	0.024	–0.052
smallmouth buffalo	0.27	0.151		0.24	0.185	
bigmouth buffalo	0.03	0.681		0.02	0.742	
shorthead redhorse	0.33	0.106		0.34	0.099	2.392
black bullhead	0.01	0.841		0.00	0.948	
channel catfish	0.00	0.908		0.02	0.720	
white bass	0.67	0.007	–0.015	0.63	0.011	–0.065
rock bass	0.19	0.236		0.35	0.093	–0.050
largemouth bass	0.01	0.810		0.03	0.646	
smallmouth bass	0.39	0.070	0.017	0.49	0.036	0.080
black crappie	0.28	0.146		0.28	0.139	
white crappie	0.44	0.052	–0.072	0.44	0.053	–0.318
yellow perch	0.10	0.407		0.09	0.423	
sauger	0.87	0.000	–0.568	0.78	0.002	–2.332
walleye	0.20	0.225		0.06	0.537	
freshwater drum	0.15	0.302		0.15	0.310	

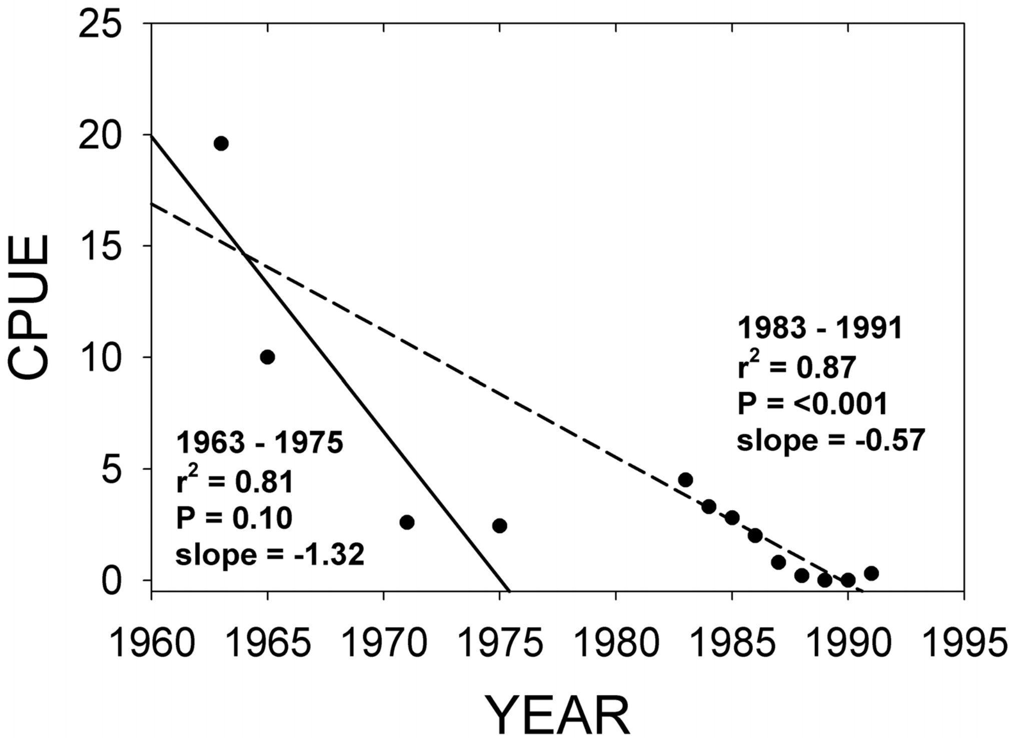

Figure 4.—Changes in mean yearly electrofishing catch per unit effort (CPUE, number/h) for sauger from the channelized Missouri River, Nebraska, downstream from Lewis and Clark Lake, which began filling in 1955. Year-CPUE regressions are calculated separately for two time periods: 1963–1975 and 1983–1991 to illustrate different trends between the two periods (data from Hesse 1994d).

Missouri.—The 890 km of Missouri River passing through Missouri to its confluence with the Mississippi River are both channelized and flow regulated. However, numerous large volume tributaries discharge to the river here because it is within the more mesic Central Lowlands and Interior Highlands physiographic provinces. Approximately one-half of the Missouri River's total discharge to the Mississippi River enters the main stem within the state of Missouri. Consequently, flood pulses have not changed dramatically within this reach since upstream impoundment. However, low flows and other ecologically relevant hydrologic variables have been more altered (Galat and Lipkin 2000). Fishes from the Ozark Highlands and Mississippi River are added to the ichthyofauna in this segment of river accounting for some of the observed increase in species richness.

Pflieger and Grace (1987) summarized changes in fishes in the Missouri River, Missouri, from surveys at approximately 20-year intervals between 1940 and 1983. Gizzard shad substantially increased in numbers, and goldeye, bluegill, channel catfish, white crappie, sauger, and freshwater drum may also have increased. Catches of common carp, river carpsucker, and bigmouth buffalo decreased markedly.

Pallid sturgeon composed 3% of river sturgeons (*Scaphirhynchus*) from 1940s collections, although river sturgeons were rare (Fisher 1962). No pallid sturgeons were collected in the 1960s or 1980s collections (Pflieger and Grace 1987). Carlson et al. (1985) examined 1,806 river sturgeons during 1978–1979 from the lower Missouri and middle Mississippi rivers, and reported only 0.3% were pallid sturgeons and four specimens were pallid–shovelnose hybrids. Pallid sturgeons were also very rare in these areas nearly 20 years later. Grady et al.

(2001) collected 5,197 sturgeons from the lower Missouri and middle Mississippi rivers between 1996 and 2000; 8 (0.15%) were wild origin pallid sturgeons and 22 were pallid–shovelnose hybrids.

Small fishes whose prominence increased included red shiners and several *Notropis* spp.: emerald, river, and sand shiners (Pflieger and Grace 1987). Relative abundance of several chubs (speckled chub, sturgeon chub, sicklefin chub, and silver chub) also was reported to increase slightly in contrast to the trends reported above for Nebraska. Small fishes whose numbers declined greatly included flathead chub and plains minnow.

