Transactions of the American Fisheries Society 133:727–742, 2004

Relations among Habitat Characteristics, Exotic Species, and Turbid-River Cyprinids in the Missouri River Drainage of Wyoming

MICHAEL C. QUIST* AND WAYNE A. HUBERT

U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit,[1]
University of Wyoming, Laramie, Wyoming 82071-3166, USA

FRANK J. RAHEL

Department of Zoology and Physiology,
University of Wyoming, Laramie, Wyoming 82071-3166, USA

Abstract.—We used data from 91 stream reaches in the Missouri River drainage of Wyoming to determine whether abiotic and biotic factors were related to the abundance of four cyprinid species associated with turbid-river environments: flathead chub *Platygobio gracilis*, sturgeon chub *Macrhybopsis gelida*, plains minnow *Hybognathus placitus*, and western silvery minnow *H. argyritis*. The abundance of these cyprinids was positively related to the percentage of fine substrate in a reach and inversely related to the percentage of gravel substrate, the percentage of large rocky substrate, and the abundance of exotic piscivores. Differences in substrate composition and abundance of exotic piscivores were largely explained by the presence and location of large, mainstem impoundments. Reaches without any large impoundments in their watershed had a high percentage of fine substrate, high catch rates of turbid-river cyprinids, few exotic piscivores, and little gravel or large rocky substrate. Reaches with a downstream impoundment (i.e., within 200 km) had habitat characteristics similar to those without impoundments but had few turbid-river cyprinids and many exotic piscivores. Reaches with an upstream impoundment (i.e., within 200 km) had little fine substrate, a high percentage of large rocky substrate, few turbid-river cyprinids, and many exotic piscivores. Our results suggest that impoundments have had a substantial influence on the distribution and abundance of cyprinid species adapted to hydrologically dynamic, turbid prairie streams and that conserving these species is dependent on maintaining natural flow and sediment transport regimes and on reducing habitat suitability for exotic piscivores.

Fishes in streams and rivers are affected by a variety of physical, chemical, and biological factors; understanding how these factors influence fish distributions and abundance is important when considering the status of native fishes (Master 1991; Allan and Flecker 1993; Richter et al. 1997). The abundance and distribution of native fishes in North America have been declining since the early 20th century largely due to extensive physicochemical and biological alterations of aquatic habitats (Williams et al. 1989; Moyle and Leidy 1992). Although the loss of fishes has been greatest in the Pacific and southwestern regions of the United States (Carlson and Muth 1989; Moyle and Williams 1990; Bestgen and Platania 1991; Gido and Propst 1999), many species also have declined in rivers and streams of the Great Plains (Williams et al. 1989; Richter et al. 1997), particularly species adapted to large, turbid-river systems (Pflieger and Grace 1987; Hesse et al. 1993; Hesse 1994; Luttrell et al. 1999).

Most lotic systems in the Great Plains have headwaters that drain the eastern slope of the Rocky Mountains and downstream reaches that traverse quaternary sediments eroded from the mountains (Matthews 1988; Fausch and Bestgen 1997). Therefore, most flow originates from snowmelt runoff during spring and early summer, and base flow is maintained by underlying aquifers. Historically, many prairie streams of the Great Plains were turbid and frequently intermittent due to the porous, sedimentary geology of the region and arid climate (Cross and Moss 1987; Matthews 1988). The geomorphology of prairie systems, coupled with the climatic characteristics of the Great Plains, resulted in variable flows and extreme fluctuations in temperature, salinity, and dissolved oxygen. Consequently, several taxa evolved morphological, physiological, and life history characteristics that allow them to survive

* Corresponding author: mcquist@uwyo.edu

[1] The Unit is jointly sponsored by the U.S. Geological Survey, University of Wyoming, Wyoming Game and Fish Department, and Wildlife Management Institute.

Received July 11, 2003; accepted November 20, 2003

in these relatively harsh systems. For example, many fish have broad physicochemical tolerances to survive abrupt changes in temperature and water quality (Matthews and Maness 1979; Bryan et al. 1984; Matthews 1987) and enhanced chemoreception senses (e.g., barbels with chemosensory and tactile sense organs) adapted for turbid conditions (Moore 1950; Branson 1963; Davis and Miller 1967). Species that build nests or attach eggs to substrate (e.g., Centrarchidae and Percidae) are generally absent due to the dynamic flow regime and shifting-sand substrate characteristic of prairie systems (Baxter and Stone 1995; Fausch and Bestgen 1997). Rather, many species have semibuoyant eggs that not only avoid the abrasive action of the substrate, but also allow the recolonization of reaches that experience frequent intermittence and local population extirpation (Lehtinen and Layzer 1988; Taylor and Miller 1990; Platania and Altenbach 1998). Because species that reside in prairie systems are adapted to hydrologically dynamic, turbid conditions, they are sensitive to anthropogenic activities that stabilize flows or alter physicochemical characteristics (Pflieger and Grace 1987; Fausch and Bestgen 1997). Alterations that stabilize habitat also allow for the establishment of nonnative fish predators and competitors (Wenke et al. 1993; Fausch and Bestgen 1997).

The Missouri River drainage is the largest river system in the Great Plains. Like most large-river systems in North America, rivers and streams in the Missouri River drainage have experienced extensive habitat modification and changes in fish assemblage structure (Pflieger and Grace 1987; Hesse et al. 1989). Although water pollution, the introduction of exotic species, the diversion of water for agriculture, and channelization have influenced rivers throughout the Great Plains (Cross and Moss 1987; Hesse et al. 1989), the construction of large impoundments has been identified as one of the most widespread and detrimental anthropogenic impacts to natural river systems (Petts 1984; Rosenberg et al. 1997). Effects of impoundments on physical habitat are largely restricted to reaches downstream of impoundments, where regulated flows and reduced fine-sediment transport results in reduced connectivity of the main channel with the floodplain, altered channel morphology, and reduced turbidity (Patton and Hubert 1993; Ward and Stanford 1995; Gregory et al. 2002). Impoundments act as barriers to fish movement and may fragment populations (Dynesius and Nilsson 1994; Luttrell et al. 1999), regardless of whether the impoundment is upstream or downstream of a reach. Similarly, reservoirs are a source of exotic species for upstream and downstream colonization (Pringle 1997). All of these factors are thought to have had a significant effect on native cyprinid species adapted to turbid-river systems (Cross and Moss 1987; Pflieger and Grace 1987; Hesse 1994; Bonner and Wilde 2000). Thus, knowledge of the effects of anthropogenic activities is necessary to provide insight into the mechanisms influencing fish assemblages in large-river systems (Dynesius and Nilsson 1994). Such studies are not only important for conserving populations of native species under current disturbance regimes, but also help to assess the potential impact of future disturbances (e.g., construction or removal of impoundments, urbanization, and oil and gas development) on native species.

Several native cyprinids occur in the prairie streams and rivers of Wyoming (e.g., fathead minnow *Pimephales promelas*, sand shiner *Notropis stramineus*, and red shiner *Cyprinella lutrensis*); however, these species are ubiquitous and their distributions are not limited to large-river systems. We focused on four native cyprinid species (hereafter termed turbid-river cyprinids) adapted to large, turbid rivers: flathead chub *Platygobio gracilis*, sturgeon chub *Macrhybopsis gelida*, plains minnow *Hybognathus placitus*, and western silvery minnow *H. argyritis*. These four species are generally restricted to turbid-river systems and were once widely distributed in prairie streams and rivers throughout the Great Plains (Pflieger and Grace 1987; Hesse 1994). However, the abundance and distribution of all four species have declined across their historic distribution (Miller 1972; Pflieger and Grace 1987; Williams et al. 1989), including Wyoming (Patton et al. 1998). Although these four species are protected or have been considered for protection in various states (Robinson et al. 1974; Reigh and Elsen 1979; Hesse et al. 1993; Burr et al. 1996; Stukel and Backlund 1997), only the sturgeon chub has been petitioned for Federal protection under the Endangered Species Act.

