



# Groundwater declines are linked to changes in Great Plains stream fish assemblages

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Groundwater pumping for agriculture is a major driver causing declines of global freshwater ecosystems, yet the ecological consequences for stream fish assemblages are rarely quantified. We combined retrospective (1950–2010) and prospective (2011–2060) modeling approaches within a multiscale framework to predict change in Great Plains stream fish assemblages associated with groundwater pumping from the United States High Plains Aquifer. We modeled the relationship between the length of stream receiving water from the High Plains Aquifer and the occurrence of fishes characteristic of small and large streams in the western Great Plains at a regional scale and for six subwatersheds nested within the region. Water development at the regional scale was associated with construction of 154 barriers that fragment stream habitats, increased depth to groundwater and loss of 558 km of stream, and transformation of fish assemblage structure from dominance by large-stream to small-stream fishes. Scaling down to subwatersheds revealed consistent transformations in fish assemblage structure among western subwatersheds with increasing depths to groundwater. Although transformations occurred in the absence of barriers, barriers along mainstem rivers isolate depauperate western fish assemblages from relatively intact eastern fish assemblages. Projections to 2060 indicate loss of an additional 286 km of stream across the region, as well as continued replacement of large-stream fishes by small-stream fishes where groundwater pumping has increased depth to groundwater. Our work illustrates the shrinking of streams and homogenization of Great Plains stream fish assemblages related to groundwater pumping, and we predict similar transformations worldwide where local and regional aquifer depletions occur.

ecology | conservation | freshwater | Great Plains | fishes

Worldwide, irrigation accounts for 90% of human water use and is sustained by the annual pumping of 545 km<sup>3</sup> of water from global groundwater sources (1). In North America, major aquifers are important sources of water for 60% of land equipped for irrigation. One of these aquifers, the High Plains Aquifer in the Great Plains, is the single greatest source of groundwater and supports \$35 billion [2007 US dollars (USD)] in US market value of agricultural products (2). The total area irrigated with groundwater from the High Plains Aquifer was 8,500 km<sup>2</sup> in 1949 when large-scale pumping began, increased to 55,000 km<sup>2</sup> by 1980, and reached 63,000 km<sup>2</sup> by 2005 (3). Sustaining this level of agricultural productivity will depend on continued extraction of water from the High Plains Aquifer, but the aquifer is experiencing substantial declines in storage (4, 5). Groundwater extraction from the aquifer is occurring faster than recharge (6) and has resulted in the depletion of 410 km<sup>3</sup> of stored groundwater, a volume equal to 85% of the water in Lake Erie, North America (5). Long-term depletion of the High Plains Aquifer has caused water tables to drop by more than 50 m in some portions of the Great Plains whereas redistribution of water through surface canals and lateral subsurface flows has

contributed to rising water tables in other locations (7, 8). Rates of groundwater depletion caused by pumping from the High Plains Aquifer are similar to those measured on portions of every continent except Antarctica, suggesting that the Great Plains is a microcosm for the effects of global groundwater pumping on the hydrologic cycle (9).

Pumping from the High Plains Aquifer has also caused surface water to decline in streams of the western Great Plains (10, 11). In the Republican River basin in southwestern Nebraska, depleting groundwater has caused streamflow declines at 70% of US Geological Survey stream gauges (12). In the Arikaree River in eastern Colorado, mean annual discharge declined 60% from the period 1932–1965 to the period 1966–2006 (13). In the western third of Kansas, historically perennial streams are now ephemeral or permanently dry, and groundwater extraction combined with surface diversions permanently dry the Arkansas River just downstream of the Colorado border (14). These losses of surface stream flow are caused by declining water tables below river beds, so much so that they no longer supply groundwater to channels. Although rainstorms can produce floods in this region, base flows are sustained by groundwater (15) and are thus sensitive to water table fluctuations close to the ground surface (16–18). As depth to groundwater increases beneath streambeds, streams become decoupled from the aquifer, and aquatic habitat becomes intermittent or completely dry (6). However, changes in depth to groundwater are not consistent across space and time so broad-scale ecological consequences of decoupling streams from the High Plains Aquifer are sparsely studied despite widely accepted

