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Complex influences of low-head dams and artificial wetlands on fishes in a Colorado River tributary system

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Abstract Low-head dams in arid regions restrict fish movement and create novel habitats that have complex effects on fish assemblages. The influence of low-head dams and artificial wetlands on fishes in Muddy Creek, a tributary of the Colorado River system in the USA was examined. Upstream, fish assemblages were dominated by native species including two species of conservation concern, bluehead sucker, *Catostomus discobolus* Cope, and roundtail chub, *Gila robusta* Baird and Girard. The artificial wetlands contained almost exclusively non-native fathead minnow, *Pimephales promelas* Rafinesque, and white sucker, *Catostomus commersonii* (Lacepède). Downstream, fish assemblages were dominated by non-native species. Upstream spawning migrations by non-native white suckers were blocked by dams associated with the wetlands. However, the wetlands do not provide habitat for native fishes and likely inhibit fish movement. The wetlands appear to be a source habitat for non-native fishes and a sink habitat for native fishes. Two non-native species, sand shiner, *Notropis stramineus* (Cope), and redside shiner, *Richardsonius balteatus* (Richardson), were present only downstream of the wetlands, suggesting a beneficial role of the wetlands in preventing upstream colonisation by non-native fishes.

KEYWORDS: artificial wetlands, dams, fish, fragmentation, impoundment, invasive species.

Introduction

Human activities can result in the creation of habitats that are uncommon or even novel for a geographic region. For example, in the treeless Great Plains of North America, woodland patches planted as windbreaks harbour bird species characteristic of eastern deciduous forests (Knopf 1986). In areas with few or no natural lakes, reservoirs provide habitat for numerous aquatic species characteristic of lentic habitats. In many cases, these novel habitats harbour non-native species that can affect native biota both upstream and downstream of source populations in the reservoir (Falke & Gido 2006; Johnson *et al*. 2008).

Shallow impoundments represent a novel habitat when they are created in areas where standing-water habitat is rare or absent (Olson 2004; Robertson 2006). Between 1998 and 2004, there was an estimated net increase of 89 140 ha of freshwater wetlands in the US, with most of the increase as a result of flooding of formerly terrestrial habitats (Dahl 2006). The benefits of human-created wetlands can include increased abundance of waterfowl and aquatic mammals, improved water quality in downstream areas, elevation of local water tables and provision of habitat for hydrophilic plant assemblages (Michael 2003; Rumble *et al*. 2004). Many small-bodied fishes benefit from wetland creation because they are tolerant of the low oxygen conditions that limit the occurrence of larger, piscivorous species in such habitats (Rahel 1984; Kobza *et al*. 2004). Fish species that make seasonal use of inundated floodplains for spawning or feeding

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benefit from the creation or restoration of wetland habitats along rivers (Galat *et al.* 1998; King *et al.* 2003). Because of these benefits, the creation of wetlands is often promoted as a way to preserve and enhance biodiversity (Hansson *et al.* 2005).

In arid landscapes, shallow impoundments are often constructed in headwater tributaries by placing low-head dams across stream channels (Olson 2004). The impoundments provide water for livestock and wetland habitat for wildlife, but the effects of such artificial wetlands on native fishes are seldom evaluated (Rumble *et al.* 2004). One negative effect is t he loss of habitat for stream-dwelling fishes when lotic habitat is converted to lentic habitat. Another negative effect is that newly created lentic habitats may support non-native species that compete with or prey upon native fishes (Schrank *et al.* 2001). Finally, structures that are built to impound water may block fish movements through the stream network (Martinez *et al.* 1994; Luttrell *et al.* 1999). Such movements are important when habitats needed by different life stages are spatially segregated (Schrank & Rahel 2004; White & Rahel 2008). Also, fish movement may be important for the recolonisation of stream reaches that periodically go dry in arid landscapes (Wilde & Ostrand 1999; Scheurer *et al.* 2003).

In this study, the influences of low-head dams and artificial wetlands on fish assemblages in Muddy Creek, a small stream in the upper Colorado River Basin in Wyoming, USA were evaluated. Like many streams in this region, Muddy Creek originates in mountains where stream flows are perennial and fish assemblages are dominated by coldwater species. As these streams flow into arid basins, they often become seasonally intermittent and fish assemblages become dominated by warmwater taxa, especially minnows (Cyprinidae) and suckers (Catostomidae). On Muddy Creek, a 526-ha wetland complex with numerous water control structures and several ponds was constructed from the 1920s to the 1950s to store water for irrigation and create standing-water habitat for wildlife (Thompson 2001). There was interest in how the wetlands might affect three native fish species of conservation concern: flannelmouth sucker, *Catostomus latipinnis* Baird and Girard, bluehead sucker, *Catostomus discobolus* Cope, and roundtail chub, *Gila robusta* Baird and Girard. The objectives of this research were to determine the extent to which the wetland complex in Muddy Creek provided habitat for native vs non-native fishes, especially during periods of low or no streamflow, and to evaluate the effect of the low-head dams and associated wetlands on fish movements throughout the Muddy Creek system.