Our objective was to examine the factors affecting the abundance of turbid-river cyprinids in the Missouri River drainage of Wyoming. Specifically, we investigated associations of turbid-river cyprinids with habitat conditions and the abundance of exotic piscivores to answer the following questions: (1) which abiotic and biotic factors are related to the abundance of turbid-river cyprinids across the Missouri River drainage of Wyoming; (2) how the presence and location of impoundments has influenced the abiotic and biotic factors

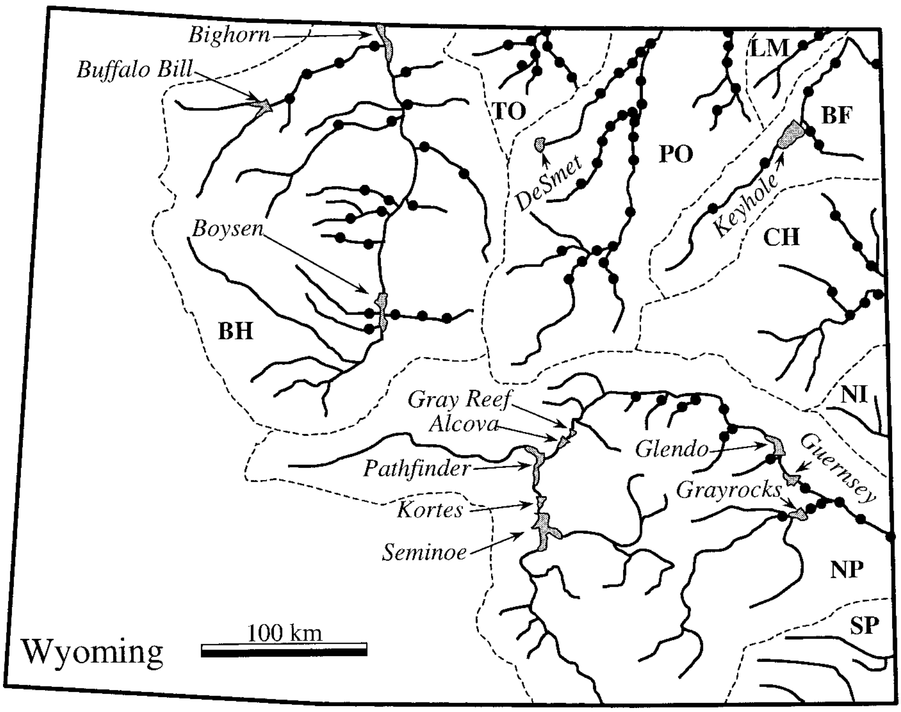

FIGURE 1.—Map of reaches (solid circles) sampled from river systems (Belle Fourche [BF], Bighorn [BH], Cheyenne [CH], Little Missouri [LM], North Platte [NP], Powder [PO], and Tongue [TO]) in the Missouri River drainage of Wyoming (1993–2000). Location of large impoundments (shaded areas; names provided in italics) and the Niobrara (NI) and South Platte (SP) river basins are also shown.

important for turbid-river cyprinids within subdrainages; and (3) how the presence and location of impoundments has influenced these abiotic and biotic factors across subdrainages of the Missouri River basin in Wyoming.

Our approach involved analyses at two scales. First, we used principal components analysis to reduce and simplify habitat data across 91 reaches from seven subdrainages within the Missouri River drainage of Wyoming. Summary habitat variables (i.e., principal components scores) and the abundance of exotic piscivores were then used in a multiple-regression framework to identify associations between the four turbid-river cyprinids and abiotic and biotic characteristics across the Missouri River drainage of Wyoming. At a smaller spatial scale, we investigated the relationship of impoundments with physical habitat, exotic piscivores, and turbid-river cyprinids. Comparisons of abiotic and biotic data were conducted within and across subdrainages to provide insight into how the presence and location of impoundments affected the factors important for turbid-river cyprinids.

Methods

Study area.—The Missouri River drainage encompasses 186,000 km^2 or 74% of the surface area of Wyoming. Major subdrainages include the Bighorn, Tongue, Powder, Little Missouri, Belle Fourche, Cheyenne, Niobrara, South Platte, and North Platte rivers (Figure 1). The Niobrara and South Platte rivers were excluded from our analysis because none of the four turbid-river cyprinid species are thought to be native to these watersheds in Wyoming (Baxter and Stone 1995). Only the North Platte River does not originate in Wyoming, and the remaining rivers originate from mountain ranges across the state. The headwaters of most river systems in Wyoming are characteristic of mountain streams, with large rocky substrate and fish communities dominated by introduced salmonids (Rahel and Hubert 1991). As streams flow onto the plains, they become characterized by low gradients, braided-channel morphology, fine substrate, and fish communities dominated by cyprinids and catostomids (Rahel and Hubert 1991; Fausch and Bestgen 1997). Irrigation diversions and impoundments are widespread across Wyoming; however, the number of large, main-stem impoundments varies among river systems. The Bighorn, Belle Fourche, and North Platte rivers have substantial water development and all contain at least one large impoundment within state boundaries. The Powder River system is relatively pristine and lacks main-stem impoundments (Hubert 1993). However, Lake DeSmet impounds water on Clear Creek, a tributary to the Powder River. The Tongue and Bighorn rivers are impounded a short distance downstream of the Wyoming–Montana border.

Fish and habitat sampling.—Information on fish assemblages and habitat characteristics was obtained from 91 reaches within the native distribution of each species across the Missouri River drainage of Wyoming (Figure 1) using data collected during 1993–2000. Fish and habitat were sampled during base flow conditions (May–August). A backpack electrofisher (Smith-Root, model 15-B) was used to sample fishes on small streams (wetted width $<$5 m) and a bank unit (Coffelt, model VVP-2C) was used on larger streams. Seining (4.6-long $\times$ 1.2-m-deep bag seine, 4.8-mm mesh) was conducted to supplement electrofishing samples in 82% of the reaches. In general, a single electrofishing pass and two to five seine hauls were conducted over a sampling reach. Even though electrofishing (i.e., single pass) over a 200-m reach has been shown to sufficiently sample all fish species in Wyoming streams (Patton et al. 2000), reaches varied from 200 to 500 m. Fish were identified in the field and voucher specimens were preserved in 10% formalin to verify field identifications.

Catch per unit effort (CPUE) of flathead chubs, sturgeon chubs, plains minnows, and western silvery minnows was calculated as the number of fish per 200 m. We also estimated CPUE of turbid-river cyprinids as a guild by summing catches for all four species. CPUE of exotic piscivores ($CPUE_{pisc}$) was estimated as the number of introduced piscivores (i.e., brown trout *Salmo trutta*, green sunfish *Lepomis cyanellus*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, rock bass *Ambloplites rupestris*, white crappie *Pomoxis annularis*, walleye *Sander vitreus*, [formerly *Stizostedion vitreum*], or yellow perch *Perca flavescens*) per 200 m. Although differences in sampling gear may have biased our CPUE estimates for a few sites, we were primarily interested in broad patterns of abundance. We addressed potential bias by categorizing CPUE estimates using percentile values of abundance, but the results were identical to those obtained using CPUE. Therefore, CPUE estimates were used in all analyses.

Channel slope (%) was estimated using 1:24,000 scale U.S. Geological Survey (USGS) topographical maps. The distance between the nearest contour lines upstream and downstream of the reach was measured along the stream using a map wheel. Channel slope was calculated as the elevation drop between contour lines divided by the stream distance between contour lines. Mean wetted width (m) was measured along six equally spaced transects, and maximum depth (m) was measured at the deepest point in each reach. Substrate was categorized using a modified Wentworth scale (i.e., silt, sand, gravel, cobble, boulder, and bedrock; Armantrout 1998), and the percentage of each substrate type in the reach was visually estimated. Silt and sand substrates are often difficult to visually discriminate in the field; therefore, we combined estimates of silt and sand to represent the amount of fine substrate. Boulder and bedrock substrates, which were relatively rare in most study reaches, were combined with cobble substrate to represent the percentage of large rocky substrate. The amount (% of total surface area) of woody debris and aquatic vegetation was obtained from visual estimates in the field and photographs made during sampling. Wang et al. (1996) reported that differences between visual estimates and intensive surveys (i.e., digitized photographs) of substrate composition were less than five percentage points. Similar results were reported for cover estimates (Wang et al. 1996), suggesting that visual estimates of substrate and cover were suitable for the purposes of this study.

Statistical analysis.—Habitat data were examined using principal components analysis (PCA) to simplify the data set and reduce the number of variables. Because habitat variables were measured using different measurement scales, the PCA was conducted on the correlation matrix rather than the variance–covariance matrix (Johnson 1998). Only axes with eigenvalues greater than one were used in further analyses. Although factor loadings provide an indication of the contribution of each variable to the principal components axis, Pearson's correlation analysis between principal component scores and habitat variables was conducted to help interpret the meaning of principal component scores. Principal component scores were calculated for each reach and used as independent variables in multiple-regression analyses.

