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Historical data reveal fish assemblage shifts in an unregulated prairie river

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Abstract. Wyoming's Powder River is considered an example of a pristine prairie river system. While the river hosts a largely native fish assemblage and remains unimpounded over its 1,146-km course to the Yellowstone River confluence, the hydrologic regime has been altered through water diversion for agriculture and natural gas extraction and there has been limited study of fish assemblage structure. We analyzed fish data collected from the mainstem Powder River in Wyoming between 1896 and 2008. Shifts in presence/absence and relative abundance of fish species, as well as fish assemblage composition, were assessed among historical and recent samples. The recent Powder River fish assemblage was characterized by increased relative abundances of sand shiner *Notropis stramineus* and plains killifish *Fundulus zebrinus*, and decreases in sturgeon chub *Macrhybopsis gelida*. Shifts in fish species relative abundance are linked to their reproductive ecology with species with adhesive eggs generally increasing in relative abundance while those with buoyant drifting eggs are decreasing. Assemblage shifts could be the result of landscape level changes, such as the loss of extreme high and low flow events and changing land use practices.

Key words: fish community shifts; Great Plains; *Macrhybopsis gelida*; native invaders; *Notropis stramineus*; pelagic spawning; prairie fish.

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Background

Freshwater systems are some of the most imperiled ecosystems worldwide (Leidy and Moyle 1998, Dudgeon et al. 2006). In North America, freshwater fish populations have been in decline since the early 20th century (Williams et al. 1989, Moyle and Leidy 1992, Jelks et al. 2008). Over the past 30 years, the number of imperiled freshwater fish taxa has increased 179 fold and approximately 39% of all native North American ichthyofauna have received conservation statuses (Jelks et al. 2008). Shifts in native fish communities have been attributed to altered flow and sediment transport regimes (Hughes et al. 2005, Durham and Wilde 2008, Taylor 2010, Perkin et al. 2014), habitat alterations and homogenization (Cross and Moss 1987, Rahel 2002, Perkin and Gido 2012), and introduction of nonnative taxa (Quist et al. 2004, Cucherousset and Olden 2011). In addition, a recently recognized mechanism leading to shifts in native fish communities is "native invasions," the disproportionate expansion of particular native species more suited to exploiting niche opportunities afforded by human activities (Simberloff 2011, Carey et al. 2012).

North American prairie ecosystems are among the most threatened biomes in North America (Samson and Knopf 1994), having been "ravaged by pump, flow and pollution" (Matthews 1988). The Great Plains ecosystem stretches east to west from the Eastern Deciduous Forest to the foothills of the Rocky Mountains. Most prairie river systems have been altered by water development which has tended to stabilize historically-intermittent and (or) widely-fluctuating flow regimes. Perhaps the largest and most well-known prairie river, the Missouri River, is now extremely regulated. One third of this river is channelized and another third is impounded, while the whole river experiences a substantially different flow regime from that in which its native fishes evolved (Rabeni 1996). Prairie streams are of ecological importance due, in part, to their highly-adapted native fishes. Over 200 species of fish in 28 families may be found in the warm-water streams of the Great Plains region (Cross et al. 1985, Rabeni 1996), but individual streams tend to support a small subset of this array. Prairie streams, along with their native fish assemblages, face increasing risks of extinction (Matthews 1988, Hubert and Gordon 2007).

The Powder River is one of the last unregulated prairie river systems in North America. As a result it is characterized by a highly-variable hydrograph and frequent intermittency (Hubert 1993). Due both to the lack of dams and the naturally wide-ranging flows, the fish assemblage is composed largely of members of the original, post-glacial ichthyofauna which are all highly adapted to the extreme environmental conditions of the basin (Hubert 1993). Of 32 species present in the Powder River drainage, 25 are native (Smith 1988, Smith and Hubert 1989). Several of these native species (shovelnose sturgeon *Scaphirhynchus platorynchus*, goldeye *Hiodon alosoides*, sturgeon chub *Macrhybopsis gelida*, and western silvery minnow *Hybognathus argyritis*) have been designated as Species of Greatest Conservation Need by the state of Wyoming (WGFD 2010) due to declining populations and habitat loss.

The Powder River represents one of the last remaining examples of a Great Plains river with unregulated flows and a fish assemblage composed predominantly of native species (Baxter and Stone 1995). Although the Powder River appears to maintain flood and physicochemical regimes similar to those of the past, both the physicochemical regime and the biotic integrity of the system are little known and under-studied. The fish assemblage has been classified as "relatively pristine" (Hubert 1993), but this was on the basis of the continued presence of native species not on an examination of species relative abundances. Other Great Plains rivers have seen substantial decreases in the relative abundance of fish in the "pelagic spawner" reproductive guild (Dudley and Platania 2007, Perkin and Gido 2011). In addition, there is evidence that sand shiners *Notropis stramineus* have substantially increased in abundance in the Powder River (Patton 1997). Historical data provides a unique opportunity to evaluate shifts in assemblage composition through time (Patton et al. 1998, Almeida et al. 2014). We used historical and contemporary fish sampling data to examine assemblage composition in the mainstem Powder River over the period of fish sampling records. Our aim was to identify and assess possible changes to the Powder River fish assemblage. We hypothesized that the "relatively pristine" characterization by Hubert (1993) may no longer be applicable to the Powder River fish assemblage.

