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The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA

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ABSTRACT

Across the western Great Plains of North America, groundwater pumping for irrigated agriculture is depleting regional aquifers that sustain streamflow for native fishes. We investigated linkages between groundwater pumping from the High Plains Aquifer and stream fish habitat loss at multiple spatial scales during spring and summer 2005–2007 in the Arikaree River, eastern Colorado, USA. Monthly low-altitude flights showed that flowing reaches were reduced from about 65 to ≤15 km by late summer, and long permanently dry segments in the lower basin prevent recolonization. Drying occurred rapidly during summer within three 6·4-km river segments, and patterns in habitat connectivity varied among segments owing to hydraulic conductivity. Most refuge pool habitats dried completely or lost more than half their volume, disconnecting from other pools by late summer. On the basis of these empirical habitat data, and historical groundwater and streamflow data, we constructed a MODFLOW model to predict how groundwater pumping will affect water table levels and fish habitat under three future scenarios. Under the most conservative scenario, we predicted that only 57% of refuge pools will remain in 35 years (2045), nearly all isolated in a 1·7-km fragment of river. A water balance model indicated that maintaining current water table levels and refuge pools for fishes would require a 75% reduction in groundwater pumping, which is not economically or politically feasible. Given widespread streamflow declines, ecological futures are bleak for stream fishes in the western Great Plains, and managers will be challenged to conserve native fishes under current groundwater pumping regimes. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS agricultural irrigation pumping; drought; Great Plains; groundwater; habitat connectivity; habitat loss; High Plains Aquifer; dryland streams

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INTRODUCTION

Arid and semi-arid ecosystems, collectively termed *drylands*, cover over 50% of the world's land surface (Parsons and Abrahams, 1994). Streams in these regions support unique and diverse aquatic habitats and biota (Deacon and Minckley, 1974), but are under tremendous pressure from human use of water. Worldwide, about 70% of freshwater used by humans is for agricultural irrigation (United Nations, 2009). Arid and variable climates place a premium on water, especially for agriculture, and most dryland rivers are subject to extensive diversion or groundwater use. Water abstraction for irrigation has led to water scarcity and significant hydrologic changes in dryland rivers worldwide, including in Australia (Walker *et al*., 1993; Kingsford, 2000; Arthington and Pusey, 2003), Spain (Bernaldez *et al*., 1993; Munoz-Reinoso, 2003; Llamas and Martínez-Santos, 2005) and Africa (Falkenmark, 1989; Meigh *et al*., 1999; Le Maitre *et al*., 2009).

In North America, dryland rivers occur not only in desert regions but also in the Great Plains, which cover the entire mid-continent. The Great Plains is the third largest ecoregion in North America (Omernik, 1987; Figure 1), and is one of the most productive and economically important agricultural areas in the world, producing approximately 25% of the world's grains (CGC, 2009). Groundwater provides a major contribution to flows in Great Plains streams, especially for those that do not receive snowmelt runoff from mountain headwaters, and maintains base flows and connections among habitats important for the persistence of aquatic biota (Winter, 2007). Widespread groundwater mining for agricultural irrigation has contributed to significant declines in groundwater levels (Gutentag *et al*., 1984; Robson and Banta, 1995; McGuire *et al*., 2003), and, as a result, stream habitat fragmentation and loss have become critical issues across the western Great Plains.

Habitat fragmentation and loss are the most important factors causing population declines and extirpations of species worldwide (Vitousek *et al*., 1997), especially in aquatic ecosystems (Ward, 1998; Dudgeon *et al*., 2006).

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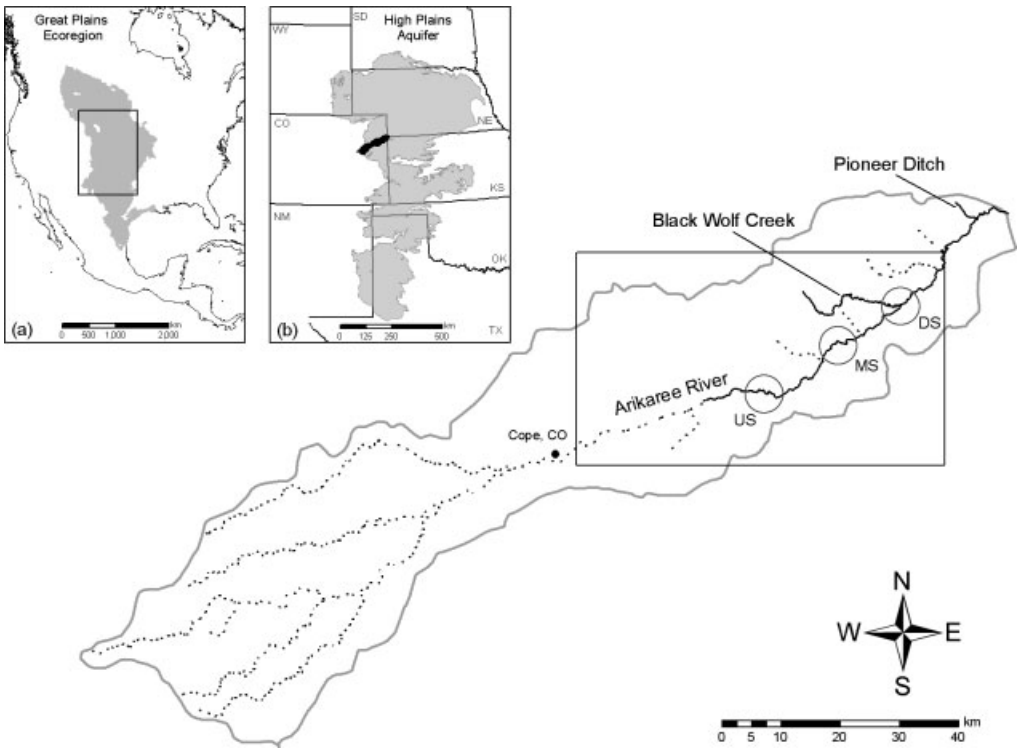

Figure 1. Location of the Great Plains ecoregion in North America (a) and the Arikaree River basin (black polygon) in eastern Colorado (b) on the western edge of the High Plains Aquifer. Within the Arikaree River basin (main), fish habitat and groundwater level data were collected along three 6·4-km segments (circled; US = upstream segment, MS = middle segment, DS = downstream segment). Solid stream reaches flow seasonally, whereas dashed reaches are dry. The locations of the town of Cope, Colorado, and two tributaries to the Arikaree River (Black Wolf Creek and Pioneer Ditch) are labeled. The black box outlines the area within which our groundwater model domain is located (Figure 4).

Streams are the most easily fragmented aquatic habitats, because of their linear and hierarchical structure (Fagan, 2002; Campbell-Grant *et al*., 2007), and connectivity is quickly lost as habitats become increasingly fragmented (Bunn and Arthington, 2002; Fausch *et al*., 2002). Worldwide, fishes in dryland streams are declining particularly rapidly, including assemblages in Australia (Humphries *et al*., 1999; Pollino *et al*., 2004) and Spain (Arparicio *et al*., 2000; Bernando *et al*., 2003). Native fishes in the western Great Plains are also in decline, which Cross and Moss (1987) attributed to habitat loss, including overuse of groundwater. For example, of 37 species native to the Platte, Arkansas and Republican river basins in eastern Colorado, 20 have become either extirpated, endangered, threatened or a species of concern in Colorado (Fausch and Bestgen, 1997; CDOW, 2007; Hubert and Gordon, 2007). However, to our knowledge, no study has quantified the linkages between groundwater pumping, connectivity and loss of fish habitat in dryland streams.

Fishes native to dryland streams have become adapted to harsh conditions, but there are limits to this resilience as habitat loss increases. In dryland streams, flow regularly becomes intermittent during the dry season, and the remaining refuges have wide fluctuations in temperature and dissolved oxygen (Matthews and Maness, 1979; Magoulick and Kobza, 2003; McMaster and Bond, 2008). During this period, fishes are often restricted to isolated pools until flows resume in wetter seasons and reconnect upstream and downstream habitats they may need for spawning and rearing (Labbe and Fausch, 2000; Scheurer *et al*., 2003; Falke and Fausch, 2010). As a result, most fishes of the western Great Plains are small-bodied, short-lived and reach maturity at an early age (Fausch and Bestgen, 1997). Many require specific habitats to complete their life history, which are reconnected when flow resumes (e.g. plains minnow *Hybognathus hankinsoni*; Taylor and Miller, 1990). Because stream habitats are easily fragmented, declines in flow due to groundwater pumping may lead to permanent fragmentation and inability of fish to complete their life history or to recolonize reaches from which they were extirpated.

