DECLINE OF NATIVE MISSOURI RIVER FISHES: THE INTRODUCED FISH PROBLEM

By Harold M. Tyus

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MO-ARK
SERVING THE MISSOURI RIVER VALLEY
P.O. Box 35024, Kansas City, Missouri 64134
Decline of Native
Missouri River Fishes: The Introduced Fish Problem

by

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ABSTRACT

The native Missouri River fish community has been greatly affected by human-induced habitat change. Populations of at least nine native fishes have declined in range and abundance in all or some portion of the river system. These declines have been mostly attributed to physical and chemical alterations of habitat. However, as physical habitats were being altered by water resources development, nonnative fishes were introduced into these modified environments. In newly-created reservoirs, turbid riverine conditions were replaced by clear lacustrine-like environments and stocked with hardy, highly aggressive, predaceous and/or competitive fishes. Some introduced fishes were “pre-adapted” to the modified environments and thrived in them. But these same conditions were alien to the native riverine fishes, which universally declined. Remaining riverine sections are more suitable to the native fishes. But introduced fishes also have increased in the remaining riverine habitats due to direct stockings, and escapement from reservoirs and tailwaters. Physical habitat changes contributed to the declines of native Missouri River fishes, but declines of some of the native fishes would not have been as precipitous if fish introductions had not occurred. Additional fish introductions and management practices favoring the spread and proliferation of introduced species could hasten native fish declines, result in more threatened or endangered listings, and reduce options for recovering species listed now and in the future. There is a critical need for management agencies to recognize the potential problems of fish introductions, to investigate these problems with well-planned research, and to develop management options for reducing the adverse interactions between introduced and the native Missouri River fishes.
# TABLE OF CONTENTS

**ABSTRACT** .................................................................................................................. ii

**TABLE OF CONTENTS** .................................................................................................. iii

**INTRODUCTION** .......................................................................................................... 1

**MISSOURI RIVER AND ITS FISHES** ........................................................................... 3
  - A History of Change ................................................................................................. 3
  - Status of the Fish Fauna ......................................................................................... 5

**ENVIRONMENTAL FACTORS AND FISH DECLINES** ............................................. 7
  - Background ............................................................................................................ 7
  - Limiting Factors ..................................................................................................... 7
  - Synthesis ................................................................................................................. 12

**THE INTRODUCED SPECIES PROBLEM** ............................................................... 13
  - Ecosystems Disrupted ............................................................................................. 13
  - Threats to the Native Missouri River Fishes ......................................................... 14
    - Coldwater introductions ....................................................................................... 15
    - Coolwater introductions ..................................................................................... 16
    - Warmwater introductions .................................................................................. 19
  - Vulnerability of Native Fishes to Nonnative Interactions ...................................... 21
    - Background ........................................................................................................ 21
    - Endangered species ............................................................................................ 23
    - Other species of concern .................................................................................... 24
LIST OF TABLES

Table 1. Numbers of native and introduced fishes in three sub-basins of the Missouri River. .........................................................6

Table 2. Factors that influence the biotic integrity of streams. ......................8

Table 3. Introduced fishes in the Missouri River ......................................10
INTRODUCTION

Native freshwater fish communities have been severely affected by anthropogenic environmental change, which has steadily increased during the last 100 years (Williams et al. 1989). As a result, 27 native North American fishes (N=1,003) have become extinct and 265 species are threatened with extinction (reviewed by Wilson 1992). Several causes have been identified for these fish extinctions, but adverse interactions with introduced species was a major factor and associated with 68% of fish extinctions (Miller et al. 1989).

Intentional stocking of nonnative fishes for recreational fishing has been a major component in fisheries management (Rahel 1997). Nonnative fish introductions were purported to fill "vacant niches" (Moyle et al. 1986, Courtenay 1995) and declines of native fish faunas were almost always attributed to physical habitat alteration. However, a growing body of knowledge also implicates species introductions as a major factor in the decline, endangerment and extinction of native fishes. As a result, management practices to increase populations of nonnative fishes are being questioned, and nonnative stocks of some sport fish that were enthusiastically introduced in the past are just as enthusiastically being removed to preserve native fishes (Wiley and Wydowski 1993, Rahel 1997).

Moyle et al. (1986) discussed six mechanisms by which introduced fishes displace native fishes. Temple (1990) pointed out that effects of introductions are often understated and urged the development of control methodologies. In a review of 31 case studies of fishes that had been introduced into stream communities, Ross (1991) reported that at least 77% of introductions caused declines in native fish populations. Lassuy (1995) found that adverse interactions with nonnative fishes were reported as a reason for 70% (N=69) of fish species listed under provisions of the Endangered Species Act. Finally, Tyus and Saunders (2000) concluded that nonnative fishes may be the major factor in the continuing decline of endangered Colorado River fishes and should be considered as a factor associated with the decline of native fishes in other systems as well.

Why have fish introductions been so detrimental to native fish populations? The reasons why harmful effects occur are logical and scientifically fundamental. In an extensive review of fish introductions in the United States, Taylor et al. (1984) stated that harmful effects to native populations should be a "foregone conclusion." The evidence was sufficiently compelling that those authors believed a "no effects" argument would be implausible to the point of straining: "... one's confidence in ecological principles." The scope of the problem is captured in a document prepared by the national interagency Aquatic Nuisance Species Task Force (ANSTF 1994).

"By competing for resources, preying on native fauna, transferring pathogens, or significantly altering habitat, the introduction of a
nonindigenous species may work synergistically with other factors, such as water diversions or pollutants, to alter the population and distribution of indigenous species. The factors are often cumulative and/or complementary. For example, habitat degradation may make a species more vulnerable to the introduction of nonindigenous species."

Fuller et al. (1999) compiled lists of nonindigenous fishes introduced into the United States. All major regions of the United States have experienced introductions of nonnative fishes, and negative impacts in some regions have been devastating, for example in California (Moyle 2002) where 148 nonnatives have been introduced and the Colorado River (Tyus and Saunders 2000) where 102 have been introduced. The Missouri River region also has been affected by introductions of a great number of nonnative fishes (111 taxa; Fuller et al. 1999), but comparatively little is known about specific effects of introductions on the native Missouri River fishes.

The historic Missouri River, second largest river in North America, was a functional floodplain river. This system was extensively altered by humans during the 20th Century, and the mainstream is now a system dams, reservoirs, and altered channels. As native habitats were changed, more than 50 nonnative fishes were introduced into them. As a consequence, the aquatic system has been in a state of flux and native biodiversity has suffered. The decline of native fishes has predominately been attributed to physical habitat alteration, and little thought apparently was given to the effects of nonnative fishes that were introduced into the newly created reservoirs and altered stream channels. This philosophy began to change in the late 1980's and early 1990's as Endangered Species Act listing and recovery guidelines mandated that all potential causes associated with the decline of listed and candidate Missouri River fishes be identified and thoroughly evaluated.

Status reviews and other information gathered by the U.S. Fish and Wildlife Service (USFWS) in the pallid sturgeon (Scaphirhynchus albus) listing process (USFWS 1993), and status reviews of sturgeon chub (Macrhybopsis meeki) and sicklefin chub (M. gelida) (USFWS 1995) concluded that nonnative fishes contributed to the decline of these species by competition, predation, and hybridization. More recent findings found that evidence is lacking to demonstrate that introduced fishes are threatening their continued existence (USFWS 2001). However, data providing specific proof that competition and predation by introduced fishes is or is not a major factor in the decline of the Missouri River fishes are conspicuously lacking. I have not been able to find a comprehensive study of Missouri River native-nonnative fish interactions, either in laboratory or field situations, that addresses the problem.

Major dams and impoundments on the Missouri River are, from a pragmatic standpoint, permanent (Sheehan and Rasmussen 1999) and the extirpation of native fishes due to impoundment (e.g., loss of about 50% of river reaches historically occupied by sicklefin and sturgeon chubs) is not likely to be reversed. As human populations continue to expand, the demand for water, power, and transportation can
only be expected to increase, and as further changes occur in the system how can anthropogenic damages be minimized? Notwithstanding the massive changes in the system that have already occurred, what are the most important problems that need to be addressed today if the pallid sturgeon is to be recovered, and declines of additional species are to be prevented?

The objective of this study is to evaluate the potential for introduced fishes to cause declines of native Missouri River fishes. This was accomplished by reviewing major factors associated with native fish declines, exploring the mechanisms by which introduced fishes might be affecting the native fauna, and identifying species that constitute a menace to the native fishes.

MISSOURI RIVER AND ITS FISHES

A History of Change

The Missouri River is included in the Mississippi Province, a large zoogeographic unit that includes those areas of the United States and Canada drained by the Mississippi-Missouri River basins. The province is the largest and most species-rich region of the North America fish fauna and the center of fish evolution in the Nearctic region (reviewed by Moyle and Cech 1996). This important region served as a refuge for fishes during glaciation episodes, providing a place where species were able to re-invoke regions as glaciers retreated (Robison 1986). The presence of relict fishes of the ancient Mesozoic (i.e., sturgeons [Acipenseridae], paddlefish [Polyodontidae], gar [Lepisosteidae], and bowfin [Amiidae] in the big-river fauna (Pfieger 1997), suggests that the area has been a refuge for these species much longer than since the Pleistocene (Moyle and Cech 1996).