Multiple-regression analysis was used to examine the relationship of CPUE of turbid-river cyprinids with physical habitat (i.e., principal component scores) and abundance of exotic piscivores. Nonlinear-regression techniques were used because the relationships between turbid-river cyprinid catch rates versus principal component scores and the abundance of exotic piscivores were curvilinear. The multiple-regression equation fit to the data was

$$Y = \beta_0 \times \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k),$$

where Y is the CPUE of turbid-river cyprinids, β_0 is the intercept, β_k is the coefficient estimate for the kth variable, and X_k represents the kth independent variable (D. Johnson and G. Milliken, Kansas State University, Department of Statistics, personal communication). The contribution of each variable was determined by comparing the residual sums of squares of reduced models (RSS_{red}) to the residual sums of squares of the full model (RSS_{full}) using an F-test (Milliken and Johnson 1992):

$$F = ([RSS_{red} - RSS_{full}]/[df_{red} - df_{full}]) \times [RSS_{full}/df_{full}]^{-1},$$

where df is degrees of freedom from the reduced (df_{red}) and full models (df_{full}). The estimated F-value was then compared against $F_{0.05,1,dffull}$ to test the null hypothesis that the reduced model was significantly better than the full model. None of the independent variables (i.e., principal component scores or $CPUE_{pisc}$) used in the multiple-regression analysis were correlated (r = 0.01–0.35, $P > 0.05$). Regression models were developed for CPUE of turbid-river cyprinids as a guild, CPUE of flathead chubs, and CPUE of plains minnows. Regression analysis was not conducted for western silvery minnows or sturgeon chubs due to the low number of reaches where they were collected (less than six reaches). Because we were interested in examining associations across the Missouri River drainage, PCA and multiple-regression analyses were conducted across subdrainages (i.e., each reach was treated as a replicate).

At a smaller spatial scale, we tested the effect of impoundments on turbid-river cyprinids, physical habitat, and exotic piscivores within each subdrainage. Because large, mainstem impoundments can have different effects on physical habitat conditions and fish assemblage structure depending on their location in a watershed, we placed reaches into three impoundment categories: (1) little or no influence (i.e., large, main-stem impoundments absent upstream or greater than 200 km downstream); (2) influenced by a large, main-stem impoundment less than 200 km downstream; or (3) influenced by at least one large, main-stem impoundment upstream. Small impoundments were present in all river basins, but classification was based only on large impoundments (i.e., greater than 200 surface ha at full pool) because information on the specific location of small impoundments was unavailable. Reaches influenced by large upstream impoundments occurred in the Bighorn, Belle Fourche, North Platte, and Powder (i.e., Clear Creek only) river basins. Reaches affected by downstream impoundments occurred in the Bighorn, Belle Fourche, North Platte, and Tongue river basins, and reaches not influenced by impoundments occurred in the Cheyenne, Little Missouri, and Powder river drainages. The closest impoundment to reaches categorized as not influenced by impoundments were nearly 400 km away in North Dakota (i.e., Little Missouri River, Powder River) or central South Dakota (i.e., Cheyenne River).

We established a priori hypotheses about the effects of impoundment on habitat and fish assemblage structure, which were tested using analysis of variance (ANOVA). Specifically, we hypothesized that abiotic and biotic characteristics differed among impoundment categories, within and across the seven subdrainages. Differences in variables that were important in the multiple-regression analysis were tested among impoundment categories within subdrainages using orthogonal contrasts (Milliken and Johnson 1992). Because comparisons were conducted between impoundment categories within a subdrainage, each sampling reach within a subdrainage was treated as a replicate (e.g., all reaches in the Powder River without impoundments compared with all reaches in the Powder River with an upstream impoundment). Differences in abiotic and biotic characteristics among impoundment categories across subdrainages were also examined using ANOVA. Specifically, the mean of each variable for a river basin by impoundment category (e.g., mean of reaches in the Powder River without impoundments) was treated as the replicate for an impoundment category rather than an individual sampling reach. Treating the river basin by impoundment category mean as the replicate was necessary because the number of sampling reaches was not equally allocated among impoundment categories and ba-

TABLE 1.—Loadings from the principal components analysis of physical habitat information from reaches in the Missouri River drainage of Wyoming sampled during 1993–2000. Abiotic variables include the percentage of fine, gravel, and large rocky substrate; mean width (m); maximum depth (m); channel slope (%); and percent of the reach covered by large woody debris (LWD) or aquatic vegetation (VEG). Numbers in parentheses represent Pearson's correlation coefficients and associated *P*-values (*r, P*) for correlations between variables and principal component scores. Eigenvalues (λ) and percentage of the variation are provided for the first three principal components axes (i.e., PRIN1, PRIN2, PRIN3).

Variable	PRIN1	PRIN2	PRIN3
Fine	−0.579 (−0.92, 0.0001)	−0.181 (−0.22, 0.12)	0.043 (0.05, 0.67)
Gravel	0.433 (0.69, 0.0001)	0.253 (0.32, 0.08)	−0.012 (−0.13, 0.23)
Large rock	0.508 (0.81, 0.0001)	0.154 (0.19, 0.10)	0.045 (0.05, 0.66)
Width	0.359 (0.43, 0.04)	−0.453 (−0.55, 0.0001)	0.168 (0.17, 0.11)
Depth	0.268 (0.39, 0.07)	−0.446 (−0.54, 0.0001)	0.175 (0.19, 0.10)
Slope	0.034 (0.05, 0.62)	0.642 (0.78, 0.0001)	0.079 (0.08, 0.44)
LWD	−0.124 (−0.19, 0.10)	0.251 (0.32, 0.08)	0.521 (0.55, 0.0001)
VEG	−0.010 (−0.02, 0.88)	−0.005 (0.01, 0.96)	−0.802 (−0.85, 0.0001)
λ	2.544	1.464	1.118
Variance (%)	31.8	18.3	14.0

sins. Using means as replicates prevented a particular subdrainage with a large number of sampling reaches from having an overriding influence on the results. All analyses were conducted using SAS (SAS Institute 1996) and α equal to 0.05.

Results

Flathead chubs were the most common of the four turbid-river cyprinid species and were sampled from every subdrainage except the North Platte River. Flathead chubs were also absent from the Little Missouri River where they are not thought to be native. Plains minnows were sampled only in the Belle Fourche, Powder, and Cheyenne river basins and were absent from the Bighorn, North Platte, Tongue, and Little Missouri rivers. Western silvery minnows were sampled from two reaches in the Little Powder River (Powder River basin) and two reaches in the Little Missouri River. Sturgeon chubs had a restricted distribution and were only sampled from five reaches in the Powder River. Exotic piscivorous fish (primarily green sunfish, rock bass, and smallmouth bass) were sampled in all subdrainages.

The first three principal component axes had eigenvalues greater than one and cumulatively explained over 60% of the variation in habitat among all reaches (Table 1). The first principal component axis could be interpreted as representing substrate composition and separated reaches dominated by fine substrate from those dominated by large substrate. Fine substrate was negatively loaded on the first axis and highly correlated with principal component scores from the first axis (PRIN1). The proportions of gravel and large rocky substrate were also highly loaded and correlated with PRIN1, but the relationships were positive. The second axis was best explained as a measure of channel morphology due to high loadings and correlations with mean width, maximum depth, and channel slope, where reaches with low gradients were wide and had high maximum depths. The third axis represented instream cover characteristics (i.e., large woody debris, or aquatic vegetation).

Catch rates of turbid-river cyprinids as a guild as well as by species were related to both habitat characteristics and the abundance of exotic piscivores. In all models, principal component scores from the second and third axes did not contribute significantly to the multiple-regression models ($P = 0.10$–0.85). Rather, catch rates of turbid-river cyprinids as a guild, flathead chubs, and plains minnows were negatively related to both PRIN1 and CPUE of exotic piscivores (Figures 2–4). Because flathead chubs were the most abundant species, they were largely responsible for the similar relationship observed for CPUE of turbid-river cyprinids as a guild. Turbid-river cyprinids were most abundant in reaches with a high proportion of fine substrate, little gravel and large rocky substrate, and few exotic piscivores. Piscivores appeared to have an overriding influence on the abundance of turbid-river cyprinids because even when habitat conditions were suitable (i.e., low PRIN1), the presence of a few exotic piscivores resulted in few, if any, turbid-river cyprinids. After we established which variables were related to higher abundances of turbid-river cyprinids across the Missouri River drainage of Wyoming, we examined whether the presence and location of impoundments explained differences in habitat conditions and the abundance of exotic piscivores.