Our purpose here is to consider what will be required to conserve a native assemblage of fishes in a western Great Plains river subject to persistent agricultural groundwater pumping and multi-year droughts. We frame our analysis by considering alternative future scenarios (i.e. ecological futures, censu Carpenter, 2002) based on the status quo of the current pumping regime and climate, as well as scenarios incorporating varying levels of groundwater conservation, to assess what must be done to create a sustainable future for these fishes. Specifically, our goals were to (1) measure current spatial and temporal distribution of fish habitat and connectivity at three spatial scales; (2) develop models of water balance and groundwater table levels and (3) use the models to project loss of fish habitat into the future based on different pumping scenarios.

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STUDY AREA AND SITE DESCRIPTION

Our research was conducted in the Arikaree River basin in the western Great Plains of eastern Colorado (Figure 1). The Arikaree River is one of three principal tributaries of the Republican River, located at the headwaters of the Kansas River basin. Historically, this region was shortgrass prairie, but current land use in the Arikaree basin is predominantly agricultural. Primary crops are corn (50%), wheat (30%) and alfalfa (<10%), and 90% of corn is irrigated by large centre-pivot systems that apply groundwater to circles 800 m in diameter (NASS, 2007). Irrigation typically begins in early June and ceases in early September, but varies annually with climate (Riley, 2009).

Groundwater pumping and river flow

The Arikaree River is fed by the High Plains Aquifer, one of the largest aquifers in North America, which underlies 451 000 km^2 of the Great Plains ecoregion (Figure 1). During the early 1960s, the total area irrigated with groundwater from this aquifer increased rapidly, from 8500 km^2 in 1949 to 55 000 km^2 in 1980 (Gutentag *et al.*, 1984). In eastern Colorado, over 4000 high-capacity wells were installed and currently irrigate over 3000 km^2. Groundwater levels have declined 8 m or more (Robson and Banta, 1995) over 5200 km^2 in this region (McGuire *et al.*, 2003). By 1990, over 21×10^9 m^3 (17 million acre-feet) of groundwater had been removed in eastern Colorado (VanSlyke and Joliet, 1990), and by 2002 the rate of groundwater stage decline was approximately 0·3 m per year (CDNR, 2002). Estimated annual groundwater used for irrigation within the Colorado portion of the Arikaree basin was approximately 82×10^6 m^3 (67 000 acre-feet) in 2007 (Riley, 2009).

Since the advent of intensive groundwater withdrawal for agricultural irrigation, mean annual discharge in western Great Plains headwater tributaries has declined precipitously (Szilagyi, 1999). In the Arikaree River, mean annual discharge declined 60% from 0·71 (±0·06 SE) m^3/s during 1932–1965 to 0·29 (±0·02 SE) m^3/s during 1966–2006 (t-test, $t = 2{\cdot}02$, $P < 0{\cdot}001$; Figure 2). Additionally, variability in mean annual flows has also declined by half ($SD = 0{\cdot}32$, 1932–1965; $SD = 0{\cdot}15$, 1966–2006). Peak flows occur in May and June from a combination of groundwater and spring precipitation, and low flows occur in late summer through early spring.

Drought conditions are relatively frequent in Great Plains basins (Figure 3; Schubert *et al.*, 2004), and the western Great Plains has been recently affected by a drought that began in 2000 (NDMC, 2008). Because groundwater is the primary source of surface flow in the Arikaree River (see Section on Geology and Groundwater Dynamics), we would not expect droughts to have a large effect on discharge. Indeed, in the past, flows in the Arikaree River were not strongly influenced by intense droughts (Figure 3). However, the proportion of days without flow at the stream gauge near the mouth has increased during the current drought (2000–2007) to almost 80%. Owing to the cumulative effects of groundwater pumping over time, the river appears to have crossed a critical threshold beyond which it is no longer resilient.

Fish assemblage

Despite the flow declines, the Arikaree River supports a relatively intact native fish assemblage compared to nearby basins (e.g. North and South Forks of the Republican River; Nesler, 2004). However, out of 16 native species, 2 have not been collected since the 1940s (flathead chub and stonecat; refer to Table I for scientific

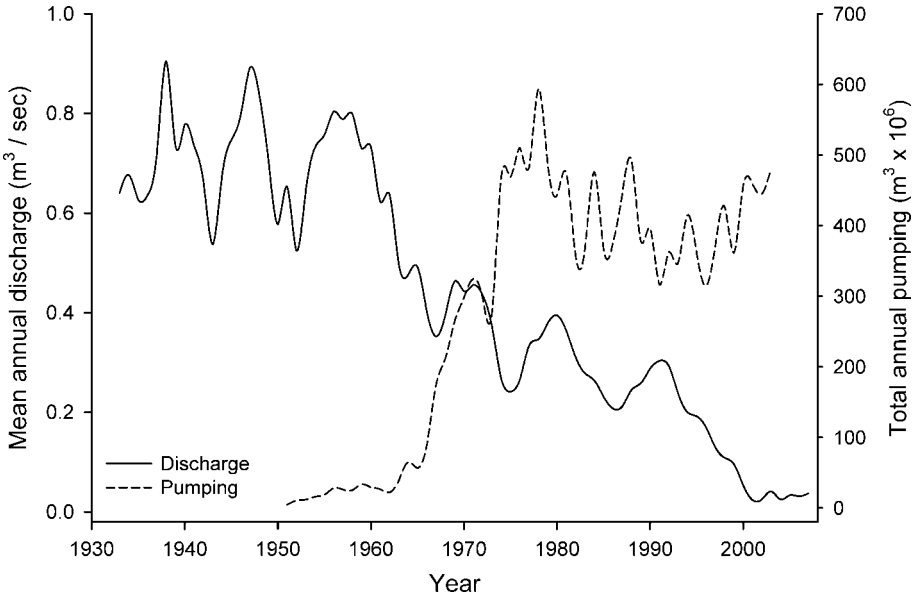

Figure 2. Five-year running means of annual discharge for the Arikaree River in eastern Colorado from 1932 to 2007 (left y-axis; solid line; USGS gauge #6821500, Haigler, NE) and the estimated amount of groundwater pumped for irrigation in Yuma County, Colorado from 1950 to 2005 (right y-axis; dashed line; Davis and Richrath, 2005). The Arikaree River and its associated aquifers are located in the southern half of Yuma County.

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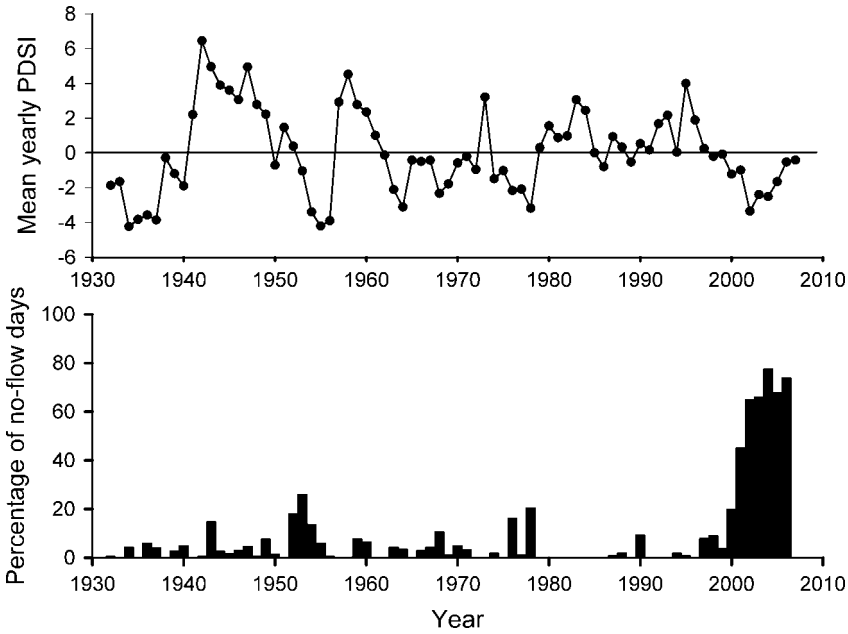

Figure 3. Relationship between drought and river flows for the Arikaree River in eastern Colorado from 1931 to 2007. Top panel is the mean Palmer drought severity index (PDSI; Palmer, 1965) over time (NOAA, 2008). The PDSI incorporates air temperature, precipitation and soil moisture. More negative values indicate harsher drought conditions. Lower panel is the percentage of days in each year the Arikaree River had no flow near its confluence at Haigler, NE (USGS gauge #6821500). No-flow days were defined as days where flow was below the detection limit of 0·028 m^3/s.

Table I. List of fish species found in the Arikaree River, Colorado (ordered by Family), and their preferred stream size, year last collected and status.