Methods

Study area

Muddy Creek originates at an elevation of 2500 m and flows through shrub steppe before joining the Little Snake River near Baggs, Wyoming at an elevation of 1920 m. The study area was a 100-km section of Muddy Creek downstream from a large rock gabion structure built to stabilise a gully formed by channel headcutting (Fig. 1). In this section, Muddy Creek is a low gradient stream with sparse riparian vegetation and often becomes intermittent. Substrata are dominated by clay and sand with sporadic patches of gravel and cobble. The hydrograph is dominated by snow melt with peak discharge occurring in late March or April. The artificial wetland complex occurs 78–84 km upstream from the confluence of Muddy Creek with the Little Snake River. Water from Muddy Creek flows through the wetland complex, which consists of impoundments, water control structures, overflow spillways, ditches and a braided channel (Fig. 2). The artificial wetland is much larger and has more barriers to fish movement than wetlands likely to have been created in the past by beaver, *Castor canadensis* Kuhl,

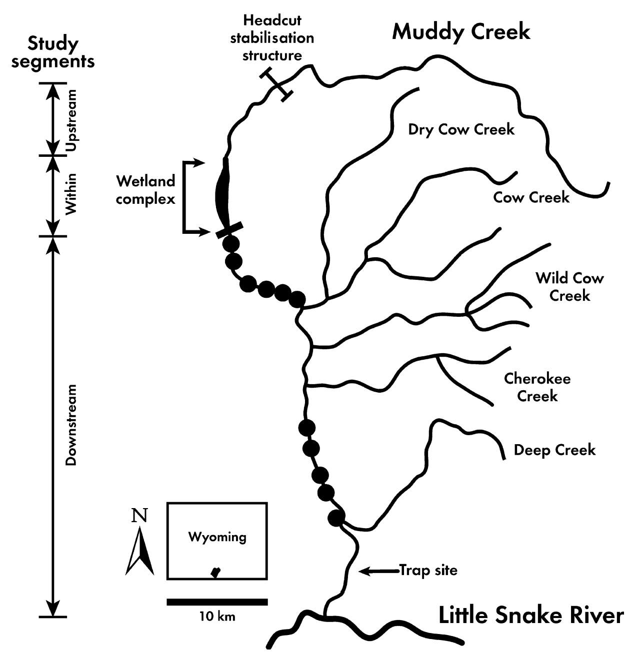

Figure 1. Muddy Creek and its tributaries. The study area was the 100-km section of Muddy Creek downstream of a large headcut stabilisation structure. A weir at the trap site was used to collect fish for implantation with radio transmitters. Circles indicate the maximum upstream locations for 11 white suckers implanted with radio transmitters at the trap site and monitored from 19 April to 18 May 2004.

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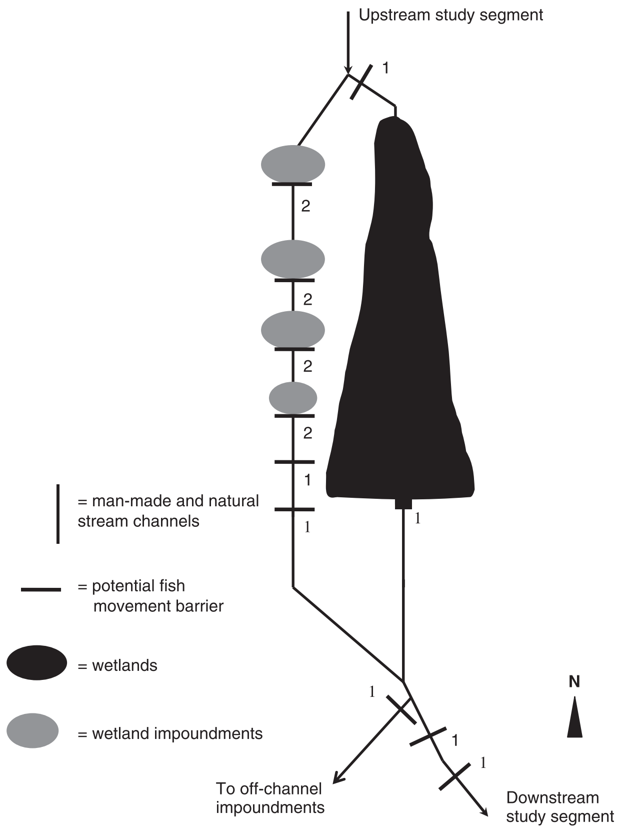

Figure 2. Muddy Creek wetland complex. Numbers correspond to the main types of water control structures: 1, low-head dam with water drop of 0.5–2.0 m; 2, overflow spillways in wetland ponds with vertical drops of 2–3 m. Channels represent primary water movement pathways within the wetland complex.

activity and thus represents a novel habitat for the Muddy Creek system.

