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Barrier Effects on Native Fishes of Minnesota

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Abstract

To evaluate the effects of barriers on aquatic biodiversity, fish distributions upstream and downstream of 32 barrier dams on the mainstem or tributaries of the Mississippi, Minnesota, St. Croix, St. Louis, Missouri, and Red River of the North were assessed. Recolonization was assessed for eleven dams that were subsequently removed and had adequate post removal surveys. On average, species richness declined by 41% for complete barriers, 37% for near-complete barriers and 20% for barriers that are/were inundated at bankfull flows. A detailed assessment of the Cottonwood River Watershed indicated that a single barrier near the mouth of the river caused a watershed-wide loss of species richness.

Habitat generalists, tolerant (e.g., common carp, fathead minnow, black bullhead, white sucker) lake-oriented, headwater, and widely stocked species were the least likely to be absent upstream of barriers. Intolerant, stream-dependent, and imperiled species were the most likely to be absent upstream of barriers. Blue sucker, mooneye, paddlefish, sauger, shovelnose sturgeon, and flathead catfish were among 27 species absent upstream of all assessed barriers for watersheds in which they were present. A number of small-bodied species, like the carmine shiner, were also sensitive to fragmentation. Channel catfish and freshwater drum, hosts to 13 and 11 mussels were absent upstream of 61% and 64% of barriers, respectively.

Subsequent removal of 11 barriers resulted in upstream recolonization of an average of 66% of the species that had been absent. Removal also resulted in substantially higher catch per unit effort for a number of species, suggesting that an impact of fragmentation is reduced abundance of remaining riverine species. Removal of the Appleton Dam on the Pomme de Terre River resulted in recolonization of elktoe, deertoe, and plain pocketbook mussels; species that had been found only as dead shells in surveys prior to the dam's removal. These findings suggest that barrier dams, while often ineffective for control of common carp, are among the most profound and definitive causes of native biodiversity losses in Minnesota waters.

The fragmentation of North American Rivers is extensive with more than 87,000 U.S. dams over 6 feet high registered in the 2013 National Dam Inventory. Of these 1,078 dams are fragmenting Minnesota streams. Additional small dams, impassable culverts, and other barriers further fragment rivers and streams throughout the nation.

The effects of dams on fish migrations and the decline of migratory species have been acknowledged for over 300 years. In France, design of fish passage facilities began by the 17th century (McDonald 1887; Rajararnam and Katopodis 1984). In North America, conflicts between dam builders and commercial fisherman became intense by 1780 with the "shad wars" as new dams extirpated anadromous American Shad from East Coast rivers (Watson 1996). In Minnesota, Woolman (1895) recommended installation of fish passage for all dams. Most of this early awareness of barrier effects was centered on anadromous game species, such as salmon (those that migrate from the ocean to freshwater or upstream to spawn).

A number of more recent studies have associated barriers with the extirpation of strictly freshwater species and with reduced biodiversity in the North Central United States and Canada (Aadland et al. 2005; Santucci et al. 2005; Catalano et al. 2007). Santucci et al. (2005) found higher fish IBI scores, higher macroinvertebrate condition index scores, higher quality habitat, and more consistent compliance with water quality standards in free-flowing reaches of the Fox River, Illinois than was found in impounded reaches.

Migration of fish is associated with spawning; optimal foraging; seasonal changes in habitat needs and accessing winter habitat; and recolonization following drought or water quality related mortality. Migration may be especially critical in northern latitudes due to harsh winter conditions that can a) cause anoxia, reduction of habitat volume, super-cooled water, frazil and anchor ice and b) result in increased stress, prevalence of disease, and mortality. For example, the majority of species found in a west central Minnesota watershed were observed making seasonal migrations through fishways on the Otter Tail River and fish densities of all species in an upstream reach declined substantially in mid-winter suggesting downstream migration out of the reach (Aadland 2010).

As with fish, the role of dam construction in the decline of mussels has been acknowledged for over a century. In an assessment of mussels in Minnesota, Wilson and Danglade (1913) state, "A dam or natural fall, impassable for fish, may mean the entire absence of mussels in the river above." Dam construction has been cited as the primary cause of all recent (roughly 20 species) mussel extinctions in North America (Haag 2009). North America is analogous to tropical rainforests in terms of mussel species richness, with more species than any other continent, but 71.7% are listed as special concern, threatened, or endangered (Williams et al. 1993). The ecological implications of mussel declines are extensive due to their roles in stabilizing stream beds (Zimmerman and de Szalay 2007), increasing diversity of other benthic invertebrates (Gutierrez et al. 2003; Spooner and Vaughn 2006), and water filtration (Newton et al. 2011).

In addition to the loss of biodiversity, dam construction and fragmentation have also been shown to increase the prevalence and dispersal of aquatic introduced species. Johnson et al. (2008) found invasive species to be 2.4 to 300 times more likely to occur in reservoirs than in natural lakes. For example, the Illinois River has been channelized, has had severe water quality impairments throughout its history, and is entirely impounded by dams. It is also believed to have the highest densities of silver carp in the world, which became established in the river around 2000 (Sass et al. 2010).

For clarity, we are defining a species as **native** (indigenous) if its presence is the result of only natural processes, with no human intervention. In contrast, a species is **introduced** (non-native, alien, exotic, non-indigenous) if it is living outside its native range and has arrived there by human activity, either deliberate or accidental.

Diagnosis of barriers as the cause of reduced biodiversity is verified where barriers have been removed and species recolonize (Garvey et al. 2012). Kanehl et al. (1997) found moderate declines in carp abundance and major increases in smallmouth bass abundance following removal of the Woolen Mills Dam, Wisconsin. Removal of the Stronach Dam, Michigan resulted in recolonization of 8 species found only downstream of the dam and an increase in abundance of 18 of 25 species sampled (Burroughts et al. 2010). The removal of dams has increased recently due to structural instability of aging dams and increased awareness of the ecological damages associated with them (Aadland 2010).

The introduction of common carp in the 1880s and later declines in their popularity initiated construction of fish barriers as early as 1927 (Hoffbeck 2001). Subsequently, numerous carp barriers have been constructed across Minnesota including dams, electric barriers, screens, and high velocity culverts. These provide the opportunity to evaluate barriers targeting common carp in terms of effects on common carp and native assemblages.

Since the effects of introduced carp and other aquatic introduced species on native species is a primary cited concern, the evaluation of barriers on native species is fundamental to evaluating the efficacy of barriers as an introduced species deterrent. Nationally, most studies have focused on the effects of barriers on game species with relatively few evaluations of the effects of barriers on aquatic biodiversity.

A fish screen on Six Mile Creek near Lake Minnetonka in 1965. *Credit Minnesota Historical Society.*

The Methods

The Effects of Dams on Fish Diversity

As a means of addressing the effects of barriers on native fishes in Minnesota, the presence/absence of fish species in the upstream versus downstream watersheds of 32 dams throughout Minnesota was analyzed. The dams assessed are, or were, located in tributaries and mainstems of the Minnesota, Red River of the North, St. Croix, St. Louis, Missouri and Mississippi river watersheds (Figure 1). Geo-referenced fish records from the Minnesota DNR-Fisheries, MN DNR-Ecological and Water Resources, Pollution Control Agency, university collections, the Bell Museum, and other reliable sources were used to tabulate the presence and absence of fish above and below the barriers. Much of the data is available through the Department's "Fish mapper" tool (Fish Mapper website: http://www.dnr.state.mn.us/maps/fom/index.html) but more recent Stream Habitat Program and Fisheries records were acquired directly from Area Offices.

Dams that are frequently inundated and passable during high flow conditions were not included in this assessment. Of the 32 dams assessed, nineteen were complete blockages, nine were near-complete blockages (may be passable during 10 year or larger floods), and four were moderate blockages (may be passable during 2 year or larger floods). Two of the complete blockage dams were built on natural barriers, Redwood Falls and St. Anthony Falls. Fourteen of the dams have been subsequently removed or modified for fish passage and safety.

Major floods can inundate even relatively large dams making them passable for a brief yet key period of time; therefore, the results needed to be put in context for the occurrence of these large floods. Many dams also have experienced partial or complete failures during their existence - some dams have failed multiple times. Flood and failure events were considered in the analysis. Inundation may or may not create passable conditions for a long enough duration or at the right time of year for recolonization by a given species.

Only the downstream-most major barriers on the chosen tributaries were assessed. Several rivers had a series of closely spaced dams with little or no sampling effort in between them so the potential affect by each barrier could not be assessed.

Since fish records comprised a wide range of gear types and sampling effort, sample abundance was not quantified in the analysis and was handled as "present" or "absent". While presence/absence data handling was necessary, barriers can substantially reduce population size without extirpating the species entirely or major floods may allow a few individuals to pass. As a result, many species identified as "present" may not represent viable populations.

Unfortunately, for most cases, the historic pre-barrier species diversity and abundance is unknown because dams were built as early as the 1850s which pre-dates fish sampling by trained fisheries biologists or taxonomists.

For each barrier dam fish distributions were handled on a watershed basis upstream and downstream. If there were records of a species within the contributing watershed upstream of a barrier, it was considered "present". The exceptions to this were a couple of cases where a native species was known to have been stocked in a relatively isolated lake in the watershed but was absent from the rest of the basin, it was considered "absent".

Only species found in the river or tributary being assessed were included in the analysis as potential species for that tributary. Species found in larger mainstem rivers downstream were not included in the analysis for that tributary. This was done to avoid inclusion of species that may require larger river habitat that may not exist in the tributary. In several cases this limited the list of potential species where dams were close to the mouth of the tributary because few samples were collected between the barrier and the mouth.

Downstream effects on fish diversity were not quantitatively assessed due to the complexities of assessing effects attributable to a single barrier. Migration barriers have caused downstream basin-wide extirpations when they block access to critical spawning habitat. Large rivers, however, may have multiple tributaries that provide suitable spawning habitat so effects were evaluated only for the tributary watershed.

Distribution after removal or failure of a dam was also assessed for some structures to separate habitat or water quality effects from those attributable to the barrier. Since most dam removals have been relatively recent, several tributaries have had no surveys since removal. For most sites, significantly less sampling effort was available post-removal than for pre-removal. Pre and post dam construction records of species that were absent upstream following dam construction

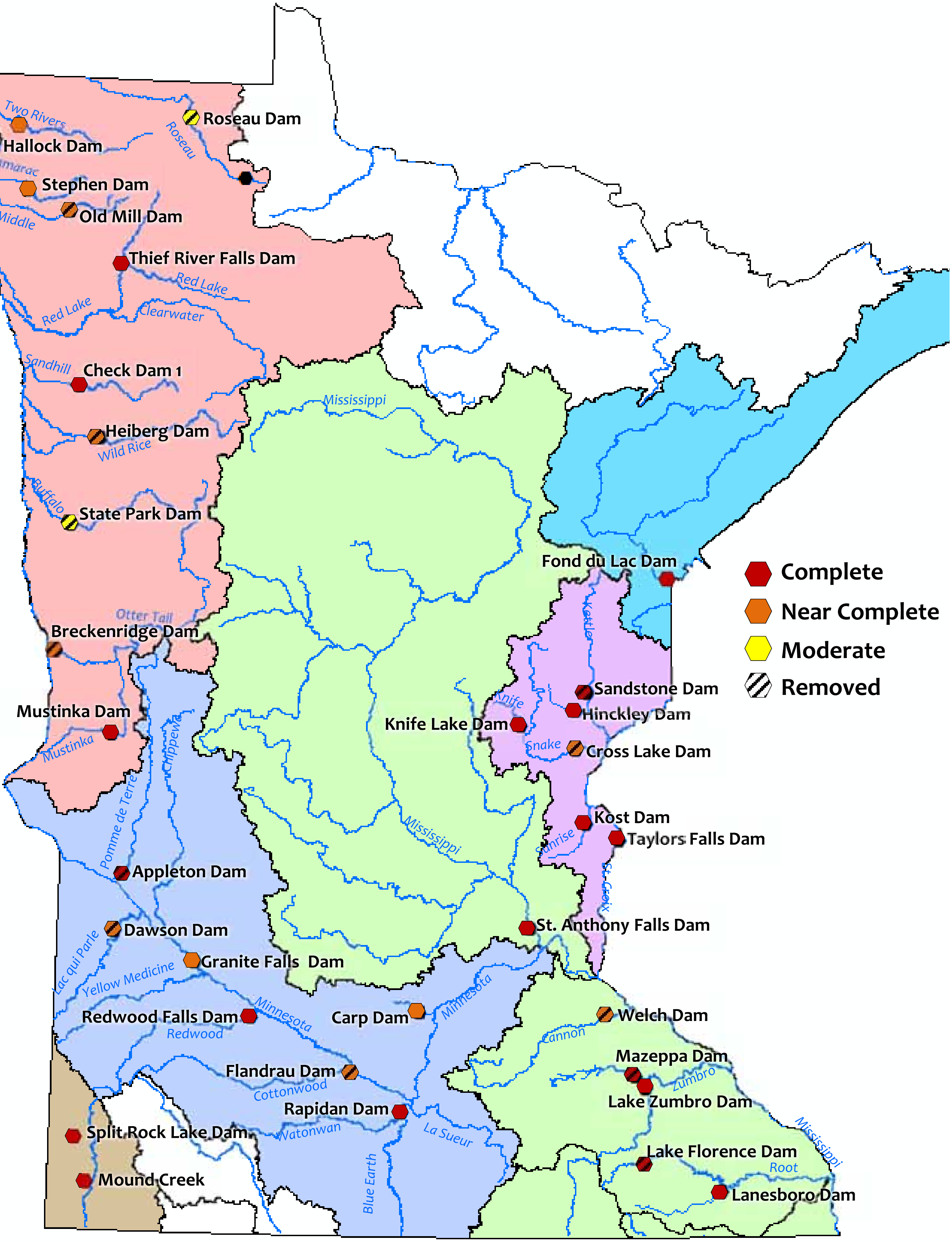


Figure 1. The locations, effectiveness, and current status of the 32 dams included in the barrier assessment.

were also considered as evidence that the barrier-caused the extirpation.

Relative vulnerability of species to barrier-caused extirpation was assessed as a percentage of watersheds where they were present in the watershed but were not found upstream of the barrier. This was put in the context of habitat, thermal regimes, introductions or stocking and other factors. Relative vulnerability was also assessed as a function of environmental tolerance (tolerant/intolerant species) and imperiled status (special concern, threatened, and endangered).

The Effects of a Dam on Watershed Scale Fish Diversity

To address relationships between watershed area, biodiversity, and barrier effects, a detailed assessment of the Cottonwood River Watershed was completed. Flandrau Dam, originally built in 1937 near the mouth of the Cottonwood River, blocked most of the watershed from the Minnesota River. The dam failed in 1947 and was rebuilt the following year but a number of fish surveys were conducted in 1948 during the time when the dam was passable. The dam also failed in 1965 and 1969 but was rebuilt each time and no available fish surveys were conducted upstream of the dam site during these dam breaches. The dam was finally removed in 1995. This dam and fish sampling history provided assessment of a short duration open river condition followed by nearly 50 years of fragmentation then a final period of surveys following the dam's removal. Watershed area and stream mile distance from the mouth of the Cottonwood River were measured for each site and associated with general habitat type and species composition.