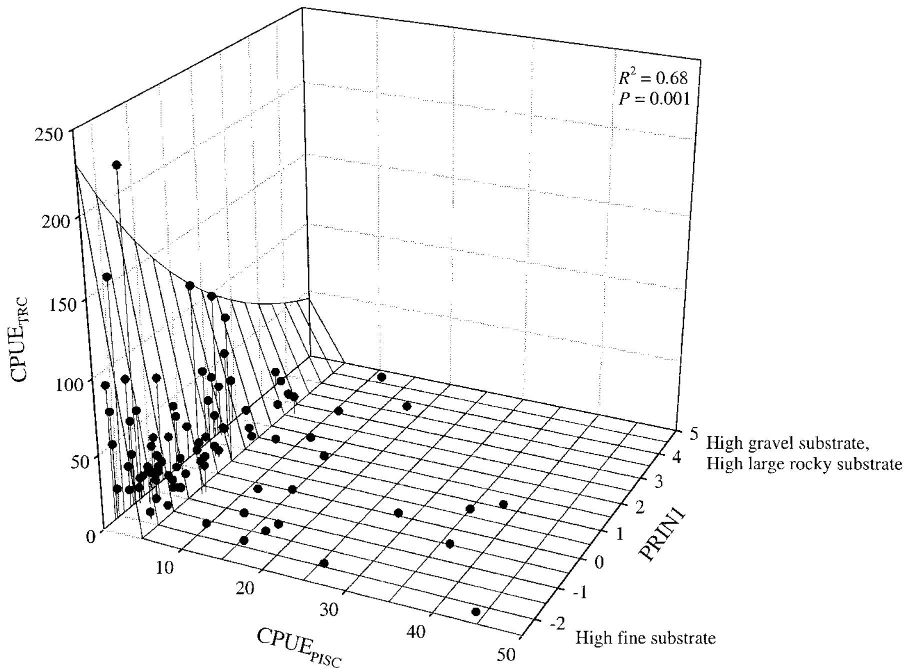

FIGURE 2.—Relationship of catch per unit effort (CPUE = number/200 m) of turbid-river cyprinids ($CPUE_{TRC}$; flathead chub, plains minnow, western silvery minnow, and sturgeon chub combined), CPUE of exotic piscivores ($CPUE_{PISC}$), and scores from the first principal component axis (PRIN1) for reaches sampled in the Missouri River drainage of Wyoming (1993–2000). Variables contributing to PRIN1 are provided in Table 1. The multiple-regression equation is: $CPUE_{TRC} = 132.95\ e^{(-0.22 \times PRIN1\ -1.19 \times CPUE_{PISC})}$.

Substrate characteristics varied among impoundment categories within river basins (Table 2). Fine substrate was significantly higher (P = 0.01–0.002) in reaches with a downstream impoundment compared with those with an upstream impoundment in the Belle Fourche, Bighorn, and North Platte river basins. Fine substrate dominated reaches without impoundments and was significantly higher (P = 0.002) than in reaches with an upstream impoundment in the Powder River. Conversely, reaches with an upstream impoundment had significantly higher (P = 0.01–0.001) proportions of gravel and large rocky substrate compared with those without impoundments in the Powder River and those with a downstream impoundment in the Belle Fourche, Big Horn, and North Platte river basins.

Catch rates of exotic piscivores were similar (P = 0.05–0.12) between reaches with an upstream or downstream impoundment within subdrainages (Table 3). In the Powder River, exotic piscivores were significantly more abundant in reaches with an upstream reservoir compared with those without impoundments. Turbid-river cyprinids were more abundant in reaches influenced by an upstream impoundment compared with reaches with a downstream impoundment in the Belle Fourche River system. In the Bighorn River basin, turbid-river cyprinids were more abundant in reaches with a downstream impoundment compared with those with an upstream impoundment. Turbid-river cyprinids were more abundant in reaches without impoundments than in reaches with an upstream impoundment in the Powder River basin. These results are largely explained by the abundance of flathead chubs and plains minnows, where flathead chubs were more abundant and plains minnows were less abundant in reaches downstream of impoundments compared with reaches upstream of an impoundment in the Belle Fourche River basin. In the Bighorn River drainage, flathead chubs were absent from reaches with an upstream impoundment. Flathead chubs were also absent from all reaches in the North Platte River basin, and plains minnows were absent from the Bighorn and North Platte river drainages regardless of impoundment category. Comparisons in the Tongue, Cheyenne, and Little Missouri river basins were not conducted because only one impoundment category was sampled (Table 3).

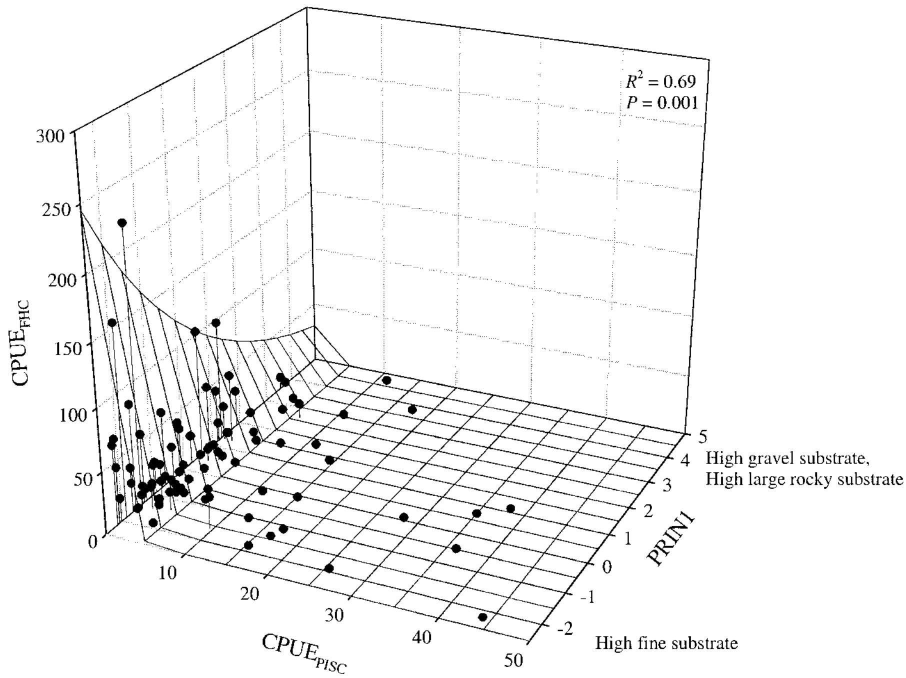

FIGURE 3.—Relationship of catch per unit effort (CPUE = number/200 m) of flathead chubs (CPUE$_{FHC}$), CPUE of exotic piscivores (CPUE$_{PISC}$), and scores from the first principal component axis (PRIN1) for reaches sampled in the Missouri River drainage of Wyoming (1993–2000). Variables contributing to PRIN1 are provided in Table 1. The multiple-regression equation is: $CPUE_{FHC} = 122.81\ e^{(-0.28 \times PRIN1\ -0.91 \times CPUE_{PISC})}$.

Differences among impoundment categories across subdrainages were consistent with the results obtained by comparing among impoundment categories within subdrainages. We found that substrate composition was similar between reaches not influenced by impoundments and those with a downstream impoundment (Figure 5), while reaches with an upstream impoundment had a significantly lower percentage of fine substrate and a higher percentage of gravel and large rocky substrate. Although exotic piscivores in reaches influenced by impoundments (upstream or downstream) were up to 10 times higher than those not influenced by impoundments, these differences were not statistically significant. Turbid-river cyprinids as a guild, flathead chubs, and plains minnows were more abundant in reaches without impoundments compared with those with either an upstream or downstream impoundment, and western silvery minnows and sturgeon chubs were only sampled from reaches without impoundments (Figure 6). Although the distribution and abundance of turbid-river cyprinids relative to impoundments are of substantial ecological importance, differences in abundance were not statistically different due to the high variability and low sample size among watersheds.

Discussion

Our results suggest that the abundance of turbid-river cyprinids in the Missouri River drainage of Wyoming was related to substrate composition and the abundance of exotic piscivores, all of which were associated with the presence and location of large, main-stem impoundments in the watershed. Although these results are correlative, our analyses provide an accumulation of evidence that illustrates consistent large-scale patterns in fish and habitat characteristics. Moreover, the accumulation of evidence presented in our study, coupled with existing knowledge on large-river systems, provides insight as to the potential mechanisms influencing turbid-river cyprinids in Wyoming.