Stream flow conditions in Muddy Creek

Because Muddy Creek has a history of intermittency during summer, it was important to relate longitudinal patterns in fish assemblages to spatial patterns of intermittency. To do this, streamflow conditions were mapped by flying over the study area during June, July and September 2004. Flights started at the confluence of Muddy Creek with the Little Snake River and progressed upstream to the headcut stabilisation structure (Fig. 1). Surface flows in tributaries were determined by starting at the tributary mouth and progressing upstream to the headwaters. Three types of flow conditions were recorded: (1) stream channel with surface flow; (2) intermittent reaches with isolated pools typically <200 m apart; and (3) dry stream channel. Approximate locations for transitions among the three types of flow conditions were recorded with a handheld GPS receiver (Trimble GeoXT®, Trimble Navigation Limited, Sunnyvale, CA, USA) while flying over the stream. Locations were downloaded to a geographical information system (ArcView 3.2®; Environmental Systems Research Institute, Redlands, CA, USA) to create maps depicting spatial patterns of flow conditions in the study area.

Fish assemblage patterns in relation to the wetland complex

To assess the influence of the wetland complex on the distribution of native and non-native fishes, fish populations were sampled in distinct segments downstream, within and upstream of the wetlands. The downstream segment began at the confluence of Muddy Creek with the Little Snake River and extended upstream 78 km to the first dam in the wetland complex (Fig. 1). The wetland segment extended from 78 to 84 km upstream of the confluence and was marked by 1–2 m high water control structures that spanned the channel at the upstream and downstream ends of the wetlands. Within the wetlands, the original stream channel had been replaced by a series of impoundments, ditches and flooded wetlands. The upstream segment extended from 84 to 100 km upstream of the confluence and went from the wetlands upstream to the headcut stabilisation structure.

Fish assemblages were sampled during two time periods. Fish were sampled in the wetland segment from 25 May to 2 June 2004 only. In the four largest impoundments (1–5 ha, maximum depth about 2 m), fish were sampled using two gill nets, 10 minnow traps and three small-mesh trap nets, each set for two 24-h periods. Gill nets were 48-m long, 2-m deep and had panels with 5-, 7- and 10-cm stretch mesh. Trap nets had small mesh (6.3 mm) that facilitated capture of small fishes and included a 10-m long by 1-m deep lead. Minnow traps were 42-cm long and 21 cm in diameter with 5-mm wire mesh and were baited with pieces of dead fish. Three 200-m stream reaches downstream of water control structures within the wetland segment were sampled using one pass with backpack electric fishing gear.

From 28 July through 18 August 2004, fish populations were sampled in all three study segments. Within the wetland segment, the same four impoundments were sampled using two gill nets and 10 minnow traps, each set for two 24-h periods. Remnant pools within channels of the wetland complex were sampled using seines. The upstream and downstream segments in Muddy Creek were largely intermittent during this

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period, so isolated pools were sampled using a 9.1-m long bag seine with 6.3-mm mesh. At least one seine haul was made in each pool, but multiple seine hauls were made in several large pools. When pools with surface water connectivity to nearby pools were seined, the downstream end of the pool was blocked to prevent fish escapement and seined in a downstream direction. Because the sampling methods were not efficient at capturing age-0 fish, the analysis was limited to fish age-1 or older based on a total length of ≥41 mm for the cyprinid species and ≥51 mm for the catostomid species (Snyder & Muth 2004).

Habitat features of pools

A suite of habitat characteristics was measured for each pool: maximum water depth (m), average pool width (m), pool length, pool area (m^2) and pool area with water ≥0.5 m deep (m^2). Pool distances from the Little Snake River were estimated with 1:24 000 hydrography imagery and ArcView GIS 3.2. One-way Analysis of Variance (ANOVA; $P \leq 0.05$) was used to test for differences in the above pool habitat characteristics among the three segments. If differences occurred, pair-wise ANOVA was done among the means to determine which segments differed. For the pair-wise comparisons, a Bonferroni-adjusted alpha level of 0.017 based an overall alpha level of 0.05 divided by the number of comparisons (three) was used.