Results and Discussion

Barrier Effects on Upstream Fish Diversity

Of the 32 barriers evaluated, an average of 37% (3% to 78%) of the species sampled in the watershed were absent from collections upstream of the barrier (Table 1 and Table 2). The fish records analyzed included a total of 150 species including 16 non-native and 134 species that are considered native to Minnesota. The extent of species absent upstream was higher among the more effective barriers.

Table 1. Summary of Barrier Effects on Species Richness

Barrier Effectiveness	# of Dams Assessed	Average % Absence
Complete	19	41%
Near Complete	9	37%
Moderate	4	20%
Overall Average	***32***	***37%***

The percentage of species absent above natural barriers at St. Anthony Falls (50%) and Redwood Falls (36%), which have likely been barriers for thousands of years, were within the range of that for complete barrier dams (15-73%). This suggests that barrier-caused extirpation can happen within a short time frame (decades). Rivers upstream of natural barriers tend to have lower species richness. It is unknown if absent species were never able to colonize upstream of the barrier or if some fish species were historically there then extirpated.

The absence of a species from surveys upstream of a barrier has several potential explanations:

1) The species was extirpated as a result of the barrier.
2) The species is present but was not collected in the surveys.
3) The upstream reach lacks suitable habitat for the species.

Significant sampling effort, a diversity of habitat upstream of the dams, and the abrupt upstream extent of the species at the dam site favors barrier-induced extirpation as the explanation of species absences for most sites and most species. However, a number of factors need to be considered in determining whether the upstream absence of a species is attributable to the barrier or if habitat, water quality, stream size, temperature regimes, hydrology, statistical probabilities, or other

Watershed	Barrier Name Year Built, Year Removed	Dam height at low flow (ft) Barrier Effectiveness	Watershed area (mi^2) upstream of dam / total % of watershed upstream of dam	Total # of native species observed in watershed Additional introduced species	# of Native MN species absent upstream of barrier (% of total)
Red River of the North Basin					
Otter Tail River	**Breckenridge Dam** 1935. Replaced with rock ramp in 2007	8 Near Complete	1,910 / 1,952 97.8%	75 1	9 (12%)
Mustinka River	**Mustinka Dam** 1940	18 Complete	163 / 861 18.9%	30 1	15 (50%)
Buffalo River	**State Park Dam** Pre-1893, 1937 Removed in 2002	3.5 Moderate	325 / 975 33.3%	58 1	21 (36%)
Wild Rice River	**Heiberg Dam** 1875. Removed in 2006	8 Near Complete	934 / 1,560 59.9%	61 1	16 (26%)
Sand Hill River	**Check Dam 1** 1955	10 Complete	308 / 420 73.3%	36 1	15 (42%)
Red Lake River	**Thief River Falls Dam** 1946	16.75 Complete	3,450 / 5,680 60.7%	64 3	13 (20%)
Middle River	**Old Mill Dam** 1886, 1938. Removed in 2001	8.5 Near Complete	225 / 779 28.9%	32 1	25 (78%)
Tamarac River	**Stephen Dam** 1975	12 Near Complete	283 / 397 71.3%	37 1	9 (24%)
Roseau River	**Roseau Dam** 1932. Replaced with rock ramp in 2001	5 Moderate	474 / 1,420 33.4%	44 1	10 (23%)
South Branch Two Rivers	**Hallock Dam** 1938	8 Near Complete	592 / 1,100 53.8%	42 1	13 (31%)
St. Croix River Basin					
St. Croix River	**Taylors Falls Dam** 1890, 1907	50 Complete	6,240 / 7,650 81.6%	106 5	31 (29%)
Snake River	**Cross Lake Dam** 1800s, 1938, 1963. Modified with rock ramp in 2013	2 Moderate	974 / 1,009 96.5%	68 1	2 (3%)
Knife/Snake River	**Knife Lake Dam** 1983	14 Complete	92/1,009 9.1%	68 1	33 (49%)
Kettle River	**Sandstone Dam** 1908. Removed in 1995	20 Complete	868 / 1,060 81.9%	64 5	22 (34%)
Grindstone River	**Hinckley Dam** 1955	10 Complete	77 / 1,060 7.3%	64 5	30 (47%)
Sunrise River	**Kost Dam** 1885	13 Complete	268 / 283 94.7%	64 2	19 (30%)

Table 2. Watersheds assessed for barrier effects on fish species richness. Barrier effectiveness is based on dam height and frequency of inundation by floods; Complete = complete barrier, Near Complete = near complete barrier that may be passable during large floods (10-year or larger), Moderate = moderate flood barrier that may be passable during moderate floods (2-year or larger).

Watershed	Barrier Name Year Built, Year Removed	Dam height at low flow (ft) Barrier Effectiveness	Watershed area (mi²) upstream of dam / total % of watershed upstream of dam	Total # of native species observed in watershed Additional introduced species	# of Native MN species absent upstream of barrier (% of total)
Lower Mississippi River Basin					
Mississippi River (upstream of Iowa border)	**St. Anthony Falls Dam** 1848, 1963	49 Complete	19,100 / 65,000 29.4%	127 8	64 (50%)
South Branch Root River	**Lanesboro Dam** 1868	28 Complete	284 / 1,250 22.7%	93 4	57 (61%)
North Branch Root River	**Lake Florence Dam** 1857. Removed in 1993	12 Complete	119 / 1,250 9.5%	92 4	65 (70%)
Zumbro River	**Lake Zumbro Dam** 1919	55 Complete	845 / 1.150 73.5%	89 4	27 (30%)
North Fork Zumbro River	**Mazeppa Dam** 1922. Removed in 2001	20 lowered to 10 Complete	174 /1,150 15.1%	89 4	65 (73%)
Cannon River	**Welch Dam** 1900. Removed in 1994	8 Near Complete	1,340 / 1,440 93.1%	82 5	19 (23%)
Minnesota River Basin					
Minnesota River	**Granite Falls Dam** 1911	17 Near Complete	6,180 / 16,200 38.1%	97 4	39 (40%)
High Island Creek	**Carp Dam** 1958	6 Near Complete	206 / 241 85.5%	47 1	30 (64%)
Blue Earth River	**Rapidan Dam** 1910	55 Complete	2,410 / 3,486 69.1%	66 1	26 (39%)
Cottonwood River	**Flandrau Dam** 1937, Was repeatedly damaged by floods & was removed in 1995	28 lowered to 12 Near Complete	1,310 / 1,313 99.8%	65 2	24 (37%)
Redwood River	**Redwood Falls Dam** 1902	34 Complete	630 / 665 94.7%	53 2	19 (36%)
Pomme de Terre River	**Appleton Dam** 1872. Removed in 1999	13 – 16 Complete	905 / 915 98.9%	65 1	17 (26%)
Lac qui Parle River	**Dawson Dam** 1913. Replaced with rock ramp in 2009	8 Moderate	472 / 1,156 40.8%	41 1	8 (20%)
Missouri River Basin					
Mound Creek	**South Dam** 1936	14 Complete	16.8 / 17.2 97.7%	29 1	9 (31%)
Split Rock Creek	**Split Rock Dam** 1937	24 Complete	45 / 320 13.9%	26 1	10 (38%)
Lake Superior Basin					
St. Louis River	**Fond du Lac Dam** 1924	78 Complete	3.600 / 3,634 99.1%	62 11	9 (15%)

factors are responsible. Conversely, the presence of an individual does not necessarily indicate that the species is unaffected by the barrier or representative of a viable population. A number of species are routinely stocked, masking barrier effects on a population. Ultimately, historical pre-barrier records or those following removal of barriers indicate the ability of a species to exist or thrive in the river reach. These considerations warrant further discussion given their implications for barrier effects.

Considerations in Fragmentation Assessment

Historical Context of Fish Distribution Data It was not possible to comprehensively determine species distributions prior to watershed fragmentation since most of the watersheds evaluated had barrier dams by the mid- to late 1800s and did not have systematic fish surveys until the mid-1900s. Archeological surveys, some early explorers like Alexander Henry (1799 – 1808), George Featherstonhaugh (1835), and others who took detailed notes provide useful historical data on easily identified food fishes like lake sturgeon, walleye, channel catfish, and freshwater drum. Most species were not targeted until much later when biological surveys started. Woolman (1895) surveyed the upper Minnesota and Red River watersheds in the 1890s to 1910s. Surber (1923) primarily surveyed eastern Minnesota streams in the 1920s. However, most fish surveys did not occur until after 1940.

The late timing of initial surveys makes the early distribution data a baseline for a significantly impaired condition, not pre-human influence, in most watersheds. Land-use changes, dam construction, unregulated overfishing, and severe water pollution likely limited or extirpated many of the pre-settlement species prior to any surveys. The Mississippi River was an anoxic "dead zone" from the Twin Cities to Hastings from the about 1885 to the 1980s due to raw sewage effluent until the Clean Water Act and other legislation forced construction of water treatment plants. Release of raw sewage was typical for municipalities located on rivers and streams. The St. Louis, Rainy, and other relatively undeveloped watersheds were heavily polluted with paper mill effluent and massive logging drives. The Otter Tail River had repeated fish kills due to discharges of whey and other cheese by-products into the early 1990s. As a result, it is likely that many species absent from early records probably existed in Minnesota waters prior to these changes. Improved treatment of human waste does appear to be allowing some species to return to Minnesota waters.

Climate change will likely have implications for what species will be here in the future as it has in the past. As a result of the relatively recent glaciation of most of Minnesota and subsequent warming of waters over the past 14,000 years, most of our fish assemblage would have been invaders as thermal regimes and habitat changed. River systems of Northern Europe are less diverse than similar sized rivers in North America due, in part, to the north-south orientation of the Mississippi River that allowed recolonization from southern refugia compared to the East-West orientation of the Danube and other European rivers that would not have had southern un-glaciated refugia (Oberdorff et al. 1997). Under current anthropogenic climate change, southern species may expand into Minnesota waters while cold-water species may decline as thermal regimes change (Stefan and Hondzo 1991). Some species have already shown changes in abundance, northerly extent of range, and timing of spawning attributable to climate change (Schneider 2010).

Species Introductions and Stocking A number of the game and bait species native to Minnesota are widely stocked and this includes water to which they may not have historically been native to. Routine stocking likely masked the effects of fragmentation for walleye, channel catfish, smallmouth bass, and other species. Walleyes are migratory and likely susceptible to effects of fragmentation but are so widely and regularly stocked that these effects are very difficult to assess. Many of these occurrences do not represent viable populations or meta-populations as indicated by the need for ongoing stocking. Stocking is less common where natural reproduction occurs.

Habitat Type, Habitat Diversity, and Length of Free-Flowing River Fish distributions are defined by habitat, which is a function of geology, watershed size, slope, hydrology, climate, and other factors. Habitat also can be defined by temporal (diurnal, seasonal, annual), life stage (spawning, eggs, fry, juvenile, adult) and spatial (microhabitat, mesohabitat, watershed) scales. For many stream fish species, habitat overlaps large spatial areas and includes a diversity of microhabitat types for successful completion of life cycles (Aadland and

Kuitunen 2006). The length of stream required is likely to be dependent on the availability of the full suite of habitats needed to complete each life history stage. Since year to year climate and hydrology can dramatically affect habitat suitability and reproductive success, a network of connected habitats increases resilience to drought and poor spawning conditions.

Lake sturgeon may require 155 to as many as 620 miles of free-flowing river to maintain a healthy population (Auer 1996). Sturgeon have been observed visiting multiple spawning rapids before actually spawning. This likely increases reproductive success as the suitability of individual rapids varies with the flows and water temperatures each year. The fact that the St. Croix River has retained a viable lake sturgeon population upstream of the St. Croix Falls dam may be due to the availability of spawning rapids, large river habitat and considerable length of free-flowing river in the watershed upstream of the dam. However, a number of species have disappeared from the St. Croix and similar watersheds despite the presence of diverse habitats. Blue sucker maintained a presence upstream of the St. Croix Falls Dam until the 1970s but haven't been sampled there since.

Conversely, tolerant, generalized species are often able to maintain populations within much shorter river reaches. For example, common carp, black bullheads, fathead minnows, and a number of other tolerant lake species can complete life histories within a single isolated lake.

Stream and Watershed Size It is logical that large fish would require a minimum stream and watershed size but amazingly large fish are found in small streams and watersheds when they have access to them. For the largest fish species, presence in smaller streams may only occur during spawning and high flows or as juveniles. Large-bodied fish like flathead catfish risk stranding or predator attacks if present or trapped in small streams as flows recede. As shown in the picture below, a large flathead was found stranded in a riffle in the Yellow Medicine River in July 2009. This fish may have been killed by the eagle observed feeding on it. The presence of connected lakes or deep pools in a watershed can provide vital refugia for these large bodied fishes.

Interestingly, the smallest watershed assessed in this study, the Grindstone River (77 mi^2), had historical records of MN's largest fish species, the lake sturgeon (which can grow to 10 feet and 400 pounds), found in Grindstone Lake (20 mi^2 watershed). Since lake sturgeon spawn in rapids, these fish, at some point in their life, would have had to leave the lake and swim up the Grindstone River, which is about 20 feet wide at the lake outlet. Lake sturgeon have been observed spawning in the Moose Horn River where the drainage area is 112 mi^2. The largest paddlefish on record was 85 inches long and weighed 198 pounds. It was speared in Lake Okoboji, Iowa where they were once abundant, but are now extirpated, likely due to barrier dams. Paddlefish also spawn in rivers (riffles and rapids) so would have needed to ascend the Little Sioux River and the outlet creek, which is about 50 feet near the lake outlet (141 mi^2). These small streams and watersheds may be very important migratory pathways as well as spawning and nursery habitat for large-bodied fish, even though spawning adults may only be present briefly during high spring flows to spawn.

Watershed size and the location of the dam in the watershed also had statistical implications due to relative sampling effort. Several of the assessed barriers were near the mouth of the watershed being assessed so that most of the sampling effort and watershed area was upstream of the barrier. The limited number of samples downstream of the barrier results in a low number of potential species listed as "absent" upstream of the barrier (as it reduced the number of potential species considered present in the watershed). For instance, 99.8% of the Cottonwood River's watershed is upstream of the Flandrau Dam site, so only samples from a very short reach downstream of the dam and upstream of the Minnesota River confluence added species to the watershed total that were inferred to potentially exist upstream in the absence of the barrier. Despite the short segment of free-flowing river in the watershed downstream of the dam, 24 species (37% of the watershed total) were collected downstream of Flandrau Dam that were not collected above it.