Family	Common name	Scientific name	Stream size	Last collected	Status	References
Cyprinidae	Brassy minnow	*Hybognathus hankinsoni*	C/S	2007	Extant[b]	Falke (2009)
	Central stoneroller	*Campostoma anomalum*	C/S/L	2007	Extant	Falke (2009)
	Creek chub	*Semotilus atromaculatus*	C/S	2007	Extant	Falke (2009)
	Fathead minnow	*Pimephales promelas*	C/S/L	2007	Extant	Falke (2009)
	Flathead chub	*Platygobio gracilis*	S/L	1940	Extirpated	Metcalf (1966)
	Plains minnow	*Hybognathus placitus*	S/L	1979	Extirpated	Cancalosi (1980)
	Red shiner	*Cyprinella lutrensis*	C/S/L	2001	Unknown	Scheurer *et al.* (2003)
	River shiner	*Notropis blennius*	S/L	1979	Extirpated	Cancalosi (1980)
	Sand shiner	*Notropis stramineus*	C/S/L	2001	Unknown	Scheurer *et al.* (2003)
	Suckermouth minnow	*Phenacobius mirabilis*	C/S/L	1979	Extirpated	Cancalosi (1980)
Catostomidae	White sucker	*Catostomus commersonii*	C/S/L	2007	Extant	Falke (2009)
Ictaluridae	Black bullhead	*Ameiurus melas*	C/S/L	2007	Extant	Falke (2009)
	Stonecat	*Noturus flavus*	C/S/L	1940	Extirpated	Metcalf (1966)
Fundulidae	Northern plains killifish	*Fundulus kansae*	C/S/L	2007	Extant	Falke (2009)
Centrarchidae	Green sunfish	*Lepomis cyanellus*	C/S/L	2007	Extant	Falke (2009)
	Largemouth bass[a]	*Micropterus salmoides*	C/S/L	2001	Unknown	Scheurer *et al.* (2003)
Percidae	Orangethroat darter	*Etheostoma spectabile*	S	2007	Extant[c]	Falke (2009)

Codes for stream size are C = creek, S = small river, L = large river, based on Frimpong and Angermeier (2009).
[a] Nonnative species.
[b] State-threatened species in Colorado (CDOW, 2007).
[c] State species of concern in Colorado (CDOW, 2007).

names; Metcalf, 1966) and 3 others (plains minnow, river shiner and suckermouth minnow) have not been found since a basin-wide survey in the late 1970s (Cancalosi, 1980). Native fishes, including the five extirpated species, once occurred in segments that are now permanently dry in the Arikaree River (Metcalf, 1966; Cancalosi, 1980; Falke, 2009). Loss of flowing habitat is the likely cause of their extirpation, especially for species that require seasonal flow to carry out critical life history events like reproduction and movement to suitable habitats. Notwithstanding the recent loss of diversity, the Arikaree River continues to provide the best remaining habitat in Colorado for two species whose distribution and abundance are declining throughout the region (Scheurer, 2001; Hubert and Gordon, 2007), the state-threatened brassy minnow and the state species of concern orangethroat darter. Previous work in the Arikaree River suggests that seasonal flows that contribute to habitat quantity and connectivity are vital for growth, survival and population persistence of native Arikaree River plains fishes (Falke

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et al., in press; Scheurer *et al*., 2003; Falke and Fausch, 2010). However, the distribution of habitat, the dynamics of seasonal habitat connectivity, and the relationship of these factors to groundwater have yet to be quantified and are critical for successful future conservation efforts.

Geology and groundwater dynamics

Surficial geology of the Arikaree River basin consists mainly of areas of highly permeable dune sand and Peorian loess underlain by the Ogalalla formation of the High Plains Aquifer (Weist, 1964). The river channel flows through alluvial deposits of unconsolidated gravel, sand, silt and clay. The alluvium is, in turn, underlain by the groundwater-bearing Ogalalla formation in the upper portion of the basin, and low permeability Pierre shale in the lower portion (Figure 4).

As a groundwater-fed stream, water levels and flow in the Arikaree River are determined by the water balance between the regional High Plains Aquifer and the alluvial aquifer in which the stream is incised. Precipitation recharges the regional aquifer, which eventually flows into the alluvial aquifer, and then into the stream channel in reaches where the aquifer head is higher than the streambed. However, mean pan evaporation in this xeric climate (152 cm/year) exceeds mean precipitation (44 cm/year; Robson and Banta, 1995). Recharge occurs mainly after snowmelt or during episodes of heavy rain when evapotranspiration rates are low. Water is lost to the atmosphere through irrigation pumping and evapotranspiration, particularly in the riparian corridor where the water table is closest to the land surface (Wachob, 2006). Therefore, we conceptualized the system as two linked aquifers (regional and alluvial), with recharge, evapotranspiration and irrigation pumping serving as the primary factors influencing groundwater dynamics and streamflow.

We focused our multi-scale analysis of fish habitat and groundwater dynamics on the downstream 110 km of the Arikaree River, because no surface water had been observed upstream since 1999 (Scheurer *et al*., 2003; Figure 1). Our initial investigation of the geology and groundwater dynamics showed that the regional and alluvial aquifers are hydraulically disconnected in the lower basin (Figure 4) because the river channel

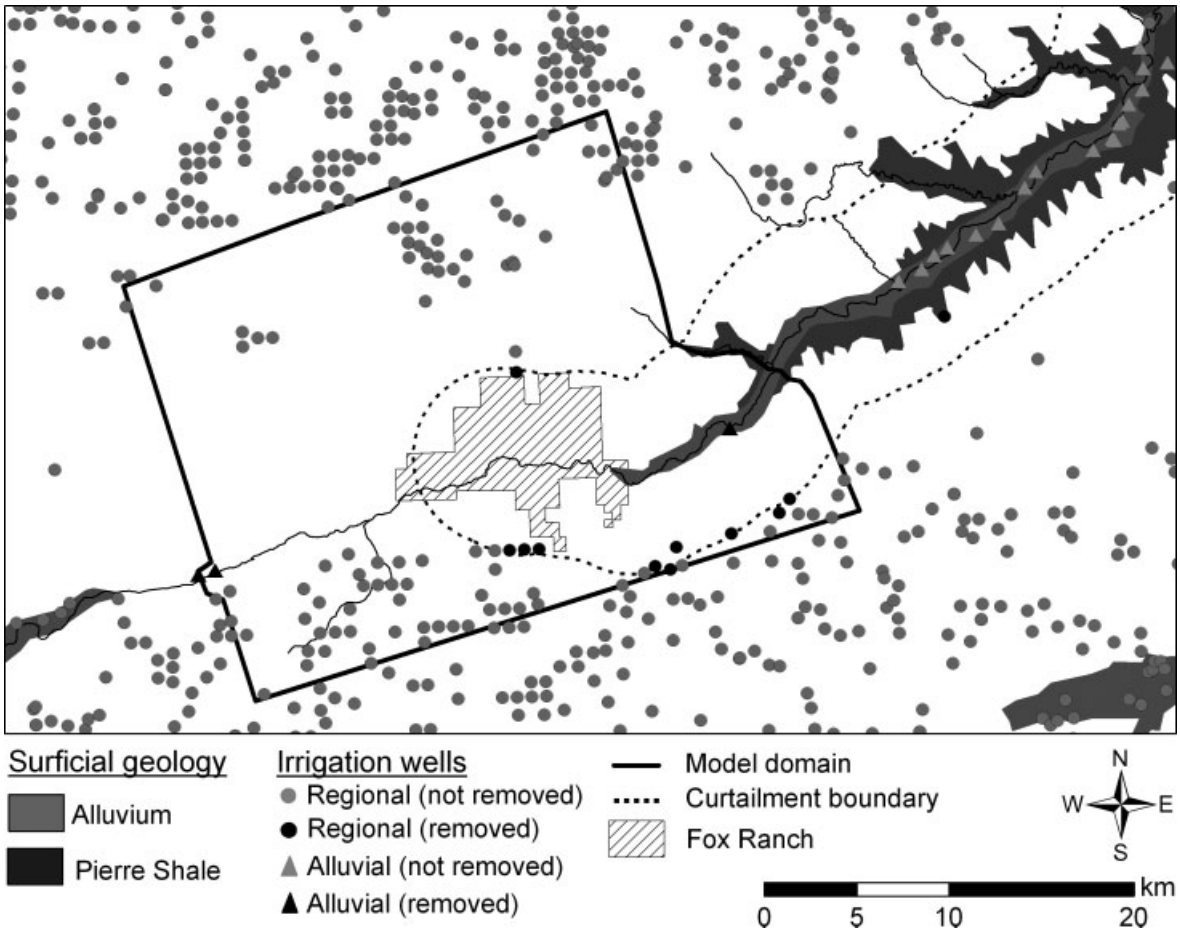

Figure 4. Map of the lower Arikaree River basin (outlined in Figure 1), showing the domain of our MODFLOW groundwater model (polygon). The model domain extends from the groundwater divides with the South Fork Republican River to the south (shown at lower right), and the North Fork Republican River to the north. Also shown are major surficial geologic units (see legend; Weist, 1964), the Fox Ranch and locations of irrigation wells within the study area (CDSS, 2007). The alluvium upstream through the Fox Ranch is narrow and not shown. Grey circles are wells pumping from the regional aquifer that were not removed in our model scenarios (see text), whereas black circles are wells that fell within the curtailment zone (dashed area) and were removed. Grey triangles are alluvial irrigation wells that were not removed in our model scenarios, whereas black triangles are alluvial wells that fell within the curtailment zone and were removed.