Effect of the wetland complex on fish movement

Sampling in 2002 suggested that non-native white sucker, *Catostomus commersonii* (Lacepède), along with native bluehead sucker and flannelmouth sucker may migrate from the Little Snake River into Muddy Creek to spawn during the peak of spring runoff in March and April (U.S. Bureau of Land Management, Rawlins, WY, USA, unpublished data). To determine the potential for fish to move into and through the wetland complex, the spawning migration of catostomids into Muddy Creek was monitored in spring of 2004. Fish were collected in a trap approximately 8 km upstream from the confluence of Muddy Creek with the Little Snake River. The trap consisted of two mesh boxes (1 m × 1 m) with associated wings that spanned the channel and captured fish moving both upstream and downstream. The trap was monitored daily from 15 March to 18 June 2004. No large bluehead suckers or flannelmouth suckers were captured in 2004, but white suckers large enough to implant with 8-g radio-transmitters equipped with mortality sensors (model F1820; Advance Telemetry Systems, Isanti, MN, USA) were captured. All implanted white suckers weighed more than 400 g, the minimum weight needed to stay within a 2% body weight burden (Winter 1996). Following surgery, fish were allowed to recover from the anaesthesia and then released upstream of the trap.

Transmitter-implanted fish were located periodically by walking the stream bank, canoeing in the channel, or flying the study area in a fixed-wing aircraft. Locations were recorded with a handheld GPS unit (Trimble GeoXT®), and later downloaded with geographical information system software (ArcView 3.2®) to depict movement patterns. Some transmitter-implanted fish that returned downstream to the trap site following upstream movements were recaptured to determine if gametes had been expelled. Several fish were released downstream of the trap to determine if downstream movements would continue to the Little Snake River.

Results

Stream flow conditions in Muddy Creek

The aerial observations indicated the progression of intermittent stream flow in Muddy Creek during the summer of 2004. On 9 June 2004, the main stem of Muddy Creek within the study area had surface flow but was approaching the point of discontinuous surface flow and pool isolation (Fig. 3). Dry stream channels and isolated pools were the dominant conditions within the tributaries on 9 June 2004. On 20 July 2004, the main stem of Muddy Creek had surface flow from the Little Snake River upstream to the mouth of Cow Creek. Upstream of Cow Creek, Muddy Creek had discontinuous surface flow and isolated pools except for an 8-km reach in the upstream segment near the headcut stabilisation structure. Within the wetland complex, the channels consisted of isolated pools with no surface flow. Portions of Cow Creek and Wild Cow Creek had temporarily resumed flowing on 20 July as a result of localised thunderstorms. On 1 September 2004, Muddy Creek and its tributaries mostly lacked surface flows and consisted of isolated pools. However, a reach in the upstream segment that extended 6 km downstream from the headcut stabilisation structure retained surface flows on this date.

Fish assemblage patterns in relation to the wetland complex

Fish assemblages in the wetlands consisted almost entirely of non-native species during both sampling

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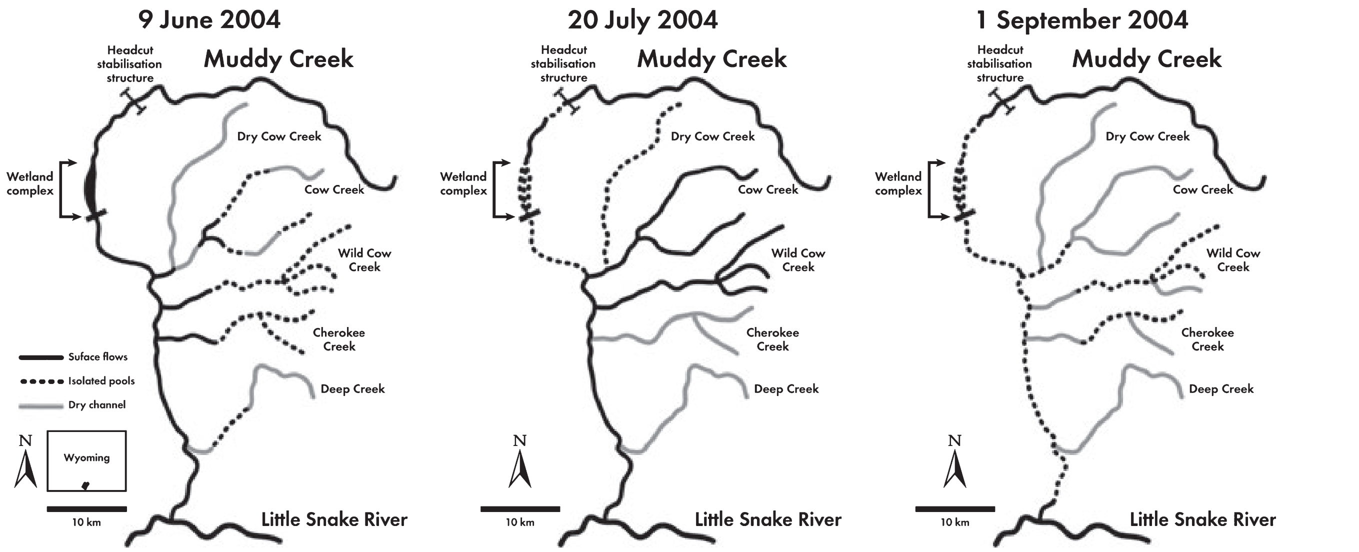