Originating in southwestern Montana, the Missouri River flows about 2,500 miles southwest to join the Mississippi River at St. Louis, Missouri. First issuing from clear headwater streams, the historic Missouri River became increasingly turbid as it receives drainage from silty tributaries. The native Big-River fauna of the Missouri-Mississippi rivers evolved in response to the prevailing historic conditions, and was superbly adapted to habitats and conditions that resulted. The mainstream Missouri River was a wide braided channel with a complex variety of habitats (e.g., backwaters, side channels, oxbows, shoals, pools, eddies, and runs) that changed seasonally as the natural flows fluctuated and shorelines eroded (Pfieger 1997, USFWS 1993). In response, a diverse fish fauna developed in the big-river region, which included large fishes of main channels and sloughs (e.g., sturgeon, paddlefish, gar, carpsucker and, buffalo [Catastomidae], and catfish [Ictaluridae]), and oxbows and backwaters (e.g, bass, bluegill, and crappie [Centrarchidae]). Common smaller fishes that occupy a variety of habitats include several species of minnows (i.e., chubs and shiners). It is difficult to separate the Missouri River fauna from that of the Mississippi River, but the distribution of several species: sicklefin, sturgeon, and flathead (Platygobio gracilis) chubs; plains and western silvery minnows (Hybognathus placitus and H. argyritus); and
pallid sturgeon, are especially related to the Missouri River (Pflieger 1997).

The present Missouri River has been extensively altered by humans and in many ways is unlike its historic condition. One of the greatest changes has been physical habitat modification due to construction and operation of mainstream reservoirs. By 1964, six large reservoirs had been constructed, which impounded 75 million acre-feet (92.4 billion m$^3$) of water, inundated thousands of miles (1,300 km) of natural riverine habitats, altered the historic flow patterns, and changed water quality, especially stream turbidity (reviewed by Werdon 1993ab). After these reservoirs were filled, major sections of the river system were isolated by impassable dams, and only about 1/3 of the Missouri River was left free-flowing. As physical habitat changes occurred, there were concomitant introductions of sport and forage fishes into the newly-created habitats, such as common carp (Cyprinus carpio), several species of trout (Salmonidae), yellow perch (Perca flavescens), northern pike (Esox lucius), walleye (Stizostedion vitreum), rainbow smelt (Osmerus mordax), and others. In addition to mainstream reservoirs, thousands of smaller impoundments on tributary streams have been constructed to augment the water supply in the arid plains region. These smaller impoundments, which have affected flows, sediment attributes, and the biota of the main channel, also have been stocked with introduced fishes prone to escapement into the main river channels. As a result, the historic fish fauna of the Missouri River, shaped by evolution over millions of years, has undergone a massive change due to anthropogenic actions that started over a century ago, and reached a massive peak with reservoir construction and operation. The change in the fish fauna has been exceptionally rapid and there are indications that this change has been recently accelerating (Pflieger 1997).

Most native fishes of the Missouri River are declining in abundance. According to the National Research Council (2002), 51 (76%) of native Missouri River fishes are: "...listed as rare, uncommon, or decreasing in numbers, and one is an endangered species." The problem is particularly acute for the so-called big-river fauna that occur only in main channel habitat. Pflieger (1997) portrays some of the adverse changes in the fauna:

"The flathead chub and plains minnow, the two dominant forage fishes in the Missouri River in 1945, have nearly disappeared, largely replaced by the emerald shiner and other sight-feeding minnows. The pallid sturgeon has declined in abundance since the early part of this century. Hybridization between this species and the shovelnose sturgeon probably is a response to changing habitat conditions in the Missouri River. Three species of chubs (speckled, sicklefin, and sturgeon) that are specialized for life in open, sandy or gravelly sections of the river channel have ...nearly disappeared in river reaches upstream..."

The pallid sturgeon has been federally listed as an Endangered Species and at least a dozen fish species (mostly native cyprinids) are considered threatened, endangered, species at risk or of special concern by state agencies, conservation
societies, and departments within state agencies (e.g., Holton and Johnson 1996, USFWS 2001). For example, in North Dakota, six of nine species identified as species with long-term population declines were native to the Missouri River system, and include the pallid sturgeon, paddlefish (*Polyodon spathula*), sicklefin chub, sturgeon chub, flathead chub and blue sucker (*Cycleptus elongatus*; Power and Ryckman 1998). Other species also have declined in other parts of the basin. Based on fish sampling of 45,500 small fishes from 1971-1993, Hesse (1994) reported that seven Missouri River fishes in Nebraska have had population reductions of 70% to 98%, and he recommended that sicklefin and sturgeon chubs, flathead chub, speckled and silver chubs (*Machrybopsis aestivalis* and *M. storeriana*), and plains and silvery minnow be listed at both the state and federal level.

**Status of the Fish Fauna**

Distribution of fishes in the Missouri River has been greatly modified by the transfer of fishes into areas where they are not native (i.e., were not present before European settlement). Waves of intentional and unintentional fish introductions began in the late 1800's and have continued to present. These introductions included exotic species imported from other continents, and nonnative species introduced from another basin, or transferred from one part of the basin where they were considered native to another part where they were nonnative.

Cross et al (1986), the most authoritative and comprehensive accounting presently available, reported 173 fishes from the Missouri River basin. Of these, 138 were native to some portion of the basin and 61 were nonnative. However, some species are native to a portion of the basin and nonnative to other portions (note also that the status assigned to some of the fishes is questioned later in this paper). There were remarkable differences in fish assemblages when the basin was divided into lower, middle, and upper sections: the upper section had less than half of the native species of the two lower sections and more introduced species. A total of 36 (43.2%) of the fishes were introduced in the upper Missouri River from other drainages (Table 1), including 18 (20.5%) from outside the basin, 17 (19.3%) from the middle or lower sub-basin, and 3 (3.4%) between drainages in the upper basin.

Table 1 provides the numbers of fishes that occur in the lower (lower Missouri, Chariton, and Nishnabotna rivers, middle (Platte, Niobrara, Sioux, Saint James, and part of the Missouri rivers), and the upper Missouri River basin (White, Little Missouri, Yellowstone, and upper Missouri rivers). Corresponding information for smaller drainage units also is provided in Cross et al. (1986).
Table 1. Numbers of native and introduced fishes in three sub-basins of the Missouri River. Lower = lower Missouri, Chariton, and Nishnabotna rivers\(^1\), Middle = Platte, Niobrara, Sioux, Saint James, and part of the Missouri rivers\(^2\), Upper = White, Little Missouri, Yellowstone, and upper Missouri rivers\(^3\). NN = non-native. (After Cross et al. 1986).

<table>
<thead>
<tr>
<th>Species Category</th>
<th>Lower</th>
<th>Middle</th>
<th>Upper</th>
<th>Basin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number</td>
<td>143</td>
<td>111</td>
<td>88</td>
<td>173</td>
</tr>
<tr>
<td>Native species</td>
<td>118</td>
<td>87</td>
<td>53</td>
<td>138</td>
</tr>
<tr>
<td>Introduced species</td>
<td>29</td>
<td>25</td>
<td>38</td>
<td>61</td>
</tr>
<tr>
<td>NN to basin</td>
<td>19</td>
<td>12</td>
<td>18</td>
<td>33(^4)</td>
</tr>
<tr>
<td>NN to sub-basin</td>
<td>6</td>
<td>11</td>
<td>17</td>
<td>21(^5)</td>
</tr>
<tr>
<td>NN within sub-basin</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>7(^6)</td>
</tr>
</tbody>
</table>

4. Excludes 2 fish of uncertain status
5. Excludes 5 fish of uncertain status

In this report, nonnative and nonindigenous are used as synonyms. However, in general usage, nonnative connotes a wider distribution; e.g., a human may be a native to the United States but nonindigenous to the southwest, or to Hawaii. In this context, Fuller et al. (1999) reported that organisms moved into areas outside their: "...historic or natural geographic range are considered nonindigenous species. This includes species transferred into the United States from foreign countries as well as those species moved from one region or watershed to another within the United States.” Typically, an exotic species is a special case that is not indigenous to a continent.

It is intuitive that a species introduced into North America from another country, or transported from one part of the country to another would be a nonindigenous species, however, the notion that it is acceptable practice to transfer a fish classified as a native in one drainage of a river basin to another needs to be questioned. Some species introduced into an adjacent watershed may pose as serious a problem as a species introduced from a foreign country (Fuller et al. 1999). This is especially pertinent for river basins in which large alterations of habitat has occurred to make
otherwise unsuitable habitats suitable to the nonnative species.

Nonnative fishes transplanted into the upper Missouri River are predominantly predaceous game fishes, including at least 9 species of salmonids, northern pike, bullheads, 2 centarchids, yellow perch, and walleye. Other species of special concern are rainbow smelt and common carp. In the lower Missouri River, transplants of exotic minnows include grass and bighead carps (Cyprinidae). All of these species may compete with native Missouri River fishes.