Partial Barriers Four of the 32 dams assessed in this study are not complete barriers during moderate floods. Furthermore, some of these and others assessed have failed periodically over their history. The occasional flood flows and dam failures potentially allowed individuals of extirpated species to migrate upstream of the barrier. This may explain the relatively intact fish community upstream of the Cross Lake Dam on the Snake River. This dam was only 2 feet high but since it was built on natural rapids with steeper slopes over bedrock, velocities were high during major floods. The fact that only

A dead flathead catfish, apparently killed by a bald eagle, in a riffle in the Yellow Medicine River, July 2009. Fingerling flathead catfish have been caught at this site suggesting that the small river, though generally lacking deep water adult habitat, may be important for reproduction. *Credit DNR Stream Habitat Program.*

2 species were absent upstream of the dam may indicate that fish were able to pass this barrier recurrently during bankfull and higher flows. Lake sturgeon, extirpated above most barrier dams, have maintained a presence upstream of this dam. However, the photo below of sturgeon caught in rapids below the upstream Bean Dam suggest that historic sturgeon populations were much higher. Sturgeon were observed below the Cross Lake Dam unsuccessfully attempting to migrate upstream. It has since been modified for fish passage.

Locks & Dams The lock & dam system on the Mississippi River is a series of partial barriers that provide limited passage through the lock chambers or during high flows when the gates are open. Passage may vary by species and by lock & dam size and height. Tagged silver carp moved upstream through lock & dam #26 through #20, up to #19, during “closed” gate conditions almost as readily as during open gate conditions and were able to pass under gates that were not entirely closed (Brooks et al. 2009). Native species generally had much lower success in passing the dams. Paddlefish and blue catfish were impeded more than other fish species. The near-extirpation of skipjack herring and declines of other native species have been attributed primarily to the construction of the 36 foot-high Lock & Dam 19, which is a complete barrier except through the lock chambers (was completed in 1913 and is located at southern tip of Iowa).

Current fish assemblages of the Upper Mississippi River, and as a result potential assemblages of Minnesota tributaries, are likely limited by the lock & dam system and the associated habitat fragmentation and inundation (when compared to historic assemblages). This is especially significant when the anoxic dead zone between the Twin Cities and Hastings is considered since all current fish and mussel species in that reach would have needed to recolonize after sewage treatment plants improved water quality in the 1980s. The limited passage of native species through the Lock & Dam System likely allows more species to exist upstream that would not be present if they were complete barriers. Improved passage through these lock and dams would allow species like skipjack herring, American eel, paddlefish, and many others to increase in abundance. Conceptual designs for nature-like fish passage through the entire lock & dam system was proposed in 2006. Commercial fisherman described catching large “shovelnose sturgeon” over 50 pounds in Minnesota waters of the Mississippi (Mike Davis, DNR ecologist, personal communications). These likely would not have been shovelnose sturgeon, which do not get that large, but similar looking pallid sturgeon. Blue catfish (for which early records exist), pallid sturgeon and other species that may have been part a free-

A large pile of sturgeon speared in rapids below Bean Dam on the Snake River in 1912. *Photo taken by Herman Schmidt.*

flowing fish assemblage in Minnesota waters may also recolonize with improved connectivity of the Mississippi River.

Presence versus Viable Population The presence of a species upstream of a barrier does not confirm that the population is maintaining a viable population. For instance, surveys on the Red Lake River in 1996 and 2001 each collected a single channel catfish upstream of the Crookston Dam. Surveys following its removal (2005) in 2005 and 2011 collected 222 and 255 catfish respectively. Some long lived species can retain a presence long after functional extirpation. Lake sturgeon can live over 150 years. Large adults were caught in large lakes of the Red River Basin as late as 1947, which is over 50 years after suitable spawning habitat had been largely eliminated or blocked. Some mussel species have been aged to over 200 years so can also retain a presence many years after they can no longer reproduce due to the loss of their host species. Following the definitions used in this study, a single individual caught anywhere in the watershed upstream of a dam precluded the species from being considered “absent”.

Thermal Regimes Many tributaries to the Mississippi River in southeastern MN have cold-water headwater reaches with warm-water downstream reaches. Some of these streams have warm headwaters starting in the plains, followed by cold, groundwater-fed middle reaches through the bluffs, and finally warmer lower reaches near their confluence with the Mississippi. These thermal regimes dictate the presence, range and migratory boundaries of coldwater species during the summer months. During winter, all Minnesota waters are cold and may allow dispersal of these coldwater species to other groundwater-fed streams. Generally, headwater species associated with cold water were not absent above barriers assessed here.

Downstream Effects Downstream effects of barriers on fish diversity were not directly assessed due to the difficulty of determining whether a specific dam was the causative factor. The decline of many species, however, has been attributed to the loss of upstream spawning habitat. Since dams are frequently built in high gradient reaches (Minnesota Falls, Granite Falls, Rapidan, Taylors Falls, etc.) they not only block migrations but inundate these critical habitats. In addition, many are known to make seasonal spring migrations up smaller tributaries to spawn followed by downstream migrations back into the larger river. This short but critical presence in the stream makes them unlikely to be collected, especially since most stream surveys are done in late summer. By eliminating spawning habitat it is likely that many of the barriers assessed have substantial effects on downstream fish communities that, based on observed migration distances, may extend hundreds of miles.

Access to Refugia To maintain populations, species require available microhabitat for all life stages (spawning, fry, juvenile, and adult). They also need to be able to survive droughts and extreme winter conditions that may reduce or eliminate available habitat. Hydrologically stable streams and those with numerous lakes that maintain suitable dissolved oxygen levels through winter in their watersheds (such as the Otter Tail, Red Lake, and Cannon Rivers) generally retained more species upstream of barriers than those prone to low flows or that have few or no lakes. The lakes or stable base flows may provide habitat refugia during drought conditions that would not exist in stream reaches that stop flowing. Lakes that become anoxic in winter, like many in the agricultural watersheds of southern Minnesota, generally do not provide suitable refugia except for species tolerant of very low oxygen. Northern pike have been shown to migrate out of winterkill lakes and into connected streams as oxygen refugia (Tonn and Magnuson 1983). These lake–stream interactions may be very important to sustaining biodiversity in these watersheds.

Relative Vulnerability to Barrier-Caused Extirpation by Species

Of the 32 dams and 150 species evaluated, most native species were found to be vulnerable to extirpation by barriers. All 134 native fish species for which there were records were ranked according to vulnerability to barrier-caused extirpation. This was determined by the percentage of barriers upstream of which they were absent divided by the number of watersheds in which they were present (Table 3. and Table 4. starting on page 28). A total of 27 native fish species were absent upstream of every barrier (100%) for watersheds where they were found. Sixty-six native species were absent upstream of at least half of the barriers for which they were assessed. As already discussed, these results must be tempered by sample size and influence of the factors discussed previously.

The data suggest that imperiled species (special concern, threatened, and endangered) are particularly vulnerable to fragmentation by barriers (Figure 2). Species that have imperiled status in Minnesota and are imperiled or extirpated in adjacent states were most prevalent in the upper quartile of vulnerability (75-100 % absence) to barriers. This is consistent with other studies that have cited dams as a primary threat to imperiled species and native biodiversity (Rinne et al. 2005).

Species designated as "intolerant" to impairment of water quality (EPA) were also vulnerable to barrier-caused extirpation while "tolerant" species were generally among the least vulnerable. The ability to survive anoxia in eutrophic lakes and agricultural watersheds allows tolerant species to maintain populations through winter and drought while other species must periodically migrate out of these watersheds or are killed. For example, black bullheads held in enclosures in Lake Christina, Minnesota were able to survive both rotenone treatment and anoxia by burying themselves in lake sediments (Thomas Carlson, retired DNR Shallow Lakes Biologist, personal communications). There may be interaction effects in addition to direct barrier effects that are responsible for this trend. The suppression or extirpation of intolerant species and decreased biodiversity due to barriers would give tolerant species a competitive advantage. Thus, tolerant species may actually benefit from fragmentation in some systems. Prominent tolerant species included common carp, fathead minnow, black bullhead, white sucker, and creek chub. These

Table 3. Summary of Barrier-caused Extirpation Fish Data

# of dams/watersheds analyzed	32
# of native fish species present in these watersheds	134
# of introduced species present in these watersheds	16
# of native species absent above every dam for watersheds in which they were present	27 (20%)
# of species listed (Endangered, Threatened, Special Concern) in MN	27 (20%)
# of species listed in MN and neighboring states and province	69 (51%)
# of intolerant species	48 (36%)

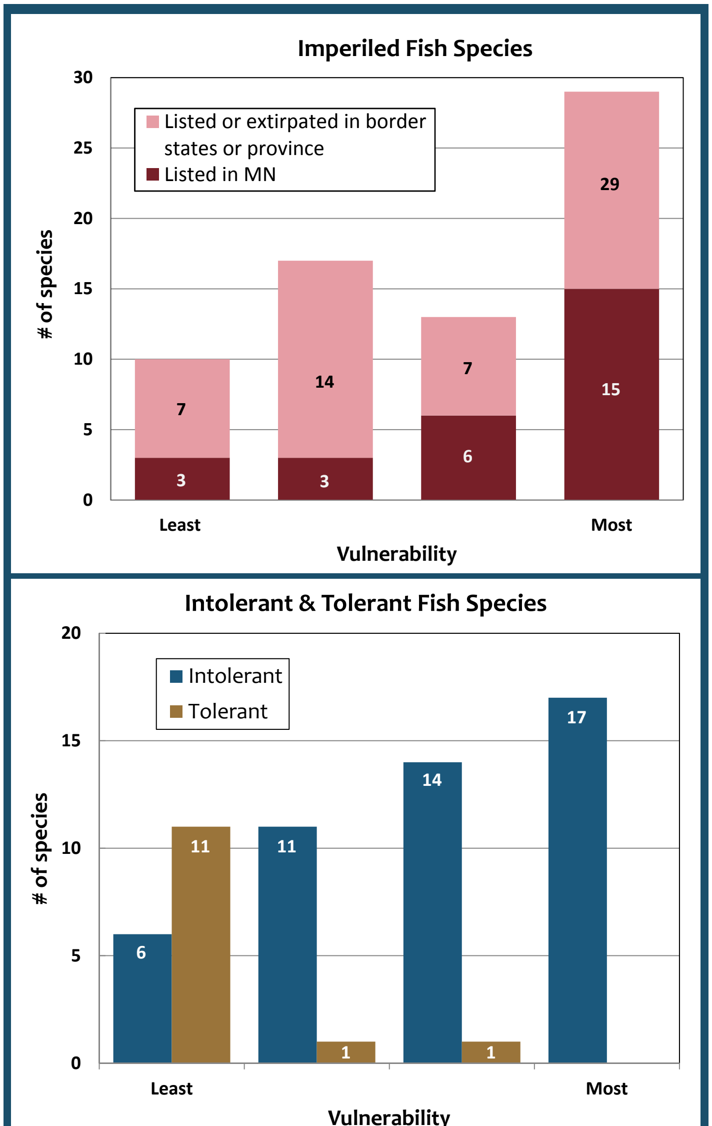


Figure 2 (top) Total number of listed species in MN and surrounding states and province, and number listed in MN, in percent absence quartiles. (bottom) Number of intolerant and tolerant native fish species (including naturalized common carp) in percent absence quartiles.

findings are consistent with those of Santucci et al. (2005) in comparisons of free-flowing and fragmented reaches of the Fox River, Illinois.

While the absence of a species upstream of a dam does not prove that it was due to the barrier, historical records prior to the dam construction and later records following dam removal do substantiate a barrier effect. The likelihood of a species return to an upstream reach following a barrier removal can also be inferred by the presence of suitable habitat and comparisons to similar-sized connected streams and watersheds. Thirteen of the 32 dams were subsequently removed. Eleven dam removals have enough post-removal sampling effort to evaluate biodiversity effects, enabling greater certainty in defining barrier effects (Table 4). A summary of the species that returned following removal is shown in Table 4.

The general lack of spring surveys limits assessment of river reaches used for spawning but not for other life stages. Many species are known to ascend smaller rivers and streams in the spring followed by post-spawning downstream migrations back into larger river reaches. While juveniles of some species will remain near spawning areas as they mature, others will drift downstream as fry. Only 1 of 54 upstream surveys following removal of Flandrau Dam was done in May, with one in June, and none in April (a peak spawning month for many species). Most surveys were done in July, August or September. Some large-bodied species like flathead catfish and lake sturgeon that may only be present for a short but critical period in smaller river reaches are likely to be missed by summer surveys.

As expected, species known to migrate long distances and large-bodied fishes were among the most likely to be absent or extirpated upstream of dams. However, the list of species sensitive to fragmentation also included a number of small-bodied species as well as a disproportionate number of species listed as endangered, threatened or special concern in Federal, Minnesota and adjacent state listings.

The least likely species to be absent upstream of barriers were tolerant habitat generalists, stocked game and bait species, headwater fishes, and species that complete all life history stages in lakes. The absence of common carp upstream of barriers was relatively rare (25%) as it was for black bullhead (6%). Interestingly, these are two species typically targeted by fish barriers in Minnesota. Common carp were most likely to be absent upstream of complete barriers on cold-water streams, watersheds lacking lakes, or in watersheds that were relatively pristine.

Barrier Effects on Specific Fish Species

The sturgeons and paddlefishes of Order Acipenseriformes are the most vulnerable group in terms of extinction (85% of this group are critically endangered) because they are long distance migrants and their habitat needs are especially vulnerable to fragmentation (IUCN, 2004).

Lake sturgeon *Acipenser fulvescens* (*Special Concern in MN, WI, ON; Endangered in IA*) were absent above 80% of assessed dams (12 of 15). The exceptions were the St. Croix River upstream of St. Croix Falls Dam, and two of its tributaries, the Kettle River upstream of Sandstone Dam and the Snake River upstream of the Cross Lake Dam, which maintained the presence of lake sturgeon, but the species appears to be much less abundant than it was historically. The Cross Lake Dam may be passable for sturgeon during moderate floods helping to maintain a metapopulation, and the St. Croix, Kettle, and Snake rivers all have high quality spawning habitat connected to lakes and deep pools that would provide adult refugia and habitat from drought and winter conditions.

Lake sturgeon were extirpated from the entire Red River Basin and from the Minnesota River watershed upstream of Granite Falls where they were historically abundant to the headwaters of both watersheds. Dams in these basins inundated or blocked access to rapids where this species spawns like Rapidan (Blue Earth River), Minnesota Falls and Granite Falls (Minnesota River), Red Lake Falls (Red Lake River), and Fergus Falls (Otter Tail/ Red River).