Methods

Study system

The Powder River flows from its headwaters in the Bighorn Mountains and high plains of south central Wyoming to its confluence with the Yellowstone River upstream of Terry, Montana (Hubert 1993; Fig. 1). The mainstem of the Powder River is unregulated by large dams for its entire length of 1146 km, 459 of which are in Wyoming. The Yellowstone River Intake Diversion Dam is located on the Yellowstone River 122 km downstream from the confluence of the Yellowstone and Powder rivers. While there are no dams on the mainstem of the Powder River, points of diversion for water withdrawals, associated predominantly with irrigation and

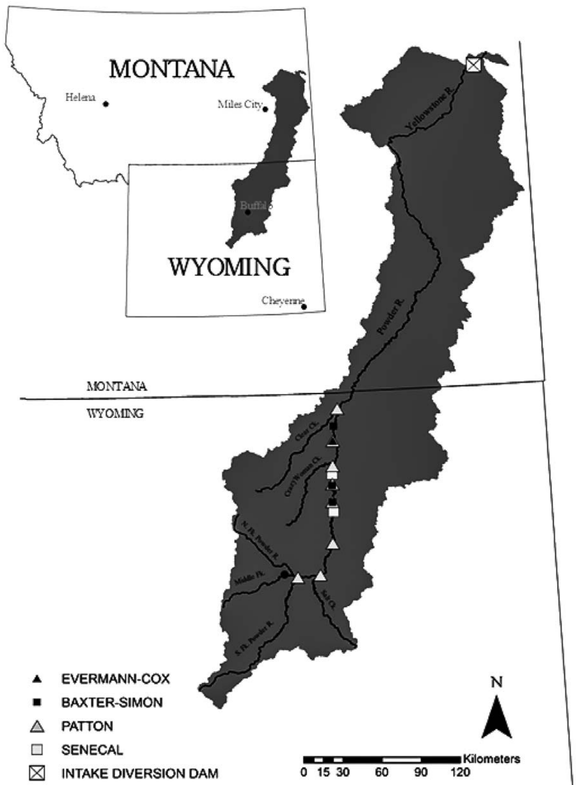

Fig. 1. Map of the Powder River basin in Montana and Wyoming. Sampling sites by source, impoundments, and major cities are shown.

energy development, are present throughout the watershed.

Predominant land use within the basin has historically been agriculture (Hubert 1993). In recent years (1994–2009) this has shifted towards energy extraction, as evidenced by the increase in numbers of wells permitted and volume of product water generated within the basin (Table 1). Additionally, magnitude and frequency of peak flows are reduced as compared to historical data. Years of prolonged drought through the 1990s and early 2000s are likely responsible for this trend. Frequency of intermittency is also reduced in recent years and intermittent periods are known to strongly influence prairie stream fish communities (Magoulick 2000, Dodds et al. 2004).

The Powder River has a diverse native fish assemblage consisting of shovelnose sturgeon, goldeye, sturgeon chub, members of the genus *Hybognathus* (western silvery, brassy, and plains minnows), fathead minnow *Pimephales promelas*, flathead chub *Platygobio gracilis*, longnose dace *Rhinichthys cataractae*, river carpsucker *Carpiodes carpio*, channel catfish *Ictalurus punctatus*, and stonecat *Nocturus flavus*. Fishes known to be non-native are common carp *Cyprinus carpio*, black bullhead *Ameiurus melas*, plains killifish *Fundulus zebrinus*, green sunfish *Lepomis cyanellus*, bluegill *Lepomis macrochirus*, and smallmouth bass *Micopterus dolomieu*. The sand shiner is currently abundant in the Powder River in Wyoming, although it was only first observed in the Powder River in Montana in the 1960s. Hence, the native status of sand shiner in Wyoming portions of the drainage is debatable. Further downstream in the Powder River in Montana and in the Yellowstone River, it is described as a native species.

We examined five data sets to assess potential changes to the Powder River fish assemblage over time (Table 2). Historical data sets ranged from the 1890s to the 1980s (Evermann and Cox 1896, Baxter and Simon 1970, Stewart 1981) while contemporary data sets covered years 1994–2008 (Patton 1997, Senecal 2009). Spatially, these collections spanned the mainstem Powder River in Wyoming from downstream of Salt Creek to the Montana border (Fig. 1).

Little information is given regarding the methods of Evermann and Cox (1896) or Baxter and Simon (1970). It is assumed that access was the predominant deciding factor in site selection. Similarly, no information on habitats sampled was included for these two historic data sets. Stewart (1981) indicates type of gear used and site locations, but little else, other than to say most successful seining attempts occurred over rocky substrate. Patton (1997) electrofished 200-m reaches and seined river margins. He noted that an effort was made to sample all habitat types present. Senecal seined river margins in 2007 and individual habitat features (pools, riffles, runs, backwaters, and shoals) were sampled in 2008. In both years, seine haul lengths were measured using a laser range finder (Senecal 2009).

Standardization

We conducted several standardization exercises to account for differences in sampling methodology among studies. We examined the effect of sampling effort, habitat targeted, and meth-

Table 1. Comparison of "historic" (1931–1993) and "contemporary" (1994–2009) hydrologic and land use factors throughout the Powder River Basin, Wyoming. Hydrologic data were obtained from the USGS gage at Arvada (06314000) for the period of record 1930–2009 (http://water.usgs.gov). Snow water equivalent data were obtained from the NRCS SNOTEL site at Soldier Park, the headwaters of Clear Creek (site number 100902060103) for the period of record 1950–2009 (http://www.wcc.nrcs.usda.gov). Coalbed natural gas (CBNG) statistics were obtained from the Wyoming Oil and Gas Conservation Commission (http://wogcc.state.wy.us).

Variable	Unit	Time period 1930–1993	Time period 1994–2009
Average daily flows >280 m^3/s	days/year	0.17	0.00
Average daily flows >140 m^3/s	days/year	0.72	0.63
Intermittency	days/year	18.40	11.80
Average snow water equivalent	inches	5.75	3.84
CBNG wells permitted	count	356	41234
CBNG produced water volume	m^3	0.00	6.50×10^8

odology utilized.

For effort standardization, we conducted a Monte Carlo simulation for each data set with more than three sampling events (Stewart 1981, $n = 80$; Patton 1994, $n = 8$; Senecal 2007, $n = 41$; and Senecal 2008, $n = 174$; Stewart 1981, Patton 1997, and Senecal 2009, respectively). Three sampling events from each data set were randomly chosen and presence/absence was determined for each species based on these three sampling events alone. The simulation was run 100 times and species' presence in a given time period was determined based on whether the species was found to be present in over 50% of the 100 trials. As a result of the effort standardization, species that were only occasionally detected in years with high effort were removed from the presence data set.