ENVIRONMENTAL FACTORS AND FISH DECLINES

Background

Riverine fishes are an important part of river biota, and certainly the most visible for humans. However, the role of fishes as indicators of environmental quality is not well appreciated (Bayley and Li 1993). Most fisheries management programs have addressed single species or groups of species (e.g., sport, or game fish) and there is a lack of basic understanding about ecological relationships that shape riverine faunas. This is unfortunate, because river systems have been greatly subjected to human modification, often with unpredictable and sometimes severe consequences.

The abundance of a natural population (excluding immigration and emigration) is determined by the balance of individuals gained through reproduction and those lost to mortality. If recruitment to the breeding population does not equal or exceed loss to all sources of mortality, other factors being equal, the population will decline. Factors contributing to recruitment and loss may be abiotic (physical or chemical), biotic, or both. Physical factors could include the quality or abundance of habitat required for one or more life history stages. Water quality, another abiotic factor, could cause mortality via pollutants, or reduce recruitment by more subtle effects like delay of spawning due to colder water temperatures. In general, however, water quality effects other than temperature (e.g. turbidity) have been studied little. Biotic limiting factors may include food supply, but are most likely related to nonnative fish predation, competition, or hybridization. In order to better understand the role of the biological component of habitat, it is instructive to review the issues in a broader geographical and biological context.

Limiting Factors

Environmental factors that regulate the abundance of a life history stage, or a population, are considered “limiting factors.” There are biotic and abiotic factors that regulate growth and mortality, and the relative importance of these limiting factors may vary in time (e.g., with season or with life history stage) or space (habitat occupied by a particular life history stage at a particular time of year). Limiting factors may be viewed as affecting the biological integrity (i.e., the natural quality of the stream biota; Karr and Dudley 1981) or the well-being of species, and include five main classes of abiotic and
biotic factors: biotic interactions, flow regimes, energy sources, water quality, and habitat structure (Table 2).

<table>
<thead>
<tr>
<th>CLASSES OF FACTORS</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biotic interactions</td>
<td>Relationships between organisms or populations, including predator-prey, competition, behavior, etc.</td>
</tr>
<tr>
<td>Water flow regimes</td>
<td>A major characteristic of streams that influences physical habitat</td>
</tr>
<tr>
<td>Energy source</td>
<td>Includes both autotrophy (food produced within the stream) and heterotrophy (food originating outside of the stream)</td>
</tr>
<tr>
<td>Water quality</td>
<td>Biological, chemical, and physical characteristics of water</td>
</tr>
<tr>
<td>Habitat structure</td>
<td>Features that result in a diversity of physical habitats</td>
</tr>
</tbody>
</table>

Abiotic factors that affect the distribution and abundance of Missouri River fishes have been changed by human development. Most native fishes are adapted to conditions of the natural stream ecosystem, but thousands of miles of the historic Missouri River ecosystem have been lost by conversion to reservoirs and clear tailwaters, fragmented by barriers, or suffered loss of complex habitats. As a result, fishes that once were superbly adapted to the natural riverine system have now been placed in a very different physical environment.

The biological component of habitat is more difficult to visualize than abiotic components. In general, biotic factors includes interacting plant and animal communities. Interactions occur according to trophic position and ontogenetic life stage, affected by changes in physical habitat (e.g., temperature, turbidity, water stage, etc.), they are shaped by behavior, and expressed by predation and competition for food and space. Of first consideration is food supply, which can regulate the size of populations, and the growth and health of individuals. As fish populations grow, intra- and inter-specific competition can greatly affect the distribution and availability of food.
Space also is important for all organisms, and fish behaviors such as territoriality and spacing aggression can limit the amount of space available for organisms. Finally, predator-prey relationships are very important and the success of the predator in capturing prey, or the success of the prey in escaping predation can depend on environmental conditions.

As changes in physical habitat were occurring in the mainstream Missouri River, fishery managers sought out aggressive and highly predaceous “game” species to fill the newly formed habitats. These fishes were predominately visual, or sight-feeding predators that were “preadapted” to the clearer waters. Additional introductions of smaller, non-game species were made to provide forage for the game fishes, while others may have been unintentional (e.g., “bait bucket”; Ludwig and Leitch 1996) introductions. Some of these introduced species were non-native to the Missouri River basin, while others were fishes that were native to some part of the basin, but not formerly adapted to living in the historic mainstream river (Table 3).

The adverse effects of introduced fishes on the decline of Missouri River fishes are relatively unknown. However, many native fishes are cyprinids and a very early (and practical) assessment of predation on cyprinid fishes provided by Forbes and Forbes and Richardson (1920) is instructional:

“Among the enemies of Cyprinidae disclosed by our study of 1,221 Illinois fishes . . . are practically all our most predaceous fishes . . . and it is safe to say that no fish-eating fish would, if hungry for fish, refuse a minnow of any kind unless it seemed too small to be worth the trouble of capturing.”

This early account simply points out the basic fact of predator-prey relationships in fishes: all fishes consume other organisms and have a dual role: to eat and to be eaten. Even small fishes commonly eat the eggs and larvae of other (and sometimes much larger) fish species if they are provided the opportunity.

The precise effects of nonnative fishes on native Missouri River fishes remain to be quantified. However, it is arguable that at least some of the native fish populations would not have declined as greatly in range and abundance in the altered river if additional species had not been translocated there. In addition, the adverse effects of fish introductions have been exacerbated by construction and operation of dams and reservoirs. Historic riverine habitats have been altered in impounded sections and the downstream river, in part due to a decrease in turbidity levels. Native and nonnative fishes now coexist in many locations where water clarity places the native fishes at a disadvantage, especially with introduced sight-feeding predators.
Table 3. Fish species introduced into the Missouri River. (After Cross et al. 1986). (See Table 1 for explanation of basin segments)

<table>
<thead>
<tr>
<th>Species</th>
<th>lower basin</th>
<th>middle basin</th>
<th>upper basin</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amia calva</em> (bowfin)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dorosoma petense</em> (threadfin shad)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Coregonus clupeaformis</em> (lake whitefish)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Oncorhynchus kisutch</em> (coho salmon)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>O. <em>nerka</em> (sockeye salmon)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>O. <em>tshawytscha</em> (chinook salmon)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>O. <em>aquabonita</em> (golden trout)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>O. <em>mykiss</em> (rainbow trout)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Salmo trutta</em> (brown trout)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Salvelinus fontinalis</em> (brook trout)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>S. <em>namaycush</em> (lake trout)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Thymallus articus</em> (Arctic grayling)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Osmerus mordax</em> (rainbow smelt)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Umbra limi</em> (central mudminnow)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Esox lucius</em> (northern pike)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>E. <em>masquinongy</em> (muskellunge)</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Carassius auratus</em> (goldfish)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Ctenopharyngodon idella</em> (grass carp)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>Cyprinus carpio</em> (common carp)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><em>Gila atraria</em> (Utah chub)</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Notemigonus crysoleucas</em> (golden shiner)</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Notropis hudsonius</em> (spottail shiner)</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Cyprinella spioptera</em> (spotfin shiner)</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>Pimephales vigilax</em> (bullhead minnow)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Species1</td>
<td>lower basin</td>
<td>middle basin</td>
<td>upper basin</td>
</tr>
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<td><em>Richardsonius balteatus</em> (redside shiner)</td>
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<td><em>Minytrema melanops</em> (spotted sucker)</td>
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<td><em>Ameiurus melas</em> (black bullhead)</td>
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<td><em>A. nebulosus</em> (brown bullhead)</td>
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<td><em>Fundulus sciadicus</em> (plains topminnow)</td>
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<td><em>Xiphophorus helleri</em> (green swordtail)</td>
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<td><em>X. variatus</em> (variable platyfish)</td>
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<td><em>Menidia beryllina</em> (inland silversides)</td>
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<td><em>M. crysops</em> (White bass)</td>
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<td><em>Ambloplites constellatus</em> (Ozark bass)</td>
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<td><em>A. rupestris</em> (rock bass)</td>
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<td><em>Micropterus dolomieui</em> (smallmouth bass)</td>
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<td><em>M. punctatus</em> (spotted bass)</td>
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<td><em>M. salmoides</em> (largemouth bass)</td>
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<td><em>Pomoxis annularis</em> (white crappie)</td>
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<td><em>P. nigromaculatus</em> (black crappie)</td>
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<td><em>Perca flavescens</em> (yellow perch)</td>
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<td><em>Stizostedion vitreum</em> (walleye)</td>
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Previous studies have demonstrated that fishes may alter habitat use due to minor changes in turbidity levels, especially to avoid predation (e.g., Miner and Stein 1996). A laboratory study of young razorback suckers (Xyrauchen texanus) that were exposed to both native and nonnative predators in clear and turbid waters had some surprising results. The suckers selected the clear water in deference to turbid conditions that would be more characteristic of their native riverine environment, but in clear water they were highly susceptible to predation by nonnative fish. When placed in higher turbidity, a more natural condition, the nonnative predator was no better at capturing the prey than the native predator (Johnson and Hines 1999). It was not anticipated that the sucker would select the clear water conditions that made it vulnerable, and this demonstrates naivete on the part of the prey that could contribute to its demise in altered habitats filled with unfamiliar nonnative predators.