A lake sturgeon caught below Minnesota Falls Dam before it was removed in 2013. *Credit Ken Peterson.*

Lake sturgeon will migrate hundreds of miles to spawn. A juvenile lake sturgeon tagged in Lake Pepin

Barrier	Native fish species absent in upstream watershed while dam was present then found upstream of dam site after removal or modification or when dam was breached	# of species returned
Breckenridge Dam Otter Tail River Built in 1935 Replaced with rock ramp in 2007	silver lamprey[L], longnose gar[L], goldeye[L,I], mooneye[L,I], stonecat[I], white bass, sauger, lake sturgeon[MN,L]*	8 species (89% of 9 absent species)
State Park Dam Buffalo River Built pre 1893 & 1937 Removed in 2002	silver lamprey[L], goldeye[L,I], spotfin shiner, carmine shiner[L,I], sand shiner, northern redbelly dace[L], blacknose dace, quillback[L], silver redhorse, channel catfish, green sunfish, smallmouth bass[I], sauger, freshwater drum	14 species (67% of 21 absent species)
Heiberg Dam Wild Rice River Built in 1875 Removed in 2006	goldeye[L,I], brassy minnow, emerald shiner, carmine shiner[L,I], finescale dace[L], quillback[L], silver redhorse, channel catfish, tadpole madtom, smallmouth bass[I], sauger, freshwater drum, lake sturgeon[MN,L]*	13 species (81% of 16 absent species)
Sandstone Dam, Kettle River Built in 1905 Removed in 1995	southern brook lamprey[MN,I], blackchin shiner[I], blacknose shiner[L,I], mimic shiner[I], northern redbelly dace[L], bluntnose minnow, tullibee, banded killifish[L], gilt darter[MN,L,I], blackside darter[L], slimy sculpin[I], emerald shiner	12 species (55% of 22 absent species)
Welch Dam Cannon River Built in 1900 Removed in 1994	paddlefish[MN,L,I], mooneye[L,I], gizzard shad, speckled chub[L,I], silver chub[L], mimic shiner[I], river carpsucker, highfin carpsucker[I], river redhorse[L,I], flathead catfish[L], Muskellunge[I], brook trout[I], sauger, lake sturgeon[MN,L]	14 species (74% of 19 absent species)
Minnesota Falls Dam Minnesota River Built in 1871 & 1904 Removed winter 2013	shovelnose sturgeon[L], lake sturgeon[MN,L], flathead catfish[L], paddlefish[MN,L,I], mooneye[L,I], American eel[MN,L], gizzard shad, highfin carpsucker[I], blue sucker[MN,L,I], black buffalo[MN,L,I], sauger, silver lamprey[L] Notes: Removal was very recent so sampling effort has been limited and focused on the large species. American eel made it around dam during 2007 flood.	12 species (31% of 39 absent species) preliminary
Lake Florence Dam North Branch Root River Built in 1857 Removed in 1993	slenderhead darter[L,I], banded darter[I], smallmouth bass[I], bluegill, greater redhorse[L,I], golden redhorse[L], black redhorse[MN,L,I], smallmouth buffalo, northern hogsucker[L,I], longnose dace[I], sand shiner, gravel chub[MN,L,I], spotfin shiner, largescale stoneroller, chestnut lamprey[L]	15 species (23% of 65 absent species
Flandrau Dam, Cottonwood River Built in 1937. Dam was damaged by floods in 1947, was rebuilt in 1960, damaged again in 1965 and 1969, finally was fully removed in 1995	shovelnose sturgeon[L], mooneye[L,I], gizzard shad, golden shiner, river shiner[L], mimic shiner[I], river carpsucker, highfin carpsucker[I], black buffalo[MN,L,I], yellow bullhead[L], brown bullhead, channel catfish, white bass, Iowa darter[I], logperch[L], sauger, carmine shiner[L,I], freshwater drum, Mississippi silvery minnow[MN,I], speckled chub[L,I], silver chub[L] Note: Returned either while dam was passable or after it was removed.	21 species (88% of 24 absent species)
Dawson Dam Lac qui Parle River Built in 1913 Replaced with rock ramp in 2009	bigmouth buffalo[L], greater redhorse[L,I], channel catfish, bluegill, walleye	5 species (63% of 8 absent species)
Appleton Dam Pomme de Terre River Built in 1872 Removed in 1999	emerald shiner, carmine shiner[L,I], quillback[L], silver redhorse, greater redhorse[L,I], channel catfish, white bass, banded darter[I], freshwater drum	9 species (53% of 17 absent species)
Carp Barrier Dam, Drywood Creek, a tributary of the Pomme de Terre River Built in 1930s, failed, built taller in 1971. Failed in 2001	spotfin shiner, spottail shiner[I], common shiner, golden shiner, quillback[L], white sucker, shorthead redhorse, channel catfish, stonecat[I], Iowa darter[I], Johnny darter, banded darter, freshwater drum	13 species (72% of 18 absent species)
		Average = 66%

Table 4. Native fish species that returned to the watershed upstream of dam barriers after the dams were removed or modified or while the dam was passable. MN = listed in Minnesota, L = listed in neighboring state or province, I = intolerant, * lake sturgeon were re-introduced since extirpation in the Red River Basin. The average does not include Minnesota Falls Dam since the removal was recent and post-removal data is limited.

was later caught below the Minnesota Falls dam in 2012, which is a distance of 300 miles. Lake sturgeon have been reintroduced to the Red River of the North since 1998. This has occurred concurrently with dam removal and fish passage projects to reconnect spawning rapids to the mainstem Red River and large lakes. Fish survey data confirm that this combined effort has been successful as sturgeon are becoming abundant in several of the large lakes.

Shovelnose sturgeon *Scaphirhynchus platorynchus* (*Federally Threatened*) were absent upstream of all assessed barriers (7). Shovelnose were absent upstream of Minnesota Falls Dam but returned to the rapids shortly after its removal. They were also absent upstream of Flandrau Dam but were caught about 25 miles upstream of the dam after its removal. Like other sturgeon species, shovelnose spawn in rapids and riffles over large substrates.

Paddlefish *Polyodon spathula* (*Threatened in MN and WI, Special Concern in ND, Extirpated in ON*) The paddlefish is a large river planktivore that spawns in riffles and rapids. Paddlefish were absent above all barriers assessed (4) but returned to the Minnesota River above Minnesota Falls Dam shortly after its removal in 2013 and to the Cannon River above Welch Dam following its removal in 1995. Fragmentation has been widely acknowledged as a primary cause of declines in this species (Unkenholz 1986). Paddlefish have been studied with particular attention as a planktivorous species which could be affected by bigheaded carp. The largest documented paddlefish, a 198 pound individual, was speared in Lake Okoboji, Iowa in 1916 where they were historically abundant. The species was extirpated from the lake, likely due to barrier dams on the Little Sioux River. Ironically an electric barrier recently installed on the outlet creek of Lake Okoboji, Iowa to prevent introduced carp from migrating into the lake also precludes reestablishment of paddlefish in the lake.

Restoration of the previously inundated Minnesota Falls should provide potential spawning habitat for paddlefish. Several paddlefish have been caught immediately downstream of the Minnesota Falls Dam over the years. Paddlefish have declined over their range due to dam construction that has blocked migrations and inundated spawning habitat.

A shovelnose sturgeon. *Credit DNR Fisheries.*

(top) A paddlefish caught in the Minnesota River near Granite Falls in 2005. *Credit DNR Fisheries.* (bottom) Paddlefish caught in 1957 just below Minnesota Falls Dam. *Credit Ken Peterson.*

Sauger *Sander canadensis* were absent upstream of all dams assessed (20). The closely related walleye may be nearly as sensitive to fragmentation, but widespread stocking masks possible barrier effects. Both species spawn in riffles and rapids in rivers or less commonly in clean wave-swept gravel or rubble shoals in lakes. Sauger returned to a number of river reaches following dam removal including: the Otter Tail after removal of Breckenridge Dam, the Cottonwood River after removal of Flandrau Dam, the Canon River after removal of Welch Dam, the Wild Rice River after

A sauger upstream of dam site after removal of Heiberg dam on the Wild Rice River. *Credit DNR Fisheries.*

An American eel. *Credit DNR Fisheries.*

removal of Heiberg Dam and the Minnesota River after removal of Minnesota Falls Dam. Walleyes similarly increased in abundance in these river reaches and successfully spawned in upstream reaches following removal of these dams.

American eel *Anguilla rostrata* (*Special Concern in MN, WI, SD, and ON*) were absent above 86% of assessed dams (6 of 7). This species is MN's only ocean-dependent species. These fish spawn in the Sargasso Sea then the catadromous (migrate from freshwater to the sea to spawn) females migrate back up the Mississippi River watershed. They have the unusual ability to occasionally pass some barriers by "swimming" out of water (usually in wet grass) and there is a single record in 1957 as far upstream as St. Anthony Falls prior to construction of the Lock. Another eel, caught by Area Fisheries staff made it past Minnesota Falls Dam in 2007, a year that lacked a flood large enough to inundate the dam. With the exception of these two individuals, they were absent above barriers for all of the assessed watersheds for which records exist. Since they spawn in the ocean, it follows that any complete barrier would extirpate them from the watershed. This has proven to be the case since American eel have declined over most of their range due to dam construction

A skipjack herring. *Credit Konrad Schmidt.*

Skipjack herring *Alosa chrysochloris* (*Endangered in MN and WI, Special Concern in SD*) was absent above all barriers assessed (3). This species was historically found in Bigstone Lake at the headwaters of the Minnesota River. They were largely extirpated from all Minnesota waters following construction of Lock and Dam 19 in 1913. This dam inundated Keokuk Rapids, which would have been an important spawning area for sturgeon, paddlefish and other rapid dependent species. It is also the tallest, 36 feet, lock & dam on the Mississippi. The loss of skipjack herring resulted in the near extirpation of elephant-ear *Elliption crassidens* and ebonyshell *Fusconaia ebena* mussels, for which skipjack herring are the sole host. Historically, ebonyshell mussels were the dominant mussel species in the Upper Mississippi and Lower Minnesota rivers of Minnesota. A few skipjack herring were caught in Lake Pepin in 1986 for the first time since 1928 and subsequently in 1993, 2001, and 2008. These fish would have had to pass through the lock chamber at Dam 19. The endangered skipjack herring and the dependent ebonyshell and elephant-ear mussels illustrate the importance of fish passage on the Mississippi River and the cascading fragmentation effects on biodiversity. Skipjack herring are also a piscivore that feed within the water column and may be an effective predator on bigheaded carp eggs, larvae, and juveniles.

Blue sucker *Cycleptus elongatus* (*Special Concern in MN, ND and SD, Threatened in WI*) were absent upstream of 100% of the barriers assessed (6). They maintained a population upstream of St. Croix Falls Dam on the St. Croix until the late 1970s. The large, relatively pristine watershed upstream of St. Croix Falls provides a suite of habitat, particularly rapids that this species prefers. Blue suckers maintained a metapopulation for a period of decades after

A blue sucker collected while electrofishing Minnesota Falls following removal of the Minnesota Falls Dam. *Credit DNR Stream Habitat Program.*

A longnose gar (left) and shortnose gar (right) caught upstream of Minnesota Falls Dam. Gar were absent from the reach above the dam prior to its removal. *Credit DNR Fisheries.*

the dam was built, but the species was ultimately lost from the reach by the late 1970s. Blue sucker were absent upstream of Minnesota Falls Dam, but an individual was caught following the 2011 flood that largely inundated the dam. The species was caught in numbers following removal of the dam in 2013. Blue sucker are a fast water species found predominantly in rapids.

Shortnose gar *Lepisosteus platostomus* and **longnose gar** *Lepisosteus osseus* (*Special Concern in SD*) both were absent upstream of 73% of barriers assessed (8 of 11). Gar may be an important predator on juvenile bigheaded carp (Duane Chapman, USGS, personal communications). The ability of juvenile bighead and silver carp to grow

A mooneye caught above Minnesota Falls dams site after dam removal. *Credit DNR Stream Habitat Program.*

vascularized lip extensions enable them to use atmospheric oxygen and inhabit warm, backwaters with low dissolved oxygen where most predators can't survive. Gar are also able to gulp oxygen due to lung-like vascularized swim bladders enabling them to live and hunt in these warm anoxic backwaters.

Mooneye *Hiodon tergisus* (*Concern in SD*) were absent upstream of all barriers assessed (15) while the closely related **goldeye** *Hiodon alosoides* (Endangered in WI) were absent above 92% of barriers (12 of 13). Both species returned to a number of river reaches following dam removal (Table 4). Mooneye and goldeye feed in the water column and at the surface on a variety of insects and small fishes. Their pelagic feeding behavior may equip them to be important predators on bigheaded carp fry and small juveniles.

Flathead catfish *Pylodictis olivaris* (*Concern in ND*) were absent upstream of all barriers assessed (11). They did return to the Canon River following removal of the Welch Dam and to the Mississippi River above St. Anthony Falls following construction the lock in 1963. Flathead catfish need deep pools, usually in larger rivers, for wintering but often migrate upstream to spawn in smaller streams. Flathead adults and fingerlings (indicating reproduction) have been found in the free-flowing Yellow Medicine River, which has an average flow of only 154 cfs and average August flows of only 66 cfs. Flathead catfish are the largest predatory fish in Minnesota and are capable of eating carp up to 30% of their body weight. Davis (1985) reported that stocked flatheads caused a 90% reduction in common carp abundance in Richardson Lake. It is known that these fish can grow very large, as a 157 pound flathead was illegally taken from the Minnesota River near Redwood Falls in 1930. Flatheads are capable of preying on adult carp and may be an important biological control.

A flathead catfish caught on the Minnesota River during Fisheries surveys. *Credit DNR Fisheries.*

A channel catfish caught on the Red River of the North. *Credit DNR Stream Habitat Program.*

Channel catfish *Ictalurus punctatus* absent upstream of 61% of assessed barriers (19 of 31), and **freshwater drum** *Aplodinotus grunniens* absent upstream of 64% of barriers (18 of 28), are two species that are especially important hosts for freshwater mussels. Freshwater drum are hosts for at least 11 species of native mussels, of which they are the sole hosts for 8 species (Figure 3). Channel catfish are hosts for at least 13 species of mussels and are the primary hosts for 6 species. Both fish species were extirpated from the Cottonwood watershed by Flandrau dam. Attempts to re-establish channel catfish by stocking failed.

A freshwater drum. *Credit DNR Stream Habitat Program.*

Following the removal of Flandrau Dam channel catfish and freshwater drum returned almost to the headwaters, 112 miles upstream of dam.

Small-bodied fish While tagging studies have shown that large-bodied fish are migratory, these results and fishway data indicate that many small fish species also migrate and are impacted by barriers.