Pflieger and Grace (1987) designated 26 species as "stragglers" in the Missouri River, Missouri (generally identified as sporadic or rare and waifs on our species list). More of these species occurred during the 1962–1966 and 1978–1983 periods than during the 1945–1949 period. Six species apparently were added to the Missouri River's fish fauna in Missouri after 1945. Skipjack herring is an anadromous big river fish from the Mississippi River that was first recorded from Missouri in approximately 1954, but numbers increased in the 1970s. Its increase in the Missouri River coincided with a decline in the upper Mississippi River following construction of locks and dams and a reduced suspended sediment load (a surrogate for turbidity) in the lower Missouri River following impoundment (Cross 1975). White bass is a nonnative species and was intentionally introduced into Lewis and Clark Lake in 1959. Alien grass carp first appeared in commercial catches in 1971 and striped bass, stocked into Lake of the Ozarks on the Osage River in 1967, first appeared in 1975. Rainbow smelt was introduced into Lake Sakakawea, North Dakota in 1971 and was first collected in Missouri in 1978. Silver carp first appeared in commercial fish catches in 1982.

In general, Pflieger and Grace (1987) observed that fishes that became more abundant were mostly pelagic planktivores and sight-feeding carnivores: skipjack herring, gizzard shad, white bass, bluegill, white crappie, river shiner, and red shiner. Fishes that decreased in abundance included big river species adapted for life in turbid waters with specialized habitat or feeding requirements (e.g., pallid sturgeon and flathead chub) or species more common in backwaters (e.g., western silvery minnow, plains minnow, and river carpsucker).

Grady and Milligan (1998) quantitatively examined changes in the minnow fauna following Pflieger and Grace's (1987) study. Presence of minnows increased from the 1940s to 1990s for five species, decreased for five species, and remained about the same for one species (Table 7). Populations of sturgeon chubs and western silvery minnows continued to decline from the 1980s. These results generally corroborated those of Pflieger and Grace (1987). Grady and Milligan (1998) and Berry et al. (2004) report that recent adoption of boat-mounted benthic trawls in channel habitats has yielded higher catches of many minnows and chubs than did historical shoreline bag seining. This suggests that channel populations of some small riverine cyprinids might not be as low as previously reported.

Commercial fishery.—The number of commercial fishers in the state of Missouri gradually decreased from 1948 (968) to 1963 (350), and then gradually increased to a peak of 1,039 in 1982 (Figure 5). Commercial fishers declined nearly continuously thereafter to 67 in 2001 (Figure 5). Factors contributing to these fluctuations through 1990 include increases in permit fees and health advisories against consumption of Missouri River fishes (Robinson 1992). Closure of the commercial catfish fishery on the Missouri River in 1992 and record flooding during the 1990s contributed to the further decreases in permit sales (V. Travnichek, personal communication).

Prior to 1997, total reported harvest was highest in 1945 at 222 metric tons (mt), and then declined gradually to 35 mt in 1966, paralleling the decline in number of fishers. Methods of estimating annual harvest changed in 1967, providing a more accurate, but higher reported harvest. Total harvest generally increased from the late 1960s until 1990 when it peaked at 432.5 mt (Figure 5). The precipitous decline thereafter is attributed to closure of the commercial catfish fishery.

Eleven groups of fishes comprised 98% of the total catch between 1945 and 2001 (Figure 6). In decreasing order of percent composition, these were

Table 7.—Summary of changes in presence-absence of cyprinid minnows in Missouri River, Missouri, between 1945 and 1997 (Grady and Milligan 1998). Grady and Milligan (1998) used logistic regression to examine if there was a significant positive (+), negative (–), or no (0) relationship between the probability of collecting a species over time (year) and distance (upriver to downriver within Missouri).

Species	Year	Distance	Notes
sicklefin chub	+	+	More abundant below Kansas City than above.
sturgeon chub	0	0	Rare at all times and locations.
plains minnow	–	0	Absent only in 1994 collections, stable otherwise.
flathead chub	–	0	Only one fish collected since 1980s.
western silvery minnow	–	–	Drastic decline in numbers collected over time.
sand shiner	+	+	Uncommon in general.
ghost shiner	–	+	More abundant below Kansas City than above.
river shiner	+	–	Increase in numbers over time.
emerald shiner	+	0	Most abundant minnow collected.
bigmouth shiner	+	–	Slight increase over time.
bluntnose minnow	–	+	More abundant in quiet backwaters.

common carp (39.0%), buffalo spp. (24.2%), flathead catfish (9.7%), channel catfish (6.5%), freshwater drum (4.5%), carpsucker spp. (4.1%), blue catfish (3.4%), grass carp (2.1%), paddlefish (1.9%), other Asian carps (*Hypophthalmichthys* spp., 1.5%), and sturgeon spp. (1.2%). Catches of grass, silver, and bighead carps have been gradually increasing (Figure 6). Shovelnose sturgeons are the only other group where catch has not shown a precipitous decline since about 1990. It declined to less than 1,800 kg during the early 1990s flood years, but gradually increased to more than 5,600 kg in 2001 (Figure 6). Increased commercial interest in sturgeons is a result of high prices paid for caviar and is a cause for concern about over harvest (Quist et al. 2002).

A 61% decline in commercial harvest of channel catfish as a result of overfishing was reported