Although most nonnative impacts can be expected to occur in riverine sections that have been converted to impoundments, native Missouri River fishes are not free of interactions with introduced fishes even in the less-altered riverine channels. Fish escapement from reservoirs, as well as some stocking directly into the river channels, contributes a steady supply of predators and competitors into riverine habitats occupied by the remaining populations of riverine fishes. In one study, 16 fish species escaped from Missouri River reservoirs, which include such species as common carp, channel catfish, various sunfishes (Centrarchidae), freshwater drum, and walleye (Walburg 1971). The number of fishes escaping reservoirs can be remarkable, and peak numbers ranged from 170,000 channel catfish to 10 million freshwater drum in a single 24 hr. period (Walburg 1971).

Synthesis

Physical habitat modification of the Missouri River system has been recognized as a major factor in the decline of native fishes. However, little has been done to identify the role of introduced fishes. As shallow, turbid, flowing stream reaches have been changed to deep, clear, lacustrine habitat, adaptations of the riverine fishes were no longer appropriate. At the same time, many other fishes that were not native in the riverine habitats were introduced into the newly-created system. The impact of these introduced fishes has been debated in various forums, but it is relatively certain that their presence has not been beneficial to the historic native riverine fishes. In other river systems where the effects of fish introductions on native fishes have been more thoroughly investigated (e.g., Tyus and Saunders 2000), adverse interactions appear to be just as important in causing declining native fish populations as habitat alteration. In fact, it is arguable whether declines and extinctions of freshwater fishes would be such a problem if native fishes were allowed to exist in physically altered habitats without the added stress imposed by introduced fishes.
THE INTRODUCED SPECIES PROBLEM

Ecosystems Disrupted

Many aquatic and terrestrial species have been introduced into North America. A study by the Office of Technology Assessment (USOTA 1993) concluded that introductions of harmful species have produced cumulative impacts and: “. . . are creating a growing economic and environmental burden for the country.” The report states that 4,500 foreign species have established populations in the United States. Many of these introductions were intentional, but others occurred unintentionally through human activities (Taylor et al. 1984).

Humans have a penchant for supplementing their local biological environment with imported plants or animals that are perceived to have special beauty or usefulness, or are simply reminders of a pleasing biological environment in another geographic location. Exotic species have been introduced from Europe and other continents with the intent of benefitting their “new ecosystem” in the United States. But most exotic species were the bane of, rather than a benefit to, new environments, and there are many examples of harmful introductions. One of the first species to be introduced into the United States was common carp. The carp was stocked across the country as a recreational and food fish by federal and state agencies, but the folly of this action soon became apparent as it caused great losses to fish habitat and displaced native fish populations (Fuller et al. 1999). For several decades, common carp has been considered one of the most undesirable species in North America, and targeted for population reduction or eradication (Wydoski and Wiley 1999). However, introductions of other fishes have continued, and predaceous and highly competitive species such as the ruffe (Gymnocephalus cernua; native to Europe and Northern Asia), which was introduced into the Great Lakes, and various species of snakeheads (Channidae; native to Africa and Asia), which now occur in several states (e.g., Oberg 2002) are recent examples of highly undesirable introductions. Finally, recent alarm over the imminent invasion of the great lakes by exotic silver, bighead, and black carp (Hypophthalmichthyes, Mylopharygodon) is due to predictions that these fishes would have even greater adverse impact on the Great Lakes ecosystem than the zebra mussel (Great Lakes Fishery Commission 2002), which imposed enormous economic hardships on water and power industries (Nalepa and Schlosser 1993).

Although most of the preceding examples of exotic introductions were due to accidental or unintentional releases, it is important to point out that many fishes have been intentionally introduced into waters of the United States where they are not native species. The overwhelming numbers of these introductions have been due to actions by responsible government agencies, ostensibly for “beneficial purposes”. These introductions have included such diverse purposes as providing food resources (e.g., the
common carp), as a biological control (e.g., the mosquitofish, *Gambusia affinis*), as bait fish (e.g., sheepshead minnow, *Cyprinodon variegatus*), and as "forage" for other introduced sport fishes (e.g. gizzard shad, *Dorosoma cepedianum*) and rainbow smelt. All of these introduced fishes, and many others, have become abundant in river systems throughout the United States. Although these introduced fishes have some practical or aesthetic value, all have caused problems in natural ecosystems and resulted in unanticipated economic and environmental costs (USOTA 1993, Taylor et al. 1984, Courtenay and Robins 1989). Even seemingly innocuous species like grass carp (*Ctenopharyngodon idella*), which was introduced in 1963 to control aquatic vegetation (Stanley et al. 1978), is now suspected of altering native fish communities (Raibley et al. 1995).

If the impact of introduced species were simply to add some individuals to the existing biological community, it would be less of a cause for concern. Introductions do not happen in a biological vacuum, however. In complex native fish communities, it is difficult to predict the outcome of introducing a new species (Li and Moyle 1981), but most introductions prove harmful and have unanticipated (usually adverse) effects on native communities. In general, the biological system receiving the invader will be altered, typically by displacement of a native species (Li and Moyle 1981, Courtenay and Robins 1989, Courtenay 1993). The problems caused by many introduced plants and animals seem to worsen with time (Leopold 1949, Laycock 1966). In the extreme, introduced species can cause the local extirpation or extinction of native species with resultant loss of biodiversity (reviewed by USOTA 1993).

**Threats to the Native Missouri River Fishes**

Data and other information needed for a direct evaluation of adverse interactions between native Missouri River fishes and nonnative introductions is generally lacking. However, some comparisons can be made with other areas where problems due to competition and predation between introduced and native species have been documented. In general, aquatic introductions: "...have been harmful; in some cases they have been catastrophic." (Fuller et al. 1999).

The fish species most likely to cause problems are well known. According to the ANSTF (1994) nonnative fish introductions related to sport fishing were most frequently cited as a reason for listing fishes under the Endangered Species Act (73% of all fish listings):

"Members of the bass and sunfish family (*Centrarchidae*) were the most frequently cited sport fish group contributing to ESA listings. The largemouth bass (*Micropterus salmoides*) was the most frequently cited individual species. Other centrarchids included green sunfish, bluegill, crappie, "other sunfish," and smallmouth bass. Members of the freshwater catfish and bullhead family (*Ictaluridae*) were the second most commonly cited group. Channel catfish
(Ictalurus punctatus) and several species of bullheads were mentioned. Various
bait species were another frequently cited group and included most commonly the
red shiner (Cyprinella lutrensis), the fathead minnow (Pimephales promelas) and
“other baitfish.” Rainbow trout (Oncorhynchus mykiss) and brown trout (Salmo
trutta) were cited in seven and six cases, respectively, primarily for having caused
problems though hybridization with native trout species or as predators of smaller
species.”

A comprehensive assessment of the relative impacts of introduced fishes on the
native Missouri River fishes will require knowledge of habitat use, food preferences, and
reproductive ecology of the native fishes. Information about the introduced fishes also
will be required, including foods consumed, space utilized, behavior, and degree of
sympathy with the native fishes. Unfortunately, very little has been reported in the
published literature about the life histories of most of the native species considered at
risk. Except for federally listed and candidate species (i.e., pallid sturgeon, sturgeon
chub, and sicklefin chub) published sources available for the other species at risk
presented in this report point out that for most, little is known about specific habitat
requirements, food preferences, or reproductive ecology (e.g., Pflieger 1997). Ideally,
this information would have been obtained before habitats were altered and populations
of the native fishes declined. However, there is a great deal of information available for
assessing the degree of threats posed by various nonnative fishes introduced into the
Missouri River, because almost all of them have caused problems with native fishes
elsewhere.

Table 3 provides an accounting of fishes (common and scientific names provided)
that have been introduced into various locations in the lower, middle and upper Missouri
River. Introduced fishes considered to be threats to the native Missouri River fishes are
discussed below by cold-, cool-, and warm-water systems:

— Coldwater introductions

Coldwater systems include streams and lakes in which the temperature rarely
exceeds about 20° C for any period of time. Fish faunas are characterized by trouts,
whitefishes, sculpins, and a few species of minnows and suckers. Because most of
these systems are at high elevations and small, they are subjected to harsh conditions,
and food webs are short.

Coldwater fishes that have been introduced into nonnative ranges in the Missouri
River basin include different taxa: Pacific salmon and nonnative cutthroat trout of the
genus Oncorhynchus, European brown trout (Salmo), and chars (Salvelinus). These
fishes historically inhabited headwater streams and cold rivers, where they rarely interact
with warmwater fishes. However, widespread introductions have been made into deep
and thus, cold reservoirs and their tailwaters and many “blue ribbon” tailwaters have
been exploited by sport fishermen. During colder portions of the year, introduced
coldwater fishes can move downstream into habitats occupied by native fishes and predation at that time may be high.

Cold water released from Glen Canyon Dam in the Colorado River supports a substantial tailwater trout fishery in Grand Canyon. Trout predation on native warmwater cyprinids that enter mainstream waters from warm tributaries has been well documented (Marsh and Douglas 1997). Valdez and Ryel (1995) estimated that brown trout consumed 230,000 humpback chub annually in the Grand Canyon, and that rainbow trout consumed 27,375 annually. These authors also reported evidence of competition.