To test for the potential effect of sampling different habitats, we analyzed 2008 data with samples from five different habitat types. The purpose was to assess whether regularly sampling all available habitat types produced different results than opportunistically sampling deeper habitats. We compared assemblage structure among differing habitat types using nonmetric multidimensional scaling (NMDS) and compared species' relative abundance calculated using all 2008 data, and only 2008 pool data. Assemblage structure overlapped highly among habitat types (Appendix A) so for the remaining analyses we did not include a habitat adjustment factor.

We used adjustment factors developed by Patton et al. (1998) to account for variation in capture probabilities among sampling gears. Patton et al. (1998) used both seining and electrofishing in his study, and developed species-specific standardization factors based on the probability of capturing each species using only a seine (number of sites where a species was collected by seining divided by the number of sites the species was collected at by electrofishing). Adjustment factors at the site level were applied to the Patton data which was the only dataset which utilized electrofishing. Adjustment

Table 2. Datasets used in analyses of Powder River fish assemblage shifts are detailed by author (Source), date of collection (Date), number of sampling events (n), whether or not habitat information was recorded (Habitat), method of collection (method: EF = bank electrofishing, HL = hook and line, S = seine) and data analysis applied (P/A = presence/absence, NMDS = community composition).

Source	Date	n	Habitat	Method	P/A	Relative abundance	NMDS
Evermann and Cox	1896	1	No	HL, S	X	...	...
Baxter and Simon	1964	3	No	S	X	X	X
Stewart	1979–1980	80	No	S	X	X	X
Patton	1994	8	Yes	EF, S	X	X	X
Senecal	2007–2008	215	Yes	S	X	X	X

Table 3. Presence by time period for all fish species found in one or more sampling event. For time periods with more than three sampling events, presence was determined based on being present in over 50% of 100 random draws of three sampling events.

Species	Presence by year					
	1896	1964	1980	1994	2007	2008
Black bullhead	...	...	...	...	...	...
Bluegill	...	...	...	...	...	...
Channel catfish	X	X	...	X	X	X
Common carp	...	...	...	X	...	...
Goldeye	...	X	...	X	...	...
Green sunfish	...	...	...	...	...	...
Fathead minnow	...	...	...	X	X	X
Flathead chub	X	X	X	X	X	X
Hybognathus sp.	X	X	X	X	X	X
Longnose dace	X	X	X	X	X	X
Longnose sucker	X	...	...	...	...	...
Mountain sucker	X	...	...	X	...	...
Northern redhorse	...	...	...	...	...	...
Plains killifish	...	...	...	X	X	X
River carpsucker	...	...	...	X	X	X
Rock bass	...	...	...	...	...	...
Sand shiner	...	...	...	X	X	X
Sturgeon chub	X	X	X	X	...	...
Smallmouth bass	...	...	...	...	...	...
Stonecat	X	...	...	X	X	...
White sucker	...	...	...	X	...	...

factors were available for all species except smallmouth bass and bluegill. For species that were more susceptible to electrofishing than seining this resulted in a decline in relative abundance for that time point (Appendix B).

Analysis

We included all sampling events and all fishes in species presence/absence plots, but corrected for sampling effort (see standardization section). For the relative abundance plots we excluded presence/absence only data and species for which fewer than 50 individuals were captured. This removed all data collected in 1893 by Evermann and Cox (1896) and five sampling events from Patton in 1994 (Patton 1997). In addition, black bullhead, bluegill, longnose sucker *Catostomus catostomus*, mountain sucker *Catostomus platyrhynchus*, northern redhorse *Moxostoma macrolepidotum*, smallmouth bass, common carp, green sunfish, and rockbass *Ambloplites rupestris* were removed from the analyses. For each sampling event we calculated the relative abundance for each species.

We examined assemblage structure for each sampling event with all species included using NMDS. Bray-Curtis distance was used to obtain the dissimilarity matrix from a matrix of fish species' relative abundances. We compared whether there was a difference between fish assemblages for historic samples (1964, 1980) and contemporary (1994, 2007, 2008) with permutational multivariate analysis of variance using distance matrices. All analyses were carried out using the vegan package (Oksanen et al. 2011) in R (R Development Core Team 2011); the metamds function was utilized for NMDS and the adonis function for comparing the contemporary and historic samples. For both the relative abundance and assemblage analysis we corrected for sampling methodology (see standardization section).

Results

Presence/absence

Four species were almost always present in samples of the fish assemblage: flathead chub, *Hybognathus* sp., channel catfish, and longnose dace (Table 3). Notable changes to the assemblage included the addition of sand shiner, plains killifish, fathead minnow, and river carpsucker in the later samples and the loss of sturgeon chub. Sand shiner and plains killifish first appeared in Patton's 1994 sampling (Patton 1997) and maintained their presence throughout Senecal's 2007–