Impoundments reduce turbidity and stabilize substrate (i.e., channel armoring) due to decreased fine sediment transport (Allan 1995). For example, average annual sediment load in the Missouri River was reduced by 81% following the construction of Gavins Point Dam (Hesse et al. 1989). As a result of the Gavins Point Dam and other large

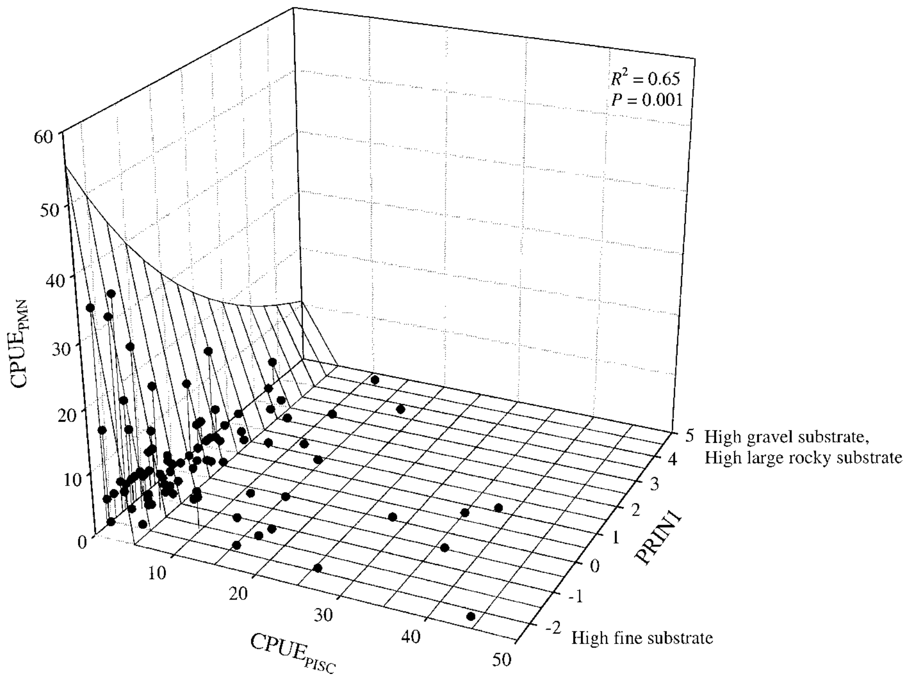

FIGURE 4.—Relationship of catch per unit effort (CPUE = number/200 m) of plains minnows ($CPUE_{PMN}$), CPUE of exotic piscivores ($CPUE_{PISC}$), and scores from the first principal component axis (PRIN1) for reaches sampled in the Missouri River drainage of Wyoming (1993–2000). Variables contributing to PRIN1 are provided in Table 1. The multiple-regression equation is: $CPUE_{PMN} = 10.01\ e^{(-0.12 \times \mathrm{PRIN1}\ -1.84 \times \mathrm{CPUE_{PISC}})}$.

impoundments, turbidity and the proportion of fine substrate have declined, and the proportion of large substrate has increased in the Missouri River (Pflieger and Grace 1987; Hesse et al. 1989; Galat et al. 1996). In Wyoming, Akashi (1988) reported a 67% reduction in the suspended sediment load of the Bighorn River after completion of the Boysen Dam with corresponding changes in habitat. Similar results have been reported in the North Platte (Wenzel 1993) and Laramie rivers (North Platte River drainage; Patton and Hubert 1993). Reduced turbidity may have direct consequences for turbid-river cyprinids. For instance, Bonner and Wilde (2000) found that a suite of turbid-river cyprinids (e.g., flathead chub, plains minnow, and peppered chub *Macrhybopsis tetranema*) historically comprised 98% of the fish assemblage in the Canadian River, Texas, prior to impoundment. However, turbid-river cyprinids decreased in abundance or were extirpated after impoundment, and the assemblage became dominated by species not characteristic of highly turbid systems such as emerald shiners *N. atherinoides*, red shiners, and various piscivores. These authors hypothesized that reduced turbidity was responsible for shifts in fish assemblage structure and tested the hypothesis using a series of experiments. Based on these experiments, Bonner and Wilde (2002) found that the feeding efficiency of species characteristic of highly turbid conditions (e.g., flathead chub) was unaffected by turbidity, while the feeding efficiency of species not commonly associated with high turbidity decreased with reduced water clarity. Similar mechanisms may explain many of the patterns observed in our study, particularly with regard to the abundance of exotic piscivores.

Substrate composition was directly related to the abundance of turbid-river cyprinids and was different among impoundment categories. Although differences in substrate composition among impoundment categories could be interpreted as an artifact of where sampling occurred, several lines of evidence support the contention that differences were due to impoundments. Many of the reaches with a downstream impoundment were located on the lower segments of tributaries, whereas reaches with an upstream impoundment were all on large rivers (>20 m wide). Substrate particle size almost always decreases in a downstream direction and is smallest in large rivers (Allan 1995). Our results illustrate the opposite trend, where large rocky substrate dominated reaches with an upstream im-

TABLE 2.—Number of reaches and the percentage of fine, gravel, and large rocky substrate by impoundment category and subdrainage. Reaches were sampled in the Missouri River drainage of Wyoming (1993–2000). Asterisks represent a significant ($P < 0.05$) difference between impoundment categories within subdrainages; NA indicates that reaches were not available for sampling.

	Impoundment category		
Subdrainage	No influence from impoundments	Influenced by downstream impoundment	Influenced by upstream impoundment
Sample size			
Belle Fourche	0	4	3
Bighorn	0	18	4
North Platte	0	7	8
Tongue	0	9	0
Powder	24	0	5
Cheyenne	7	0	0
Little Missouri	2	0	0
Fine substrate			
Belle Fourche	NA	85.0 (15.0)*	40.0 (5.2)
Bighorn	NA	97.5 (5.5)*	45.0 (5.0)
North Platte	NA	52.9 (13.7)*	20.2 (6.7)
Tongue	NA	83.8 (5.4)	NA
Powder	94.6 (1.8)*	NA	61.6 (3.5)
Cheyenne	98.3 (1.7)	NA	NA
Little Missouri	97.5 (2.5)	NA	NA
Gravel substrate			
Belle Fourche	NA	12.5 (6.2)	15.0 (7.6)
Bighorn	NA	8.1 (3.2)*	30.0 (10.2)
North Platte	NA	12.1 (10.1)*	32.5 (8.8)
Tongue	NA	9.0 (7.5)	NA
Powder	7.2 (3.8)*	NA	25.3 (5.2)
Cheyenne	6.7 (3.6)	NA	NA
Little Missouri	6.5 (4.5)	NA	NA
Large rocky substrate			
Belle Fourche	NA	0.1 (0.1)*	35.0 (23.6)
Bighorn	NA	13.0 (4.0)*	55.0 (5.0)
North Platte	NA	10.1 (4.2)*	51.2 (8.3)
Tongue	NA	12.2 (3.2)	NA
Powder	2.5 (1.0)*	NA	10.4 (2.1)
Cheyenne	1.2 (0.1)	NA	NA
Little Missouri	0	NA	NA

poundment. Furthermore, this result was observed not only across basins but among reaches within a particular subdrainage.

The relationship between large impoundments and instream habitat was particularly evident in the North Platte River, which contains more large impoundments than any other system in Wyoming and has been impounded since the early 1900s. Prior to impoundment, the North Platte River was much like other Great Plains rivers in Wyoming (e.g., the Powder River) with fine substrate and fish assemblages composed of turbid-river species such as flathead chubs, sturgeon chubs, shovelnose sturgeon *Scaphirhynchus platorynchus*, and goldeyes *Hiodon alosoides* (Evermann and Cox 1896; Baxter and Stone 1995). However, substrate composition is now dominated by gravel, cobble, and boulder substrates, and the native fish assemblage has been replaced by exotic salmonids (e.g., brown trout), percids (e.g., walleye), and centrarchids (e.g., smallmouth bass). Although similar effects have been observed in the Bighorn and Belle Fourche river systems (both systems were impounded in 1952), main-stem impoundments have had a longer time to influence channel morphology and fishes in the North Platte River. Thus, our results support the hypothesis that reservoirs have decreased the amount of fine sediment and increased the amount of rocky substrate in downstream reaches, which has had consequent effects on turbid-river cyprinids. Although substrate characteristics and the conditions that altered substrate composition likely reflect (e.g., flow regime and turbidity) were directly related to the abundance

TABLE 3.—Catch per unit effort (CPUE) (number/200 m) of exotic piscivores, turbid-river cyprinids as a guild, flathead chubs, plains minnows, western silvery minnows, and sturgeon chubs by impoundment category and subdrainage. Reaches were sampled in the Missouri River drainage of Wyoming (1993–2000). Asterisks represent a significant ($P < 0.05$) difference between impoundment categories within subdrainages; NA indicates that reaches were not available for sampling, and a dash indicates that a particular species is not thought to be native to the subdrainage in Wyoming.