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downcuts beneath the Ogallala formation and the alluvial aquifer is underlain by impermeable Permian shale. Upstream, in the middle of the river basin, the alluvial aquifer is hydraulically connected to the regional aquifer, and groundwater flowing into the alluvium and the stream channel maintains fish habitat during dry conditions. In contrast, fish habitat in downstream reaches is maintained only by flow from upstream reaches, supplemented by episodic precipitation events.

Groundwater pumping affects fish habitat through these complex connections among the regional and alluvial aquifers and the stream channel. Pumping for irrigation from the regional aquifer has caused a long-term decline in groundwater levels, leading to reduced inflow to the alluvial aquifer and to the river in the middle reaches. In turn, groundwater and surface flow from the middle to downstream reaches has been reduced, so fish habitat has declined markedly there (Falke, unpublished data; Scheurer *et al*., 2003). Moreover, 17 irrigation wells pump directly from the alluvium in this downstream region (Figure 4), further depleting alluvial groundwater and reducing river flow. Given the high incidence of drying in the downstream reaches (Scheurer *et al*., 2003), we surmised that habitat to sustain viable populations of native fishes like brassy minnow and orangethroat darter would persist primarily in the middle reaches where the regional and alluvial aquifers are hydraulically connected. Therefore, we focused our analysis of the link between groundwater and fish habitat on this region (see Section on Materials and Methods).

MATERIALS AND METHODS

Fish habitat at multiple scales

We made direct measurements of the amount and connectivity of fish habitat at three spatial scales: throughout the downstream half of the basin, among three long river segments (Figure 1) and among pools within those segments. Among-habitat connectivity (hereafter referred to as *connectivity*) was classified into three categories: flowing (all pools connected), intermittent (disconnected pools) and dry.

Basin scale. Flights with a fixed-wing aircraft were conducted 200–300 m above the stream channel in May 2005, and monthly from May through July 2006 and May through October 2007. Each flight surveyed the downstream 110 km of the Arikaree River from Cope to its confluence with the North Fork Republican River (Figure 1). Stream reaches were classified visually by connectivity category and their boundaries marked using a Garmin GPSmap 60 Global Positioning System (GPS; Garmin International Inc., Olathe, Kansas, USA). A Geographic Information System (ArcGIS ver. 9·1, Environmental Systems Research Institute, Redlands, California, USA) was used to measure the lengths of reaches in the three connectivity categories.

Segment scale. Fish habitats were measured on the ground in three 6·4-km segments that represent a gradient of intermittency and were studied previously (Figure 1; refer to Scheurer *et al*., 2003 for detailed description). Briefly, the upstream segment is on The Nature Conservancy Fox Ranch, in the region where the regional and alluvial aquifers are connected, and is most perennial. Long reaches sustain flow in all but the driest conditions, and habitats include alternating runs and deep, persistent pools. The middle segment lies in the region where the two aquifers become disconnected, and is intermittent most of the year. The upper half has well-developed pools and a riparian gallery forest of cottonwood (*Populus deltoides*), whereas the lower half is wide and shallow with sand substrate and no riparian canopy. The downstream segment is in the lower, hydraulically disconnected reach where alluvial wells are prevalent, and is nearly dry by early summer. A few pools persist at its upstream end in some years (Scheurer *et al*., 2003). A perennial tributary, Black Wolf Creek, enters near the midpoint and often sustains a short reach of flowing habitat in the main channel.

At the segment scale, connectivity was measured twice a month from May through August 2005, and weekly from late May to mid August in 2006 and 2007. During each survey, each segment was traversed on foot, and the presence of water recorded throughout. Boundaries of reaches in the three different connectivity classes were georeferenced with the GPS, a GIS layer was produced of each segment and lengths of reaches in each connectivity class were measured using ArcGIS.

Pool scale. Refuge pools that provided fish habitat in each segment were censused at the lowest water levels during late July each year (2005–2007). Surveys were also conducted in August 2006, to compare drying between July and August. All pools in each segment were identified and georeferenced. For each pool, we measured (in metres) length, width at the midpoint, and maximum depth; we used these measurements to estimate pool surface area (in square metres) and volume (in cubic metres).

Groundwater and pool habitats. We installed six groundwater monitoring wells in the upstream segment in August 2005 to measure the relationship between groundwater levels and refuge pool depths. The wells were spaced evenly along the segment, about 10 m from the stream channel. The bottom sections of the well casings (5-cm diameter PVC pipe) were slotted (0·6-cm spacing, 0·05-cm slot width) to allow groundwater entry. Pressure-based HOBO U20 water level loggers (Onset Corp., Bourne, Massachusetts, USA) in each well recorded groundwater stage hourly (±0·5 cm). In 2007, we monitored maximum depth (in centimetres) in ten deep pools distributed throughout the segment and near these wells to measure the relationship between groundwater level and pool depth. Pool maximum depth (centimetres) was

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recorded weekly from March through August, and periodically through October, from fixed stage gauges in each pool.

Groundwater models

We developed two models to project the future effects of groundwater pumping on fish habitat, a simple water balance model (Squires, 2007) and a numerical groundwater model (Magelky, 2010). The control volume for both models was in the middle of the basin where the regional and alluvial aquifers are hydraulically connected (Figure 4) and fish habitats will likely persist longest (see Section on Geology and Groundwater Dynamics). The domain for the water balance model included all of the Arikaree River groundwater basin in Yuma County, whereas the numerical model (Figure 4) encompassed a smaller, 45-km river segment that included the Fox Ranch and had northern and southern boundaries near the groundwater divides with the adjacent river basins.

Water balance model. We developed a water balance model for the regional and alluvial aquifers within our control volume to compare the change in storage (ΔS), inputs (Q_{in}) and outputs (Q_{out}) between pre-development (pre-1958, before pumping) and 2007 conditions (Squires, 2007). The model for the aquifer and stream system was evaluated using estimates of the total inflow to, and outflow from, the aquifer to develop an initial estimate of aquifer fluxes and a general estimate of pumping effects. Although the model does not account for spatial or temporal variability in parameters such as recharge, evapotranspiration and pumping, it is an important initial step in understanding the hydrologic system.

Pre-development groundwater flow into and out of the control volume was estimated from a 1958 groundwater contour map (Weist, 1964). Stream outflow was estimated from a stream gauge (United States Geological Survey #06821500) at Haigler, Nebraska. Recharge for the High Plains Aquifer was initially estimated to be about 7% of the average precipitation of 44 cm/yr from 1951 to 2006, or approximately 2·9 cm/yr (Scanlon *et al.*, 2006; Squires, 2007). Recharge for the alluvial aquifer was estimated to be approximately 6·3 cm/yr, or 15% of the average precipitation based on a lysimeter study in the alluvium along the nearby South Platte River (Willard Owens Consultants, 1988). Groundwater flux from the regional aquifer to the alluvium and the total evapotranspiration from the alluvium were calculated so that the change in storage in each control volume was zero for pre-development, pseudo-equilibrium conditions.

Using the pre-development water balance model, we then developed a second model assuming current irrigation pumping rates. On the basis of the loss of storage due to pumping, we estimated an average yearly decline in water table levels of 0·25 m/yr in the regional aquifer, assuming an apparent specific yield (*Sya*; unitless) of 0·17 calculated by Squires (2007). This estimate was similar to the mean rate measured in seven wells south of the Arikaree River from 1965 to 2007 (mean = 0·27 m/yr, SE = 0·01, range 0·21–0·31; CDSS, 2007).

Finally, we used our post-development water balance model to estimate how much irrigation pumping would need to be reduced to maintain current groundwater levels. This was done by reducing streamflow to 2007 levels, reducing flow out of the aquifer (Q_{out}) to equal flow in from upgradient (Q_{in}) and reducing irrigation pumping (Q_w) until the change in storage (ΔS) equalled zero. This conservation water balance model was parameterized using 2007 data.

Groundwater model. We constructed a numerical groundwater model using MODFLOW-2000, a block-centred finite-difference code for simulating groundwater flow systems (Harbaugh *et al.*, 2000). MODFLOW is a widely used, well-documented and verified groundwater flow modelling software package (Anderson and Woessner, 1992). Simulations were run using extension packages developed by Hill (1990) and Harbaugh *et al.* (2000), and pre- and post-processing, including finite grid development, were performed using Visual MODFLOW version 4·0 (Waterloo Hydrogeologic Inc., Waterloo, Ontario, Canada).