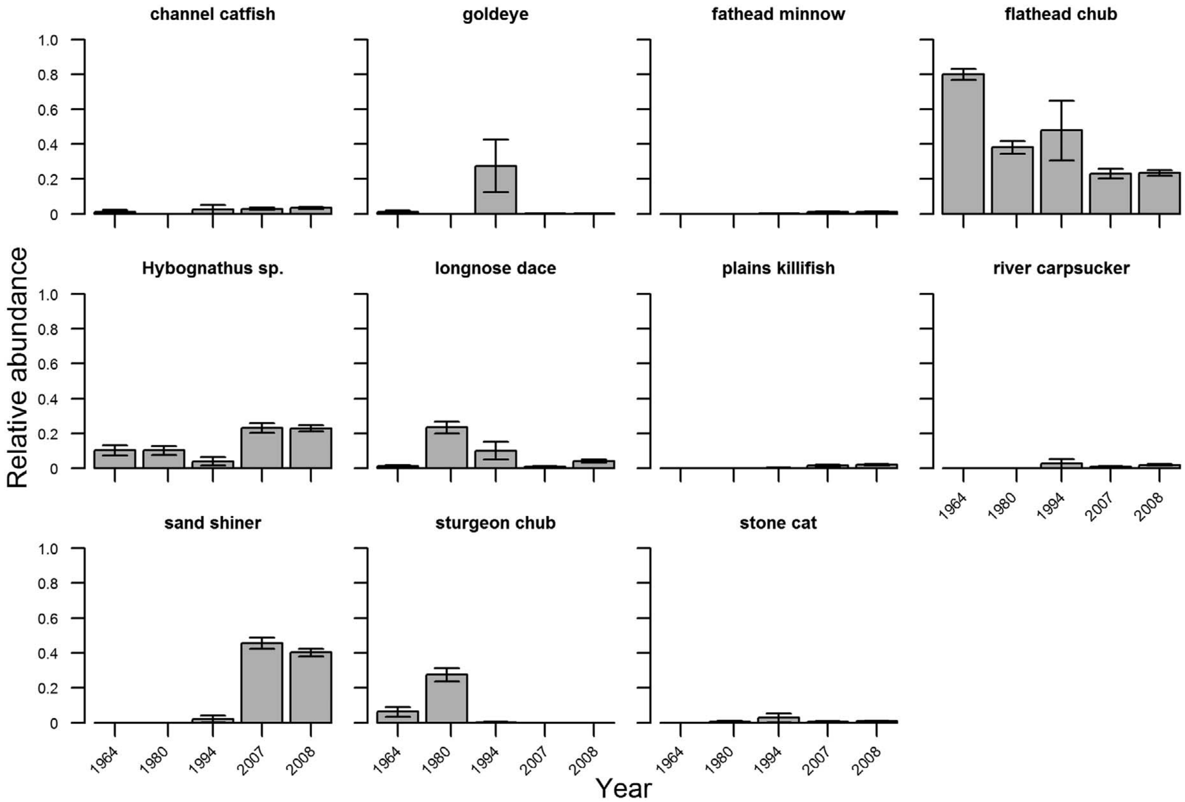

Fig. 2. Relative abundance of common fish species (more than 50 individuals captured) through time. Plots are the average relative abundance + 1 SE.

2008 sampling (Senecal 2009). Although presence of sturgeon chub was occasionally detected in 2007–2008 sampling, effort standardization removed them from the presence data set.

Four species were considered to be absent for all time periods: black bullhead, bluegill, green sunfish, and smallmouth bass. These introduced species were all found for the first time in 2007–2008 sampling but were caught so rarely that effort standardization removed them from the presence data set.

Relative abundance

Eleven species were common in the samples describing the fish assemblage (more than 50 individuals captured; Fig. 2). Channel catfish, longnose dace, and *Hybognathus* sp. comprised a consistently small proportion of the fish sampled. The largest directional shifts in species' relative abundances were decreases in flathead chub and sturgeon chub, and increases in sand shiner. Average flathead chub relative abundance decreased by 71% between 1964 and 2008 sampling events. Sturgeon chub made up between 6.2% (Baxter and Simon 1970) and 27.4% (Stewart 1981) of the fish sampled in early samples, but decreased to less than 1% (0.02 %; Senecal 2009) in later samples. Sand shiner saw marked increases in relative abundance. Sand shiner were first detected in Patton's 1994 sampling (Patton 1997) and increased by 96% between 1994 and 2007 sampling events. Sand shiner made up 39% of the fish sampled in the 2007–2008 samples. In addition to sand shiner, relative abundances also increased for plains killifish and fathead minnow.

Assemblage composition

Assemblage composition from recent sampling events (1994, 2007, and 2008) diverged from historical sampling events (1964, 1980), though 1994 appeared to be intermediate (Fig. 3). The permutational multivariate analysis of variance found significant differences among the groups

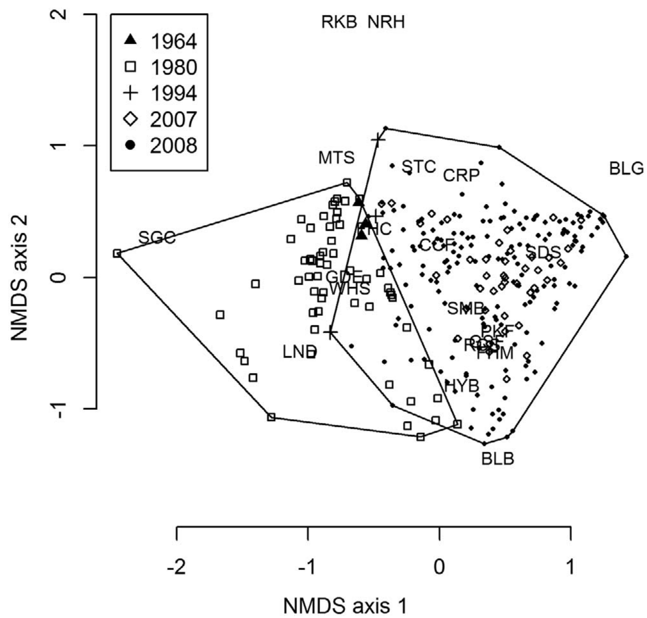

Fig. 3. Nonmetric multidimensional scaling plot (stress = 0.14) of fish assemblage structure for each sampling event. Historic (1964, 1980) and contemporary (1994, 2007, 2008) sampling events are boxed separately. Species codes are BLB = black bullhead, BLG = bluegill, CCF = channel catfish, CRP = common carp, GDE = goldeye, GSF = green sunfish, FHC = flathead chub, FHM = fathead minnow, HYB = *Hybognathus* sp. (plains and western silvery minnow), LND = longnose dace, MTS = mountain sucker, NRH = northern redhorse, PKF = plains killifish, RCS = river carpsucker, RKB = rockbass, SDS = sand shiner, SGC = sturgeon chub, SMB = smallmouth bass, STC = stonecat, and WHS = white sucker.

($F_{1,299} = 104.34$, $p < 0.001$) but this only explained 26% of the variation ($R^2 = 0.26$). Species that were indicative of contemporary assemblage structure included sand shiner and plains killifish, while sturgeon chub were highly associated with historical assemblages.