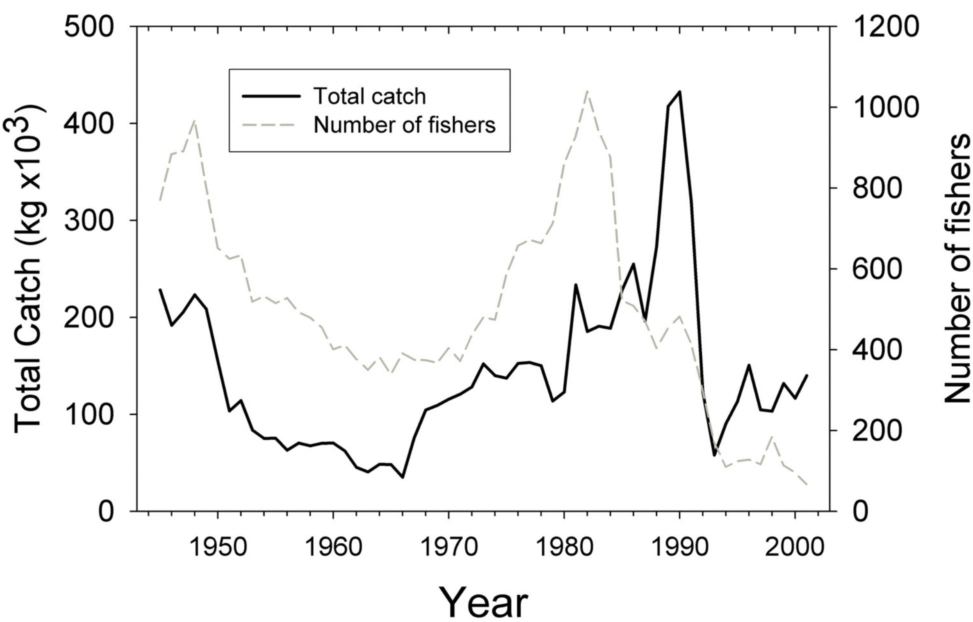

Figure 5.—Changes in number of commercial fishers and their reported total annual harvest of all fish species from Missouri River, Missouri between 1945 and 2001 (data from V. Travnichek, Missouri Department of Conservation).

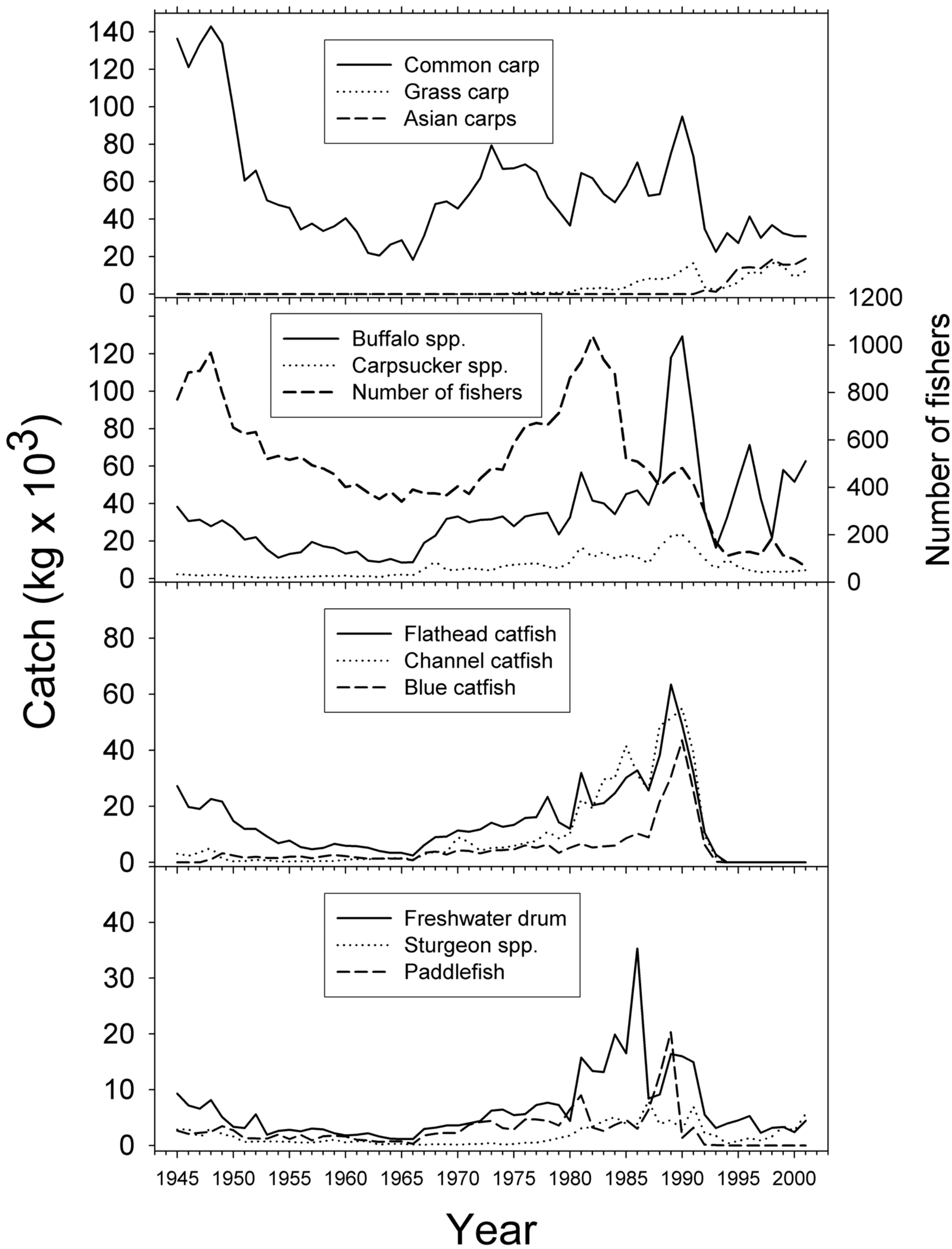

Figure 6.—Changes in reported total annual harvest of 11 fish taxa from Missouri River, Missouri, between 1945 and 2001 (data from V. Travnichek, Missouri Department of Conservation).

for Nebraska (Zuerlein 1988 in Hesse 1994a) over four, 10-year periods between 1944 and 1983. Closure of the commercial catfish fishery in 1992 resulted in noticeable changes in population structure of Missouri River channel catfish in Nebraska (Mestl 1999) and of channel, flathead, and blue catfishes in the Missouri River recreational fishery in Missouri (Stanovick 1999). Mean length and percentage of quality-sized channel catfish (>410 mm) in Nebraska catches increased significantly after the closure (Mestl 1999). Percentage of ages four to seven catfish made up 9% of standing crop before closure (1974–1975) and 58% after closure (1996–1997). Although annual production decreased from 199 to 83.5 kg/100 kg of standing stock between these periods, most of this production was in fish below harvestable size. Seventy-two percent of production of age 2–3 channel catfish was lost through mortality during 1974–1975, whereas only 35% was lost through mortality in 1996–1997.