Within our model domain (Figure 4), grid spacing of 201 m (0·4 km^2 each) resulted in 17 326 active cells. The model was constructed with general head boundaries north and south representing the groundwater divides with the adjacent basins, using the GBH6 package. For both the regional and alluvial aquifers, the east and west boundaries were constructed as general head boundaries representing aquifer water levels, and the east model boundary just north of the Arikaree River was represented as a drain element to incorporate a small intermittent tributary. The river was represented using the STR6 package to enable stream routing of water through the model domain. Precipitation recharge was modelled using the RCH6 package and riparian evapotranspiration using the EVT6 package. The model was constructed as a single-layer unconfined aquifer, assumed to be homogeneous and isotropic, and base elevations were set at the top of the Pierre shale.

The rate of evapotranspiration for the riparian areas of 86 cm/yr determined by Squires (2007) was applied for the growing season. Apparent specific yield for the High Plains Aquifer and alluvium were based on previous modelling studies (Table II; RRCA, 2003; Squires, 2007). The number of irrigation wells and their spatial position on the landscape within our model domain were obtained from the Colorado Decision Support System (CDSS, 2007) and pumping rates for individual wells were set at 60% of their rated capacities (Fardal, 2003).

The model was calibrated using an iterative process, by first calibrating a steady-state model to pre-development water levels, and then refining the calibration to best match historical trends in water levels from pre-development to the present. The steady-state model was calibrated by adjusting hydraulic conductivity to minimize the root mean squared error (RMSE) of the

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Table II. Numerical model parameters for the High Plains (regional) and alluvial aquifers within the lower Arikaree River basin, Colorado. Recharge values are 15 and 25% of precipitation for the regional and alluvial aquifers, respectively.

Model parameter	Units	Regional aquifer	Alluvial aquifer
Hydraulic conductivity	m/d	9	152
Recharge	cm/yr	6·3	10·5
Apparent specific yield (*Sya*)	Unitless	0·17	0·125

modelled versus 1958 pre-development water table levels (Weist, 1964). The output from the steady-state model was then passed to a transient model for calibration to the 1958–2007 data.

Historical groundwater level measurements were available for five wells in the High Plains Aquifer and one in the alluvial aquifer (CDSS, 2007) within our model domain, allowing a second, transient calibration. To simulate the regional decline in water levels from pumping outside the model domain, the general head boundaries were decreased 0·25 m/year to match declines in wells near the groundwater divide (see Section on Water Balance Model). The iterative calibration minimized the RMSE of the modelled water levels compared to the 1958 contours and the 1958–2007 water level records (refer to Table II for final model parameters). The final recharge values determined in the calibration process for the High Plains Aquifer and alluvial aquifer were greater than the estimate from the lysimeter study in the nearby South Platte River Basin that was used in the water balance model. This was probably owing to the relatively high proportion of dune sands within the numerical model domain versus the larger domain for the water balance model. The RMSE for the final transient calibration was 2·5 metres, 2·7% of the range in measured water levels across the study area. The RMSE of the history matching calibration was 2·9 cm/year.

We performed a sensitivity analysis of two parameters likely to influence our steady-state model results, recharge and evapotranspiration (Magelky, 2010). Both were varied from the calibrated values (Table II) by modifying these parameters up to ±50%. The results indicated that the model is most sensitive to larger rates of recharge, and less sensitive to changes in evapotranspiration. This difference is likely due to the proximity to boundary conditions and the area to which each is applied. For example, evapotranspiration stresses are limited to the area near the stream boundary condition because this is the only area where water levels are close to the ground surface, whereas recharge is applied across the entire model domain.

Model scenarios. We used the MODFLOW model to predict groundwater levels for three realistic scenarios of future water use to evaluate their impact on alluvial water table levels and fish habitat (i.e. refuge pool) depths. These predictions were based on the historical transient model, with two periods per year representing the pumping (growing) season and the non-pumping season. There was no significant trend in total annual rainfall (in centimetres) as a function of year from 1958 to 2007 (slope = −0·05, $P = 0{\cdot}06$), and so we used the same recharge and evapotranspiration rates as in the steady-state calibrated model. First, for the status quo scenario (SQ), the current number of wells and pumping rates were continued into the future. Second, for the alluvial well removal scenario (AW), the three wells located directly in the alluvium within our model domain were removed, whereas all wells in the regional aquifer (Figure 4) continued pumping. This scenario was based on a proposal by The Nature Conservancy to buy water rights and retire several alluvial wells for conservation purposes (W. Burnidge *personal communication*). Third, for the three-mile band scenario (TM), we removed all wells within our model domain identified by the Colorado State Engineers Office (CDWR, 2007) as within a 4·8 km (3 miles) band of the river, from the Fox Ranch downstream. These represented 19% of the total pumping volume in the SQ scenario. The TM scenario is based on the current state policy designed to curtail pumping and restore river flows for delivery downstream to Kansas to meet an interstate water compact.

We evaluated the three future scenarios by calculating the number of refuge pools remaining, in August, at lowest flow in the upstream segment, from 2007 to 2045. For our initial state, we set the pool surface elevation and shallow alluvial groundwater elevation in August 2007 to be equal. Owing to the close relationship between pool stage and groundwater stage during summer (see Section on Results), we assumed that future pool depths would correspond to alluvial water table levels. We considered a pool to dry completely when the water table dropped below the elevation of the stream bed, based on measured pool maximum depths. Subsequently, we calculated the percentage and spatial location of pools remaining over time under each scenario.

We quantified uncertainty in our estimates of pool drying by calculating a 95% prediction interval (95% PI; Helsel and Hirsch, 2002) based on observed and predicted rates of water table level declines for the six wells in our model domain for which data were available. This prediction interval provided an estimate of the uncertainty in modelled water table level predictions based on the assumptions that future decline rates are within the range of historical decline rates and future pumping will remain similar to rates used in the model based on the period 1965–2007. As no trend in model error was found in our modelled water table level decline predictions, we proceeded with the uncertainty analysis using the following steps.

First, linear regression was used to estimate the observed average rate of decline (i.e. slope of the water table level as a function of time relationship) at each of the six wells. Second, we calculated the difference between the observed and predicted decline rates for each well across years with data. Third, these prediction errors were normalized to a percent of the average decline rate

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at each well and applied across the range of predicted decline rates within the model domain. Finally, based on these normalized prediction errors, the 95% PI (Helsel and Hirsch, 2002) was calculated to provide a range of uncertainty in the decline rate estimates for pools.

Trends in discharge for other tributaries

We made a regional comparison of trends in streamflow, by assembling the USGS data available on mean annual discharge for all Republican River tributaries in Colorado, Nebraska and Kansas. We calculated the slope of mean annual discharge (in cubic metres per second) as a function of calendar year for each stream, using SPSS version 11·0 (SPSS Inc., Chicago, IL).

RESULTS

Climate

A drought that started in 2000 continued during 2005–2007 (Figure 3), although mean annual flow in 2005 was the highest since 2001 (0·05 m^3/s). Total precipitation for 2005 of 53·2 cm measured in the basin (CoAgMet, 2008) was the highest since 1995, and above the long-term mean for 1895–2005 (mean = 44·3 cm; $SD = 8·8$). Total precipitation for 2006 and 2007 (32·8 cm and 33·0 cm, respectively) was well below the long-term mean, and both years ranked among the lowest 10% over the period of record. The mean flow declined in 2006 to 0·02 m^3/s, the third lowest over the period of record (1933–2007), and remained low in 2007 (0·04 m^3/s). However, abundant snowfall in December 2006 (30–45 cm; NOAA, 2008) contributed to relatively higher flows in the basin in spring 2007 (see Section on Fish Habitat).

Fish habitat

Basin scale. Low-altitude flights over the 110 km stretch of the lower Arikaree River during 3 years showed that fish habitat was permanently disconnected from downstream basins and dried to a relatively short segment by late summer. During all spring flights, flows began 30–35 km downstream from Cope (Figure 1), and in May 2005 (the only survey that year), it continued for 43 km. Downstream from that point, the channel was dry for 25 km to the confluence with the Pioneer Canal which diverts flow from the North Fork Republican River into the Arikaree River. Flow resumed here and continued 7 km to the confluence of the Arikaree with the North Fork Republican River.

Lower precipitation in 2006 reduced spring flows, and more of the river channel was dry than in 2005. In May 2006, flows again began about 35 km downstream of Cope, but continued for only 28 km, followed by a set of intermittent reaches along the middle segment for 6 km, and then flowing reaches for 10 km. Downstream, the river was mostly dry to the confluence with the Pioneer Canal, and then flowed 7 km to the confluence. Flowing reaches declined in June, and by July, only one 11-km flowing reach remained, centred on the upstream segment, representing only 10% of the original 110 km of flowing habitat. No flows were present below the Pioneer Canal to the confluence during this dry period.