	Impoundment category		
Subdrainage	No influence from impoundments	Influenced by downstream impoundment	Influenced by upstream impoundment
	CPUE of exotic piscivores		
Belle Fourche	NA	37.5 (35.5)	16.5 (8.6)
Bighorn	NA	0.8 (0.5)	2.0 (0.9)
North Platte	NA	8.5 (0.6)	12.7 (5.6)
Tongue	NA	10.2 (2.7)	NA
Powder	0.4 (0.2)	NA	5.3 (1.4)
Cheyenne	1.2 (0.2)	NA	NA
Little Missouri	2.1 (1.3)	NA	NA
	CPUE of turbid-river cyprinids		
Belle Fourche	NA	0.3 (0.2)*	7.0 (1.7)
Bighorn	NA	10.7 (4.4)*	0
North Platte	NA	0	0
Tongue	NA	5.6 (2.9)	NA
Powder	68.1 (16.7)*	NA	17.4 (10.8)
Cheyenne	13.0 (4.6)	NA	NA
Little Missouri	2.0 (0)	NA	NA
	CPUE of flathead chubs		
Belle Fourche	**NA**	**0***	**7.0 (1.7)**
Bighorn	**NA**	**10.7 (4.4)***	**0**
North Platte	**NA**	**0**	**0**
Tongue	**NA**	**5.6 (2.9)**	**NA**
Powder	**64.2 (17.5)***	**NA**	**17.2 (11.0)**
Cheyenne	**13.0 (4.6)**	**NA**	**NA**
Little Missouri	**—**	**NA**	**NA**
	CPUE of plains minnows		
Belle Fourche	**NA**	**0.3 (0.2)**	**0**
Bighorn	**NA**	**0**	**0**
North Platte	**NA**	**0**	**0**
Tongue	**NA**	**0**	**NA**
Powder	**3.1 (0.8)***	**NA**	**0.2 (0.2)**
Cheyenne	**6.7 (2.1)**	**NA**	**NA**
Little Missouri	**0**	**NA**	**NA**
	CPUE of western silvery minnows		
Belle Fourche	**NA**	**0**	**0**
Bighorn	**NA**	**0**	**0**
North Platte	**NA**	**—**	**—**
Tongue	**NA**	**0**	**NA**
Powder	**0.3 (0.2)**	**NA**	**0**
Cheyenne	**—**	**NA**	**NA**
Little Missouri	**2.0 (0)**	**NA**	**NA**
	Catch per unit effort of sturgeon chubs		
Belle Fourche	NA	—	—
Bighorn	NA	0	0
North Platte	NA	0	0
Tongue	NA	0	NA
Powder	0.5 (0.3)	NA	0
Cheyenne	—	NA	NA
Little Missouri	0	NA	NA

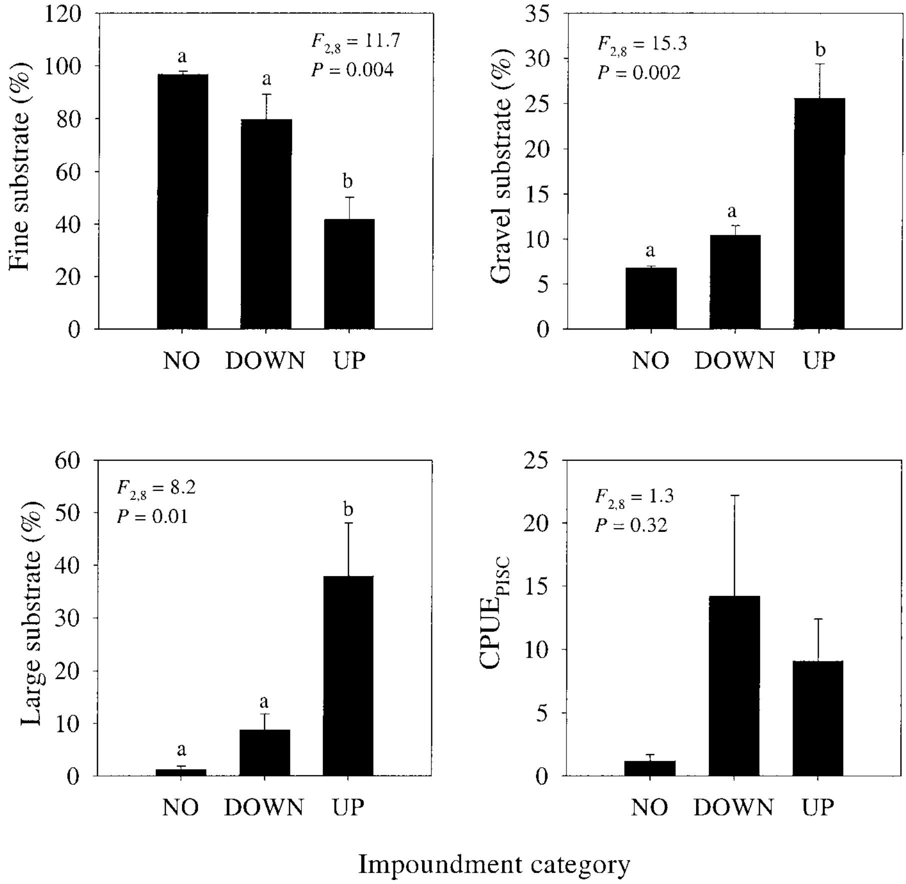

FIGURE 5.—Mean percentage of fine, gravel, and large rocky substrate, and catch per unit effort of exotic piscivores ($CPUE_{PISC}$ = number/200 m) from reaches sampled in the Missouri River drainage of Wyoming (1993–2000) by impoundment category (NO = no influence from an upstream or downstream impoundment, N = 3; DOWN = influenced by downstream impoundment, N = 4; UP = influenced by upstream impoundments, N = 4). Mean substrate percentage and $CPUE_{PISC}$ were calculated by subdrainage and impoundment category. Error bars represent one standard error and impoundment categories with different letters indicate a significant difference ($P \leq 0.05$).

of turbid-river cyprinids, the low abundance or absence of turbid-river cyprinids in reaches upstream of reservoirs with apparently suitable habitat suggest that exotic piscivores can have an overriding influence on turbid-river cyprinids.

The river and stream systems of the Great Plains historically exhibited extremes in flow and physicochemical conditions, and many species evolved in these relatively harsh environments (Matthews 1988; Fausch and Bestgen 1997). Although our study did not directly address changes in flow or floodplain dynamics, previous research clearly illustrates that peak flows, intermittence, and floodplain connectivity have been altered by large, main-stem impoundments in Wyoming. For example, the North Platte River has been affected by four large impoundments constructed between 1909 and 1961, which have reduced peak annual flows by about 40% (Wenzel 1993). In the Bighorn River, Akashi (1988) reported a 38% reduction in peak flows and a decrease in the frequency of overbank flow from once every 2 years to less than once every 10 years following completion of Boysen Dam in 1952. In addition to reduced peak flows and floodplain connectivity, impoundments have decreased annual flow variation, increased annual low flows by about 50–60%, and eliminated the intermittent characteristics of the North Platte and Bighorn rivers (Akashi 1988; Wenzel 1993; Bray 1996). In other systems without impoundments, such as the main stem of the Powder River, flows are highly variable where overbank and no flow conditions (i.e., intermittence) occur almost yearly (Hubert 1993; Baxter and Stone 1995). Centrar-