Shiners & minnows

Shiners are a keystone forage species. Many shiner species are not tolerant of low dissolved oxygen, which may make them vulnerable to extirpation due to barriers. Their vulnerability to extirpation has obvious implications on the productivity of fisheries and for the bait industry. The following species were often absent upstream of barriers:

- **speckled chub** *Macrhybopsis aestivalis* (Threatened in WI) 100% of 11 barriers,
- **Mississippi silvery minnow** *Hybognathus nuchalis* (*Special Concern in MN*) 100% of 7,
- **gravel chub** *Erimystax x-punctatus* (*Threatened in MN, Endangered in WI, Extirpated from Canada*) 100% of 3,
- **silver chub** *Macrhybopsis storeriana* (Special Concern *in WI, SD, ND, and Canada*) 92%, 12 of 13,
- **slimy sculpin** *Cottus cognatus* 70%, 7 of 10
- **river shiner** *Notropis blennius* (Special Concern in SD) 70%, 7 of 10,
- **carmine shiner** *Notropis rubellus* (Threatened in *Canada, Concern in ND and SD*) 59%, 13 of 22, and
- **emerald shiner** *Notropis atherinoides* 52%, 12 of 23
- **spotfin shiner** *Notropis spiloptera* 44%, 12 of 27.
- **sand shiner** *Notropis stramineus* 40%, 12 of 30
- **spottail shiner** *Notropis hudsonius* 37%, 7 of 19.

Darters

Darter diversity is an important indicator of ecosystem health and a metric for the index of biological integrity.

The following species tended to be absent upstream of barriers:

- **western sand darter** *Ammocrypta clara* (*Threatened in IA, Special Concern in WI*) 100% of 7 barriers,
- **crystal darter** *Crystallaria asprella* (*Endangered in MN & WI, Extirpated from IA*) 100% of 6,
- **river darter** *Percina shumardi* (*Special Concern in ND*) 88%, 7 of 8,
- **mud darter** *Etheostoma asprigene* (*Special Concern in WI*) 75%, 3 of 4
- **gilt darter** *Percina evides* (*Threatened in WI, Special Concern in MN, Extirpated from IA*) 71%, 5 of 7,
- **banded darter** *Etheostoma zonale* 64%, 7 of 11.

Mussels Mussel surveys were more limited than those for fish but followed similar trends. Since most mussels require fish hosts, extirpation of the host will ultimately result in the extirpation of the mussel. However, due to the long life span of mussels, up to 200 years for one species (Haag and Rypel 2011), individuals may persist well after being functionally extirpated. Still, mussel diversity has decreased in many waters, particularly in the Minnesota River watershed where 23 of 41 species no longer exist. Unlike fish, historic mussel communities can be determined by the presence of dead shells. Like fish, poor water quality, sedimentation, and habitat alteration and changes in hydrology can adversely affect mussels.

The recolonization of 3 mussel species following removal of the Appleton Dam, on the Pomme de Terre River, is evidence that fragmentation was the cause of their extirpation. Pre-dam removal surveys found only dead shells of elktoe *Alasmidonta marginata*, deertoe *Truncilla truncate* and plain pocketbook *Lampsilis cardium* mussels upstream of the dam. Archeological surveys along the shores of Lake Christina, near the headwaters of the Pomme de Terre River, found plain pocketbook mussel shells indicating that this species was historically found in the headwaters of this watershed. Extirpation of these mussels upstream of the dam and their subsequent recolonization following the dam's removal may have different explanations based on the presence or extirpation of host fish species.

Freshwater drum, also extirpated upstream of the dam, are the sole host for deertoe mussels (Figure 3). The disappearance of this fish species would have led to the extirpation of this mussel species by the inability to reproduce. Return of the drum following removal of the dam is the likely explanation for the recolonization of deertoe mussels.

Rock bass and three sucker species (shorthead redhorse, white sucker, and northern hogsucker) have been identified as hosts (naturally infected; successful transference has not yet been determined) for elktoe mussels. Except for northern hog sucker, these species were present upstream of the dam. However, northern hogsucker and three additional sucker species (greater redhorse, silver redhorse, and quillback carpsucker) that were absent upstream of the dam recolonized following its removal. The return of these species may have been important in the recolonization of elktoe mussels. Functional mussel hosts need to be physiologically compatible, but habitat preferences and behavior also determine the success of mussel reproduction.

Plain pocketbook mussels also use species (walleye, black bass, and several sunfish species) that were present prior to the dam's removal. This suggests that the two latter species may have died out due to drought or other factors and lacked the ability to recolonize due to the dam. Like many rivers, the Pomme de Terre River has stopped flowing during droughts in several periods including the 1934, 1936, 1976, 1988, and 1989. Host fish cannot facilitate reproduction unless they can be infected by glocidia released by viable adults. Removal of the dam would have enabled both existing host fishes and extirpated hosts to become infected in downstream mussel beds and facilitate mussel recolonization of reaches upstream of the dam.

Watershed Scale Biodiversity Effects

Fish diversity was assessed along the Cottonwood River and its tributaries for periods with and without the presence of Flandrau Dam (see Figure 4).

Biodiversity effects of the dam extended to the entire watershed. Cumulative species richness and species per survey are shown in Figure 5. The species richness of the free-flowing Cottonwood River compared to the fragmented river was significantly greater based on a randomization t-test ($t = 2.998$, $\rho = .0016$).

In the absence of the dam, species richness increased by an average of 35% in the watershed and this increase extended to upper reaches of the watershed. For instance, channel catfish and freshwater drum were sampled in Double Lake (drainage area of 2.2 mi^2 , 112 miles upstream of the dam); these two species were not collected in any

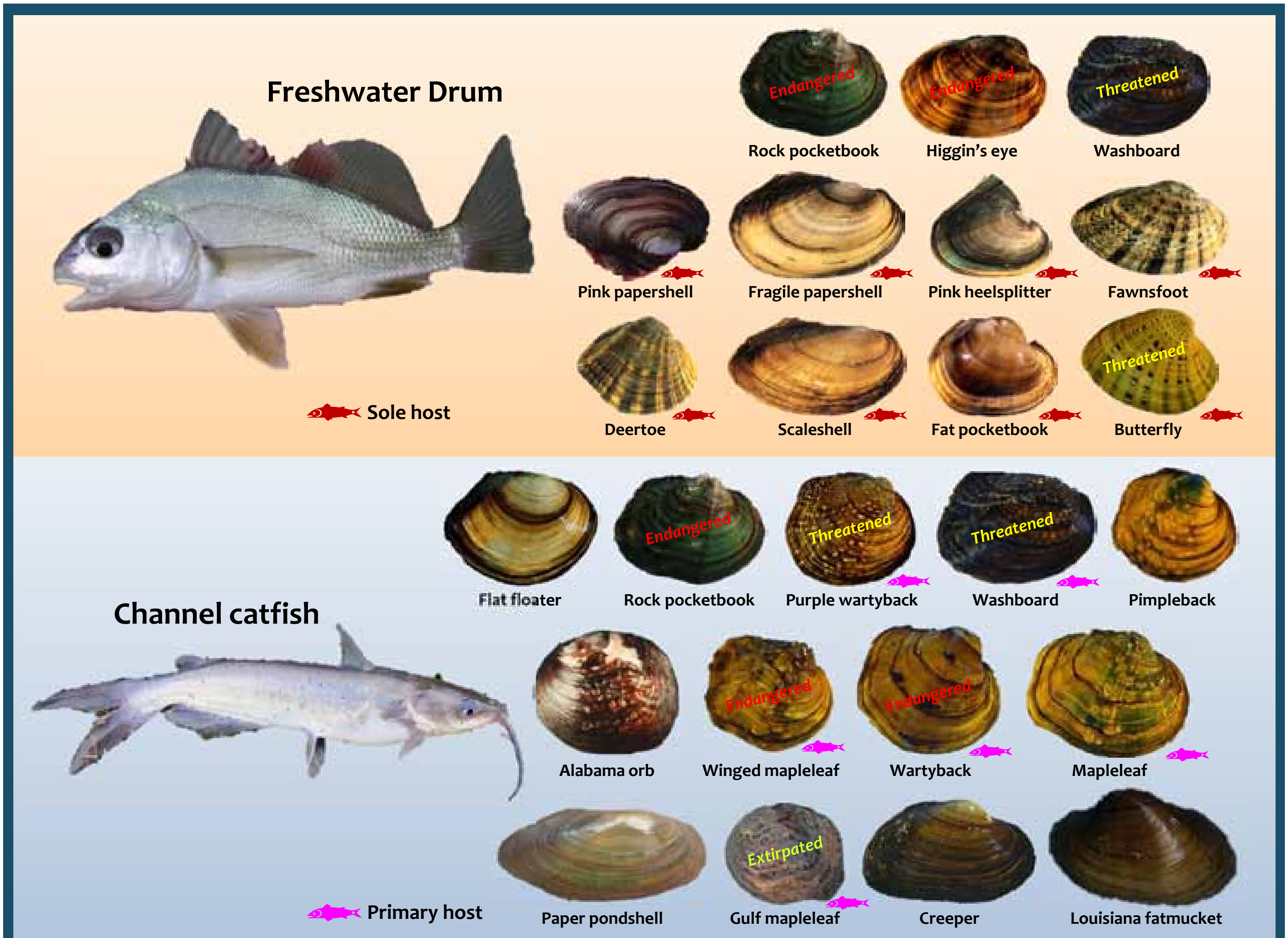


Figure 3. Freshwater drum and channel catfish and the mussels for which they are hosts.

samples upstream of Flandrau Dam prior to the dam's removal. The lake flows into Highwater Creek so these fish would have needed to ascend the creek, which is only about 10 feet wide at the lake's outlet. Removal of the dam also provided access to boulder rapids that are key spawning habitat for walleye, sauger, paddlefish, lake sturgeon, blue sucker, black buffalo and others.

Twenty-one of the twenty-four species that were absent upstream of Flandrau Dam were collected upstream of the dam site during the period when it was breached in 1948 or after it was removed in 1995 (Table 4).

Silver chub, Mississippi silvery minnow, and carmine shiner were present upstream of the dam in 1948 when it was breached, but have not yet been caught upstream of the dam site since removal. Land use changes like ditching, tiling, wetland drainage, use of nitrogen and phosphorous fertilizer, and pesticide use have caused significant habitat and water quality changes that may be unsuitable for these species. These minnows tend to migrate later in the spring and may still be blocked by low-head dams like Kuhar Dam near Lamberton, which is submerged during high spring flows, but would become a barrier as flows decrease. Rates of recolonization likely vary with species as well and these species are relatively rare. In addition to those already mentioned, flathead catfish, shortnose gar and longnose gar, speckled chub, and black buffalo, caught downstream of the dam, have not yet been collected upstream of the dam.

The presence or absence of species does not provide a full perspective of fragmentation effects since it does not show changes in abundance. A number of riverine species that were present in small proportions of the surveys while the river was dammed increased in prevalence (percent occurrence) when the main stem was free-flowing (Figure 6). For instance, the proportion of samples

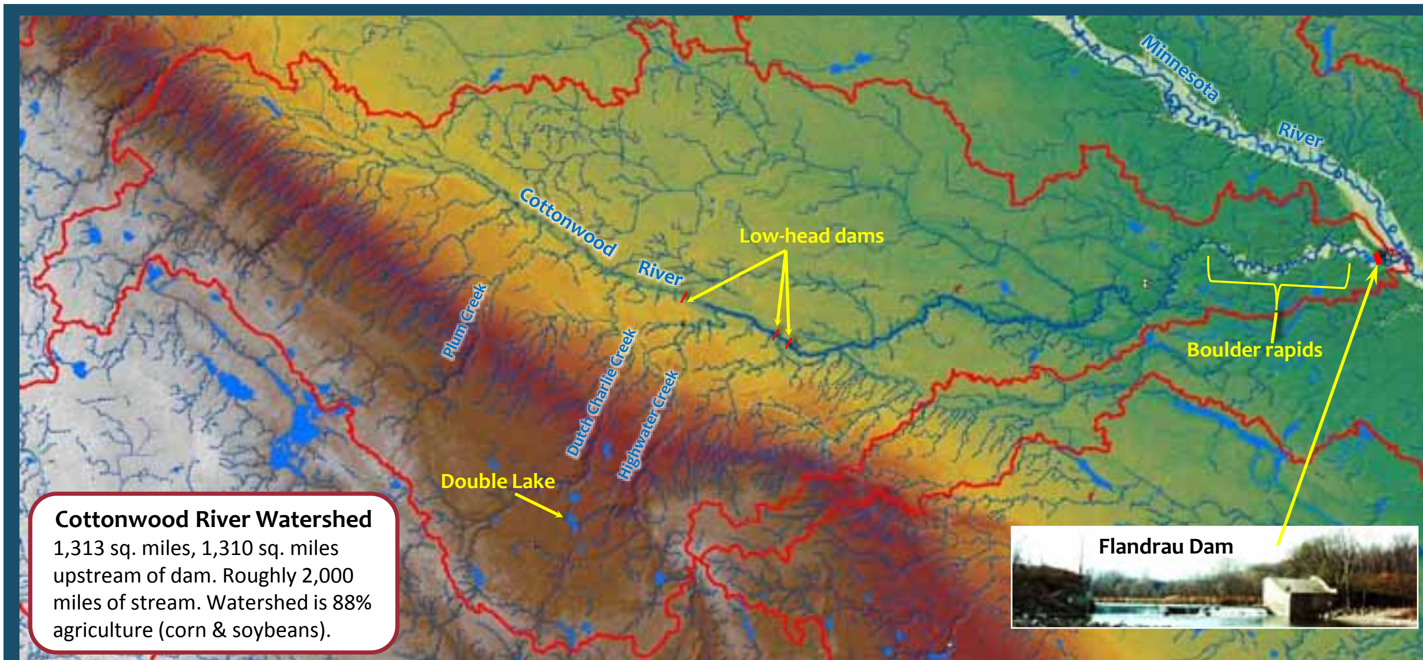
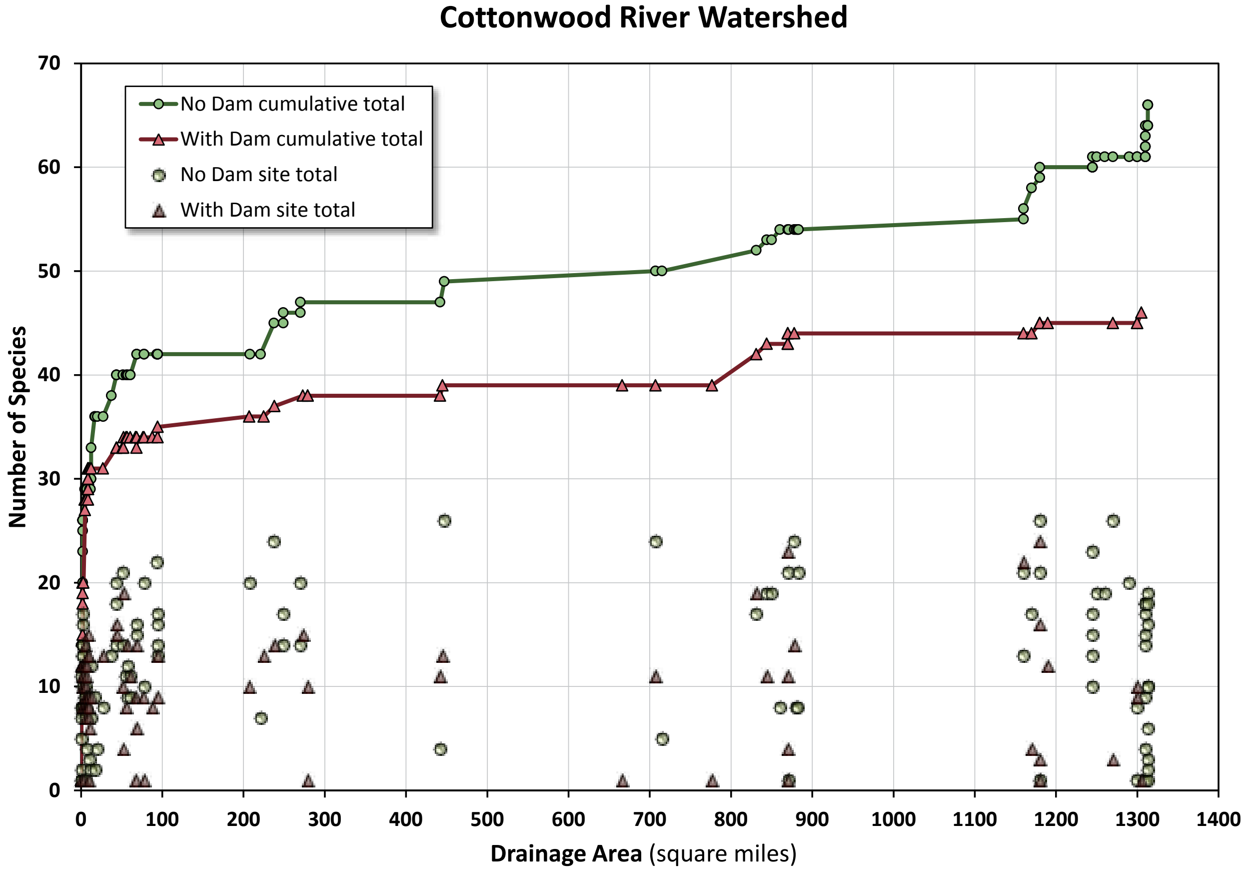