Size of channel, flathead, and blue catfish in the Missouri River, Missouri, recreational harvest also increased significantly from before (1991–1992) to after (1995–1996) the commercial ban (Stanovick 1999). Additionally, angler harvest rates and release rates for all three species were higher after the commercial ban. This was most noticeable for flathead catfish where harvest rates more than tripled and release rates more than doubled following the commercial ban.

Discussion

The Missouri River possesses a diverse ichthyofauna. It is distinguished by native species well adapted for life in an environment with continuous high turbidity, a swift current, a scarcity of quiet backwaters, and an unstable sand-silt bottom (Pflieger 1971). The term "big river" fishes in common use today was coined by Pflieger (1971) to describe this distinctive assemblage of fishes inhabiting the Missouri–Mississippi system. Here resides a preponderance of benthic specialists exhibiting a panoply of ecomorphological adaptations, including inferior mouth position, dorsoventral flattening of the head, streamlined or deep humpbacked body shape, sickle-shaped or enlarged pectoral fins, reduced eyes, and an array of well-developed electrosensory and chemosensory organs (e.g., sturgeons, paddlefish, chubs, buffaloes, carpsuckers, blue sucker, catfishes, burbot, and freshwater drum). Environmental factors that molded ecomorphology of Missouri River's fishes are perhaps most similar to those operating in other largely turbid, dryland rivers like the Colorado (Mueller et al. 2005) and Rio Grande (Calamusso et al. 2005). However, unlike the Colorado, Missouri River fishes also evolved within a community rich in native piscine predators and competitors. Indeed, flathead catfish, one of the most damaging, nonnative piscivores to the lower Colorado River basin's native fishes (Minckley et al. 2003) is an archetypical Missouri–Mississippi big river predator.

Spatiotemporal changes across the Missouri's riverscape are a consequence of complex interactions between natural and anthropogenic factors. Predominant landscape factors that shape its present-day fish distributions include basin climate, physiography, zoogeography, and hydrology. Collectively, these constitute the "historical ecology" of a river's fish assemblage (Matthews 1998). Distribution patterns of native fishes along the Missouri River well illustrate the classic phenomenon of "longitudinal zonation" in riverine fish assemblages (Hawkes 1975; Matthews 1998). Additions of more Ozarkian (e.g., black redhorse and golden redhorse) and Mississippian fishes (e.g., Alabama shad, flathead, and blue catfish,) and replacement of coolwater species (e.g., longnose dace and longnose sucker) by warmer-water species (e.g., speckled chub and quillback) in the lower river contribute to the biogeographic longitudinal patterns observed.

These abiotic and biotic determinants constitute a series of filters (sensu Tonn 1990; Poff 1997) upon which human activities have further molded the patterns reported herein. Impoundments have fragmented the main-stem Missouri River and created longitudinal barriers to long-distance migrants like pallid sturgeon. Similarly, several small-bodied chubs are now extirpated from over more than one-half of the river's length. Temperature reductions below hypolimnetic-release dams impounding Ft. Peck Lake and Lake Sakakawea have been implicated in lack of recruitment of pallid sturgeon (Gardner and Stewart 1987; Dryer and Sandvol 1993), chubs (Galat and Clark 2002), and native larval fishes in general (Wolf et al. 1996). Reduction in channel complexity and changes to the natural flow regime have been particularly damaging to its big river fauna as is evidenced by the predominance of imperiled fluvial specialist and fluvial dependant fishes. Lateral fragmentation of the river from its floodplain by levees has been implicated in population declines of fishes that use the floodplain for spawning and/or nursery (Galat et al. 1998). Clear water and dense submergent vegetation associated with delta formation in reservoirs supports a greater density of centrarchids (e.g., largemouth bass and bluegill) and certain cyprinids (e.g., spotfin shiners) than other segments of the river or reservoirs (VanZee 1997; Wickstrom 2001) and may have contributed to range expansion of grass pickerel (VanZee and Scalet 1997).

The most recent anthropogenic impact to the Missouri River may be the population explosion of introduced Asian carps, particularly bighead and silver carp below Lewis and Clark Dam. They are often the most abundant larval fish collected (Galat et al. 2004) and adults also frequently dominate in experimental gill net catches (D. Chapman, U.S. Geological Survey, personal communication). Pflieger (1997) warned that bighead carp may compete for food with native planktivores, including paddlefish and bigmouth buffalo, as well as larvae of most native Missouri River fishes. Research is currently underway to determine if diet overlap exists in the lower Missouri River (D. Chapman, personal communication).

Richness of the Missouri River's native fish fauna remains relatively intact despite these assaults; no native fishes have yet been extirpated. Proportion of native fishes is higher in the Missouri River than the Colorado or Columbia rivers, and it had the lowest proportion of imperiled fishes of eight north-temperate rivers reviewed by Galat and Zweimüller (2001). Nevertheless, the widespread and long history of human intervention has contributed to spatiotemporal declines of about 25% to its ichthyofauna. Our review substantiates consistent population declines throughout much of the main channel Missouri River for the following species that are not federally listed: sicklefin chub, sturgeon chub, plains minnow, western silvery minnow, highfin carpsucker, and sauger. In contrast, over one-half of additions to fish biodiversity of the Missouri River since Cross et al. (1986) have been intentional and unintentional introductions, contributing to a homogenization of its ichthyofauna (sensu Rahel 2002). These changes, in part, prompted the National Research Council (2002) to warn that, "Degradation of the Missouri River ecosystem will continue unless some portion of the hydrologic and geomorphic processes that sustained the preregulation Missouri River and floodplain ecosystem are restored—including flow pulses that emulate the natural hydrograph, and cut-and-fill alluviation associated with river meandering. The ecosystem also faces the prospect of irreversible extinction of species."

Restoration Activities

Several events during the past decade have directed national attention to impairment of the Missouri River. Declines in populations of archetypical Missouri River fishes and birds resulted in listing the least tern *Sterna antillarum* and the before-mentioned pallid sturgeon as endangered and the piping plover *Charadrius melodus* as threatened under the Endangered Species Act. The conservation organization, American Rivers, designated the Missouri River as the nation's most endangered river in 1997 and again in 2001. Basin-wide droughts in the late 1980s and early 2000s and catastrophic flooding in the lower river in the early to mid 1990s have highlighted conflicts over water allocation. Socioeconomic values for the river and floodplain are changing from primarily transportation and agriculture uses, respectively, to an increase in reservoir and river based recreation, and there is a recognized need for more balance among all of the river's designated beneficial uses. The Lewis and Clark "Corps of Discovery" bicentennial in 2004–2006 is anticipated to boost tourism and general public interest in the history and status of the "Big Muddy." Activities along the Missouri River are moving from chronicling offenses to its ecological integrity towards designing and implementing rehabilitation and restoration programs (Galat et al. 1998; U.S. Fish and Wildlife Service 1999; U.S. Army Corps of Engineers 2004) within an adaptive management framework (National Research Council 2002; Prato 2003).