Figure 3. Flow conditions in Muddy Creek based on aerial surveillance on 9 June, 20 July and 1 September 2004.

periods. During the 25 May to 2 June period when water was flowing through the wetland complex, no native fish species were captured in the four wetland impoundments and only five individuals of one native species, speckled dace, *Rhinichthys osculus* (Girard), were captured in the wetland channels (Table 1). Non-native fathead minnows, *Pimephales promelas* Rafinesque, accounted for 97.9% of the catch in the four impoundments and 96.1% of the catch in the channels. Two other non-native species, white sucker and creek chub, *Semotilus atromaculatus* (Mitchill), were also present in the wetland impoundments and channels.

Table 1. Composition of fish assemblages in impoundments and in stream channels within the wetland complex during 25 May to 2 June 2004 and 28 July to 18 August 2004. Values are the percent of the total catch represented by each species in a given habitat during a time period

	25 May to 2 June 2004		28 July to 18 August 2004	
	Impoundments	Channels	Impoundments	Channels
Native fish species				
Speckled dace	0.0	0.9	0.0	1.6
Non-native fish species				
Fathead minnow	97.9	96.2	44.8	88.3
White sucker	1.9	0.4	55.2	2.7
Creek chub	0.2	2.5	0.0	7.4
No. individuals	2162	569	125	188

During the 28 July to 18 August sampling period when water was not flowing through the wetland complex, fish assemblages in the four impoundments consisted of fathead minnows and white suckers. No native species were captured. Channels within the wetland complex contained only remnant pools and these were dominated by three non-native species: fathead minnow, creek chub and white sucker. The only native fish captured were three speckled dace that represented 1.6% of the total catch.

During 28 July to 18 August, in addition to the wetlands, fish assemblages were sampled in the downstream and upstream segments of Muddy Creek. The stream was largely intermittent, but fish age 1 or older were present in 86 of 100 pools sampled in the downstream segment of the study area, 14 of 20 pools sampled in the wetland segment and 50 of 53 pools sampled in the upstream segment. There was a clear pattern in the spatial distribution of fishes in Muddy Creek with non-native species dominating the wetland complex and downstream reaches but native species prevalent in upstream reaches (Fig. 4). The downstream segment was dominated by four non-native species: white sucker, creek chub, fathead minnow and redside shiner, *Richardsonius balteatus* (Richardson) (Table 2). The redside shiner and another non-native species, sand shiner, *Notropis stramineus* (Cope), were found only in the downstream segment. Only three native species were captured in the downstream segment, and they occurred in low abundance: speckled dace, roundtail chub and flannelmouth sucker. Remnant pools in channels within the wetland

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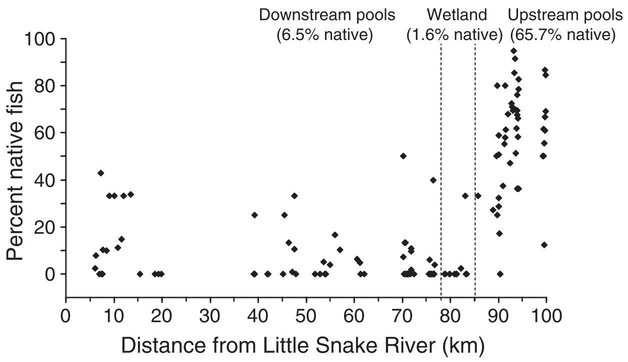

Figure 4. The percent of the total catch consisting of native fishes in pools located downstream, within and above the wetland complex. Data are for pools where two or more fish ≥ age-1 were collected. The dashed lines segregate the three study segments, and numbers below segment names are the percent native fishes averaged across all pools in that segment. Sampling was done from 28 July to 18 August 2004.

complex were dominated by three non-native species: white sucker, creek chub and fathead minnow, with the only native fish being a few speckled dace. In the upstream segment, four native species were prevalent and collectively constituted 65.7% of the catch: bluehead sucker, flannelmouth sucker, roundtail chub and speckled dace. The three non-native species present were white sucker, creek chub and fathead minnow.

Habitat features of pools

Habitat features of pools during the period of intermittency in Muddy Creek were similar among the three study segments. Pool length, maximum pool depth and pool area ≥0.5-m deep were not significantly different (Table 3). Pool width and pool area were similar in the upstream and downstream segments but were greater than for pools within the wetland segment.