Figure 4. The Cottonwood River watershed.

in which river-oriented suckers were caught increased for all species. Percent occurrence of shorthead redhorse was 330% higher, silver redhorse 182% higher, golden redhorse 325% higher, northern hogsucker 236% higher, quillback 247% higher, and highfin carpsucker were 240% higher in the free-flowing compared to the dammed condition. Among facultative riverine game species, the proportion of samples in which smallmouth bass were caught was 88% higher in the free-flowing condition and walleye were 105% higher while sauger and channel catfish were absent in the dammed condition but were found in 8% and 24% of free-flowing samples. Abundant tolerant species like white sucker, fathead minnow, and black bullhead did not appear to be affected by fragmentation and tended to be present in virtually the same proportion of samples during the free-flowing and dammed condition.



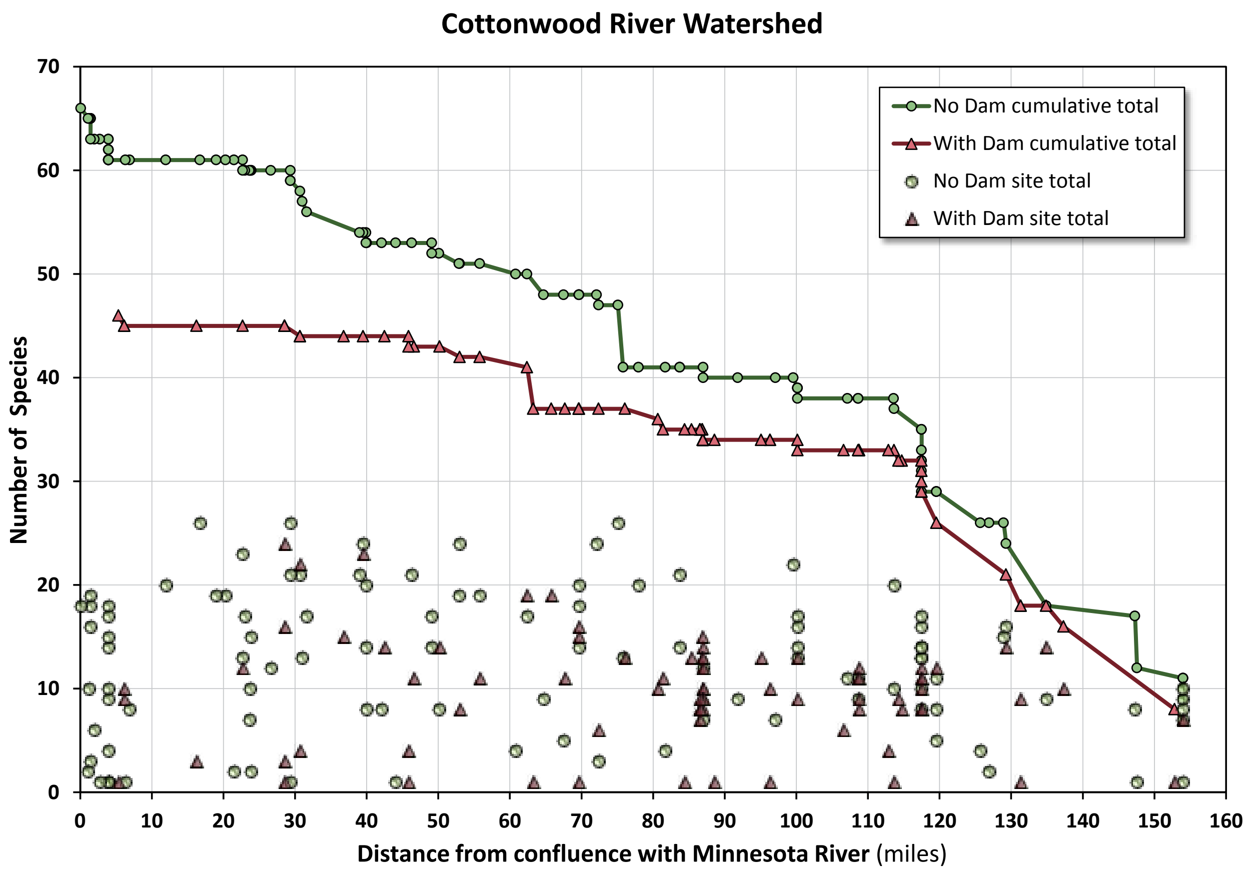


Figure 5. Number of species found in the Cottonwood River watershed. Points are the total number of species collected at a site. The line is the cumulative total. (top) Species richness is correlated with drainage area (bottom) Species richness correlated with distance from the mouth of the Cottonwood River.

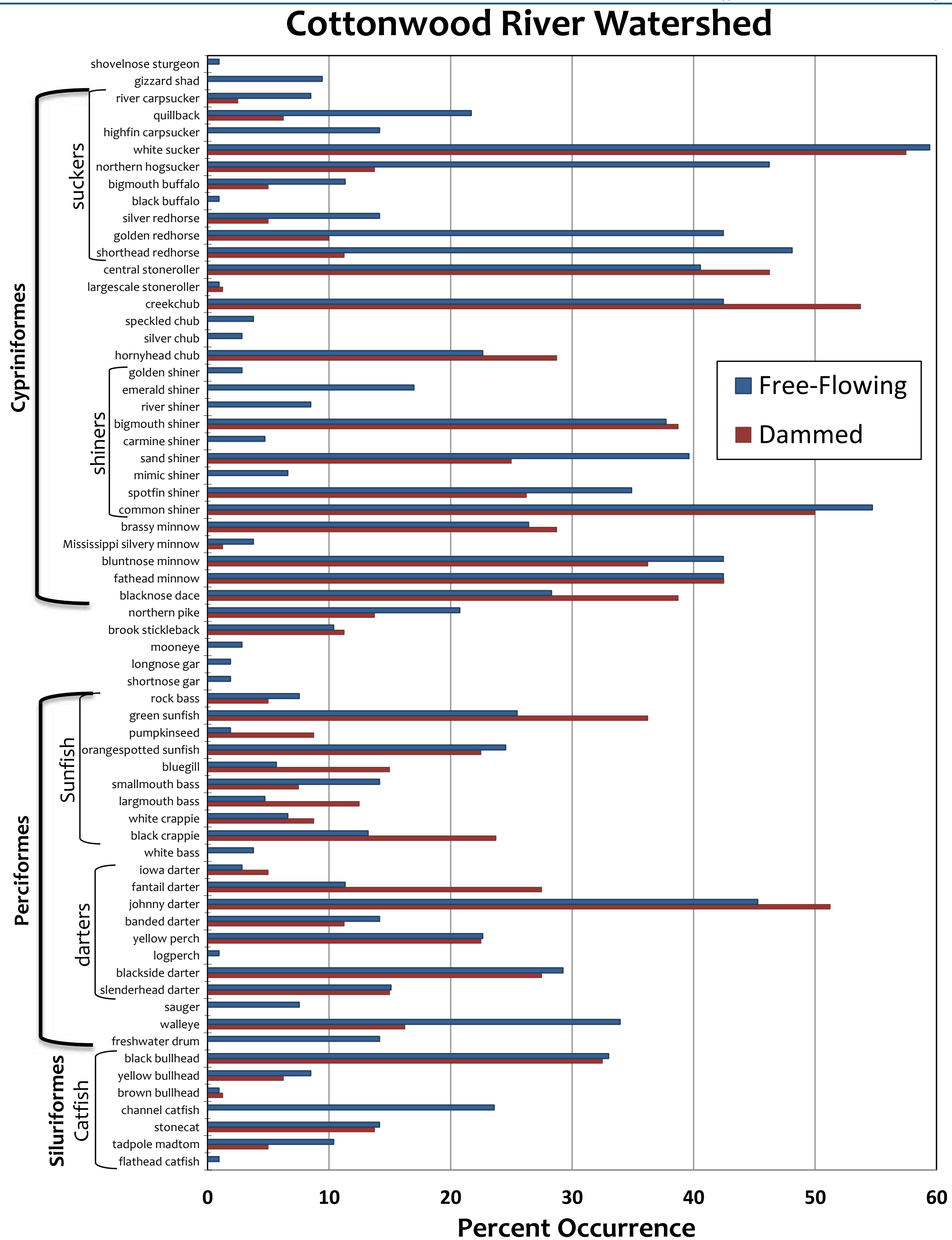


Figure 6. Percent occurrence of fish species from fish surveys in the Cottonwood River watershed separated into periods when Flandrau Dam was a barrier - dammed and when the dam was breached or removed - free flowing.

Summary and Conclusions

There are few impairments that have been shown to have as dramatic an influence on aquatic biodiversity as does the construction of barriers. To summarize:

1) Complete and near complete barriers reduced upstream species richness by an average of 41% and 37 % respectively.

2) Moderate barriers (may be passable during 2-year or larger floods) also reduced species richness by 20%. This is evidence that even partial barriers have an upstream impact.

3) Loss of species richness due to barriers extended watershed-wide.

4) Imperiled and intolerant species were the most vulnerable to extirpation by barrier dams.

5) Tolerant species, including common carp, were among the species least affected by barriers.

6) An average of 66% of species absent above barrier dams returned after the barrier was removed.

7) Based on this analysis and other studies the ability to migrate (or connectivity of migration pathways) is equally important to fish as it is to neotropical birds.

Ecological Implications of Dams The implications of barrier effects extend to fundamental elements of ecological health. Dams can have additional effects by interrupting sediment transport causing reservoir sedimentation and downstream incision, altering nutrient dynamics and causing cyanobacteria blooms, propagating non-native species, inundating important river habitat, altering flow regimes, altering temperature regimes, propagating fish diseases and parasites, and causing massive erosion when they fail. However, the effects on native species shown by this analysis are primarily due to the blockage of fish migrations since most of the reservoirs were relatively small in comparison the watershed-wide effects. Blocking seasonal fish migrations directly affects nutrient processing and water quality since fish carry these nutrients in their bodies and eggs. While this paper assessed barrier dams, any type of barrier that is effective in blocking fish migrations should be expected to cause significant declines in the diversity of fish and mussels.

This analysis has shown that barriers have direct negative effects on recreation as a number of game fish species were vulnerable to barrier related extirpation. Flathead catfish, sauger, white bass, yellow bass, and paddlefish were absent upstream of all barriers evaluated while lake sturgeon, channel catfish, and white bass were absent upstream of most barriers in watersheds where they were present. Smallmouth bass, in spite of being artificially maintained by stocking in some watersheds, were absent upstream of a number of barriers. The return of these species following dam removal supports fragmentation as the cause of their extirpation. Walleye may also be vulnerable to barrier extirpation, based on spawning habitat needs and the sensitivity of sauger (a close relative to walleye) to fragmentation, but walleyes are artificially maintained by extensive stocking.

Predatory game species are also affected by barrier effects on forage species. Several shiner and minnow species were frequently extirpated by barrier dams (again validated by their return following dam removal). Mimic shiner, emerald shiner, carmine shiner, weed shiner, silver chub, Ozark minnow, pugnose minnow, and river shiner were all absent upstream of half or more of the barrier dams in watersheds they were present.

The extirpation of native mussels that follows the loss of host fish species above dams eliminates the water filtration role of these mussels. Water filtration by mussels of the Upper Mississippi River has been estimated at 53.1 million cubic meters per day or 76 times the capacity of the Minneapolis - St. Paul metropolitan wastewater treatment plant, one of the largest in the USA (Newton et al. 2011). Mussels also stabilize stream beds (Zimmerman and de Szalay 2007) and increase the density and biodiversity of other benthic invertebrates (Spooner and Vaughn 2006; Gutierrez et al. 2003). Mussels are declining globally and this catastrophic loss in biomass may significantly alter river ecosystem functions (Spooner and Vaughn 2006). The recolonization of three extirpated mussel species following removal of the Appleton dam suggests that this trend is reversible for the species that have not yet gone extinct.

The Minnesota River The Minnesota River, one of the watersheds for which invasive species barriers are being considered, has been well documented for its water quality and sediment impairments. Nevertheless, the river between Granite Falls and its confluence with the Mississippi River is the longest reach of free-flowing, undammed river in Minnesota, a distance of 240 miles. Where free-flowing, the river mainstem and tributaries have a remarkable diversity of fish, with records of 98 native species. While the watershed has lost much of its mussel diversity, dam removal has proven to be an effective strategy in reestablishing extirpated species of fish and mussels.

While landuse impacts on water quality, hydrology, and channel erosion continue to degrade habitat in the Minnesota River and other watersheds, it is notable that where dams have been removed, the loss of biodiversity has actually been reversed and has resulted in substantial increases in species richness. This demonstrates the necessity of migration for reproduction, accessing changing habitat needs with seasons and life stage, and recolonization following drought, anoxia and water quality related mortality. Connectivity may be particularly important in watersheds subject to low winter flows, anoxia, and high summer water temperatures associated with drought since the fish and mussel assemblages of these streams depend on frequent recolonization.