Three recent publications have provided a catalyst for this shift. First, is the U.S. Fish and Wildlife Service's (USFWS) *Biological Opinion on Operation of the Missouri River Main-Stem Reservoir System and Operation and Maintenance of the Bank Stabilization and Navigation Project* (U.S. Fish and Wildlife Service 2001). The USFWS concluded that past and current operating plans and actions have jeopardized the continued existence of federally listed least tern, piping plover, and pallid sturgeon. To avoid jeopardy, the USFWS directed the U.S. Army Corps of Engineers to implement five "reasonable and prudent alternatives" (RPAs): (1) implement flow enhancement below Ft. Peck and Gavins Point dams (i.e., variability, volume, timing, and temperature) to provide hydrologic conditions necessary for species reproduction and recruitment; (2) restore, create, or acquire shallow-water, low-velocity channel and floodplain habitats, and sandbars in the lower river; (3) unbalance storage among the upper three reservoirs to benefit spawning fishes and increase availability of tern and plover sandbar habitat in riverine segments below reservoirs; (4) implement an interagency coordination team and a robust monitoring program to allow adaptive modification and implementation of management actions; and (5) increase pallid sturgeon propagation and augmentation efforts. The philosophy behind these recommendations is that both flow and habitat restorations are required to reduce jeopardy and recover the listed species. Evaluation of these projects is also necessary to assess progress towards these goals, and flexibility in actions is needed to respond to the uncertainty inherent in ecological systems.

Second, the U.S. Army Corps of Engineers' *Master Water Control Manual* directs operation of the main-stem dams on the Missouri River and is undergoing its first major revision since the reservoir system became operational in 1967. Its revision, as described in the *Revised Draft Environmental Impact Statement* (RDEIS, U.S. Army Corps of Engineers 2001), will affect future Missouri River flow management and be an integral part of implementing the USFWS's RPAs. Six alternative operating plans for the reservoirs were evaluated. One is the status quo or Current Water Control Plan. A second alternative contains four features: increased drought conservation measures, changes in Ft. Peck Dam releases to provide warmer water temperatures and a spring flow pulse for pallid sturgeon spawning, unbalancing the upper three reservoirs to benefit recreational fisheries, and adaptive management. The four other alternatives include a range of spring-rise enhancements and decreased summer releases from Gavins Point Dam to more closely approximate historical conditions. Differences among the four alternatives relate largely to magnitude of release modifications and downstream river stage changes (see Jacobson and Heuser [2001] for a comparison of flow alternatives). As of this writing, no final alternative has been selected for implementation.

A third publication that should influence Missouri River management is a National Research Council Report: *The Missouri River Ecosystem: Exploring the Prospects for Recovery* (2002). It recommends four steps to lay the groundwork for Missouri River recovery: (1) legitimize and empower Missouri River managers with the authority and responsibility to actively experiment with river operations to enhance ecological resources; (2) convene a representative stakeholder committee to develop a basin-wide strategy, conduct assessments, review plans, and provide oversight of implementation of adaptive management strategies; (3) develop long-term goals and short-term measurable objectives for adaptive management actions; and (4) work with stakeholders to build commitment to, and acceptance of, changes in current patterns of benefits delivered from the river and reservoir system.

Numerous flow and habitat enhancement projects are ongoing within the Missouri River corridor. Instream flow reservations for fisheries have been secured for the Missouri and Yellowstone rivers and many of their tributaries in the upper Missouri drainage unit. Negotiations are ongoing between Montana Fish Wildlife and Parks and the U.S. Bureau of Reclamation to provide spring flow pulses out of Canyon Ferry Dam. A new program called the Conservation Reserve Enhancement Program

(CREP) expands the Conservation Reserve Program by allowing the U.S. Department of Agriculture to work with states and local interests to meet specific conservation objectives. Land along part of the Madison and Missouri rivers to Fort Peck Lake (919 km total) can be enrolled for conservation easements such as riparian protection from poor agriculture practices and for development assistance to farmers so they do not have to subdivide their land to survive. Most land is eligible that falls within 3.2-km along the river corridor.

Habitat acquisition and improvement projects in the lower Missouri River accelerated during the past 20 years and particularly since the floods of the 1990s. Over 20,000 ha of floodplain in Missouri have come under public ownership since the 1993 flood. Most of these lands will be managed using a combination of intensive and passive strategies to enhance river–floodplain connectivity and expand river channel top width (Galat et al. 1998). The newly established Big Muddy National Fish and Wildlife Refuge is targeting a total of 24,300 ha purchased from willing sellers. An additional 48,000 ha are authorized for acquisition and development by the Corps under the Water Resources Development Act of 1999 for the expanded Missouri River Bank Stabilization and Navigation Mitigation Project (U.S. Army Corps of Engineers 2004). Numerous Corps habitat mitigation projects have created or enhanced secondary channels and sandbars along the lower Missouri River, and expansion of this program is in progress. Should planned programs reach their acquisition and development goals, nearly 20% of the former lower Missouri River floodplain may be managed for natural resource benefits. Flood stages will be reduced as the river is allowed to expand laterally. Sandbars and braided channels will once again be common riverine features. Urban areas will be protected from devastating floods and the majority of the floodplain will remain dedicated to agriculture. Populations of native river and floodplain fishes are expected to benefit greatly from these actions.