Effect of the wetland complex on fish movement

Eleven white suckers were implanted with transmitters between 15 April and 9 May 2004. Total lengths of these fish ranged from 355 to 481 mm and weights

Table 2. The number (*n*) and percent species composition (% catch) of ≥ age-1 fish collected in pools throughout the three study segments during 28 July–18 August 2004. Also shown is the percent of pools (% pools) where a species was present based on 100 pools in the downstream segment, 20 pools in the wetland segment and 53 pools in the upstream segment

	Downstream segment			Wetland segment			Upstream segment		
	n	% catch	% pools	*n*	% catch	% pools	*n*	% catch	% pools
Native species									
Bluehead sucker	0	0.0	0.0	0	0.0	0.0	14	0.5	15.1
Flannelmouth sucker	1	0.1	1.0	0	0.0	0.0	1	< 0.1	1.9
Roundtail chub	44	2.5	12.0	0	0.0	0.0	1020	36.6	62.3
Speckled dace	70	3.9	28.0	3	1.6	10.0	795	28.5	81.1
Non-native species									
White sucker	186	10.5	36.0	5	2.7	10.0	29	1.0	20.8
Creek chub	536	30.2	66.0	14	7.4	20.0	578	20.7	83.0
Fathead minnow	488	27.5	66.0	166	88.3	60.0	352	12.6	71.7
Redside shiner	393	22.1	23.0	0	0.0	0.0	0	0.0	0.0
Sand shiner	59	3.3	22.0	0	0.0	0.0	0	0.0	0.0
Total catch	1777			188			2789		

Table 3. Comparison of pool attributes among the three stream segments

	Downstream segment	Wetland segment	Upstream segment	
	$n = 100$	$n = 20$	$n = 53$	*P*-value
Length (m)	16.9 ± 0.8 (5.3–45.5)	14.0 ± 2.0 (4.0–35.0)	15.9 ± 1.0 (6.5–36.0)	0.277
Width (m)	3.1 ± 0.1^a (1.6–10.8)	2.4 ± 0.2^b (1.2–4.7)	3.3 ± 0.1^a (2.0–5.2)	0.008
Area (m^2)	56.5 ± 4.4^a (12.9–243.6)	32.5 ± 4.5^b (4.8–71.3)	51.7 ± 3.4^a (15.5–138.0)	0.038
Maximum depth (m)	0.7 ± 0.1 (0.3–1.3)	0.6 ± 0.1 (0.4–1.0)	0.7 ± 0.1 (0.4–1.1)	0.115
Area (m^2) > 0.5 m deep	7.2 ± 1.1 (0–60.0)	4.0 ± 1.3 (0–21.0)	4.0 ± 0.7 (0–18.0)	0.536

Values are mean ± standard error with the range in parentheses. *P*-values are for results of ANOVA. For a given attribute, segments with the same superscript did not differ based on pairwise comparisons with a Bonferroni-adjusted *P*-value of 0.017.

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ranged from 559 to 1220 g. Following release upstream of the trap site, all fish made upstream movements of at least 300 m within 48 h. A beaver dam with a 0.2- to 0.5-m vertical drop did not impede upstream movements. The maximum extent of upstream movements was approximately 62 km to an area downstream from the wetland complex (Fig. 1). No transmitter-implanted fish were observed to move into the wetland complex or enter any of the tributaries of lower Muddy Creek. Following upstream movements, transmitter-implanted white suckers made relatively synchronous downstream movements to the trap site prior to the onset of intermittency in June 2004. Six of the white suckers were recaptured at the trap site and all appeared to have spawned based on a lack of gamete expression when ventral pressure was applied. Four transmitter-implanted white suckers that were recaptured upstream of the trap were released downstream of the trap and these fish continued moving downstream toward the Little Snake River.

The distribution of two non-native species also provided insight into movement patterns of fishes in the study area. Non-native redside shiners and sand shiners were documented for the first time in Muddy Creek. These species were introduced into the Yampa River in Colorado and have been spreading into upstream tributaries such as the Little Snake River (Woodling 1985). In Muddy Creek, the distribution of redside shiners and sand shiners extended to a pool just below the farthest downstream dam of the wetland complex. These species were not captured in the wetland segment or the upstream segment, suggesting that the dam at the downstream end of the wetlands was preventing these species from moving further upstream.

Discussion

Much of the work on impoundments as habitat for invasive species has focused on reservoirs that provide deepwater habitat (Havel *et al.* 2005; Johnson *et al.* 2008; Gido *et al.* 2009). Such reservoirs are often stocked with large piscivorous sport fishes that reduce or eliminate native species through predation (Martinez *et al.* 1994; Tyus & Saunders 2000). The results indicate that shallow impoundments can also be a source of non-native fishes, although they are likely to be small non-game species that affect native species through competition for space or food or by predation on larval stages (Minckley *et al.* 2003). Others have also noted that wetlands can be a source habitat for non-native fishes. In France, artificial wetlands facilitated invasion by a non-native catfish, *Ameiurus melas* (Rafinesque) (Cucherousset *et al.* 2006). In the Mojave Desert of the southwestern US, conversion of a stream to a marsh created habitat conditions that favoured non-native fishes rather than the native Amargosa pupfish, *Cyprinodon nevadensis* Eigenmann and Eigenmann (Scoppettone *et al.* 2005).