## Significance

Nature and society depend on groundwater to sustain aquatic ecosystems and human livelihoods, but local and regional groundwater supplies are dwindling where human water extraction exceeds aquifer recharge. Although groundwater depletion is a global problem, ecological consequences for aquatic species such as fishes are rarely examined. We demonstrate that more than half a century of groundwater pumping from the United States High Plains Aquifer has been associated with collapses of large-stream fishes and expansion of small-stream fishes where hydrologic conditions were altered most. Projections indicate that these habitats will continue to shrink over the next half-century if groundwater pumping practices are not modified. Our findings highlight a mechanism for biotic homogenization with global implications given the worldwide extraction of groundwater.

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linkages between groundwater and the ecology of surface streams (6, 19, 20).

Although stream drying is a natural and pervasive process in Great Plains streams, the combination of groundwater pumping and habitat fragmentation by diversion dams, reservoirs, and other anthropogenic barriers now prevent many fishes from finding refuge from increased drying (21–23). Across the western Great Plains, stream fish biodiversity declined during 1950–2010 as the area of irrigated land and pumping for irrigation increased, diversion dams and reservoirs fragmented surface habitats, and stream flows diminished due to reduced groundwater input (13, 24–26). The combined effects of increased drying and surface fragmentation “ratchet down” Great Plains fish diversity because barriers prevent recolonization of dry stream segments once precipitation restores flow (27). However, despite the implied connections between groundwater levels and stream fish communities, few studies have explicitly linked groundwater depletion with stream fish community change (6, 13). Conservation of stream fishes in groundwater-dependent ecosystems in the Great Plains and worldwide requires a better understanding of how groundwater pumping reduces streamflow, and how reduced streamflow affects stream fish assemblages (9, 19, 28). Ecological change associated with groundwater depletion represents a rarely studied mechanism of biotic homogenization that ultimately results in loss of freshwater natural resources (29). The ecological and evolutionary consequences of reduced taxonomic, functional, and molecular diversity affect global human livelihoods because biotic homogenization ultimately compromises ecosystem function, services provided, and resiliency to disturbance while simplifying food-web structures and increasing community susceptibility to species invasions (30). Collectively, these consequences of freshwater resource loss represent human diminishment of the very resource required for long-term persistence (31).

We used a retrospective approach to assess the effects of 60 y of historical depletion of the High Plains Aquifer on fish assemblages inhabiting large and small streams in the western Great Plains and combined this approach with prospective modeling to develop baseline expectations for fish assemblage change through 2060. We used historical groundwater-level data from 3,431 observation wells distributed across the upper Kansas River Basin of Colorado, Kansas, and Nebraska (Fig. 1) to create annual interpolated surfaces representing depth to groundwater during 1950–2010. These interpolated depths were subtracted