Unfortunately, Missouri River rehabilitation efforts have seldom included explicit ecologically based objectives and performance measures. They are often site specific and driven by political realities rather than recovery of ecological processes. Equally important, they generally lack adequate pre- and postproject appraisals to evaluate progress towards restoration objectives and their outcomes. The result is that the "learning-by-doing" feedback loop essential to adaptive management is often missing. Other river (e.g., Kondolf 1995) and native fish (e.g., Minckley et al. 2003) restoration programs have experienced mixed success for similar reasons. Management agencies are encouraged to adopt a more holistic perspective for their activities to benefit the biological integrity of the Missouri River hydrosystem, rather than the single species approach emphasized by endangered species recovery plans. The National Research Council (2003) recently recommended that the Corps of Engineers adopt a set of principles and guidelines for successful restoration programs. We urge Missouri River restorationists to consider these in their project planning, execution, and evaluation. A well-designed, performance-based, restoration program should include relevant stakeholders and treat habitat rehabilitation and flow reregulation as an adaptive management experiment. Perhaps then, the public may one day experience a Missouri River more similar to what Lewis and Clark witnessed while enhancing diversity of contemporary socioeconomic benefits the river provides.

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Appendix A.—Distribution of Missouri River fishes by freshwater ecoregion, drainage unit, and physiographic province. Habitat use guild, habitat distribution, global conservation status, and population status are summarized by species. Numbers in parentheses refer to drainage units in Figure 1.

		Freshwater ecoregion/drainage unit																
		Upper Missouri		~Middle Missouri		Central Prairie		Physiographic province			Habitat use guild			Habitat distribution			Status	
Species name	Common name	Upper Missouri (18)	Little Missouri-White (16)	James-Sioux-Niobrara- Platte (15+14)	Nishnabotna-Chariton (12)	Lower Missouri (11)	Northern Rocky Mountains	Great Plains	Central Lowland	Ozark Plateaus	Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Main channel	Floodplain	Reservoir	Heritage global	Population
Ichthyomyzon castaneus	chestnut lamprey			N	N	N		S	M	M		X		C			G4	0
I. unicuspis	silver lamprey		N	N				S	S			X		C			G5	
Acipenser fulvescens	lake sturgeon			N	N	N			S	S		X		C	X		G3	–
Scaphirhynchus albus	pallid sturgeon	N	N	N	N	N		S	S	S	X			C		X	G1	–
S. platorynchus	shovelnose sturgeon	N	N	N	N	N		P	P	P	X			C		X	G4	–
Polyodon spathula	paddlefish	N	N	N	N	N		P	P	M		X		C	X	X	G4	–
Lepisosteus oculatus[1]	spotted gar			N	N	N			S	S			X	B	X		G5	U
L. osseus	longnose gar			N	N	N		M	P	P		X		C	X	X	G5	–
L. platostomus	shortnose gar	N	N	N	N	N		S	P	S			X	C	X	X	G5	0,–
Amia calva	bowfin				I	I			S	S			X	B	X		G5	U
Anguilla rostrata	American eel			D	D	D		M	S	P		X		C			G5	U
Alosa alabamae	Alabama shad					D				S		X		C			G3	–
A.chrysochloris	skipjack herring			N	N	N		S	S	S		X		C			G5	–
A. pseudoharengus[a]	alewife			I	I			S					X	C		X	G5	
Dorosoma cepedianum	gizzard shad		N	N	N	N		P	P	S			X	C	X	X	G5	+
D. petenense	threadfin shad					N			M	M			X	C		X	G5	+
Hiodon alosoides	goldeye	N	N	N	N	N		P	P	P		X		C	X	X	G5	0,–
H. tergisus	mooneye				N	N			S	S		X		C			G5	–
Coregonus artedi[a]	cisco, lake herring	I	I					S					X	W		X	G5	0
C. clupeaformis	lake whitefish	I	I					S					X	W		X	G5	0

Appendix A.—Continued.

		Freshwater ecoregion/drainage unit																
		Upper Missouri		-Middle Missouri		Central Prairie	Physiographic province				Habitat use guild			Habitat distribution			Status	
Species name	Common name	Upper Missouri (18)	Little Missouri-White (16)	James-Sioux-Niobrara Platte (15+14)	Nishnabotna-Chariton (12)	Lower Missouri (11)	Northern Rocky Mountains	Great Plains	Central Lowland	Ozark Plateaus	Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Main channel	Floodplain	Reservoir	Heritage global	Population
Oncorhynchus clarkii	cutthroat trout	N	I				M	M				X		W		X	G4	–
O. mykiss	rainbow trout	I	I	I		I	C	M		S		X		C		X	G5	+
O. nerka	sockeye salmon, kokanee	I					M					X				X	G5	0
O. tshawytscha	Chinook salmon	I	I					S				X		W		X	G5	+
Prosopium williamsoni	mountain whitefish	N					C	S				X		C		X	G5	U
Salmo trutta	brown trout	I	I	I			C	S				X		C		X	G5	0
Salvelinus fontinalis	brook trout	I					S	S				X		W		X	G5	U
S. namaycush	lake trout	I	I					S				X		W		X	G5	U
Percopsis omiscomaycus	trout-perch			N	N	N			S	S			X	W			G5	–
Osmerus mordax	rainbow smelt	I	I	I	I	I		S	S	S		X		C		X	G5	0,+
Esox americanus	grass pickerel			N		N		S	S	S			X	B	X		G5	U
E. lucius[2]	northern pike	I	N	N	I	I	S	P	P	S			X	B	X	X	G5	0,+
E. masquinongy	muskellunge		I	I		I		S		S			X		X	X	G5	U
Campostoma anomalum	central stoneroller		N	N	N	N		M	M	P	X			W		X	G5	+
C. oligolepis	largescale stoneroller					N				P	X			W			G5	
Carassius auratus	goldfish	I		I	I	I	S	S	S	S			X	C	X	X	G5	+
Couesius plumbeus	lake chub	N	N				P	M					X	B			G5	0
Ctenopharyngodon idella	grass carp			I	I	I		S	S	S		X		C	X		G5	+

Appendix A.—Continued.