The yellowfin cutthroat trout (Onchorhynchus clarki macdonaldi) of the east slope of the Rocky Mountains was one of the earliest cases of a native trout driven to extinction. Native to the upper Arkansas drainage its last populations were reported in Twin Lakes, Colorado, where they were abundant in the 1870's. However, their extinction was attributed to overfishing and introduction of rainbow trout, brook trout, lake trout, and Atlantic salmon (Salmo salar) in 1890. By 1903, the rainbow trout were dominant, and no yellowfin trout were found then or later (Ellis 1914, USFWS 1998).

The major factor in the decline of the greenback cutthroat trout in the South Platte and Arkansas drainages in Colorado was the introduction of non-native salmonids: rainbow, brook, brown, and Yellowstone cutthroat trouts. The greenback trout hybridizes with rainbow trout and other subspecies of cutthroat trouts, it is displaced by brook trout, and prey to rainbow and brown trouts (USFWS 1998).

An exhaustive accounting of the adverse interactions between various species of salmonids is presented by Fuller et al. 1999. These accounts leave little doubt that introduced salmon, trout, and other salmonid fishes can and do compete with, prey upon, and hybridize with native salmonids, and compete with and prey upon many other species as well.

— Coolwater introductions

Coolwater lakes are transitional between coldwater and warmwater systems. Coolwater lakes are characterized by predatory fishes such as northern pike, muskellunge, walleye, yellow perch and smallmouth bass. These species also can thrive in both cold and warmwater habitats, which they tend to move into depending on season.

Northern pike and walleye are avidly sought by recreational fishing interests, thus these species are the most popular coolwater fishes for introductions. However, stockings of these species have met with controversial results due to reduction of prey species, piscivory on salmonids, and invasions into adjoining watersheds, and there is concern about risks associated with additional introductions (McMahon and Bennett 1996).
Northern pike—This circumpolar species is restricted to cold and temperate parts of the northern hemisphere, holarctic in distribution north of about 40° latitude. It is considered native to the middle portion of the Missouri River (i.e., units 14 and 15, Cross et al. 1986), and nonnative to the upper and lower portions. A voracious piscivore, northern pike can alter fish communities via predation. A sight-feeding and ambush predator, northern pike thrive in slower rivers, ponds and lakes.

Northern pike prefer soft-rayed fishes, but will eat almost anything, including bluegill, yellow perch, walleye, other pike, and various species of waterfowl (Scott and Crossman 1973, Rast 1988), even extirpating their prey (Fuller et al. 1999). Introduced pike are capable of rapid invasion into downstream warmwater streams (Tyus and Beard 1990). As northern pike populations increased in the Yampa River of Colorado, endangered Colorado pikeminnow numbers have decreased (John Hawkins, Personal Communication 2001). As a result, a massive effort to eradicate northern pike from waters that support endangered species is in progress in the Colorado River system. Fuller et al. (1999) provide other examples of pike predation on native fishes.

Walleye—Walleye occur in most of the same drainages as northern pike. The range of the fish includes the upper Mississippi River drainage, and it is included as a native fish in portions of the Missouri River by Lee et al. (1980) and Cross et al. (1986). However, there has been some controversy about the appropriateness of the native fish designation, which is of interest because it concerns the coevolution of walleye and other native Missouri River fishes.

The status of walleye as a native Missouri River fish recently has been questioned by Captain Bill Beacom of Sioux City, Iowa, who has carefully researched the topic as an avocation. Beacom has uncovered substantial evidence that walleye are not native to the Missouri River. This evidence includes reports of the Iowa Fish Commissioner that indicate walleye were present only in the Mississippi River in Iowa (State Fish Commissioners of Iowa 1876), and that presence of the fish in the Missouri River system originated from translocation of fishes from the Mississippi River and from hatcheries (State Fish Commission of Iowa 1883, Bean 1893). In South Dakota, walleye are considered native, but the records from which this status is based are from lakes that historically have dried up during droughts or were susceptible to winter die-off ("winter kill"). In North Dakota there apparently is no proof that walleye were ever native to that state, and Beacom (personal communication) has linked the presence of walleye in the Missouri River with potential stockings from railroad sources that occurred 15 years or more before definitive surveys were conducted.

My review of the status of walleye also suggests that the fish is not native to the Missouri River, based on the following reasons: (1) Primarily a lacustrine species, walleye is a highly desirable sport and food fish and it was widely introduced before its native range was fully documented (a stocking from Vermont to California occurred as early as 1874; Fuller et al. 1999); (2) The fish is similar in appearance and easily confused with native sauger—some records of walleye were likely reported due to
misidentification; and (3) walleye were not reported in early surveys of the Missouri River drainage. The fish was not present in 1855 to 1857 collections from the Missouri River and tributaries that were identified at the Smithsonian Institution (Warren 1875), nor was the Missouri River included in the distribution account provided by Jordan and Evermann (1898). An extensive review of faunal lists by Evermann and Cox (1896) reveal the conspicuous absence of walleye from all of the earlier collections that predated widespread introductions.

In general, the walleye is widely distributed from the central United States north to arctic regions of Canada, forming a major part of the fish fauna of the boreal forest zone. Its preferred habitats include large, shallow somewhat turbid lakes where they will prey on any species of fish provided them (Scott and Crossman 1973). Walleye introductions often affect salmonid fisheries, and cause their collapse in reservoirs and tailwaters. The status as a top predator on salmonids is well established: walleye consumed 500,000 fingerling trout in a few weeks in Seminoe Reservoir, Wyoming, and consume an estimated 2 million salmon smolts in the Columbia River annually (reviewed by McMahon and Bennett 1996). In their native environments walleye extensively prey on yellow perch, whose populations are often depleted, and can displace sauger in some environments (Scott and Crossman 1973, Fuller et al. 1999). The fish has been introduced into reservoirs throughout the Missouri River basin and thrives in many of them. The walleye has "dramatically" expanded its range in the past 40-50 years (Cross et al. 1986). Although walleye and native sauger are closely related species, they differ in habitat use and prey selection (Scott and Crossman 1973, Rawson and Scholl 1978).

Rainbow smelt—A native of the New England region in the United States, the fish has been widely introduced as a large (up to 12" in length) forage fish in a variety of cool- to warmwater systems. This fish is a predator of young fishes and it has been implicated in the decline of lake trout, whitefish, cisco, and blue pike due to predation on larval fishes. It is considered to be an aquatic nuisance species in Lake Superior and elsewhere (Cornelius 2000). Rainbow smelt feed on a variety of prey items including eggs and larval fishes, and it is a threat to native fishes through competition for food and predation on young (Hrabik et al. 1998).

Courtney and Robins (1989) provided a discussion of of a proposed rainbow smelt introduction into Lake Powell of the Colorado River in Utah. Opposition to this introduction was contested by environmental groups and natural resource agencies due to potential predation by the smelt on eggs and young of federally endangered fishes. As a result the proposal was withdrawn by the State of Utah, and rainbow smelt introductions have not occurred.

Rainbow smelt was not present in the Missouri River until 1976 when it was introduced into Lake Sakakawea. Since that time, it has increased "explosively", dispersing upstream and downstream in the Missouri River, and entering other reservoirs (Cross et al. 1986). This relatively large "forage" fish is expected to prey on any fish eggs or larval fishes encountered.
— Warmwater introductions

Warmwater systems are typically found at lower elevations, and summer water temperatures exceed 23-25 C. These are the most diverse aquatic systems, the number of fishes can be large (over 40), and food webs diverse. Prominent warmwater piscivores such as largemouth basses, have been coveted as recreational game fish, cultured, and stocked into every conceivable habitat. But warmwater gamefish are thought to have had a great adverse effect on native fishes wherever they have been introduced. The ANSTF (1994) reported that centrarchids (i.e., largemouth bass, green sunfish, bluegill, black crappie, and smallmouth bass) and ictalurids (i.e., channel catfish and bullheads) were frequent contributors to the demise of native fishes nationwide.

A total of 11 nonnative centrarchids and 3 ictalurids have been introduced into portions of the Missouri River. Many of these fishes have been linked with the extirpation of native species, especially cyprinids (e.g. Lemly 1985, Fuller et al. 1999). Although it can be anticipated that the predaceous adults of these species attack native Missouri River species, it has been demonstrated that juvenile life stages also pose a threat. Sabo et al. (1996) documented 18 types of agonistic behavior, including threats and attempts to injure, in juvenile large- and smallmouth bass that were less than 50 days post-hatch.

— largemouth bass. Adapted to warm lakes and slow-moving streams, this is one of the most aggressive and predaceous freshwater fish in the world. Its introduction into nonnative environments can alter entire systems. Carlander (1977) gives a listing of food items consumed by various ontogenetic stages, which includes many taxa of fishes, birds, crustaceans, reptiles, and amphibians. Fuller et al. (1999) provides a long list of species that have suffered declines, extirpation, and extinction due to predation by largemouth bass in the United States. Largemouth bass also have been transported to exotic locations, and one account of an introduction into Lake Atitlan, Guatemala is especially revealing because of impacts attributed to the fish, which included: "... elimination of several native species of fish, reduction in total biomass of fish, predation on young flightless giant grebes, and competition for the insects and crustaceans eaten by the grebes" (Carlander 1977).

Largemouth bass has been widely introduced throughout the Missouri River basin, and its range has expanded from the eastern parts of the Dakotas, Kansas, and Nebraska all the way to the western limits of the basin. This fish is expected to be the top piscivore in warmer (and especially more lacustrine) aquatic habitats.