No systematic sampling of Muddy Creek that included the wetlands had been done prior to the present study. However, sporadic previous sampling indicated that the patterns seen in this study were persistent. Wheeler (1997) sampled a site just upstream of the wetlands in 1995 and found the same mix of fish species as found in this study, with native species being relatively common. The U.S. Bureau of Land Management (Rawlins, Wyoming office, unpublished data) sampled two sites in Muddy Creek downstream of the wetlands in 1999 and found that non-native fishes comprised 98% of the specimens collected. These earlier samples are consistent with the spatial patterns in fish assemblages observed in the present study. In Bitter Creek, a nearby drainage that lacks artificial wetlands that could serve as habitat for non-native fishes, native species common to Muddy Creek dominate the fish fauna, even in reaches that become intermittent during the summer (Carter & Hubert 1995). This suggests that the downstream portions of Muddy Creek historically contained a fish fauna dominated by the same native species found upstream of the wetlands.

Two factors likely account for the low abundance of native fishes in artificial wetlands along Muddy Creek. First, the native fishes within the study area (bluehead sucker, flannelmouth sucker, roundtail chub and speckled dace) are adapted to spawn and feed in flowing water with gravel substrates (Baxter & Stone 1995). These species cannot complete their life cycles in the standing-water, detritus-substrate environment of the wetland complex. White sucker and creek chub are more generalised in their habitat requirements and diet than the native species (Baxter & Stone 1995) and probably can meet their life cycle requirements in the wetlands. Native fishes were absent from the Muddy Creek wetlands in the spring when water was entering and exiting the wetlands and in late summer when there was no surface flow of water through the wetlands. This indicates that the wetland complex does not serve as a refuge for native fishes when Muddy Creek becomes intermittent. Thus, replacement of 6 km of Muddy Creek by a wetland complex has resulted in a loss of habitat for native riverine fishes.

A second factor that may be responsible for the inability of native stream fishes to maintain populations

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in wetlands is development of stressful abiotic conditions during winter. Oxygen concentrations in ice-covered wetland ponds in northern climates can reach low levels that are lethal to many fish species (Rahel 1984; Zimmer *et al.* 2002). Although winter oxygen conditions were not monitored, the Muddy Creek wetlands are ice-covered for extended periods each winter and hypoxic conditions seem likely. Fathead minnows, which dominated the fish assemblages in the Muddy Creek wetland impoundments, are more tolerant of hypoxia than speckled dace (Castleberry & Cech 1992) and often dominate fish biomass in wetland ponds in northern climates (Zimmer *et al.* 2002). The other non-native species, white sucker and creek chub, are not as tolerant of hypoxia as fathead minnows (Smale & Rabeni 1995), and their occurrence in the wetland ponds may depend upon periodic colonisation from upstream sources. The oxygen requirements of the native bluehead sucker, flannelmouth sucker and roundtail chub, have not been investigated, but they are moderate to large-bodied species that are likely to be less tolerant of hypoxia than small-bodied species such as the fathead minnow (Robb & Abrahams 2003).

Water control structures built to create wetlands may prevent upstream movement by fish and thus contribute to fragmentation of stream systems. In Muddy Creek, white suckers moved upstream only as far as the wetland complex during their spawning migration in 2004. It is likely that at least some white suckers would have continued moving upstream if they could have moved over dams that span the channel. Bluehead suckers and flannelmouth suckers are known to enter Muddy Creek from the Little Snake River in some years and it is likely that their upstream movements also are blocked by these structures. The structures consist of rock gabions that lack plunge pools and have waterfall heights of 1.0 to 1.5 m. Such heights would exceed the leaping ability of many stream fish species (Bjornn & Reiser 1991; Holthe *et al.* 2005).

Downstream movements of native fishes and colonisation of the wetland ponds would seem feasible during high flow periods but the results did not support this. Of the 3044 fish age 1 and older collected within the wetlands, the only native fishes were eight speckled dace found at the upstream end of the wetland complex. Native fishes do not enter the wetland complex or do not survive if they do.

Muddy Creek becomes intermittent downstream from the wetland complex in most years. No data exist to document the composition of the fish assemblage in this segment prior to the introduction of non-native fishes but it probably contained the same native species found above the wetlands. Support for this hypothesis comes from Bitter Creek, an adjacent drainage that also becomes intermittent during summer. A road culvert at the downstream end of Bitter Creek likely reduces the upstream movement of non-native fish species into the watershed. Also, Bitter Creek has no wetlands that could serve as habitat for non-native species such as fathead minnow. Only native fishes, including flannelmouth sucker and speckled dace, are present upstream of the culvert, even in reaches that become intermittent during the summer (Carter & Hubert 1995). Native fishes also dominated the intermittent segment of Muddy Creek upstream of the wetland complex. Thus, intermittency, by itself, would not appear to be the reason native fishes are rare in Muddy Creek downstream of the wetlands.