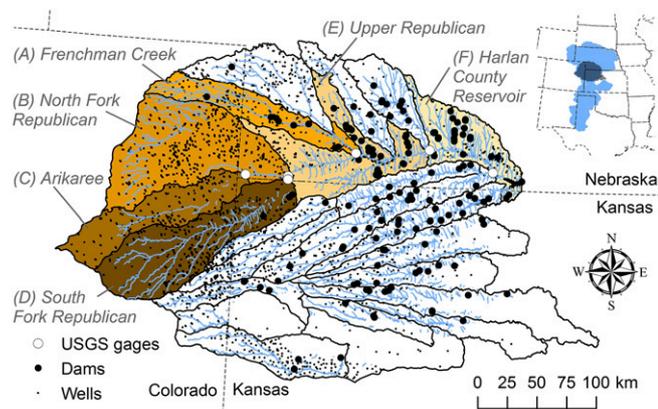
from a digital elevation model for the region (with a resolution of 0.5-km cells) to create spatially continuous estimates of depth to groundwater across the study area. We then used stream locations derived from the National Hydrography Dataset Version 2 Plus (32) to classify stream segments into two categories regarding coupling with the aquifer: “coupled” (i.e., depth to groundwater <1 m under stream location) or “uncoupled” (depth to groundwater >1 m under stream location) (*SI Methods*). We classified all segments across the region for each year and summed the length of coupled segments to quantify spatiotemporal change in habitat for stream fishes. We used historical fish collections (*Table S1–S5* and *Fig. S1*) made across the region during 1950–2010 to establish relationships between length of coupled stream segments and species occurrences using generalized regression models. Based on these retrospective relationships, we forecasted (2011–2060) change in fish assemblage structure for large streams (order  $\geq 4$ ) (33) and small streams (order <4). Our analysis focused on two spatial scales: the regional scale combining 24 subwatersheds in the upper Kansas River basin and the subwatershed scale that focused on 6 subwatersheds arranged across a gradient of groundwater decline.

## Results

Rapid and expansive increases in groundwater pumping and dam construction during 1950–2010 drastically modified stream habitats across the study region. Annual groundwater pumping from the High Plains Aquifer in the Kansas portion of the study area increased almost exponentially from 0 in 1950 to a peak of 1.31 km<sup>3</sup> in 1980, and the number of diversion dams and reservoirs throughout the study area increased from 37 to 141 during 1950–1980 (Fig. 2A). During this same period, the total length of stream coupled with the High Plains Aquifer decreased from 2,640 to 2,082 km (558 km lost) (Fig. 2B). During 1980–2010, groundwater extraction in Kansas varied annually from 0.55 to 1.30 with an average of 0.91 km<sup>3</sup>, and the number of diversion dams and reservoirs increased to 154. Meanwhile, the total length of stream coupled with the aquifer varied from 2,046 to 2,194, with an average of 2,117 km. Projections for the period 2011–2060 indicated a further decrease in length of coupled stream to 1,796 km (another 286 km lost). Most of this loss was driven by declines in length of large (primarily fourth-order) streams although small (second- and third-order) stream length declined rapidly during 1950–1980 and then remained relatively constant or increased slightly during 1980–2060 (Fig. 2B). Although the length of fourth-order coupled streams was 1.4 times greater than second-order coupled streams in 1950, by 2060, lengths of both stream orders are projected to be similar (second, 495 km; fourth, 524 km). The coupled stream length of fifth-order streams was reduced by 58 km during 1950–2010 and is projected to decline by a total of 103 km by 2060.