Discussion

Comparison of historic (1964–1980) and contemporary (1994, 2007, 2008) Powder River sampling efforts in Wyoming indicates that the fish assemblage, while composed largely of native fishes, may not be as pristine as once presumed (Hubert 1993). The most striking change is the rapid expansion of one species—the sand shiner. Sand shiner expansion may have been unintentionally aided by human vectors such as bait fishermen or resource managers (Rahel 2004). In their surveys of fishes of the Missouri River Basin during the late 1800s, Evermann and Cox (1896) sampled five species of minnow from the Powder River, none of which were sand shiner. Baxter and Simon (1970) sampled sand shiner at one of seven Powder River basin survey sites in Wyoming, the headwaters of Salt Creek (Fig. 1). This location was a privately-stocked, cool-water pond, and it is likely that sand shiner were brought to that location by bait fisherman or accidentally introduced along with intentionally stocked species. No sand shiner were collected from five sites sampled on the mainstem of the Power River (Baxter and Simon 1970). Smith (1988), however, sampled sand shiner at the mouth of Crazy Woman Creek in 1986. Although sand shiner were found in the Powder River in Montana as early as the late 1960s (Rehwinkel et al. 1978), and are native to the Missouri River basin (Gilbert 1978), they have since expanded their distribution and abundance in Wyoming to the extent that they could negatively impact other species through competitive exclusion.

The expansion of one species can contribute to the decline of other species (Grossman et al. 1982). Biological interactions, such as competition, have been found to play major roles in the organization of shallow, warm-water stream fish assemblages (Felley and Cothran 1981, Matthews 1988). Assuming that there is some overlap in resource utilization of sand shiner, plains killifish, and other small-bodied fishes, it is possible that the concept of competitive exclusion, coupled with changing habitats and other environmental factors, has contributed to a shift in the structure of the Powder River fish assemblage.

In most cases, assemblage shifts are thought of in terms of new species introductions, or native species declines due to competition or habitat loss. Increasingly, however, disproportionate or gross increases in native species, dubbed "native invaders" are being considered in these cases (Carey et al. 2012). Native invasion has been associated with anthropogenic changes in the environment (e.g., climate change) or habitat conditions that favor one native species and/or cause declines in another (Simberloff 2011). While some native Powder River fishes have experienced slight to appreciable declines, sand shiner relative abundance has increased steadily and is a candidate for being considered as a native invader in the Powder River, though its native status is debated. Similar increases in sand shiner relative abundance are documented in south central Kansas where reductions in peak flows are hypothesized to have favored this native species (Perkin et al. 2014).

Another fish species that has seen substantial increases in abundance and distribution is the plains killifish. The plains killifish is native to the North Platte River drainage in Wyoming. It was not reported to occur in the Powder River drainage by Baxter and Simon (1970). It was introduced at some point to the Cheyenne River and Bighorn River drainages in Wyoming, likely by bait fishermen prior to the 1960s (Baxter and Stone 1995). The range of the plains killifish has since expanded to include the Powder River drainage. Patton et al. (1998) were the first to record the presence of the plains killifish in the Powder River system in Wyoming (in both the South Fork as well as the mainstem of the river). The plains killifish may pose the greatest threat to native fishes of all introduced, naturalized Powder River fishes. Although this small fish likely does not pose a direct predatory threat to the native fish, indirect effects relating to interspecific competition are likely as cohabitation of habitat by animals requires a partitioning of resources, such as space and forage, between individuals (Matthews 1988).

Species expansions in the Wyoming's Powder River have taken place in concert with declines in the relative abundances of both flathead chub and sturgeon chub. Flathead chub relative abundance decreased from 30% in 1980 to 19% in 2008. Similarly, sturgeon chub decreased from 10% in 1980 to less than 1% in 2008. Sturgeon chub, once the third most abundant fish in the Powder River mainstem (after flathead chub and *Hybognathus* sp.; Baxter and Simon 1970), were exceedingly rare in 2008 samples and are considered a Wyoming Species of Greatest Conservation Need (WGFD 2010).

Differences among species' reproductive ecology have informed assemblage shifts in other Great Plains systems (Perkin and Gido 2011) and could be applicable to the Powder River. Several of the declining species, such as sturgeon chub (Moore 1944, Hoagstrom et al. 2006), *Hybognathus* sp. (Raney 1939, Pfleiger 1997) and flathead chub (Cross et al. 1985, Durham and Wilde 2008), belong to a reproductive guild of fishes, termed "pelagic spawners." Although there is some debate as to whether flathead chub belong to the pelagic or "lithopelagic" spawner guild (Hoagstrom and Turner 2013), for the purposes of this paper we consider them to be pelagic spawners. These species time the release of absorbent ova into the water column with peaks in the hydrograph, producing neutrally buoyant zygotes that are suspended in the water column (Moore 1944, Platania and Altenbach 1998, Dudley and Platania 2007, Durham and Wilde 2008, Perkin and Gido 2011, Hoagstrom and Turner 2013). These species' shared reproductive strategy enables reproduction in streams with high suspended sediments and unstable sand or silt substrates, and facilitates the repopulation of downstream habitats that may be fragmented by intermittency. However, localized extirpation of pelagic spawners has been seen in fragmented river segments due to instream migration barriers preventing the upstream movement of adults (Luttrell et al. 1999, Walters et al. 2014) and reduced downstream dispersion and recruitment of drifting eggs and larvae (Dudley and Platania 2007). The Powder River is undammed upstream of its confluence with the Yellowstone River, but habitat fragmentation could still be occurring due to irrigation diversion structures which can act as barriers to upstream migration. While relative abundance of pelagic spawners has declined, those producing adhesive ova attached to the substrate have increased. Species producing adhesive ova include sand shiner (Platania and Altenbach 1998) and fathead minnow (Gale and Buynak 1982).