During March through May 2007, the Arikaree River flowed continuously from 30 km downstream of Cope for 59–63 km (Figure 5), below which was a 10–14-km long dry segment. The Pioneer Canal contributed flow as during spring in the other 2 years. Intermittent and dry reaches increased rapidly in June and July, as in 2006. By September 2007, only 15 km of continuously flowing habitat remained upstream of the confluence with

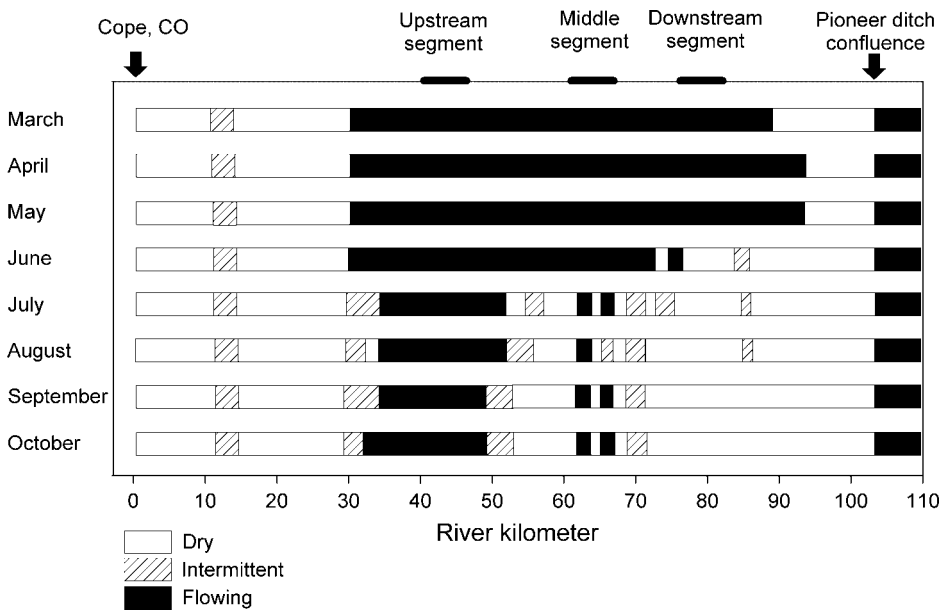

Figure 5. Among-habitat connectivity measured at the basin scale from low-altitude flights over the Arikaree River, Colorado during 2007. Survey month is on the *y*-axis, and river kilometer is on the bottom *x*-axis (flow is from left to right). Black bars represent flowing reaches, hatched bars are intermittent reaches and open bars are dry reaches. The position of Cope, Colorado, the Pioneer diversion canal, and three 6·4-km study segments are indicated along the top *x*-axis.

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the Pioneer Canal, centred on the upstream segment, similar to 2006. The Pioneer Canal contributed flow at the downstream end of the river throughout summer 2007.

Segment scale. Twenty-six segment-scale connectivity surveys were conducted in each of the three river segments during summers 2005–2007 (2005, $N = 7$ surveys; 2006, $N = 9$; 2007, $N = 10$). For clarity, we present only the final survey for each summer month across years (Figure 6). At this scale, the segments clearly differed in intermittency, but varied consistently across the 3 years with different climate. Segments were wettest in 2005, driest in 2006 and intermediate in 2007 due to abundant winter snowfall (see Section on Climate). For example, nearly all reaches in the upstream segment had flow in 2005, whereas in 2006 flows declined beginning in June so that by August approximately 60% of the stream length was intermittent and 30% completely dry. In 2007, flows declined less during summer, so that about 60% was intermittent in August.

The middle segment dried more each summer than the upstream segment, so that in 2005 about 40% was wet and 35% intermittent by July, the driest period. In 2006, the driest year, only about 20% was flowing during the driest period in August, and about 70% was dry. A similar pattern of drying occurred in 2007. The downstream segment was the driest, and dried quickly during June in the 2 wetter years (2005 and 2007), so that no habitat remained by July. There was never any surface water in the downstream segment in 2006. Overall, the amount and connectivity of fish habitat at the segment scale reflected both connections to the alluvial groundwater aquifer (see Section on Geology and Groundwater Dynamics) and inter-annual climate variability.

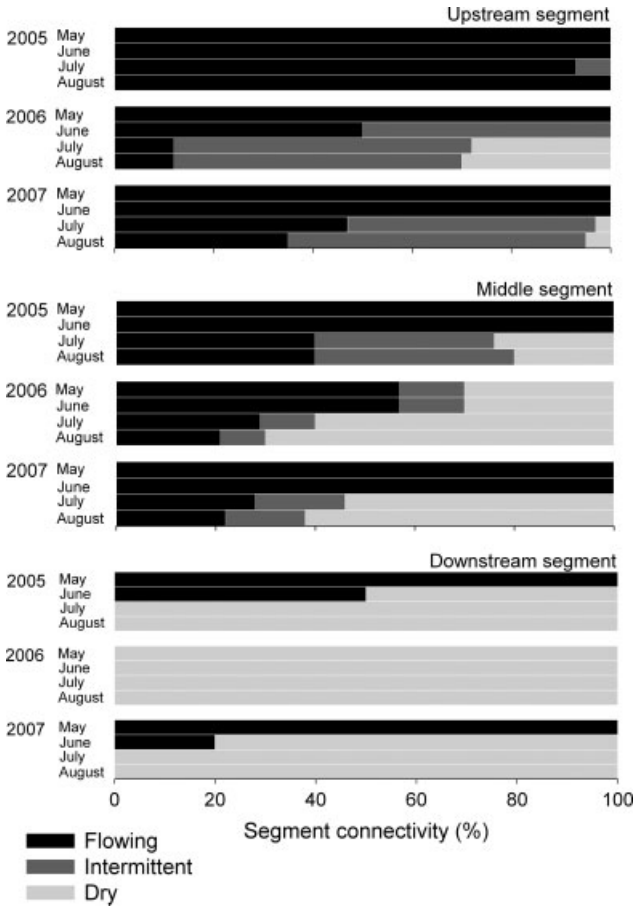

Figure 6. Among-habitat connectivity measured at the segment scale from foot surveys during summer months from 2005 to 2007 along three 6·4-km segments of the Arikaree River, Colorado. Survey month and year are on the *y*-axis, and the percent of the segment in each connectivity class (flowing, intermittent and dry) is on the *x*-axis.

Pool scale. Late summer censuses of refuge pools showed that no pools were ever present in the downstream segment during any of the 3 years. In 2006, we found a marked decrease in the number of refuge pools in the upstream segment from July to August, and in the total volume of pools in both upstream and middle segments during this short period (Table III). For example, by late August, 30% (56 of 180) of the pools present in the upstream segment in late July had dried completely, and about half of those remaining ($N = 57$) had dried to less than 50% of their late-July volumes. Overall, the upstream segment contained more than an order of magnitude more pool volume than the middle segment during the driest portion of the summers 2005–2007, and the largest refuge pools in the upstream segment had much greater volume.

Groundwater and pool habitats. Alluvial water table elevation (in metres) was directly related to pool depth (in centimetres) across six pairs of wells and pools in the upstream segment from April through October 2007. As water table elevation declined during summer, pool depths also declined. We tested the correlation between mean daily groundwater table elevation and measured pool depth ($N = 14$ dates measured). Pearson correlation coefficients ranged from 0·81 to 0·99 ($P < 0{\cdot}05$) for all six pairs, indicating that the pool depths were directly related to alluvial water table levels in this segment of the Arikaree River.

Model scenarios and conservation water balance model

The 95% PI was determined to be ±30% of the model predicted water level decline rate. The range of 70–130%

Table III. Number and volume (in cubic metres) of refuge pools censused along two 6·4-km segments of the Arikaree River, CO during summer 2005–2007.

Survey	Segment	N	Pool volume (m^3)		
			Total	Mean (SE)	Range
July 2005	US	172	6095	20·5 ± 3·4	1–433
	MS	35	556	15·9 ± 3·1	2–68
July 2006	US	180	4235	23·5 ± 3·1	1–253
	MS	27	321	11·9 ± 4·9	1–51
August 2006	US	124	2809	15·6 ± 2·8	1–207
	MS	27	197	7·3 ± 3·1	1–32
July 2007	US	218	7532	34·7 ± 9·4	1–502
	MS	31	321	17·9 ± 3·3	2–91

Codes for segment are US = upstream segment, MS = middle segment. See Figure 1 for locations.

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of the predicted rate of decline was applied to decline rates calculated for individual pools to provide an upper and lower bound to the percentage of pools remaining over time under each scenario resulting from uncertainty in the model.

Status quo scenario. Under the status quo of current pumping rates in the Arikaree River basin, our model predicted that 50% (predicted range: 40–58%) of the 218 pools that remained in the upstream segment during the driest period of summer 2007 will be dry by 2035, about 25 years in the future (Figure 7). Pools in the middle and downstream segments most likely would also be permanently dry by this time. However, by 2045 only 36% (predicted range: 29–49%) of pools will remain, and most will be isolated in a 1-km reach near the downstream end of the segment (Figure 8). Many of these pools are created by beaver dams.