Interactions with non-native species could be an important reason for the low abundance of native species in Muddy Creek downstream of the wetlands. This section of Muddy Creek was dominated by fathead minnow, creek chub, white sucker and redside shiner. These are among the most invasive fishes in the Colorado River basin (Bezzerides & Bestgen 2002; Olden & Poff 2005). Fathead minnows are trophic generalists that can depress food resources for other vertebrates and be aggressive toward other fishes (Karp & Tyus 1990; Zimmer *et al.* 2002). There is high diet overlap between creek chub and roundtail chub in Muddy Creek (Quist *et al.* 2006), which indicates the potential for competition between these species. White suckers can compete with native catostomid species for food (Bezzerides & Bestgen 2002). Thus, non-native fishes appear likely to compete with native fishes for food and space in the downstream reaches of Muddy Creek.

Because of its intermittent nature, the occurrence of fish in Muddy Creek downstream of the wetlands probably depends on periodic recolonisation. Such recolonisation is a common feature of streams in arid climates (Labbe & Fausch 2000; Scheurer *et al.* 2003). The influence of the wetlands on the ability of fish to recolonise the lower section of Muddy Creek likely differs between non-native and native fish species. Non-native species such as fathead minnow, creek chub and white sucker, might originate from upstream of the wetlands or from within the wetlands, but in either case are able to persist in the wetlands until high spring flows provide an opportunity to move downstream. Thus, the wetlands are likely to be a source habitat for non-native species in the downstream reaches of Muddy Creek. By contrast, virtually no

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native fishes were found in the wetlands either during the high water period in the spring or during the low period in the summer. As suggested earlier, either native fish do not enter the wetland or do not survive if they do enter. In the latter case, the wetland complex would be acting as a sink habitat for native fishes from the upstream segment. By acting as a source habitat for non-native species and a sink habitat for native species, the wetlands are important in structuring fish assemblages in the Muddy Creek system.

The effects of artificial wetlands in Muddy Creek differ from situations where creation or rehabilitation of wetlands has been beneficial to native fishes in other regions. Wetlands constructed along the shores of Conesus Lake in New York were comparable or superior to natural wetlands in providing spawning and rearing habitat for northern pike, *Esox lucius* L. (Morrow *et al*. 1997). Native fishes dominated constructed freshwater marshes in Florida that contained all of the species present in nearby natural marshes (Streever & Crissman 1993). In these situations, wetlands were historically part of the ecosystem and did not provide a novel habitat that could support species not native to the region. Also in these situations, the native fishes had life histories that included the use of wetlands. This is not the case for native fishes in the upper Colorado River basin that generally have life history strategies adapted for fluvial environments (Olden *et al*. 2006).

Tributaries in the Muddy Creek system do not appear to play an important role in determining fish distributions. Most of the tributaries downstream of the wetlands dry up in the summer and the few intermittent pools that remain are fishless or contain the same non-native fishes that dominate the reaches of Muddy Creek downstream of the wetlands (U.S. Bureau of Land Management, Rawlins, WY, USA, unpublished data). The tributaries do not serve as a refuge habitat for native fishes and do not appear to be important as spawning areas for large-bodied species such as white suckers that enter the main stem of Muddy Creek to spawn in the spring.

There may be circumstances where movement barriers are beneficial because they prevent the spread of non-native species throughout a drainage (Scheerer 2002; Novinger & Rahel 2003; Kerby *et al*. 2005; Rahel 2007). In Muddy Creek, this appeared to be the case for sand shiner and redside shiner, which have been expanding their distribution throughout the Little Snake River basin. These species were found in pools below the wetland complex but not within or upstream of the wetland complex. Both of these are small-bodied species that are not likely to leap over the water control structures that create the wetland complex (Holthe *et al*. 2005).

Muddy Creek illustrates the difficulties of manipulating ecosystems to benefit a wide range of human and wildlife/fisheries needs simultaneously. Constructed wetlands may store water for irrigation, create waterfowl habitat, provide riparian areas important to terrestrial wildlife, and reduce sediments to rivers downstream. These are important societal benefits that, coupled with legal mandates to avoid the net loss of wetlands in many countries, provide strong motivation to construct artificial wetlands (Robertson 2006). Impounding streams with low-head dams may be an economical way to create wetlands in tributary streams, but this approach can be detrimental to native fishes when it causes a loss of lotic habitat, provides a novel habitat that supports non-native species and blocks fish movements.

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