Vulnerability to Fragmentation Tolerant native and introduced species have been successful in fragmented, degraded, and altered systems. These species can survive drought and often concurrent warm water temperatures and low dissolved oxygen, in addition to other water quality impairments. Tolerant species are often generalized and adapted to homogenized, silt laden microhabitat. Common carp were abundant upstream of most barriers, especially in eutrophic watersheds. This included barriers specifically designed to target carp. The extirpation of native species by barriers may actually increase the success of invasive species by eliminating competition and predation influences associated with a diverse, free-flowing river.

The high vulnerability of intolerant and imperiled species and relatively low vulnerability of tolerant species to extirpation by barriers has significant implications for ecosystem health and biological assessments. The Index of Biological Integrity, IBI (Karr et al. 1986), widely used as a measure of biological health and water quality, uses metrics that include the number of intolerant species, darter species, and sucker species as positive metrics. This study supports the usefulness of the IBI as a measure of biological health but suggests that fragmentation may significantly reduce scores. A fragmented system is more likely to be dominated by tolerant species that can survive periods of poor water quality while a free-flowing system allows periodic recolonization by intolerant species.

Since 1) protection of native species is a primary objective of invasive species management and 2) this and other studies suggest that barriers are the single most definitive cause of declines in native biodiversity, barriers on naturally connected rivers and streams should not be considered a viable invasive species control strategy. Rather, reconnecting rivers by removing barriers has been shown to increase the diversity and resilience of native species while decreasing the prevalence of invasive species. Restoration of free-flowing, resilient ecosystems is likely to be the most effective means of increasing native biodiversity and preventing dominance by non-native species.

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Most Vulnerable Species : 75% to 100% Absence

Common Name *Scientific Name*	Adult Habitat *Spawning Habitat*	Adult Feeding Habits	% Absent Upstream of Barriers # Absent / Sample size	Conservation Status *Tolerance* Management (if any)
shovelnose sturgeon *Scaphirhynchus platorynchus*	pools in rivers rapids in rivers & streams	benthic invertivore	**100%** 7/7	**Federally Threatened** Intermediate
paddlefish *Polyodon spathula*	pools in large rivers riffles & rapids in rivers	planktivore/benthic invertivore	**100%** 4/4	**T** (MN, WI), **SCP2** (ND), **Ext** (ON) Intolerant
mooneye *Hiodon tergisus*	pools in rivers, connected lakes pelagic, rivers	surface & water column invertivore/piscivore	**100%** 15/15	SU (SD) Intolerant
skipjack herring *Alosa chrysochloris*	pools in rivers, connected lakes pelagic, rivers	surface & water column invertivore/piscivore	**100%** 3/3	**E** (MN, WI), **S3** (SD) Intermediate
gizzard shad *Dorosoma cepedianum*	pools in rivers, connected lakes pelagic, rivers	surface & water column planktivore/invertivore	**100%** 12/12	Intermediate
Mississippi silvery minnow *Hybognathus nuchalis*	pools & backwater in rivers & streams glides, riffles, hornyhead chub nests	benthic invertivore	**100%** 7/7	**SC** (MN) Intolerant
gravel chub *Erimystax s-punctatus*	riffles in coolwater rivers glides, riffles	herbivore, filamentous algae, diatoms	**100%** 3/3	**T** (MN), **E** (WI), **Ext** (ON) Intolerant
speckled chub (shoal chub) *Macrhybopsis aestivalis*	sandy riffles in rivers semi-pelagic	benthic invertivore	**100%** 11/11	**T** (WI) Intolerant
Topeka shiner *Notropis topeka*	streams sunfish nests	generalized invertivore	**100%** 2/2	**Federally Endangered**, **T** (IA), **SC** (MN), **S3** (SD) not rated
channel shiner *Notropis wickliffi*	pools in rivers glides, riffles	generalized invertivore	**100%** 3/3	Intermediate
ghost shiner *Notropis buchanani*	eddies & backwaters in rivers glides, riffles	generalized invertivore	**100%** 3/3	Intolerant
pugnose minnow *Opsopoeodus emiliae*	clear vegetated streams under objects	omnivore	**100%** 4/4	**SC** (IA, WI, ON) Intolerant
longnose sucker *Catastomus catastomus*	streams, Great Lakes, brackish water riffles and shoals	benthic invertivore	**100%** 1/1	**T** (SD) Intermediate
blue sucker *Cycleptus elongatus*	rapids in rivers glides, riffles & rapids	benthic invertivore	**100%** 6/6	**T** (WI), **SC** (MN), **SCP1** (ND), **S3** (SD) Intolerant
black buffalo *Ictiobus niger*	runs & pools in coolwater rivers backwaters & floodplains	benthic invertivore	**100%** 3/3	**T** (MN, WI), **SC** (ON), **PSC** (Canada), **SU** (SD) Intolerant
spotted sucker *Minytrema melanops*	clearwater rivers glides, riffles & rapids	benthic invertivore	**100%** 5/5	**SC** (Canada, ON) Intolerant
slender madtom *Noturus exilis*	riffles in streams under rocks	generalized invertivore	**100%** 1/1	**E** (MN, WI) Intolerant
flathead catfish *Pylodictis olivaris*	deep pools in rivers nests in cavities	piscivore, top predator	**100%** 11/11	**SCP3** (ND) Intermediate

Table 4. Fish species listed by percent absence upstream of dam barriers analyzed and listed in Table 1. Table is sorted by percent absence. Fish habitat and feeding data from Aadland & Kuitunen 2005 and Becker 1983. Conservation status: **E** = Endangered, **T** = Threatened, **SC** = Special Concern, **Ext** = Extirpated from Minnesota DNR (MN), Iowa DNR (IA), Wisconsin Natural Heritage Working List (WI), North Dakota Game & Fish Department (ND, Species of Conservation Priority, **SCP**, Levels 1 - 3), South Dakota Game Fish & Parks (SD, State Rank **S1 - S5**), U.S. Fish & Wildlife Service, and Government of Canada (Canada, Ontario=ON, **PSC**=Proposed Special Concern). Species tolerance ratings from US EPA.

Most Vulnerable Species : 75% to 100% Absence

Common Name ***Scientific Name***	**Adult Habitat** ***Spawning Habitat***	**Adult Feeding Habits**	**% Absent Upstream of Barriers** # Absent / Sample size	**Conservation Status** *Tolerance* **Management** (if any)
pirate perch *Aphredoderus sayanus*	sluggish streams, backwaters, wetlands **nest in vegetation**	generalized invertivore	**100%** 1/1	**SC** (MN, IA, WI) Intermediate
plains topminnow *Fundulus sciadicus*	streams **vegetation**	generalized invertivore	**100%** 1/1	**T** (MN), **S3** (SD) not rated
starhead topminnow *Fundulus dispar*	vegetated streams & backwaters **vegetation**	generalized invertivore	**100%** 1/1	**E** (WI) Intolerant
threespine stickleback *Gasterosteus aculeatus*	streams, lakes, and brackish bays **nest in shallow water**	generalized invertivore	**100%** 1/1	**E** (Canada) Intermediate
yellow bass *Morone mississippiensis*	pools in rivers, connected lakes **glides & riffles in streams**	planktivore, piscivore	**100%** 5/5	**SC** (MN) Intermediate
white perch *Morone americana*	rivers, lakes, and brackish bays **broadcast in rivers**	piscivore	**100%** 1/1	Intermediate
western sand darter *Ammocrypta clara*	sandy riffles in rivers **glides & riffles, sand**	generalized invertivore	**100%** 7/7	**T** (IA), **SC** (WI) Intolerant
crystal darter *Crystallaria asprella*	sandy riffles in rivers & streams **glides & riffles**	generalized invertivore	**100%** 6/6	**E** (MN, WI), **Ext** (IA) Intolerant
sauger *Sander canadensis*	pools in rivers, lakes **glides, riffles & shoals**	piscivore	**100%** 20/20	Intermediate Occasionally stocked game species
goldeye *Hiodon alosoides*	pools in rivers, connected lakes **pelagic, rivers**	surface & water column invertivore/piscivore	**92%** 12/13	**E** (WI) Intolerant
silver chub *Macrhybopsis storeriana*	pools in rivers **semi-pelagic**	benthic invertivore	**92%** 12/13	**SC** (WI, Canada) **S2** (SD), **SCP2** (ND) Intermediate
highfin carpsucker *Carpiodes velifer*	runs & pools in rivers & streams **backwaters**	omnivore	**91%** 10/11	Intolerant
bullhead minnow *Pimephales vigilax*	rivers & backwaters **underside of objects**	omnivore	**88%** 7/8	Intermediate
river darter *Percina shumardi*	riffles in rivers & streams **glides & riffles**	generalized invertivore	**88%** 7/8	**SCP3** (ND) Intermediate
American eel *Anguilla rostrata*	rivers (females) **Sargasso Sea**	piscivore	**86%** 6/7	**SC** (MN, WI, ON), **S3** (SD) Intermediate
silver lamprey *Ichthyomyzon unicuspis*	pools in rivers **glides, riffles**	parasite on fish	**82%** 14/17	**SCP3** (ND) Intermediate
lake sturgeon *Acipenser fulvescens*	pools in rivers, connected lakes **rapids in rivers & streams**	benthic invertivore	**80%** 12/15	**E** (IA), **SC** (MN, WI, ON) Intermediate Reintroduced in some waters
smallmouth buffalo *Ictiobus bubalus*	pools in rivers, lakes **backwaters & floodplains**	generalized invertivore	**80%** 8/10	Intermediate
black redhorse *Moxostoma duquesnei*	fast riffles & runs in streams **glides, riffles**	benthic invertivore	**80%** 4/5	**E** (WI), **T** (IA, Canada, ON), **SC** (MN) Intolerant
mud darter *Etheostoma asprigene*	rivers & backwaters **riffles on gravel or vegetation**	generalized invertivore	**75%** 3/4	**SC** (WI) Intermediate

Common Name *Scientific Name*	Adult Habitat *Spawning Habitat*	Adult Feeding Habits	% Absent Upstream of Barriers # Absent / Sample size	Conservation Status *Tolerance* Management (if any)
longnose gar *Lepisosteus osseus*	pools in rivers, connected lakes **vegetated backwaters & bays**	piscivore	**73%** 8/11	**S3** (SD) **Intermediate**
shortnose gar *Lepisosteus platostomus*	pools in rivers, connected lakes **vegetated backwaters**	piscivore	**73%** 8/11	**Intermediate**
brook silverside *Labidesthes sicculus*	ubiquitous in rivers, connected lakes **nearshore over vegetation or gravel**	surface & water column invertivore, fish fry	**73%** 8/11	**Intermediate**
gilt darter *Percina evides*	fast riffles in rivers & streams **glides & riffles**	generalized invertivore	**71%** 5/7	**T** (WI), **SC** (MN), **Ext** (IA) **Intolerant**
white bass *Morone chrysops*	pools in rivers, connected lakes **glides & riffles in streams, shoals**	planktivore, piscivore	**71%** 12/17	**Intermediate**
river shiner *Notropis blennius*	slow riffles in rivers & streams **glides, riffles**	generalized invertivore	**70%** 7/10	**S2** (SD) **Intermediate**
river carpsucker *Carpiodes carpio*	pools in rivers & streams **near banks or backwaters**	omnivore	**70%** 7/10	**Intermediate**
slimy sculpin *Cottus cognatus*	riffles in rivers & streams **nest under rocks in glides & riffles**	generalized invertivore	**70%** 7/10	**Intolerant**
southern brook lamprey *Ichthyomyzon gagei*	riffles in streams **glides, riffles**	do not eat, juveniles filter feed	**67%** 4/6	**SC** (MN) **Intolerant**
Ozark minnow *Notropis nubilus*	riffles in rivers & streams **glides, riffles, hornyhead chub nests**	omnivore, mostly vegetation	**67%** 4/6	**T** (WI), **SC** (MN) **Intolerant**
warmouth *Lepomis gulosus*	pools in low gradient streams, lakes **nest near wood or vegetation**	generalized invertivore, piscivore	**67%** 2/3	**SC** (MN, Canada, ON) **Intermediate**
freshwater drum *Aplodinotus grunniens*	pools in river, lakes **pelagic**	generalized invertivore, piscivore	**64%** 18/28	**Intermediate**
largescale stoneroller *Campostoma oligolepis*	slow riffles in rivers & streams **glides, riffles**	herbivore/benthic invertivore	**64%** 7/11	**SCP3** (ND) **Intermediate**
banded darter *Etheostoma zonale*	riffles in rivers & streams **glides & riffles**	generalized invertivore	**64%** 7/11	**Intolerant**
American brook lamprey *Lethenteron appendix*	riffles in streams **glides, riffles**	do not eat, juveniles filter feed	**63%** 5/8	**T** (IA) **Intolerant**
channel catfish *Ictalurus punctatus*	pools in rivers **nests in cavities**	piscivore, generalized invertivore	**61%** 19/31	**Intermediate** Occasionally stocked game species
bigmouth buffalo *Ictiobus cyprinellus*	pools in rivers & streams, lakes **backwaters & floodplains**	planktivore, benthic invertivore	**61%** 11/18	**SC** (Canada), **Intermediate**
mimic shiner *Notropis volucellus*	shallow pools in rivers & streams **vegetation**	generalized invertivore	**61%** 14/23	**Intolerant**
quillback *Carpiodes cyprinus*	pools in rivers & streams **backwaters**	omnivore	**60%** 15/25	**S3** (SD) **Intermediate**

Vulnerable Species : 50% to 74% Absence

Table 4 (cont.). Fish species listed by percent absence upstream of dam barriers analyzed and listed in Table 1. Table is sorted by percent absence. Fish habitat and feeding data from Aadland & Kuitunen 2005 and Becker 1983. Conservation status: **E** = Endangered, **T** = Threatened, **SC** = Special Concern, **Ext** = Extirpated from Minnesota DNR (MN), Iowa DNR (IA), Wisconsin Natural Heritage Working List (WI), North Dakota Game & Fish Department (ND, Species of Conservation Priority, **SCP**, Levels 1 - 3), South Dakota Game Fish & Parks (SD, State Rank **S1 - S5**), U.S. Fish & Wildlife Service, and Government of Canada (Canada, Ontario=ON, **PSC**=Proposed Special Concern). Species tolerance ratings from US EPA.