Alluvial well removal scenario. Removal of alluvial wells from the model, two upstream and one downstream of the Fox Ranch (Figure 4), had negligible effect on increasing pool persistence in our model (Figures 7 and 8). The trajectory of pools remaining over time was virtually identical to that of the status quo scenario. Although curtailing actively pumping alluvial wells will generally increase streamflows, the vertical separation of the water levels in the alluvium from the stream bed, coupled with the long distance of the three alluvial wells from the study area, limits the effectiveness of this scenario.

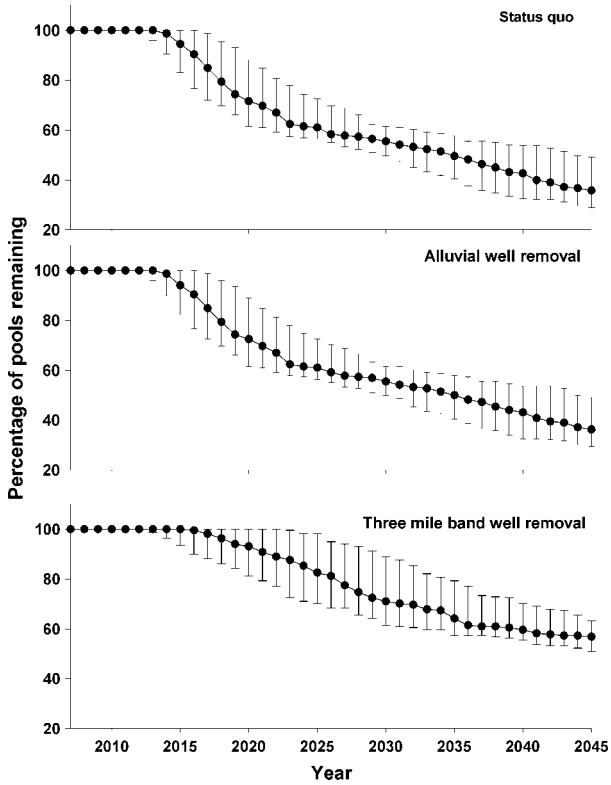

Figure 7. The percentage of refuge pools remaining over time under three scenarios of groundwater pumping for irrigation along the 6·4-km upstream segment of the Arikaree River, Colorado. Error bars represent the ±95% prediction interval. The status quo scenario (top panel) represents continued current (2007) irrigation pumping rates. Under the alluvial well removal scenario (middle panel), pumping by three irrigation wells from the alluvial aquifer is stopped. The bottom panel represents a scenario where wells within a specific 3-mile band of the river are taken out of service (see text and Figure 4).

Three-mile band scenario. Removing wells within three miles (4·8 km) of the river within the curtailment zone (Figure 4) would allow more of the pools present in 2007 to remain in 2035 than the other two scenarios (64%, predicted range: 57–79%). However, by the end of our modelling period in 2045, only 57% (predicted range: 51–63%) would remain (Figure 7). Unfortunately, similar to the other scenarios, most of these refuge pools would be isolated in only 1·7 km of the segment (Figure 8) and would most likely constitute the only fish habitat refuge in 105 km upstream from the Pioneer Ditch. Additionally, average depth of the remaining pools would decrease 32% from 67 cm (±1·8 SE) to 46 cm (±2·1 SE) during 2007–2045.

Conservation water balance model. The results of our conservation water balance model indicate that at least a 75% reduction in irrigation pumping within our model domain is needed to reach equilibrium conditions ($\Delta S = 0$), where water table levels in the regional and alluvial aquifers are no longer declining (Table IV) so that the current amount of fish habitat is conserved. This is based on the assumption that the flow out of the aquifer (Q_{out}) has been reduced to be equal to the flow into the study area portion of the aquifer from upgradient portions of the groundwater basin (Q_{in}). We also found that streamflow into and out of our control volume had declined by 2007 due to pumping. However, compared to groundwater flow, streamflow constituted a small proportion of the water balance. Overall, for water levels to recover and sustain more pools than found during August 2007, a reduction greater than 75% would be required for a prolonged period of years (Magelky, 2010).

Trends in annual discharge

All 11 Republican River tributaries with streamflow data showed significant, negative linear trends ($P < 0{\cdot}001$) in discharge over time (Table V). This analysis confirms that the effects of streamflow reduction, likely owing to groundwater pumping, are not restricted to the Arikaree River basin, but are widespread across Republican River tributaries.

DISCUSSION

Measurement of fish habitats at multiple scales showed that only about 10–15 km of the original 110 km of habitat in the Arikaree River that formerly flowed at least seasonally persisted through the driest period of the summer in 2006 and 2007. Additionally, many of the remaining habitats are seasonally disconnected from one another and all are permanently cut off from adjacent

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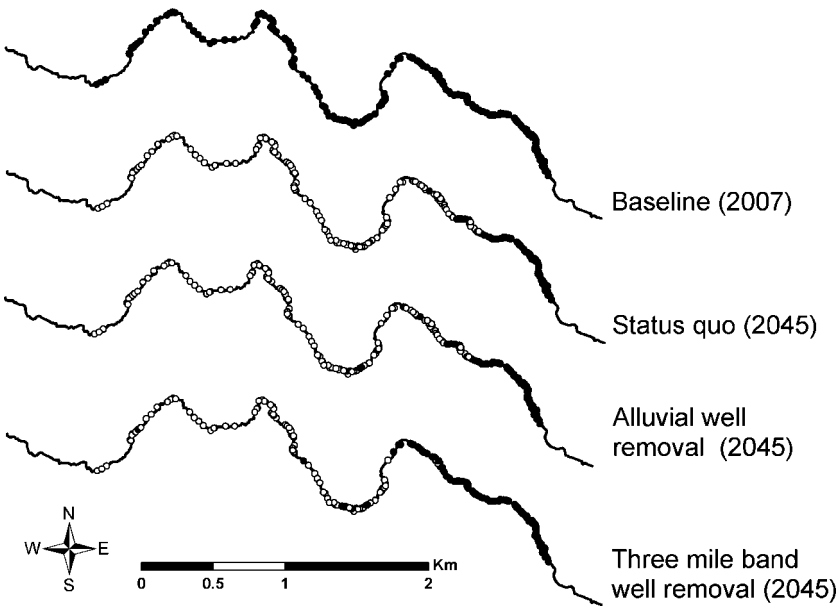

Figure 8. Projected persistence of refuge pools in August 2045 under three scenarios of irrigation pumping along the 6·4-km upstream segment (Figure 1) of the Arikaree River, Colorado, compared to baseline conditions in August 2007. Solid circles represent extant pools, and open circles dry pools. See the text for description of the three scenarios modelled.

Table IV. Results of three water balance model scenarios for a portion of the lower Arikaree River basin, CO (Figure 4), and the time period of each model. Inputs from groundwater flow (Q_{in}), surface flow (SF_{in}) and aquifer recharge (R), and outputs from riparian evapotranspiration (ET), irrigation pumping (Q_w), groundwater flow (Q_{out}) and surface flow (SF_{out}) are shown. All units are volumes in ha-m/yr × 10^3. Surface flows (SF_{in}, SF_{out}) and groundwater outflow (Q_{out}) were reduced to 2007 levels to calculate the conservation scenario. The change in storage (ΔS) represents the difference in groundwater volume within the model per year. Under the conservation model scenario, irrigation pumping must be reduced by 75% to reach equilibrium ($\Delta S = 0$).

Water balance model	Time period	Inputs			Outputs				ΔS
		Q_{in}	SF_{in}	R	ET	Q_w	Q_{out}	SF_{out}	
Pre-development	Pre-1965	2·39	0·23	5·32	3·02	0	2·60	2·32	0
Post-development	Average of 1965–2007	2·39	0·11	5·32	3·02	8·02	2·60	1·1	−6·92
Conservation	Post-2007	2·39	0·03	5·32	3·02	2·02	2·39	0·31	0

Table V. Trends in mean annual discharge (in cubic metres per second) over time (year) for 11 Republican River tributaries in Colorado, Nebraska and Kansas. Slope of the linear regression of year versus mean annual discharge, number of years in the analysis, range of years with flow records and the USGS gauge number are shown. All slopes were significantly less than zero ($P < 0·001$).

Stream	Slope	Number of years	Range of years	Gauge number
Arikaree River, NE	−0·0136	75	1933–2007	6821500
Beaver Creek, KS	−0·0169	61	1947–2007	6846500
Buffalo Creek, NE	−0·0029	67	1941–2007	6823500
Driftwood Creek, NE	−0·0040	61	1947–2007	6836500
Frenchman Creek, NE	−0·0490	57	1951–2007	6835500
North Fork Republican River, CO	−0·0091	71	1936–2007	6823000
Prairie Dog Creek, KS	−0·0284	64	1930–2007	6848500
Red Willow Creek, NE	−0·0055	46	1962–2007	6838000
Rock Creek, NE	−0·0033	67	1941–2007	6824000
Sappa Creek, KS	−0·0520	61	1947–2007	6845110
South Fork Republican River, NE	−0·0306	70	1938–2007	6827500

basins owing to a long, dry segment in the lower basin. Habitat alteration and loss of connectivity are likely key factors in the extirpation of five fish species from the basin since the 1940s (Table I). For example, one extirpated species, plains minnow, produces neutrally bouyant eggs that drift downstream and hatch quickly. Successful reproduction by this species requires periodic high flows and long segments of unfragmented stream

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habitats (Taylor and Miller, 1990; Dudley and Platania, 2007). Indeed, all five extirpated species were originally found in large rivers (Table I), and several apparently require continuous river habitats to complete their life histories (Cross and Collins, 1995; Pflieger, 1997). These conditions are now rare in the Arikaree River, and based on our model predictions, will soon disappear.