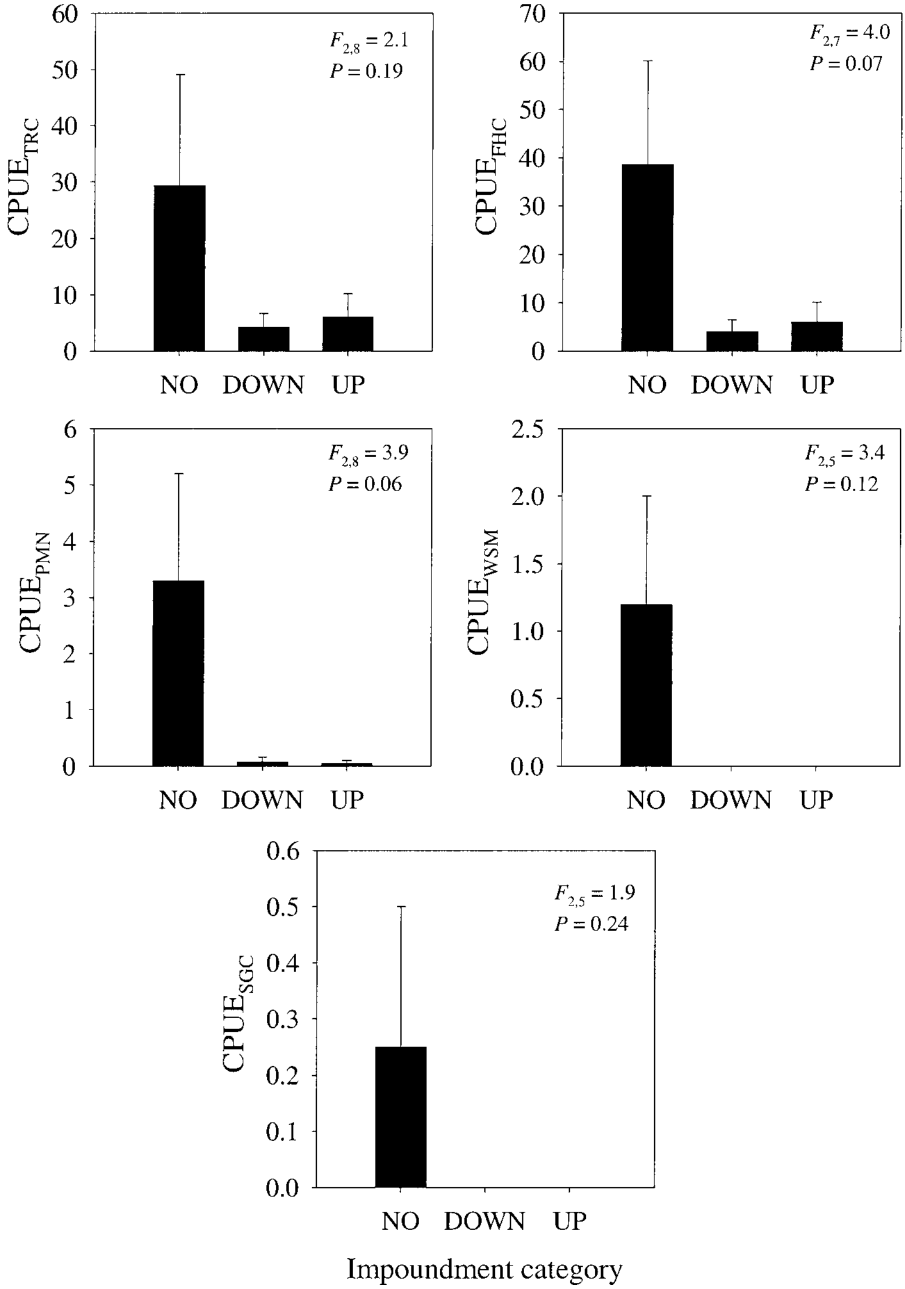

FIGURE 6.—Mean catch per unit effort (CPUE = number/200 m) of turbid-river cyprinids as a guild ($CPUE_{TRC}$), flathead chubs ($CPUE_{FHC}$), plains minnows ($CPUE_{PMN}$), western silvery minnows ($CPUE_{WSM}$), and sturgeon chubs ($CPUE_{SGC}$) from reaches sampled in the Missouri River drainage of Wyoming (1993–2001) by impoundment category (NO = no influence from an upstream or downstream impoundment, N = 2–3; DOWN = influenced by downstream impoundment, N = 3–4; UP = influenced by upstream impoundments, N = 2–4). Mean catch rates were calculated by subdrainage and impoundment category.

chids and most percids were historically absent from the turbid systems of the western Great Plains because the shifting-sand substrate, dynamic flows, and frequent intermittence were not conducive for reproduction or survival, and high turbidity prevented predation by sight-feeding piscivores (Baxter and Stone 1995; Fausch and Bestgen 1997). In Wyoming, large impoundments have stabilized flows and substrate, enhanced low flows, and decreased turbidity and frequency of intermittence. Thus, large impoundments not only enhance the same physicochemical and flow characteristics (i.e., in reaches downstream from impoundments) that prevented the occurrence of exotic piscivores in prairie streams, but they act as continual sources of exotic piscivores. Because species adapted to dynamic, turbid rivers evolved in the absence of abundant piscivores, it is not surprising that they are sensitive to predation. For example, Wenke et al. (1993) found that a reservoir on the Republican River, Kansas, enhanced low flows, stabilized substrates, and reduced turbidity in downstream reaches of the Kansas River. Consequently, smallmouth bass and white bass *Morone chrysops* increased in abundance while plains minnows became rare and sturgeon chubs and speckled chubs *Macrhybopsis aestivalis* were extirpated. Similar interactions have been described in the Rio Grande (Platania and Altenbach 1998), San Juan (Gido and Propst 1999), and Colorado rivers (Carlson and Muth 1989; Minckley et al. 2003).

Predation on stream fishes is not limited to reaches downstream of large impoundments because reservoirs serve as sources for upstream invasion by exotic piscivores (Pringle 1997). Winston et al. (1991) found that impoundment of a prairie stream in Oklahoma resulted in the upstream extirpation of four turbid-river cyprinid speciess due to the introduction of predators. In our study, reaches upstream from impoundments generally had the same number of exotic piscivores as reaches downstream from reservoirs despite differences in habitat. The most common piscivores were smallmouth bass, green sunfish, and rock bass, which have been shown to be important predators on native fishes in the Great Plains (Schlosser 1988; Winston et al. 1991; Lohr and Fausch 1996). Although our results do not identify specific mechanisms, predation probably has a large influence on the distribution and abundance of turbid-river cyprinids, and in reaches downstream of impoundments, the influence of exotic species likely interacts with other impoundment effects such as stabilized flows and substrate, and reduced turbidity.

Determining the direct effects of impoundments on fish assemblages is difficult because of the inability to conduct experimental manipulations and the confounding effects of multiple abiotic and biotic changes. Most river systems in the western United States have been altered by impoundments. Therefore, the preservation of unaltered river systems should be a priority for conserving native fishes. Although maintaining a natural flow regime (i.e., both peak and low flows) is important for turbid-river species in river systems that have already been altered, our results suggest that the restoration of sediment transport dynamics and reducing habitat suitability for exotic piscivores are also important for conserving turbid-river species.

Acknowledgments

We thank W. LaVoie, T. Lipsey, T. Marwitz, A. Parker, A. Patton, C. Patton, T. Patton, R. Tudek, and M. Williams for collecting the data used in this study. C. Berry, K. Bestgen, D. Miller, I. Schlosser, L. Thel, and four anonymous reviewers provided helpful comments on an earlier version of the manuscript. Funding was provided by the Wyoming Game and Fish Department.

References

Akashi, Y. 1988. Riparian vegetation dynamics along the Bighorn River, Wyoming. M. S. thesis. Department of Botany, University of Wyoming, Laramie.

Allan, J. D. 1995. Stream ecology, structure and function of running waters. Chapman and Hall, New York.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43:32–43.

Armantrout, compiler. 1998. Glossary of aquatic habitat inventory terminology. American Fisheries Society, Bethesda, Maryland.

Baxter, G. T., and M. D. Stone. 1995. Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne.

Bestgen, K. R., and S. P. Platania. 1991. Status and conservation of the Rio Grande silvery minnow, *Hybognathus amarus*. Southwestern Naturalist 36: 225–232.

Bonner, T. H., and G. R. Wilde. 2000. Changes in the fish assemblage of the Canadian River, Texas, associated with reservoir construction. Journal of Freshwater Ecology 15:189–198.

Bonner, T. H., and G. R. Wilde. 2002. Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society 131: 1203–1208.

Branson, B. A. 1963. The olfactory apparatus of *Hybopsis gelida* (Girard) and *Hybopsis aestivalis* (Girard) (Pisces: Cyprinidae). Journal of Morphology 113:215–229.

Bray, T. J. 1996. Changes in channel morphology and riparian mosaics on the Bighorn River, Wyoming. M. S. thesis. Department of Rangeland Ecology and Watershed Management, University of Wyoming, Laramie.

Bryan, J. D., L. G. Hill, and W. H. Neill. 1984. Interdependence of acute temperature preference and respiration in the plains minnow. Transactions of the American Fisheries Society 113:557–562.