— smallmouth bass. A fish of cooler temperate streams and lakes, smallmouth bass also are aggressive predators. This fish hybridizes with several other centrarchids (including spotted bass) and can decimate populations of small fishes by predation (Fuller 1999).

— sunfishes. Several sunfishes have expanded their previous ranges further west in the
Missouri River basin due to introductions. These smaller and more laterally compressed centrarchids include a variety of fishes stocked as game fish, including the crappies, which are predaceous species that prey on small fishes, and redbear sunfish, which mainly prey on crustaceans, and bluegill, which are mainly insectivores. Other species that are incidentally stocked include green sunfish, which is an especially aggressive species with a relatively large mouth. Green sunfish preys on or competes with many other fishes (e.g., Lemly 1985), and can eliminate native plains fishes from preferred habitats (Lohr and Fausch 1996). All sunfishes should be suspected of preying on eggs and/or young of other species.

– ictalurid bullheads and catfishes. Ictalurids eat a wide variety of food items, but all should be suspected of consuming eggs and young of other species. As bullheads and channel catfishes attain large adult sizes they also become more piscivorus. Bullheads and channel catfishes are known to consume endangered chubs in the Colorado River (Marsh and Douglas 1997). Because of their aggressive nature and inclination to eat anything (see Tyus and Nikirk 1990) stockings of channel catfish are thought to be an agent in the decline of humpback chub in the Yampa River of Colorado (Tyus 1998).

– exotic carps. Now one of the most abundant fish in the Missouri River basin, common carp were widely introduced into the United States beginning in 1877 (Laycock 1966). Prior to extensive habitat alteration, few introduced fishes established populations in the mainstream Missouri River, but common carp, introduced in 1879 has been the most successful (Pfieger 1997). This highly-competitive and hardy species was widely extolled as the "wonder fish from Europe" in the 19th century, but in the early 20th century the fish was considered a "scourge and without friends" (Laycock 1966). Common carp has been accused of degrading native fish habitats in the U.S. for over 100 years. Carp eat the eggs of other fishes, including those of sturgeons, and have been implicated in the decline of the endangered razorback sucker (Fuller et al. 1999).

Grass carp and bighead carp populations also are established in the Missouri River, and silver and black carps also have been reported. The effects of these latter carps, referred to as "Chinese carps" on native fishes is unknown, but at least one or more of these species may compete with paddlefish, bigmouth buffalo, and other species (Pfieger 1997).

The Great Lakes Fishery Commission (19 June 2002 letter from U.S. Chairman Henson to the U.S. Subcommittee on Energy and Water) and the U.S.– Canadian Joint Committee (5 July 2002 letter to the U.S. Secretary of State and the Canadian Minister of Foreign Affairs) have requested immediate action pursuant to the Boundary Waters Treaty of 1909, to stop the spread of three species of Asian carp (bighhead, black and silver carp) into the Great lakes. These agencies fear greater adverse impact on the Great Lakes than has occurred from invasions of the parasitic sea lamprey that destroyed the Lake Trout fisheries, or from the zebra mussel that resulted in catastrophic losses to the power industry and has substantially altered Lake Erie and Lake St. Clair ecosystems.
Vulnerability of Native Fishes to Nonnative Interactions

— Background

Li and Moyle (1999) provided an overview of ecological concepts that are important for understanding the effects of introduced species and Moyle et al. (1986) identified six mechanisms that allow introduced fishes to displace native fishes, especially in habitats that have undergone extensive physical habitat alteration. These mechanisms are summarized below:

1. Competition: nonnative fishes can affect the use of food and space by native fishes by interference (e.g., denying access of another species to limited resources, usually through aggression), and exploitation (e.g., better at utilizing resources, such as a visual feeder in clear water as opposed to a fish adapted to turbid conditions).

2. Predation: all fishes are consumers and most can be predaceous at some life stage. Predation may be difficult to observe in riverine systems, and eggs or larvae are so quickly digested that even stomach contents analyses can be misleading (e.g., see Langhorst and Marsh 1986).

3. Reproductive inhibition: nonnatives can reduce reproductive success of native fishes by a variety of agonistic actions whereby spawning and/or parental care of eggs and young are disrupted.

4. Environmental modification: natural habitat complexity can be changed by fishes that destroy vegetation (grass carp) or create unusual conditions (turbidity; common carp), thereby placing native fishes at risk.

5. Parasites and disease: Asian tapeworm and whirling disease are examples of parasites and diseases introduced by nonnative fishes that have caused declines in native fish populations.

6. Hybridization: altered environments can break down reproductive isolating mechanisms between related native species, but nonnatives that are placed in different environments also pose a threat due to hybridization with native species.

The preceding list summarizes the many ways that introduced fishes can adversely affect native fish communities. The interactions can be complex, difficult to predict, and in some cases difficult to imagine. However, it has been universally appreciated by naturalists and morphologists for centuries that animals reduce or
eliminate their vulnerability to enemies through adaptation, both behavioral and morphological (Fryer 1986). How do fishes reduce vulnerability to enemies, and how can species introductions can be so devastating?

It has been known for centuries that: "... major aspects of species' lifestyles are moulded by the impact of natural enemies..." (Jefferies and Lawton 1984), and even the morphology of a species can be changed by this interaction. One of the most interesting fish examples is predator-induced morphological change in crucian carp (Carassius carassius), whose populations increase their body depth in the presence of northern pike to avoid being eaten (Bronmark and Minor 1992). This morphological change is so dramatic that affected individuals have been mistakenly identified as a separate species.

It takes time to develop the strategies that adapt one species to the activities of others, and once developed, these strategies can be made less effective with physical or biological alterations of habitat. Evolution usually occurs slowly (i.e., over geologic time scales), but abrupt changes such as caused by human activities can disrupt the relationships previously developed between species. For example, a reduction in turbidity in the Missouri River could be expected to favor predation by native sauger on chubs, sturgeon, or other species adapted to life in turbid water. However, the introduction of nonnative fishes that may be "preadapted" to life in the altered environments may place native predator and prey at a disadvantage. In this case, lack of exposure to the nonnative species also could result in a naivete to predation (e.g., see Johnson et al. 1993), perhaps due to different foraging tactics, and etc. In this case, defense strategies that evolved in response to sauger predation may not be appropriate for introduced walleye, who are more adaptable, occupy different habitats, forage differently, select different prey, and as a consequence are even known to displace sauger in some habitats (Scott and Crossman 1973, Rawson and Scholl 1978). The addition of other predators such as pike, bass, sunfishes, rainbow smelt, etc., to a system that continues to be changed by physical habitat alteration makes it hard to imagine how the native prey could survive for long.

But not all impacts caused by nonnative fishes are due to predation. Competition for food and space also can be a powerful force (e.g., Schoenherr 1981, Taylor et al. 1984), especially with an increased vulnerability to predation. For example, a decrease in turbidity can be expected to result in shifts in habitat use by predator-wary prey (Miner and Stein 1996). In this case, less food and fewer places to hide greatly exacerbate problems caused by increased predation and can result in species extirpations and possibly extinctions over time.

A better understanding of vulnerability to other species can be aided by an appreciation of interactions that develop by coevolution (i.e., evolution of 2 interacting species that adapt to characteristics of the other and each enhances the fitness of the other). In this case, coevolution can be considered "reciprocal evolution" among
interacting species, even including predator and prey. In this case, adaptations of the sauger that were successful in obtaining prey, as well as those that reduce the vulnerability of the prey to the sauger may have been important attributes of native fish communities, but would not be effective with introduction of nonnative predator and prey species.

The great difficulty for fishery managers is that these adverse interactions occur underwater and are hard to detect. Not only is it difficult to detect predation by examining stomach contents of suspected culprits, but seemingly innocuous forage fishes like fathead minnows, rainbow smelt, and other species can prey on eggs and larvae of native fishes, or compete for food and space (reviewed by Tyus and Saunders 1996, 2000).

— Endangered Species

The only fish in the Missouri River basin that is presently listed pursuant to provisions of the Endangered Species Act is the pallid sturgeon. Reasons for the decline and endangerment of pallid sturgeon include blockage of spawning migrations, habitat fragmentation due to dams, habitat alteration (both physical and biological), over harvest; pollution and contaminants, and hybridization (USFWS 1993). Of special relevance to this paper is the change in the biological components of habitat and how the pallid sturgeon might be affected. This issue is addressed in the Pallid Sturgeon (Scaphirhynchus albus) Recovery Plan (USFWS 1993; page 12):

The turbidity caused by suspended sediment also provided the pallid sturgeon and other native fish, adapted to living in a nearly sightless world, with cover while moving from one snag or undercut bank to another. Today, water clarity has increased dramatically, and this essential cover is gone. Under such conditions, predation by sight-feeding predators, such as northern pike (Esox lucius), walleye (Stizostedion vitreum) and smallmouth bass (Micropterus [sic] dolomieui), can be expected to significantly impact native species not equipped by evolution with good eyesight.