Variation in the response of pelagic spawners may be related to drift distance of buoyant eggs and larvae. Average drift distances vary from 140 to 550 km, depending upon species, water velocities and habitat complexity (Platania and Altenbach 1998, Dudley and Platania 2007, Durham and Wilde 2008, Perkin and Gido 2011, Hoagstrom and Turner 2013). Sturgeon chub have the longest reported drift distances with an average of 550 km, and an estimated minimum river fragment length required for species persistence (threshold) of 297 km (Perkin and Gido 2011). Flathead chub have relatively short thresholds of 183 km and are comparatively long-lived, sometimes surviving more than 7 years (Scarnecchia et al. 2000). Recent research also shows that habitat fragmentation hinders adult dispersal of flathead chub by impeding summer upstream spawning migrations (Walters et al. 2014). In contrast to the steep declines in abundance seen in sturgeon chub, flathead chub have experienced slow, steady declines in Powder River samples. This discrepancy in persistence could be related to longer generation times in flathead as compared to sturgeon chub (Scarnecchia et al. 2000). Among the species with the shortest fragment thresholds are plains minnow *Hybognathus placitus* (115 km; Perkin and Gido 2011) which could explain the relative stability of *Hybognathus* sp. within Powder River samples. Given its short life span and long drifting distance, sturgeon chub is likely the Powder River species most sensitive to changes in flow regime and habitat alteration and fragmentation.

Members of the pelagic spawning guild comprise 25–40% of imperiled fishes throughout the Great Plains ecoregion (Jelks et al. 2008). Declines in these species are largely attributed to reduced reproductive success (Durham and Wilde 2014), reduced retention rates owing to loss of habitat complexity and lateral flood plain connectivity (Dudley and Platania 2007, Widmer et al. 2010, Hoagstrom and Turner 2013) and reduced recolonization of upstream habitats (Brown and Armstrong 1985, Winston et al. 1991, Walters et al. 2014) due to channelization and fragmentation of large river systems. While undescribed, it follows that river fragmentation thresholds for species producing adhesive ova would be much lower than those with drifting zygotes. Relatively recent extirpations or declines of pelagic spawners, including plains minnow and speckled chub *Macrhybopsis aestivalis*, have been documented in Great Plains Rivers of Oklahoma, Texas and Wyoming, respectively. These species' declines corresponded with gross increases in relative abundances of sand shiner and associated species (Winston et al. 1991, Bonner and Wilde 2000, Lionberger and Hubert 2007, Wilhite 2007, Perkin et al. 2014).

In addition to habitat fragmentation, Great Plains streams have also experienced substantial shifts in hydrology. Extreme floods, periods of intermittency and drought historically contributed to the evolution of a highly-adapted Great Plains fish assemblage (Fausch and Bramblett 1991, Hubert 1993, Matthews and Marsh-Matthews 2006). However, moderating effects have been observed at both ends of the Powder River at Arvada hydrograph for the period of record, 1930–2013 (USGS real time stream gage data: http://www.usgs.gov). Comparison of hydrograph characteristics for time periods 1930–1993 and 1994–2009 reveals appreciable changes (Table 1). Occurrence of average daily flows exceeding 280 m^3/s has declined by 100% (from 0.2 d/yr to 0 d/yr) and those exceeding 140 m^3/s have declined by 14% (from 0.7 d/yr to 0.6 d/yr). Similarly, zero flow days have declined by approximately 40% (from 18.4.0 d/yr to 11.8 d/yr). Reductions in Powder River peak flows correspond to reduced snow pack levels and may also be influenced by increased water withdrawals related to development. Mainstem Powder River permitted water withdrawals of 37 m^3/s (WRDS 2014) exceeded mean average daily flows of 8 m^3/s for the period of record. Agricultural and municipal water withdrawals have been implicated in species' declines in other systems (Gido et al. 2010). While predominant agricultural land uses persist throughout the basin, production of coalbed natural gas has increased precipitously in recent years (Table 1). Decreasing occurrences of zero flow days, despite reduced precipitation regimes, may be linked to direct discharge of coalbed methane effluent water to the Powder River watershed in Wyoming (Senecal 2009).

Periods of low or no flow, in addition to high flow periods, are integral in shaping and maintaining native fish assemblages in unfragmented prairie river systems (Labbe and Fausch 2000, Dodds et al. 2004). Alterations to stream habitat, and the timing and intensity of extreme flow events may make the Powder River system more hospitable to nonnative species (Cross et al. 1985, Gale 1986, Smith 1988, Hubert 1993, Rabeni 1996, Clearwater et al. 2002), or native fishes with physiological or ecological traits favored over other native species in altered environments (Perkin and Gido 2011). Population level declines in pelagic spawners have been linked to reductions in peak flows in other Great Plains river systems (Durham and Wilde 2014). Similar mechanisms may be at play in the Powder River, despite its unregulated status. Increases in species with adhesive ova have also been correlated with reductions in peak flows, theoretically resultant from reduced bed scour (Perkin et al. 2014).

Several authors have made connections between localized extirpations of pelagic spawners in fragmented systems following prolonged periods of drought conditions (Kelsch 1994, Perkin et al. 2013, 2014, 2015). In a situation eerily similar to that observed in the Powder River, sampling revealed local extirpation of sturgeon chub from fragmented portions of the Little Missouri following drought conditions (Kelsch 1994). Similar observations have surfaced from Great Plains river systems in Kansas and Texas where species declines have been linked to isolation and drought (Perkin et al. 2013, 2014). Although undammed, the Powder River is dotted by points of irrigation diversion (WRDS 2014). Operation of these structures coupled with groundwater withdrawal for coalbed natural gas production may have contributed to increasing fragmentation of the Powder River over the last three decades. In addition, a period of extreme drought took place from 1999–2007. Following trends observed in other Great Plains systems, it is possible that reduced colonization post drought due to a highly fragmented landscape accounts for observed changes in the Powder River fish assemblage. It seems that the factors that once favored the evolution of pelagic spawners may now, in fragmented systems, foretell their demise.