Burr, B. M., K. M. Cook, D. J. Eisenhour, K. R. Piller, W. J. Ply, R. W. Sauer, C. A. Taylor, E. R. Atwood, and G. L. Seegert. 1996. Selected Illinois fishes in jeopardy: new records and status evaluations. Transactions of the Illinois State Academy of Science 89: 169–186.

Carlson, C. A., and R. T. Muth. 1989. The Colorado River: lifeline of the American southwest. Pages 220–229 *in* D. P. Dodge, editor. Proceedings of the international large rivers symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106.

Cross, G. B., and R. E. Moss. 1987. Historic changes in fish communities and aquatic habitats in plains streams of Kansas. Pages 155–165 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Davis, B. J., and R. J. Miller. 1967. Brain patterns in minnows of the genus *Hybopsis* in relation to feeding habits and habitat. Copeia 1967:1–39.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266:753–762.

Evermann, B. W., and U. O. Cox. 1896. A report upon the fishes of the Missouri River basin. Report to the U. S. Commission of Fish and Fisheries 20(1894): 325–429.

Fausch, K. D., and K. R. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131–166 *in* F. L. Knopf and F. B. Samson, editors. Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York.

Galat, D. L., J. W. Robinson, and L. W. Hesse. 1996. Restoring aquatic resources to the lower Missouri River: issues and initiatives. Pages 49–72 *in* D. L. Galat and A. G. Frazier, editors. Overview of river-floodplain ecology in the upper Mississippi River basin. Washington D. C.

Gido, K. B., and D. L. Propst. 1999. Habitat use and association of native and nonnative fishes in the San Juan River, New Mexico and Utah. Copeia 1999: 321–332.

Gregory, S., H. Li, and J. Li. 2002. The conceptual basis for ecological responses to dam removal. BioScience 52:713–723.

Hesse, L. W. 1994. The status of Nebraska fishes in the Missouri River, selected chubs and minnows (Cyprinidae): sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*M. gelida*), silver chub (*M. storeriana*), speckled chub (*M. aestivalis*), flathead chub (*Platygobio gracilis*), plains minnow (*Hybognathus placitus*), and western silvery minnow (*H. argyritis*). Transactions of the Nebraska Academy of Sciences 21:99–108.

Hesse, L. W., G. E. Mestl, and J. W. Robinson. 1993. Status of selected fishes in the Missouri River in Nebraska with recommendation for their recovery. Pages 327–340 *in* L. W. Hesse, C. B. Stalnaker, N. G. Benson, and J. R. Zuboy, editors. Restoration planning for the rivers of the Mississippi River ecosystem. U. S. Department of Interior, Special Publication 19, Washington, D. C.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pages 352–371 *in* D. P. Dodge, editor. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106.

Hubert, W. A. 1993. The Powder River: a relatively pristine stream on the Great Plains. Pages 387–395 *in* L. W. Hesse, C. B. Stalnaker, N. G. Benson, and J. R. Zuboy, editors. Restoration planning for the rivers of the Mississippi River ecosystem. U. S. Department of Interior, Special Publication 19, Washington, D. C.

Johnson, D. E. 1998. Applied multivariate methods for data analysts. Duxbury Press, Pacific Grove, California.

Lehtinen, S. F., and J. B. Layzer. 1988. Reproductive cycle of the plains minnow, Hybognathus placitus (Cyprinidae), in the Cimarron River, Oklahoma Southwestern Naturalist 33:27–33.

Lohr, S. C., and K. D. Fausch. 1996. Effects of green sunfish (*Lepomis cyanellus*) predation on survival and habitat use of plains killifish (*Fundulus zebrinus*). Southwestern Naturalist 41:155–160.

Luttrell, G. R., A. A. Echelle, W. L. Fiser, and D. J. Eisenhour. 1999. Declining status of two species of the *Macrhybopsis aestivalis* complex (Teleostei: Cyprinidae) in the Arkansas River basin and related effects of reservoirs as barriers to dispersal. Copeia 1999:981–989.

Master, L. L. 1991. Assessing threats and setting priorities for conservation. Conservation Biology 5: 559–563.

Matthews, W. J. 1987. Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. Pages 111–120 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Matthews, W. J. 1988. North American prairie streams as a system for ecological study. Journal of the North American Benthological Society 7:387–409.

Matthews, W. J., and J. Maness. 1979. Critical thermal maxima, oxygen tolerances, and population fluctuations in southwestern stream fishes. American Midland Naturalist 102:374–377.

Miller, R. R. 1972. Threatened freshwater fishes of the United States. Transactions of the American Fisheries Society 101:239–252.

Milliken, G. A., and D. E. Johnson. 1992. Analysis of messy data, volume I: designed experiments. Chapman and Hall, New York.

Minckley, W. L., P. C. Marsh, J. E. Deacon, T. E. Dowling, P. W. Hedrick, W. J. Matthews, and G. Mueller. 2003. A conservation plan for native fishes of the lower Colorado River. BioScience 53:219–234.

Moore, G. A. 1950. The cutaneous sense organs of the barbeled minnows adapted for life in the muddy streams of the Great Plains region. Transactions of the American Microscopy Society 69:69–95.

Moyle, P. B., and R. A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 127–169 *in* P. L. Fielder and S. K. Jain, editors. Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York.

Moyle, P. B., and J. E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology 4:475–484.

Patton, T. M., and W. A. Hubert. 1993. Reservoirs on a Great Plains stream affect downstream habitat and fish assemblages. Journal of Freshwater Ecology 8: 279–285.

Patton, T. M., W. A. Hubert, F. J. Rahel, and K. G. Gerow. 2000. Effort needed to estimate species richness in small streams of the Great Plains in Wyoming. North American Journal of Fisheries Management 20:394–398.

Patton, T. M., F. J. Rahel, and W. A. Hubert. 1998. Using historical data to assess changes in Wyoming's fish fauna. Conservation Biology 12:1120–1128.

Petts, G. E. 1984. Impounded rivers: perspectives for ecological management. Wiley, New York.

Pflieger, W. L., and T. B. Grace. 1987. Changes in the fish fauna of the lower Missouri River, 1940–1983. Pages 166–177 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Platania, S. P., and C. S. Altenbach. 1998. Reproductive strategies and egg types of seven Rio Grande basin cyprinids. Copeia 1988:559–569.

Pringle, C. M. 1997. Exploring how disturbance is transmitted upstream: going against the flow. Journal of the North American Benthological Society 16:425–438.

Rahel, F. J., and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120:319–332.

Reigh, R. C., and D. S. Elsen. 1979. Status of the sturgeon chub (*Hybopsis gelida*) and sicklefin chub (*Hybopsis meeki*) in North Dakota. Prairie Naturalist 11: 49–52.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Robinson, H. W., G. A. Moore, and R. J. Miller. 1974. Threatened fishes of Oklahoma. Transactions of the Oklahoma Academy of Science 54:139–146.

Rosenberg, D. M., F. Berkes, R. A. Bodaly, R. E. Hecky, C. A. Kelly, and J. W. M. Rudd. 1997. Large-scale impacts of hydroelectric development. Environmental Reviews 5:27–54.

SAS Institute. 1996. SAS/STAT user's guide, version 6.11. SAS Institute Inc., Cary, North Carolina.

Schlosser, I. J. 1988. Predation rates and the behavioral response of adult brassy minnow (*Hybognathus hankinsoni*) to creek chub and smallmouth bass predators. Copeia 1988:691–698.

Stukel, E. D., and D. C. Backlund. 1997. Animal species monitored by the South Dakota natural heritage program. Prairie Naturalist 29:179–213.

Taylor, C. M., and R. J. Miller. 1990. Reproductive ecology and population structure of the plains minnow, Hybognathus placitus (Pisces: Cyprinidae), in central Oklahoma American Midland Naturalist 123: 32–39.

Wang, L., T. D. Simonson, and J. Lyons. 1996. Accuracy and precision of selected stream habitat estimates. North American Journal of Fisheries Management 16:340–347.

Ward, J. V., and J. A. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers 11: 105–119.

Wenke, T. L., G. W. Ernsting, and M. E. Eberle. 1993. Survey of river fishes at Fort Riley military reservation in Kansas. Prairie Naturalist 25:317–323.

Wenzel, C. R. 1993. Flushing flow requirements of a large, regulated Wyoming river to maintain trout spawning habitat quality. M. S. thesis. Department of Range Management, University of Wyoming, Laramie.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America: endangered, threatened, or of special concern. Fisheries 14(6):2–20.

Winston, M. R., C. M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. Transactions of the American Fisheries Society 120:98–105.