A living representative of ancient ray-fin fishes, it is presently listed as an endangered species by the U.S. Fish and Wildlife Service, the pallid sturgeon is the rarest fish in the Missouri-Mississippi River basin (USFWS 1993). Pallid sturgeon was formerly common in portions of the Missouri River where they constituted about one-fifth of the sturgeons captured (Forbes and Richardson 1905), but only a few individuals have been recently reported (USFWS 1993). Only 11 of 4,366 sturgeons captured were pallid sturgeons, and an additional 12 fish were pallid X shovelnose sturgeon hybrids (Carlson et al. 1985), making hybrids (0.3%) about as common as pure-strain fish (0.2%).

Pallid sturgeon is adapted to a benthic life in large turbid floodplain rivers. As a group, sturgeons are migratory (Nikolskii 1961), but pallid sturgeons declined in abundance before their specific migrations were charted. Early accounts documented
upstream spawning migrations of its close relative, the shovelnose sturgeon (e.g., Goode 1884, Jordan and Evermann 1923) and it is likely that construction of mainstream dams blocked spawning migrations of both species. Loss, reduction, or blockage of spawning habitat would have reduced the number of sturgeon larvae and exacerbated predation impacts, especially in less turbid environments. As a result of all these factors, recovery of pallid sturgeon and a reduction in the rate of decline of the shovelnose sturgeon population will require increased recruitment. In the present system few easy options exist. Adult sturgeon are large fishes and their size provides safety from predation by other native fishes. However, larvae and juvenile sturgeon are at risk.

The level of recruitment of sturgeons in the historic Missouri River is unknown. However, present recruitment of shovelnose and pallid sturgeons is apparently very low because sturgeon larvae are rarely captured (e.g., 2 sturgeon larvae in 147,000 fish larvae captured from 1983-1991; USFWS 1993). Among the factors that could be associated with the low numbers of sturgeon larvae is a higher predation rate due to increased predator density, or an increase in predator efficiency in the changed Missouri River environment. Although the sturgeons evolved with predaceous fishes such as the sauger, the present environment (e.g., less turbid, slower flows, less habitat complexity) could enhance predation rate. Also, addition of so may new predators places prey at a greater risk due to different foraging tactics of nonnative predators. In this case, predator-induced defenses gained through evolution would be lacking.

— Other Species of Concern

This category includes paddlefish and seven species of minnows (sturgeon, sicklefin, flathead, silver, and speckled chubs; plains and silvery minnows) that have declined in distribution and abundance in the Missouri River. Little is known about the life history of most of these fishes, and specific information about their reproductive ecology is lacking.

Two species previously considered for federal listing as threatened or endangered (USFWS 1995, 2001) are the sturgeon and sicklefin chubs. The USFWS (2001) recently removed the two chubs as candidates for listing for two reasons: (1) collections with benthic trawls in some locations indicated that the fish was more widely distributed than previously thought, and (2) conservation measures proposed for the listed pallid sturgeon also would benefit the two species. But this action warrants review.

Sturgeon and sicklefin chubs have had extensive range reductions and threats to their survival continue. A major concern in some fisheries is the destruction of benthic life, which may include the younger life stages of the fishes and the invertebrates they prey upon (DeAlteris and Morse 1997). Uniquely adapted to life under very turbid conditions of the mainstream river, both of these small species are vulnerable to predation from a variety of sight-feeding predators that have been introduced into altered riverine habitats.
— *Sturgeon chub*: Once reported from 14 states, this species is probably extant in only 5 states (Werdon 1993b). USFWS (2001) reported that the species exists in 11 of 30 tributaries (37%) that supported sturgeon chub habitat. Hesse (1994) reported that sturgeon chub were either extirpated or present in such low numbers as to be functionally extirpated in the Missouri River in Nebraska. The fish has been listed as threatened, endangered, or a species of concern in Kansas, North and South Dakota, Missouri, Kentucky, Tennessee, Missouri, Nebraska, Montana, and Wyoming (Power and Ryckman 1998, USFWS 1995, 2001). The fish is considered extirpated from Iowa.

The sturgeon chub is morphologically adapted for life in turbid plains rivers. The slender fish has a depressed head, small eyes, highly developed olfactory structures, and unique dermal keels (Branson 1966, Cross 1967, Reno 1969).

— *Sicklefin chub*: Once reported from 13 states, this species is probably extant in only 4 states (Werdon 1993a). Hesse (1994) reported that sicklefin chub were either extirpated or present in such low numbers as to be functionally extirpated in the Missouri River in Nebraska. The fish has been listed as threatened, endangered, or a species of concern by Kansas, Iowa, Missouri, North Dakota, South Dakota, Kentucky, Tennessee, Kansas, Nebraska, and Montana (Werdon 1993a, Power and Ryckman 1998, USFWS 1995, 2001).

The sicklefin chub is specialized for living in the main channels of large turbid rivers, where it is adapted to deep water, strong currents, and turbid water (Cross 1967). The fish has small eyes that are partially covered to protect them and abundant sensory structures for detecting prey in dim light (Moore 1950, Reno 1969). This fish is unique among other barbeled minnows due to its very long pectoral fins. Threats to the survival of this fish include habitat fragmentation, habitat loss and alteration, competition and predation from introduced fishes, and contaminants (Werdon 1993a).

— *Flathead chub*: Historically one of the most abundant fishes in the Missouri River, numbers of the fish sharply declined beginning with the construction of large mainstream reservoirs. Formerly amounting to 31% of small fishes taken in seine hauls in the 1940's, by the 1980's the fish was only 1.1% of collections (Pfieger 1997). This decline was also documented by Hesse (1994) in the Missouri River in Nebraska, where the fish declined in catch/effort 98% from 1971 to 1993. The flathead chub has been listed as endangered or a species of concern in Missouri, Arkansas, Kansas, and North Dakota.

The flathead chub is a rather large (to 12½ in) barbeled minnow, having a distinctive broad and flattened head, and large pointed sickle-shaped dorsal and pectoral fins (Page and Burr 1991). The fish has small eyes and depends more on external taste buds to find food in its native turbid water environment (Pfieger 1997). Clear water conditions places the fish at a disadvantage with introduced, sight-feeding fishes. It is presumably in competition with the emerald shiner, whose numbers have increased as flathead chubs have decreased (Pfieger 1997). Predation on its young by introduced predators, such as walleye or largemouth bass is likely a factor in its decline.
— **Plains and silvery minnows**: These two small minnows are very similar in appearance and historically common to abundant in preferred habitats in the central U.S. (Page and Burr 1991). Both minnows have been listed by Missouri as endangered, and species of concern in Kansas. Formerly abundant species in the upper Missouri River, both of these minnows have undergone a “drastic” decline and are anticipated to become extirpated if this trend continues (Pflieger 1997). Hesse (1994) reported the catch/effort of plains/silvery minnow decreased in the Nebraska portion of the Missouri River by 96% from 1971-1993. The fish has been extirpated from Arkansas (Robison and Buchanan 1988).

The plains minnow is ecologically separated from its close relative by habitat preference: it prefers river channels with sandy substrate, while the western silvery minnow prefers protected areas with a silt bottom. Decline of these small fishes in altered environments is likely due to competition and predation by introduced and native fishes.

— **Speckled chub**: This intermediate-sized (to 3 in) barbeled minnow has a long bulbous mouth and small black spots on sides and back (Page and Burr 1991). It is listed as a species of concern by Kansas. Population shifts have recently occurred in this species, and it has decreased in numbers in the upper Missouri and Mississippi rivers (Pflieger 1997). Hesse (1994) documented a 77% decline in catch/effort in the Missouri River in Nebraska from 1971-1993. Little is known about its life history needs, but its progressive decline in upstream areas that are affected by reservoirs is suggestive of the loss of important habitats or nonnative fish interactions.

— **Silver chub**: This large (to 9 in) barbeled minnow has a large eye and bright silver-white sides (Page and Burr 1991). It has been listed as endangered in Missouri, a species of concern in North Dakota, and a peripheral species in South Dakota (Power and Ryckman 1998). Historically, this was one of the most common minnows of the Missouri, Mississippi, and large prairie rivers, however, populations have declined (Pflieger 1997). Hesse (1994) reported that catch/effort of silver chub declined 70% from 1971 to 1993. Information about this fish is scant, but it seems to have declined most rapidly in prairie regions that have been the most affected by reservoir construction. Because this fish evidently does well in quiet habitats of large streams but it evidently does not do well in reservoir habitats, which is suggestive of adverse interactions with reservoir fishes.

— **Paddlefish**: The paddlefish is one of the largest freshwater fish in North America, and is represented by two extant species that are relicts of an ancient line of fishes, one in the Mississippi-Missouri river system and one in the Yangtse River of China. This sharklike fish with an elongated, paddle-like snout averages about 60 lb, but can reach sizes of over 160 lb and over 6 feet (Pflieger 1996). A commercially important species, catches of about 2.5 million pounds were reported prior to 1900, but the fish has declined, and catches seldom exceed 16,000 pounds (Pflieger 1997).
The paddlefish has been listed as endangered in Missouri, and North and South Dakota (Power and Ryckman 1998) and a fish of special concern to a number of states (Williams et al. 1989). Sport fishing is allowed in all of these states, however many of the fish caught are hatchery-reared fishes that are stocked. Causes of the decline in paddlefish stocks have mainly been attributed to stream blockage by dams, habitat alteration, and overfishing (Dillard et al. 1983). However, as in sturgeons, paddlefish larvae drift downstream with flow after swim-up (Russell 1986) presumably to reach more suitable habitats. In the present system reduced turbidity results in increased loss due to predation, and especially if the larvae move into lacustrine areas that are dominated by nonnative predators. Also, some fishes like common carp are presumed to be in competition with paddlefish (Pflieger 1997).