Accurate, well-documented historical and baseline data is integral to describing assemblage shifts over time and is crucial for the effective management and conservation of animal populations (Courtenay 2007). Unfortunately, few ecological studies exist prior to 1950 over time frames that account for important ecological disturbances (Brown 1995, Jackson et al. 2001, Gido et al. 2010). As sources for fish sampling and accurate records of hydrologic and land use changes along the Powder River are limited, the story of the evolving Powder River fish assemblage is piecemeal at best. Caution should be taken when making broad generalizations on fish assemblage changes due to differences in sampling gear, methodology and metadata documentation (Patton et al. 1998). For example, without taking sampling effort into consideration, another notable change in the fish assemblage would be the presence of centrarchids and black bullhead in recent samples. Particulars of the environment during the time span covered by Evermann and Cox (1896) and Baxter and Simon (1970) are difficult to discern due to gaps in the hydrologic record. Given gaps in available data, the inability of gages to accurately report zero flow, and the tendency for the Powder River to be flowing in some sections, while becoming isolated pools in others, historic periods of intermittency are difficult, if not impossible, to track.

Despite the data limitations, it is difficult to argue that the fish assemblage of the Powder River in Wyoming has remained unchanged from early records. While the Powder River is largely unregulated with relatively little development, it seems to be following familiar trajectories seen in rivers across the Great Plains that are more heavily impacted and fragmented. The Powder River in Wyoming is a good example of how small, cumulative changes on the landscape may result in large, directional changes in the fish assemblage.

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Literature Cited

Almeida, D., A. Ellis, J. England, and G. H. Stone. 2014. Time-series analysis of native and non-native crayfish dynamics in the Thames River Basin (south-eastern England). Aquatic Conservation: Marine and Freshwater Ecosystems 24:192–202.

Baxter, G. T., and J. R. Simon. 1970. Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

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

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

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Brown, W. V., and M. L. Armstrong. 1985. Propensity to drift downstream among various species of fish. Journal of Freshwater Ecology 3:3–17.

Carey, M. P., B. L. Sanderson, K. A. Barnas, and J. D. Olden. 2012. Native invaders—challenges for science, management, policy, and society. Frontiers in Ecology and the Environment 10:373–381.

Clearwater, S. J., B. A. Morris, and J. S. Meyer. 2002. A comparison of coal bed natural gas product water quality versus surface water quality in the Powder River basin of Wyoming, and an assessment of the use of standard aquatic toxicity testing organisms for evaluating the potential effects of coal bed natural gas product waters. University of Wyoming, Laramie, Wyoming, USA.

Cross, F. 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, Oklahoma, USA.

Cross, F. B., W. Moss, and J. T. Collins. 1985. Assessment of dewatering impact on stream fisheries in the Arkansas and Cimarron rivers. Museum of Natural History, University of Kansas, Lawrence, Kansas, USA.

Courtenay, Jr., W. R. 2007. Introduced species: What species do you have and how do you know? Transactions of the American Fisheries Society 136:1160–1164.

Cucherousset, J., and J. D. Olden. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36 (5):215–230.

Dodds, W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life of the edge: the ecology of Great Plains prairie streams. BioScience 54:205–216.

Dudgeon, D., et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

Dudley, R. K., and S. P. Platania. 2007. Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. Ecological Applications 17:2074–2086.

Durham, B. W., and G. R. Wilde. 2008. Composition and abundance of drifting fish larvae in the Canadian River, Texas. Journal of Freshwater Ecology 23:273–280.

Durham, B. W., and G. R. Wilde. 2014. Understanding complex reproductive ecology in fishes: the importance of individual and population-scale information. Aquatic Ecology 48:91–106.

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 20:325–429.

Fausch, K. D., and R. G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. Copeia 1991:659–674.

Felley, J. D., and E. Cothran. 1981. *Notropis bairdi* (Cyprinidae) in the Cimarron River, Oklahoma. Southwest Naturalist 25:564.

Gale, W. F. 1986. Indeterminate fecundity and spawning behavior of captive red shiner: fractional, crevice spawners. Transactions of the American Fisheries Society 115:429–437.

Gale, W. F., and G. L. Buynak. 1982. Fecundity and spawning frequency of the fathead minnow: a fractional spawner. Transactions of the American Fisheries Society 111:35–40.

Gido, K. B., W. K. Dodds, and M. E. Eberle. 2010. Retrospective analysis of fish community change during a half-century of landuse and streamflow changes. Journal of the North American Benthological Society 29:970–987.

Gilbert, C. R. 1978. *Notropis stramineus* (Cope) sand shiner. Page 314 *in* D. S. Lee, C. R. Gilbert, C. H. Hocutlt, R. E. Jenkins, D. E. McAlister, J. A. Stauffer, Jr., editors. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, North Carolina, USA.

Grossman, G. D., P. B. Moyle, and J. O. Whitaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. American Naturalist 120:423–454.

Hoagstrom, C. W., C. A. Hayer, J. G. Kral, S. S. Wall, and C. R. Berry, Jr. 2006. Rare and declining fishes of South Dakota: a river drainage scale perspective. Proceedings of the South Dakota Academy of Science 85:171–211.

Hoagstrom, C. W., and T. F. Turner. 2013. Recruitment ecology of pelagic-broadcast spawning minnows:

paradigms from the ocean advance science and conservation of an imperilled freshwater fauna. Fish and Fisheries 16(2)282–299.

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. Biological Report 19. National Biological Survey, Washington, D.C., USA.

Hubert, W. A., and K. M. Gordon. 2007. Great Plains fishes declining or threatened with extirpation in Montana, Wyoming, or Colorado. Pages 3–13 *in* M. J. Brouder and J. A. Scheurer, editors. Status, distribution, and conservation of native freshwater fishes of western North America: a symposium proceedings. Symposium 53. American Fisheries Society, Bethesda, Maryland, USA.

Hughes, R. M., J. N. Rinne, and B. Calamusso. 2005. Introduction to historical changes in large river fish assemblages of the Americas. Pages 1–12 *in* J. N. Rinne, R. M. Hughes, and B. Calamusso, editors. Historical changes in large river fish assemblages of the Americas. Symposium 45. American Fisheries Society, Bethesda, Maryland, USA.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Jelks, H. L., et al. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33:372–407.

Kelsch, S. W. 1994. Lotic fish-community structure following transition from severe drought to high discharge. Journal of Freshwater Ecology 9:331–341.