Group	**Common Name** ***Scientific Name***	**Adult Habitat** ***Spawning Habitat***	**Adult Feeding Habits**	**% Absent Upstream of Barriers** # Absent / Sample size	**Conservation Status** *Tolerance* **Management** (if any)
Vulnerable Species : 50% to 74% Absence	**carmine shiner** *Notropis percobromus*	riffles in rivers & streams **glides, riffles**	omnivore	**59%** 13/22	**T** (Canada), **S2** (SD), **SCP3** (ND) *Intolerant*
	river redhorse *Moxostoma carinatum*	fast runs in rivers **glides, riffles**	benthic invertivore	**55%** 6/11	**T** (WI), **SC** (Canada, ON) *Intolerant*
	brook trout *Salvelinus fontinalis*	coldwater rivers & lakes **glides & riffles in rivers & streams**	generalized invertivore, piscivore	**54%** 7/13	*Intolerant* Widely stocked game species
	emerald shiner *Notropis atherinoides*	shallow pools in rivers & streams **glides, riffles**	generalized invertivore	**52%** 12/23	*Intermediate*
	northern brook lamprey *Ichthyomyzon fossor*	pools in streams **glides, riffles**	don't eat, juveniles filter feed	**50%** 2/4	**SC** (MN, ON), **PSC** (Canada) *Intolerant*
	red shiner *Cyprinella lutrensis*	ubiquitous in rivers & streams **sunfish nests in vegetated backwaters**	omnivore	**50%** 1/2	*Tolerant*
	redside dace *Clinostomus elongatus*	riffles & raceways in streams **glides, riffles, creek chub nests**	benthic invertivore	**50%** 3/6	**T** (ON), **SC** (MN, WI), **PSC** (Canada) *Intolerant*
	weed shiner *Notropis texanus*	pools in clearwater streams & lakes **unknown**	omnivore	**50%** 5/10	**E** (IA), **SC** (WI) *Intolerant*
	silver redhorse *Moxostoma anisurum*	runs, glides & pools in rivers & streams **glides, riffles**	benthic invertivore	**50%** 14/28	*Intermediate*
	Muskellunge *Esox masquinongy*	pools in rivers, lakes **vegetated backwaters & side channels**	piscivore, top predator	**50%** 6/12	*Intolerant* Widely stocked game species
	ninespine stickleback *Pungitius pungitius*	headwater streams, shoals of large lakes **nests of vegetation between rocks**	omnivore	**50%** 1/2	*Intermediate*
Somewhat Vulnerable Species : 25% to 49% Absence	**greater redhorse** *Moxostoma valenciennesi*	runs & glides in rivers & streams **glides, riffles**	benthic invertivore	**47%** 7/15	**T** (WI) *Intolerant*
	mottled sculpin *Cottus bairdii*	riffles in rivers & streams **nest tunnel under rocks in riffles**	generalized invertivore, piscivore	**46%** 6/13	*Intolerant*
	spotfin shiner *Cyprinella spiloptera*	slow riffles in rivers & streams **crevices, glides, riffles**	generalized invertivore	**44%** 12/27	*Intermediate*
	blackchin shiner *Notropis heterodon*	shallow pools, clearwater streams, lakes **vegetation**	generalized invertivore	**43%** 6/14	*Intolerant*
	burbot *Lota lota*	rivers (pools) & lakes **pelagic over gravel or rocks**	piscivore	**42%** 8/19	**T** (IA), **SCP2** (ND) *Intermediate*
	slenderhead darter *Percina phoxocephala*	fast riffles in rivers & streams **glides & riffles**	generalized invertivore	**42%** 8/19	**SX** (SD) *Intolerant*
	sand shiner *Notropis stramineus*	slow riffles in rivers & streams **glides, riffles**	surface and water column invertivore	**40%** 12/30	*Intermediate*
	redfin shiner *Lythrurus umbratilis*	pools in headwater streams **nests in glides & riffles**	benthic invertivore	**40%** 2/5	**T** (WI), **SC** (MN) *Intermediate*

Somewhat Vulnerable Species : 25% to 49% Absence

Common Name *Scientific Name*	Adult Habitat *Spawning Habitat*	Adult Feeding Habits	% Absent Upstream of Barriers # Absent / Sample size	Conservation Status *Tolerance* **Management** (if any)
orangespotted sunfish *Lepomis humilis*	pools in rivers, streams **nest in backwaters & bays**	generalized invertivore	**39%** 7/18	**SC** (ON), **PSC** (Canada) **Intermediate**
spottail shiner *Notropis hudsonius*	slow riffles, rivers & streams **glides, riffles**	generalized invertivore	**37%** 7/19	**Intolerant** Common bait species
shorthead redhorse *Moxostoma macrolepidotum*	runs & glides in rivers & streams **glides, riffles**	benthic invertivore	**34%** 11/32	**Intermediate**
blacknose shiner *Notropis heterolepis*	pools in clearwater streams & lakes **vegetation**	generalized invertivore	**33%** 5/15	**E** (SD), **T** (IA), **SCP3** (ND) **Intolerant**
suckermouth minnow *Phenacobius mirabilis*	slow riffles in rivers & streams **glides, riffles**	generalized invertivore	**33%** 2/6	**SC** (MN), **SH** (SD) **Intermediate**
golden redhorse *Moxostoma erythrurum*	runs & pools in rivers & streams **glides, riffles**	benthic invertivore	**33%** 10/30	**SH** (SD) **Intermediate**
stonecat *Noturus flavus*	riffles & runs in rivers & streams **glides, riffles**	generalized invertivore, piscivore	**33%** 10/30	**Intolerant**
trout-perch *Percopsis omiscomaycus*	pools in rivers, large lakes **glides & riffles in streams**	generalized invertivore	**33%** 5/15	**SCP2** (ND), **S2** (SD) **Intermediate**
rainbow darter *Etheostoma caeruleum*	fast riffles in rivers & streams **glides and riffles**	generalized invertivore	**33%** 4/12	**Intolerant**
blackside darter *Percina maculata*	slow riffles in rivers & streams **glides & riffles**	generalized invertivore	**33%** 3/10	**S2** (SD) **Intermediate**
bowfin *Amia calva*	pools in rivers, connected lakes **nest, vegetated backwaters**	piscivore	**31%** 4/13	**Intermediate**
northern redbelly dace *Chrosomus eos*	clear, headwater streams & ponds **filamentous algae**	herbivore	**29%** 6/21	**T** (SD), **SCP2** (ND) **Intermediate**
least darter *Etheostoma microperca*	clearwater streams, lakes & ponds **vegetation, roots or rubble**	generalized invertivore	**29%** 2/7	**E** (IA), **SC** (MN, WI) **Intolerant**
logperch *Percina caprodes*	fast riffles in rivers & streams, large lakes **glides, riffles, shoals**	generalized invertivore	**29%** 6/21	**SCP3** (ND), **S3** (SD) **Intermediate**
smallmouth bass *Micropterus dolomieu*	raceways in rivers, lakes **nest in backwaters and bays**	generalized invertivore, piscivore	**27%** 6/22	**Intolerant** Widely stocked game species
fantail darter *Etheostoma flabellare*	fast riffles in rivers & streams **glides & riffles**	generalized invertivore	**27%** 3/11	**Intermediate**
Iowa darter *Etheostoma exile*	shallow pools in rivers & streams, lakes **nest in riffles or in vegetation**	generalized invertivore	**26%** 7/27	**Intolerant**
chestnut lamprey *Ichthyomyzon castaneus*	riffles & pools in rivers & streams **glides, riffles**	parasite on fish	**25%** 4/16	**T** (IA), **SCP3** (ND), **PSC** (Canada) **Intermediate**
central stoneroller *Campostoma anomalum*	slow riffles in rivers & streams **glides, riffles**	herbivore/benthic invertivore	**25%** 5/20	**SCP3** (ND) **Intermediate**

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	Common Name ***Scientific Name***	**Adult Habitat** ***Spawning Habitat***	**Adult Feeding Habits**	**% Absent Upstream of Barriers** # Absent / Sample size	**Conservation Status** *Tolerance* **Management** (if any)
Somewhat Vulnerable	**finescale dace** *Chrosomus neogaeus*	cool, headwater streams & ponds **logs & branches in backwaters or bays**	generalized invertivore	**25%** 4/16	**E** (SD), **SCP3** (ND) Intermediate
	lake whitefish *Coregonus clupeaformis*	deepwater lakes **glides& riffles in streams, lake shoals**	water column invertivore, piscivore	**25%** 1/4	Intermediate
	walleye *Sander vitreus*	pools in rivers, lakes **glides, riffles & shoals**	piscivore	**25%** 8/32	Intermediate Widely stocked game species
Least Vulnerable Species : 0% to 24% Absence	**Northern pearl dace** *Margariscus nachtriebi*	pools in cool, headwater streams **glides, riffles**	omnivore	**24%** 4/17	**E** (IA), **T** (SD), **SCP1** (ND) Intermediate
	bigmouth shiner *Notropis dorsalis*	shallow pools in rivers & streams **unknown**	generalized invertivore	**23%** 7/31	Intermediate
	pugnose shiner *Notropis anogenus*	clearwater streams & lakes **vegetation**	herbivore, crustaceans	**22%** 2/9	**E** (IA, Canada, ON), **T** (MN, WI), **SCP3** (ND) Intolerant
	banded killifish *Fundulus diaphanus*	backwaters in clear rivers, lakes **vegetation**	generalized invertivore	**21%** 3/14	**E** (SD), **SC** (Canada) Tolerant
	northern hogsucker *Hypentelium nigricans*	fast runs in rivers & streams **glides, riffles & rapids**	benthic invertivore	**21%** 4/19	**SH** (SD) Intolerant
	white crappie *Pomoxis annularis*	pools in river, & lakes **nest in backwaters & bays**	planktivore, piscivore	**21%** 4/19	Intermediate Widely stocked game species
	central mudminnow *Umbra limi*	headwater streams **flooded ephemeral wetlands**	generalized invertivore, piscivore	**20%** 5/25	**S1** (SD) Tolerant
	tulllibee *Coregonus artedi*	deepwater lakes **pelagic over lake shoals**	water column invertivore, piscivore	**20%** 2/10	Intermediate
	lake trout *Salvelinus namaycush*	deepwater lakes **deep shoals**	piscivore	**20%** 1/5	Intermediate Occasionally stocked game species
	brassy minnow *Hybognathus hankinsoni*	pools in rivers & streams **vegetated backwaters**	herbivore/benthic invertivore	**19%** 5/27	Intermediate
	yellow bullhead *Ameiurus natalis*	clear rivers, streams, lakes, & ponds **nests in cavities**	generalized invertivore, piscivore	**17%** 4/23	**SCP3** (ND) Intermediate*
	tadpole madtom *Noturus gyrinus*	pools in streams **under rocks**	generalized invertivore	**17%** 5/29	Intermediate
	rock bass *Ambloplites rupestris*	pools in rivers & streams, lakes **nest in backwaters & bays**	generalized invertivore, piscivore	**17%** 5/29	Intolerant
	golden shiner *Notemigonus crysoleucas*	pools in rivers, lakes & ponds **vegetated backwaters & bays**	omnivore	**17%** 4/24	Tolerant Widely stocked bait species
	southern redbelly dace *Chrosomus erythrogaster*	clear, headwater streams & ponds **glides, riffles**	herbivore	**17%** 1/6	**S1** (SD) Intermediate
	blacknose dace *Rhinichthys atratulus*	riffles and pools in rivers & streams **glides, riffles**	generalized invertivore	**17%** 5/30	Tolerant
	bluntnose minnow *Pimephales notatus*	slow riffles in rivers & streams, lakes, ponds **underside of objects**	omnivore	**16%** 4/25	Tolerant

Least Vulnerable Species : 0% to 24% Absence

Common Name ***Scientific Name***	**Adult Habitat** ***Spawning Habitat***	**Adult Feeding Habits**	**% Absent Upstream of Barriers** # Absent / Sample sizee	**Conservation Status** *Tolerance* **Management** (if any)
common shiner *Luxilus cornutus*	pools in rivers & streams **glides, riffles, hornyhead chub nests**	omnivore	**16%** 5/32	**Intermediate** Common bait species
brown bullhead *Ameiurus nebulosus*	rivers, streams, lakes, & ponds **nests in cavities**	generalized invertivore, piscivore	**13%** 3/23	**Intermediate***
johnny darter *Etheostoma nigrum*	ubiquitous in rivers, streams & lakes **nest in backwaters in vegetation**	generalized invertivore	**13%** 4/32	**Intermediate**
green sunfish *Lepomis cyanellus*	pools in rivers & streams, lakes **nest in backwaters & bays**	generalized invertivore, piscivore	**12%** 3/25	**Tolerant**
brook stickleback *Culaea inconstans*	shallow pools in streams, wetlands **nests in vegetation**	omnivore	**10%** 3/30	**Intermediate**
bluegill *Lepomis macrochirus*	pools & backwater in river, lakes **nest in backwaters & bays**	generalized invertivore	**10%** 3/30	**Intermediate** Widely stocked game species
longnose dace *Rhinichthys cataractae*	fast riffles in rivers & streams **glides, riffles**	generalized invertivore	**10%** 2/21	**Intolerant**
northern pike *Esox lucius*	pools in rivers & streams, lakes **vegetated backwaters & wetlands**	piscivore, top predator	**9%** 3/32	**Intermediate** Widely stocked game species
hornyhead chub *Nocomis biguttatus*	ubiquitous in streams **gravel nests in glides, riffles**	benthic invertivore	**8%** 2/25	**SCP3** (ND), **S3** (SD) **Intolerant** Common bait species
largemouth bass *Micropterus salmoides*	pools & backwaters in rivers, lakes **nest in backwaters & bays**	top predator, piscivore	**7%** 2/30	**Intermediate** Widely stocked game species
yellow perch *Perca flavescens*	pools in rivers & lakes **vegetation & brush**	generalized invertivore, piscivore	**7%** 2/30	**Intermediate**
black bullhead *Ameiurus melas*	rivers, streams, lakes, & ponds **nests in cavities**	generalized invertivore, piscivore	**6%** 2/31	**Tolerant***
white sucker *Catostomus commersonii*	rivers, streams, & lakes **glides, riffles**	omnivore	**6%** 2/32	**Tolerant** Widely stocked bait species
creek chub *Semotilus atromaculatus*	pools in rivers and streams **glides, riffles**	generalized invertivore, piscivore	**6%** 2/32	**Tolerant**
pumpkinseed *Lepomis gibbosus*	pools in rivers, lakes **nest in backwaters & bays**	generalized invertivore	**5%** 1/22	**Intermediate**
black crappie *Pomoxis nigromaculatus*	pools in rivers, lakes **nest in backwaters & bays**	planktivore, piscivore	**3%** 1/29	**Intermediate** Widely stocked game species
fathead minnow *Pimephales promelas*	rivers, streams, lakes, & ponds **underside of objects**	omnivore	**3%** 1/31	**Tolerant** Widely stocked bait species
lake chub *Couesius plumbeus*	Great Lakes **streams and shoals**	omnivore	**0%** 0/1	**SC** (MN), **S1** (SD) **Intermediate**
Northern longear sunfish *Lepomis peltastes*	clearwater lakes **nest in bays**	generalized invertivore	**0%** 0/3	**T** (WI), **SC** (MN) **Intolerant**

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