**DISCUSSION**

Native fish communities can be affected by physical and biological changes in habitat. Physical changes in habitat are usually obvious, but changes in the biological component of habitat are not easily observed and are not as well understood. However, in the last 20 years, much attention has been given to the unintended consequences associated with fish introductions, and well-designed studies are producing alarming results (e.g., see reviews by Moyle et al. 1986, Courtenay 1995, Tyus and Saunders 2000).

Adverse effects caused by fish introductions have been recognized by the American Fisheries Society (AFS), the premier professional fisheries organization in North America. While acknowledging the benefits that stocking has brought to recreational and commercial fisheries, the AFS states that stocking has had “undesirable effects on native species” and that stocking policy should be tempered by the need for preserving biological diversity (Kohler and Courtenay 1986, Starnes et al. 1996).

Surprisingly, there is no comprehensive basinwide evaluation of the effects that nonnative fishes have had on the native Missouri River fish fauna. However, all of the mainstream reservoirs were constructed before passage of the Endangered Species Act and before an environmental awareness of the world-wide biodiversity problem. When the impoundments were filled, state fish management agencies were mostly concerned with how to manage the huge new reservoirs for recreational sport fishing, and hatchery production offered the potential for mitigating losses of desirable species such as paddlefish.

Prior to 1950, fisheries programs in North America were devoted largely to stocking gamefish. There were few ecologists, and “virtually all fisheries biologists were fish culturists” (Wiley 1996). Although introductions of nonnative fishes were causing considerable damage to native fish populations, little concern was registered in the scientific literature. Only recently have federal and state fisheries agencies developed management measures for nongame species. It is pertinent to note that little attention
was given to introductions prior to scrutiny from an endangered species perspective (e.g. Werdon 1993ab, USFWS 1995,1997). Nonnative species were not even considered as a factor in the decline of Missouri River fishes in major symposia dealing with status (e.g., Dilliard et al. 1983) and given little attention in other published accounts. As with recovery efforts in the Colorado River and elsewhere there has been a preoccupation with physical habitat change and potential nonnative problems have been largely ignored.

The roles and responsibilities of federal and state agencies for protecting natural ecosystems have evolved gradually. Changes in policies of traditional fish and wildlife agencies have occurred in response to a growing perception that biodiversity is worth preserving. The nonnative problem is so serious and pervasive that proposals to extend federal responsibilities, which would have caused considerable controversy with state agencies in the past, now have been met with a majority of acceptance (63% of state game and fish agencies; USOTA 1993). Even so, gaps in federal and state efforts “constitute a serious threat to the Nation’s ability to exclude, limit, and rapidly control harmful fish and wildlife” (USOTA 1993). Recovery efforts for sensitive species in the Missouri River Basin will require the cooperation of federal and state agencies, as well as local governments to reduce the impacts of introduced species.

Which species may be placing native Missouri River fishes at risk of decline and potential extinction? A list of candidates is not difficult to obtain. Based on the present introductions, Fuller et al. (1999) provided convincing evidence that every one of the following species could prey upon or compete with the native fish: northern pike, walleye, largemouth and smallmouth basses, salmon, rainbow trout, brown trout, rainbow smelt, and common carp.

Why is the decline and loss of native Missouri River fish such an issue that control of nonnatives species is needed? Biological diversity is at risk when nonnative species are introduced. Biological diversity is not simply the number of native species present, but also encompasses the “ecological roles they perform, and the genetic diversity they contain” (Wilcox 1984). Because biodiversity is a characteristic of natural ecosystems, it is not enhanced by the introduction of nonnative species. Biodiversity can be reduced by shifts in the natural patterns of relative abundance (Temple 1990), but there is no doubt that biodiversity is declining on the planet. Such a decline may hold serious and unanticipated consequences for humans (Ehrlich and Ehrlich 1983, Wilson 1992, Ward 1995).

Extinction results in an irrevocable loss of biodiversity. Three sets of factors are thought to contribute to extinction: biotic factors, isolation, and habitat alteration (Frankel and Soulé 1981). Most extinctions involve a combination of the three sets of factors in which the adverse effects of one set of factors may make the native species more susceptible to the effects of other factors (Frankel and Soulé 1981, Soulé 1983, Wilson 1992). For example, biotic factors such as predation and competition from introduced species may reduce or alter the density, range, and habitat use of a native species.
While these alterations may not eliminate a robust and widespread species, they are likely to cause its decline and make the native population more susceptible to the effects of habitat alteration or isolation. Similarly, habitat alteration may reduce the range and abundance of a native species, and make the native species more susceptible to predation or competition from introduced species, especially where the introduced species is favored by habitat changes. Population decline results in small population size, and small populations are prone to problems such as demographic stochasticity, genetic deterioration, social dysfunction, and extrinsic forces (reviewed by Raup 1991). Habitat fragmentation also could reduce the size of isolated populations. Extinction is more likely to occur in small populations that have fallen below the size of minimum viability (Soule’ 1983; Raup 1991).

The case for conservation becomes most urgent as the population size of a species becomes very small. Random events such as a chemical spill that would have a relatively minor impact on a large and widely distributed population, could have catastrophic and perhaps permanent effects on a smaller, restricted population. In the interest of preserving the species and maintaining biodiversity, extraordinary measures may be required to prevent extinction. For the big river fauna of the Missouri River that are threatened by biotic factors, control of introduced species becomes imperative. The task is not necessarily a simple one: control of introduced species has been called the “nasty necessity [because of] misconceptions about the nature and magnitude of the problem, fears of the negative public reactions...and intimidation by the inefficient labor-intensive nature of current eradication technologies” (Temple 1990). In hindsight, the best policy is not to introduce nonnative species in the first place.

CONCLUSIONS

At least nine native fishes have experienced significant declines in abundance in all of some portion of the river system. These declines have been overwhelmingly attributed to physical and chemical alterations of habitat, and by comparison, the introduced fish problem has been largely ignored.

Excluding common carp, early introductions into the mainstream Missouri River did not generally result in the establishment of new fish populations (Pflieger 1997). However, as stream habitats were altered by water resources development, nonnative fishes were more successful in these modified environments. In the newly-created reservoirs, turbid riverine conditions were replaced by clear lacustrine-like environments and stocked with hardy, predaceous, highly aggressive, and/or competitive fishes. Some introduced fishes were “pre-adapted” to the modified environments and thrived in them. But these same conditions were alien to the native riverine fishes, which universally declined. Remaining riverine habitats are more suitable to the native fishes, and some have persisted with “viable” populations. Numbers of predaceous fishes in the remaining riverine habitats have steadily increased due to direct stockings, and escapement from stocked reservoir and tailwater reaches.
There is a prevailing thought among management agencies that it is acceptable to stock native fishes, predator or prey species, anywhere into the Missouri River system. Presumably the rationale behind this notion is that all of the species evolved together and have adaptations to tolerate interspecific interactions. However, the validity of this notion must be called into question. Not only have historic habitats changed, altering niches and straining long-established relationships, but the distinction between native vs. nonnative fishes has become clouded by several issues:

(1). Some fishes (e.g. walleye) were stocked before studies demonstrating their presence or absence were completed and there were some problems with misidentification.

(2). Natural or "native" Missouri River habitats have been so heavily influenced by anthropogenic changes that it is arguable whether any native habitats remain in the mainstream river. Thus, from the standpoint of damage to listed or sensitive species, it makes little difference whether a nonnative fish is stocked into a native habitat, or a native fish is introduced into a "nonnative" habitat.

(3). In the historic river, a mix of complex riverine habitats occurred and different conditions supported different species. For example, centrarchids were adapted to quiet, clear backwaters and oxbows, and chubs were adapted to the turbid conditions of the fast flowing river channels. While "native" to a river reach, neither were "native" to habitats used by the other.

(4). If biodiversity is to be maintained, management actions should be judged relative to their affect on listed, rare, or declining native Missouri River fishes.

The notion that physical habitat changes caused the declines of native fishes, and that introduced fishes have had little affect remains untested. There are no areas of the Missouri River in which physical habitat changes have occurred without fish introductions, whether intentional or nonintentional. However, it is clear that introduced fishes have not benefitted native fish populations, and it is likely that declines of some of the native fishes would not have been as precipitous if fish introductions had not occurred. Additional fish introductions and management practices favoring the spread and proliferation of introduced species will undoubtedly harm the native fish fauna, resulting in more listings of native fishes, and reducing the prospects for recovering species that are listed now and will be listed in the future.

The consequences of introducing so many nonnative fishes into habitats where they may compete with and prey upon native fish populations seems obvious in view of the extensive body of knowledge that has accumulated in the past 15 years. There remains a critical need for management agencies to recognize the potential problems of fish introductions, to investigate these problems with well-planned research, to share research findings in open forum with concerned agencies and individuals, and to formulate appropriate management actions.
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