Labbe, R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Leidy, R. A., and P. B. Moyle. 1998. Conservation status of the world's fish fauna: an overview. Pages 187–227 *in* N. P. L. Fiedler and P. M. Kareiva, editors. Conservation biology for the coming decade. Chapman and Hall, New York, New York, USA.

Lionberger, P. S., and W. A. Hubert. 2007. Introduced species and abiotic factors affect longitudinal variation in small fish assemblages in the Wind River Watershed, Wyoming. Journal of Freshwater Ecology 22:287–295.

Luttrell, G. R., A. A. Echelle, W. L. Fisher, 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 1999:981–89.

Magoulick, D. D. 2000. Spatial and temporal variation in fish assemblages of drying stream pools: the role of abiotic and biotic factors. Aquatic Ecology 34:29–41.

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

Matthews, W. J., and E. Marsh-Matthews. 2006. Persistence of fish species associations in pools of a small stream of the southern Great Plains. Copeia 2006:696–710.

Moore, G. A. 1944. Notes on the early life history of *Notropis girardi*. Copeia 1944:209–214.

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, New York, USA.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2011. vegan: community ecology package. R package version 2.0-2. http://CRAN.R-project.org/package=vegan

Patton, T. M. 1997. Distribution and status of fishes in the Missouri River drainage in Wyoming: implications for identifying conservation areas. Dissertation. University of Wyoming, Laramie, Wyoming, USA.

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.

Perkin, J. S., and K. B. Gido. 2011. Stream fragmentation thresholds for a reproductive guild of Great Plains fishes. Fisheries 36:371–383.

Perkin, J. S., and K. B. Gido. 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. Ecological Applications 22:566–579.

Perkin, J. S., K. B. Gido, A. R. Cooper, T. F. Turner, M. J. Osborne, E. R. Johnson, and K. B. Mayes. 2015. Fragmentation and dewatering transform Great Plains stream fish communities. Ecological Monographs 85:73–92.

Perkin, J. S., K. B. Gido, K. H. Costigan, M. D. Daniels, and E. R. Johnson. 2014. Fragmentation and drying ratchet down Great Plains stream fish diversity. Aquatic Conservation: Marine and Freshwater Ecosystems 25(5):500–516.

Perkin, J. S., Z. R. Shattuck, J. E. Gerken, and T. H. Bonner. 2013. Fragmentation and drought legacy correlate with distribution of burrhead chub in subtropical streams of North America. Transactions of the American Fisheries Society 142:1287–1298.

Pfleiger, W. L. 1997. The fishes of Missouri. Revised edition. Missouri Department of Conservation, Jefferson City, Missouri, USA.

Platania, S. P., and C. S. Altenbach. 1998. Reproductive strategies and egg types of seven Rio Grande Basin cyprinids. Copeia 3:559–569.

Quist, M. C., W. A. Hubert, and F. J. Rahel. 2004. Relations among habitat characteristics, exotic species, and turbid-river cyprinids in the Missouri

River drainage of Wyoming. Transactions of the American Fisheries Society 133:727–742.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabeni, C. F. 1996. Prairie legacies-fish and aquatic resources. Pages 111–124 *in* F. B. Samson and F. Knopf, editors. Prairie conservation: preserving America's most endangered ecosystem. Island Press, Washington, D.C., USA.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33:291–315.

Rahel, F. J. 2004. Unauthorized fish introductions: Fisheries management of the people, for the people, or by the people? Pages 431–444 *in* M. J. Nickum, P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, editors. Propagated fishes in resource management. American Fisheries Society, Bethesda, Maryland, USA.

Raney, E. C. 1939. The breeding habits of the silvery minnow, *Hybognathus regius* Girard. American Midland Naturalist 221:674–680.

Rehwinkel, B. J., M. Gorges, and J. Wells. 1978. Powder River aquatic ecology project. Final report. Montana Department of Fish and Game, Helena, Montana, USA.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.

Scarnecchia, D. L., K. Grabenstein, and S. Hiebert. 2000. Biology of the flathead chub in the lower Yellowstone River, Montana. Intermountain Journal of Sciences 6:10–17.

Senecal, A. C. 2009. Fish assemblage structure and flow regime of the Powder River, Wyoming: an assessment of the potential effects of flow augmentation related to energy development. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Simberloff, D. 2011. Native invaders. *In* D. Simberloff and M. Rejmánek, editors. Encyclopedia of biological invasions. University of California Press, Berkeley, California, USA.

Smith, J. B. 1988. Movement and spawning of fishes in Crazy Woman Creek, a tributary to the Powder River, Wyoming. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Smith, J. B., and W. A. Hubert. 1989. Use of a tributary by fishes in a Great Plains river system. Prairie Naturalist 21:27–38.

Stewart, D. D. 1981. The biology of the sturgeon chub (*Hybopsis gelida Girard*) in Wyoming. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Taylor, C. M. 2010. Covariation among plains stream assemblages, flow regimes, and patterns of water use. Pages 447–459 *in* K. B. Gido and D. A. Jackson, editors. Community ecology of stream fishes: concepts, approaches, and techniques. Symposium 73. American Fisheries Society, Bethesda, Maryland, USA.

Walters, D. M., R. E. Zuellig, H. J. Crockett, J. F. Bruce, P. M. Lukacs, and R. M. Fitzpatrick. 2014. Barriers impede upstream spawning migration of flathead chub. Transactions of the American Fisheries Society 143:17–25.

Water Resources Data System [WRDS]. 2014. Water rights permits for the Powder/Tongue River basin plan, Wyoming. http://waterplan.state.w.us/plan/powder/gis/shape/PTIiiirghts.dbf.zip

Widmer, A. M., J. J. Fluder, III, J. W. Keymeier, C. N. Medley, and R. A. Valdez. 2010. Drift and retention of pelagic spawning minnow eggs in a regulated river. River Research and Applications 28:192–203.

Wilhite, J. W. 2007. Use of infrared aerial photographs to identify and assess habitat needed by native fish in rivers. Thesis. University of Wyoming, Laramie, Wyoming, USA.

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.

Wyoming Game and Fish Department [WGFD]. 2010. State Wildlife Action Plan. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Supplemental Material

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/ES14-00361.1.sm