Fishes in the Arikaree River are presently cut off from adjacent basins due to permanently dry reaches in the lower basin. Connectivity with other basins is critical to provide demographic support and gene flow among populations (Neville *et al*., 2006, 2009; Fausch *et al*., 2009). Isolating fishes in short stream fragments increases the chances that random environmental events such as a severe drought will extirpate these populations from the basin (Rieman and McIntyre, 1995; Lande, 1998; McElhany *et al*., 2000). Once populations are extirpated, the long, permanently dry segments of river in the lower basin prevent any chance of recolonization from adjacent basins.

The best remaining fish habitat in the Arikaree River occurred in the upstream segment, in the 10–15 km of core habitat supported by hydraulic conductivity with the regional aquifer. Our data showed that at the pool scale, even within this wettest segment, refuge pools declined markedly and were much reduced in volume during summer drying. Reduced depth and volume of pools can lead to decreased fitness and increased mortality of fishes in these shallow habitats due to degraded water quality (e.g. high temperatures, low dissolved oxygen, freezing in winter; Labbe and Fausch, 2000; Durham *et al*., 2006), increased parasitism rates (Medeiros and Maltchik, 1999) and increased predation from terrestrial and avian predators (Power, 1987). Although plains fishes are well adapted to the harsh conditions typical of intermittent Great Plains streams, this tolerance extends only so far. At this local scale, thresholds of survival likely occur below which plains fish populations cannot persist under multiple years of extreme conditions, leading to extirpations such as those recorded (Scheurer *et al*., 2003; Falke, 2009).

Coupling measured pool depths in the most perennial river segment to a detailed groundwater model allowed us to forecast habitat at the summer minimum into the future, and to create a spatially explicit map of the remaining pools. Our results show that refuge habitats for fishes in the Arikaree River are not sustainable under any of the three ecological futures modelled. Under the current pumping regime, half of the modest number of pools remaining at low water in 2007 are projected to be completely dry within 25 years, and after 35 years nearly all of the remaining refuge pools for fish will be concentrated in less than 1 km of river. Moreover, at this low groundwater stage, this is likely to be the only set of connected pools remaining in the entire 105 km of the Arikaree River above the Pioneer Ditch. Likewise, even under the scenario in which wells within 4·8 km (3 miles) of a large segment of the river are retired, a similar fate will occur within 35 years. Reducing refuge habitats for fishes by continued pumping will hasten the extirpation of most remaining fish species in the Arikaree River.

Our analysis rests on coupling a modern groundwater model with a multi-scale analysis of fish habitat dynamics. Results of our transient groundwater model were based on several assumptions. The first was that current irrigation pumping rates within the Arikaree River basin will continue during the period we forecasted (2007–2045). Since large-scale agricultural irrigation began in Yuma County during the 1960s, the volume of groundwater used for irrigation has been relatively constant since 1975 (Figure 2), so rates likely will be similar in the future.

The second assumption was the value of apparent specific yield (*Sya*) of the regional aquifer within our model domain, which was set to 0·17. Apparent specific yield is defined as a unitless ratio of the volume of water released from storage (e.g. pumped) in a saturated unconfined aquifer to the change in the volume of water below the water table. Squires (2007) modeled *Sya* for our study area, and compared the results to empirically estimated values developed for similar systems. Because she found a similar value, we reasoned that our estimate of *Sya* was realistic for our study area.

The third assumption was that the irrigation wells do not pump at their maximum rated capacity. Through surveys of irrigators and published values, Fardal (2003) estimated that irrigation systems within our study area pump at about 60% of their rated capacity, due to declining efficiency over time and the variable cost of electricity. We considered this estimate of pumping rates to be more realistic than simply applying the maximum rated capacity to each well. Moreover, if pumping rates are higher, then fish habitat would decline faster.

Our water balance model showed that pumping would need to be reduced by at least 75% to maintain the current depleted state of aquatic habitat in the Arikaree River, and even more reduction would be required to reverse the downward trend. Given the socioeconomic importance of irrigated agriculture in this region, reduction by such a large amount is most likely an unrealistic goal. However, some level of water conservation should be considered, if only to prevent total extirpation of all fishes in the basin. What could be done to decrease the decline of groundwater levels, and conserve fishes into the future? Two possible solutions are (1) reducing water use by changing from crops with high water requirements (e.g. irrigated corn and alfalfa) to those that require less water (e.g. dryland corn or winter wheat), or increasing irrigation efficiencies, and (2) increasing water availability through artificial aquifer recharge or trans-basin diversions. However, changing crops may prove to be difficult to implement because of the current increase in farm revenues generated from growing corn for biofuel (discussed below). Likewise, although artificial aquifer recharge or trans-basin water diversion would supplement river flows, it involves risk. Concerns include facilitating the introduction of non-native species, alteration of

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hydrologic regimes in both basins and habitat alteration (Davies *et al*., 1992; Meador, 1992).

Habitat loss and fragmentation due to declining groundwater levels may be influenced by two factors that we did not explicitly incorporate into our model scenarios. The first is the increasing demand for, and profitability of, corn for biofuels (Hill *et al*., 2006; Tilman *et al*., 2006). Although no new well permits have been allowed in Yuma County since the 1970s, it is possible that fields with old wells that have been set aside for conservation or converted to dryland agriculture could be used again. More irrigation pumping within the Arikaree River basin can only exacerbate the decline in groundwater and fish habitats that our models predict. Secondly, in general, the western Great Plains ecoregion is predicted to become warmer and drier in the future due to global climate change. Specifically, recent climate models for northeast Colorado predict more extreme weather events (e.g. droughts), increased average temperatures in winter and spring, and decreased overall precipitation (Joyce *et al*., 2001; Ojima and Lackett, 2002). These changes are predicted to result in increased irrigation water demand, higher rates of evapotranspiration and intensified competition for water resources. Although we detected no significant changes in precipitation patterns over the past 100 years in the Arikaree River basin, the trend was negative. Moreover, climate change may have driven the recent major drought. Regardless, the short-term effects of climate change on the hydrology of western Great Plains streams will likely be much smaller than those of excessive groundwater consumption. Moreover, climate change will only increase the variability of groundwater and fish habitat declines, potentially driving fishes to extinction sooner than we projected.

CONCLUSION

The spatial distribution of intermittency in dryland streams is difficult to measure and predict, but both are critical for identifying refugia across the broad spatial scales over which fishes in these ecosystems carry out their life histories (Falke and Fausch, 2010). When linked to groundwater models that incorporate water abstraction, multi-scale habitat surveys like those we conducted provide much information which can be used to identify habitats critical for the persistence of fishes. Moreover, models like those we developed can be used to project conditions into the future under different realistic scenarios, allowing managers to strategically assess the quantity and distribution of remaining habitats, providing a spatially explicit approach to habitat preservation in dryland streams. A further step would be to explicitly link groundwater-fish habitat models to population or community responses (refer to Perry and Bond, 2009 for an example) to quantify viability under various scenarios of water use and climate change. However, for the Arikaree River, the implications of our research were quite clear. Given the huge amount of pumping reduction needed to sustain even the current reduced level of habitat, the rapid decline in the remaining habitat and the inability of the sociopolitical system to respond quickly, all results indicate that ecological futures are bleak for this fish assemblage.

Moreover, we found that declines in streamflow are not restricted to the Arikaree River, but are in fact widespread across the western Great Plains. A significant negative trend in mean annual streamflow over the last 50–75 years is present in all 11 Republican River headwaters for which data were available in eastern Colorado, western Nebraska and western Kansas, including the Arikaree River (Table V). Extirpation and population declines of stream fish species are widespread across this region (Gido *et al*. in press; Fausch and Bestgen, 1997; Haslouer *et al*., 2005; Hubert and Gordon, 2007), and our results indicate that with continued overuse of groundwater resources, we can expect further losses of stream fish habitats. This will lead to declining and more fragmented populations, and local extinctions similar to those that we found in the Arikaree River. Ultimately, species inhabiting these primarily east–west drainages will shrink eastward and decline in range and abundance (cf. Matthews and Zimmerman, 1990), becoming more imperilled as groundwater declines and climate change continue. Managers across the Great Plains will be challenged to address these issues, and should consider what options are available to conserve native plains fishes in these basins.

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