Species name	Common name	Freshwater ecoregion/drainage unit: Upper Missouri: Upper Missouri (18)	Little Missouri-White (16)	~Middle Missouri: James-Sioux-Niobrara Platte (15+14)	Nishnabotna-Chariton (12)	Central Prairie: Lower Missouri (11)	Northern Rocky Mountains	Physiographic province: Great Plains	Central Lowland	Ozark Plateaus	Habitat use guild: Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Habitat distribution: Main channel	Floodplain	Reservoir	Status: Heritage global	Population
Cyprinella lutrensis	red shiner		N	N	N	N		P	P	P			X	C	X	X	G5	0,+
C. spiloptera	spotfin shiner			N	N	N		S	S	S	X			C		X	G5	
Cyprinus carpio	common carp	I	I	I	I	I	P	P	P	P			X	C	X	X	G5	0,–
Erimystax x-punctatus	gravel chub					N				P	X			W			G4	–
Gila atraria	Utah chub	I					M						X			X	G5	0
Hybognathus argyritis	western silvery minnow	N	N	N	N	N		P	P	S		X		C	X		G4	0,–
H. hankinsoni	brassy minnow	N	N	N	N		S	S	P				X	C	X	X	G5	0,+
H. nuchalis[a]	Mississippi silvery minnow		N	N		N		S	S	S		X		C		X	G5	U
H. placitus	plains minnow	N	N	N	N	N		S	P	P		X		C			G4	0,–
Hypophthalmichthys molitrix[a]	silver carp				I	I			P	P		X		C	X		G5	+
H. nobilis[a]	bighead carp			I	I	I		P	P	P		X		C	X		G5	+
Luxilus chrysocephalus	striped shiner					N				S	X			W			G5	
L. cornutus	common shiner		N	N	N	N		S	P	S		X		W		X	G5	0
Lythrurus umbratilis	redfin shiner				N	N			P	P	X			W			G5	0
Macrhybopsis aestivalis	speckled chub			N	N	N		P	P	P	X			C			G3G4	+,–
M. gelida	sturgeon chub	N	N	N	N	N		S	S	M	X			C			G3	–
M. meeki	sicklefin chub	N	N	N	N	N		S	S	M	X			C			G3	–
M. storeriana	silver chub			N	N	N		S	P	M			X	C	X		G5	–
Margariscus margarita	pearl dace	N	N					S				X		W			G5	U

Appendix A.—Continued.

Species name	Common name	Freshwater ecoregion/drainage unit: Upper Missouri: Upper Missouri (18)	Little Missouri-White (16)	~Middle Missouri: James-Sioux-Niobrara- Platte (15+14)	Nishnabotna-Chariton (12)	Central Prairie: Lower Missouri (11)	Physiographic province: Northern Rocky Mountains	Great Plains	Central Lowland	Ozark Plateaus	Habitat use guild: Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Habitat distribution: Main channel	Floodplain	Reservoir	Status: Heritage global	Population
Notemigonus crysoleucas	golden shiner	I	U	U	N	N		S	P	S			X	W	X	X	G5	U
Notropis atherinoides	emerald shiner	N	N	N	N	N		P	P	P			X	C	X	X	G5	+
N. blennius	river shiner			N	N	N		M	P	P	X			C			G5	+,–
N. boops	bigeye shiner					N			S	S	X			W			G5	0
N. buchanani	ghost shiner			N	N	N		S	S	S	X			C	X		G5	0,–
N. dorsalis	bigmouth shiner		N	N	N	N		P	P	S	X			C			G5	–
N. hudsonius	spottail shiner	I	I	I		N		P	S	S			X	C	X	X	G5	0,+
N. rubellus	rosyface shiner					N				P		X		W			G5	0,–
N. shumardi	silverband shiner		N	N	N	N		M	P	S	X			C			G5	
N. stramineus	sand shiner	N	N	N	N	N		M	P	M	X			C		X	G5	0,–
N. volucellus	mimic shiner			N	N	N		M	M	M			X	C	X		G5	0
N. wickliffi[a]	channel shiner					N			S	S	X			C			G5	
Phenacobius mirabilis	suckermouth minnow		N	N	N	N	S	P	P	M	X			C			G5	
Phoxinus eos	northern redbelly dace		N	N				S	S				X	W		X	G5	U
P. erythrogaster	southern redbelly dace					N				S		X		W			G5	+
P. neogaeus	finescale dace		N	N				S					X	W		X	G5	
Pimephales notatus	bluntnose minnow		I	N	N	N		S	P	P			X	B	X		G5	0,+
P. promelas	fathead minnow	N	N	N	N	N	M	P	P	S			X	C	X	X	G5	0,–
P. vigilax	bullhead minnow			I		N			M	M			X	C		X	G5	
Platygobio gracilis	flathead chub	N	N	N	N	N	M	P	S	S	X			C			G5	0,–
Rhinichthys atratulus	blacknose dace		N	N	U			S	S			X		W			G5	U
R. cataractae	longnose dace	N	N				P	P					X	C		X	G5	

Appendix A.—Continued.

		Freshwater ecoregion/drainage unit																
		Upper Missouri		~Middle Missouri		Central Prairie	Physiographic province				Habitat use guild			Habitat distribution			Status	
Species name	Common name	Upper Missouri (18)	Little Missouri-White (16)	James-Sioux-Niobrara Platte (15+14)	Nishnabotna-Chariton (12)	Lower Missouri (11)	Northern Rocky Mountains	Great Plains	Central Lowland	Ozark Plateaus	Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Main channel	Floodplain	Reservoir	Heritage global	Population
Semotilus																		
atromaculatus	creek chub	N	N	N	N	N		S	P	P			X	W		X	G5	0,+
Carpiodes carpio	river carpsucker	N	N	N	N	N		P	P	P			X	C	X	X	G5	0,–
C. cyprinus	quillback			N	N	N		P	S	S			X	C	X		G5	–
C. velifer	highfin carpsucker			N	N	N			S	S	X			C	X		G4G5	–
Catostomus catostomus	longnose sucker	N	N				P	P					X	C			G5	0,+
C. commersonii	white sucker	N	N	N	N	N	P	P	P	S		X		C		X	G5	0,+
C. platyrhynchus	mountain sucker	N					M	M			X			C			G5	0
Cycleptus elongatus	blue sucker	N	N	N	N	N		P	P	M	X			C		X	G3G4	0,–
Hypentelium nigricans	northern hog sucker					N				M	X			W			G5	U
Ictiobus bubalus	smallmouth buffalo	N	N	N	N	N		P	P	S			X	C	X	X	G5	–
I. cyprinellus	bigmouth buffalo	N	N	N	N	N		P	P	S			X	C	X	X	G5	–
I. niger	black buffalo			N	N	N			S	M			X	C	X		G5	–
Moxostoma erythrurum	golden redhorse			N	N	N			S	S		X		C			G5	U
M. macrolepidotum	shorthead redhorse	N	N	N	N	N		P	P	S		X		C		X	G5	0
Ameiurus melas	black bullhead	I	N	N	N	N		S	P	S			X	B	X	X	G5	–
A. natalis	yellow bullhead	I	I	N	N	N		M	M	S			X	B	X	X	G5	–
Ictalurus furcatus	blue catfish			N	N	N			P	P	X			C			G5	–
I. punctatus	channel catfish	N	N	N	N	N		P	P	P			X	C	X	X	G5	0,+
Noturus exilis	slender madtom				N	N			M	S	X			W	X		G5	U
N. flavus	stonecat	N	N	N	N	N	M	P	P	S	X			C			G5	0
N. gyrinus	tadpole madtom	N	N	N	N	N		S	P	S			X	B	X		G5	

Appendix A.—Continued.

		Freshwater ecoregion/drainage unit																
		Upper Missouri		~Middle Missouri		Central Prairie	Physiographic province				Habitat use guild			Habitat distribution			Status	
Species name	Common name	Upper Missouri (18)	Little Missouri-White (16)	James-Sioux-Niobrara- Platte (15+14)	Nishnabotna-Chariton (12)	Lower Missouri (11)	Northern Rocky Mountains	Great Plains	Central Lowland	Ozark Plateaus	Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Main channel	Floodplain	Reservoir	Heritage global	Population
N. nocturnus	freckled madtom					N			P	S	X			W			G5	
Pylodictis olivaris	flathead catfish		N	N	N	N		M	P	P		X		C		X	G5	0,–
Lota lota	burbot	N	N	N	N	N	P	P	S	S			X	C		X	G5	0,–
Fundulus diaphanus	banded killifish		U					S					X	W	X		G5	
F. notatus	blackstripe topminnow					I			M	S			X		X		G5	+
F. sciadicus	plains topminnow		N	N		N		S	S	S			X	W	X		G4	0
F. zebrinus	plains killifish	I	I	N	N	N		S	S	S			X	W	X		G5	0
Gambusia affinis	western mosquitofish				I	I			S	M			X	B	X	X	G5	+
Labidesthes sicculus	brook silverside				N	N			S	S			X	C			G5	0
Menidia beryllina	inland silverside					I			S	S			X	C		X	G5	+
Culaea inconstans	brook stickleback	N	N					M					X	W	X		G5	U
Morone americana	white perch			I	I	I		S	S	S		X		W		X	G5	
M. chrysops	white bass		I	U	N	N		P	P	S		X		C		X	G5	0,+
M. mississippiensis	yellow bass				N	N			S	S		X		C	X		G5	U
M. saxatilis	striped bass				I	I			S	S		X		W	X		G5	+
Ambloplites rupestris	rock bass		I	N		I		S	S	S			X	W		X	G5	0
Lepomis cyanellus	green sunfish	I	U	N	N	N		S	P	P			X	B	X	X	G5	U

Appendix A.—Continued.

		Freshwater ecoregion/drainage unit: Upper Missouri		~Middle Missouri		Central Prairie	Physiographic province				Habitat use guild			Habitat distribution			Status	
Species name	Common name	Upper Missouri (18)	Little Missouri-White (16)	James-Sioux-Niobrara- Platte (15+14)	Nishnabotna-Chariton (12)	Lower Missouri (11)	Northern Rocky Mountains	Great Plains	Central Lowland	Ozark Plateaus	Fluvial specialist	Fluvial dependent	Macrohabitat generalist	Main channel	Floodplain	Reservoir	Heritage global	Population
L. gibbosus[b]	pumpkinseed	I	I	I	I		S	S	S				X	W	X	X	G5	
L. humilis	orangespotted sunfish		U	N	N	N		S	P	M			X	B	X	X	G5	U
L. macrochirus	bluegill	I	I	U	U	N		P	P	P			X	B	X	X	G5	0,+
L. megalotis	longear sunfish					N		S	P	S			X	W			G5	0
L. microlophus	redear sunfish			I		I		M	M	S			X	B	X	X	G5	U
Micropterus dolomieu	smallmouth bass	I	I	I		N		P	S	S			X	C		X	G5	+
M. punctulatus	spotted bass			I	I	I		S	S	S			X	C			G5	U
M. salmoides	largemouth bass	I	I	N	N	N		P	P	S			X	B	X	X	G5	–
Pomoxis annularis	white crappie	I	I	N	N	N		P	P	M			X	B	X	X	G5	0,–
P. nigromaculatus	black crappie	I	I	N	I	N		P	S	M			X	B	X	X	G5	0,–
Etheostoma exile	Iowa darter	N	N	N				S	S				X	W	X		G5	
E. nigrum	johnny darter		N	N	N	N		P	S	S			X	B	X	X	G5	+,–
Perca flavescens	yellow perch	I	U	U			M	P	P				X	W	X	X	G5	0,–
Percina caprodes	logperch					N			M	S			X	W			G5	U
P. phoxocephala	slenderhead darter					N			M	S	X			W			G5	0,–
Sander canadensis	sauger	N	N	N	N	N		P	P	M			X	C	X	X	G5	0,–
S. vitreus[b]	walleye	I	U	U	U	U	M	P	P	S			X	C	X	X	G5	+
Aplodinotus grunniens	freshwater drum	N	N	N	N	N		P	P	P			X	C	X	X	G5	0,+
Cottus bairdii	mottled sculpin	N	N			N	P	S		S			X	C			G5	U

[a] species added since Cross et al. (1986); [b] status changed from Cross et al. (1986), see text for explanation. Symbols: N = native, U = uncertain, D = diadromous, I = introduced; P = prevalent/common, M = marginal/uncommon, S = sporadic/rare; C = channel, B = channel border, W = waif, X = present; + = increasing, 0 = stable, – = decreasing, blank = unknown, U = too uncommon to rank. Intermediate or differing intra-river trends reported as pairwise combinations of +, 0, and –. See text for explanation of Heritage Global "G" rankings.