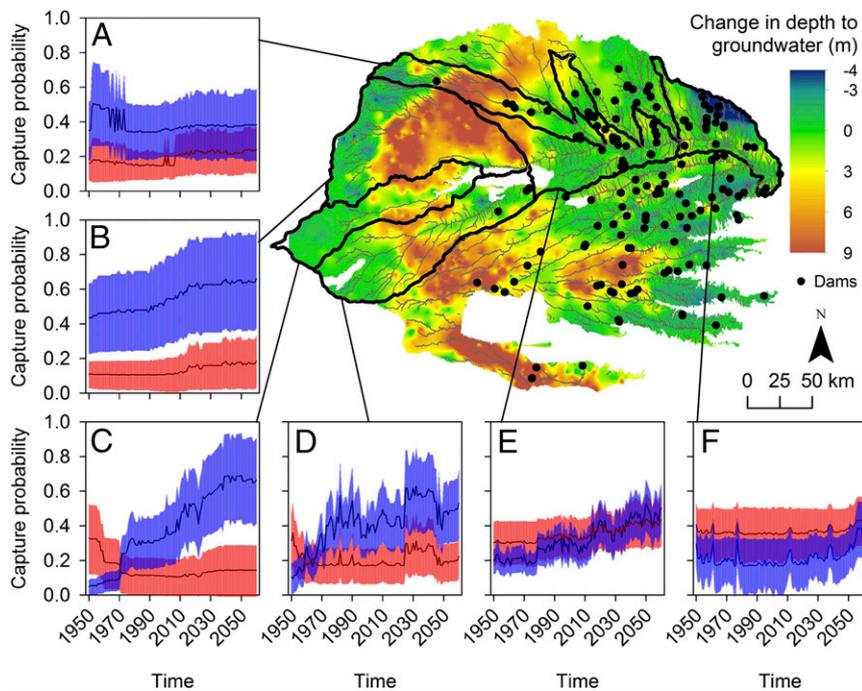
At the regional scale, the fish assemblage was transformed from dominance by large-stream fishes to small-stream fishes during 1950–1980. The assemblage remained relatively stable during 1980–2010, but projections for 2011–2060 indicate additional suppression of large-stream fishes and expansion of small-stream fishes (Fig. 2C). The average capture probability for large-stream fishes decreased by half, from 0.42 [95% confidence interval (CI) = 0.28–0.56] in 1950 to 0.20 (95% CI = 0.11–0.29) in 1980 and is predicted to decrease further to 0.16 (95% CI = 0.09–0.24) by 2060. The average capture probability for small-stream fishes nearly doubled, from 0.20 (95% CI = 0.18–0.29) in 1950 to 0.39 (95% CI = 0.26–0.51) in 1980 and is predicted to reach 0.49 (95% CI = 0.33–0.65) by 2060.

At the subwatershed scale, minimum stream flows, the number of barriers to fish movement, and total length of coupled stream varied among subwatersheds. From 1950 to 2010, the 90-d minimum flow declined in all but one subwatershed (*Table S6* and *Fig. 3*). The number of barriers remained at zero during 1950–2010 for two subwatersheds (*Fig. 3 B* and *C*), increased from 3 to 4 in one (*Fig. 3 D*), increased from 3 to 8 in one (*Fig. 3 A*), and increased from <3 to 27 in two subwatersheds (*Fig. 3 E* and *F*).



**Fig. 1.** Study region in the Great Plains of Colorado, Kansas, and Nebraska, United States showing streams over the High Plains Aquifer, groundwater observation wells, dams, and US Geological Survey streamflow gauges. Hydrologic units (shaded areas) define six subwatersheds in which detailed analyses of hydrology and fish communities were conducted. The *Inset* illustrates the upper Kansas River Basin boundary (dark shading) within the broader extent of the High Plains Aquifer (blue shading). Data are from refs. 32, 53, and 56.





**Fig. 4.** Change in estimated depth to groundwater between 1950 and 2060 for the study region. Change through time in mean (95% confidence interval) capture probability for fishes characteristic of small (<fourth-order, blue line and band) and large ( $\geq$ fourth-order, red line and band) streams are shown for six subwatersheds as follows: (A) Frenchman Creek, (B) North Fork Republican River, (C) Arikaree River, (D) South Fork Republican River, (E) Upper Republican River, and (F) Harlan County Reservoir.

caused by groundwater pumping have been reported elsewhere in the basin (34), across western Kansas (4), throughout the High Plains Aquifer (2), and globally (9).

The disproportionate decline in the prevalence of larger streams, in turn, contributed to disproportional declines in large-stream fishes. However, decline of large streams and large-stream fishes at the regional scale was confounded by a concurrent increase in the number of barriers, which are demonstrated to have negative effects on some large-stream fishes (24, 28). Our approach of scaling down to subwatersheds disentangled the relative effects of barriers and groundwater declines. Specifically, barrier numbers were greatest, and increased rapidly, in eastern subwatersheds where large-stream fish capture probabilities were highest among all subwatersheds through time. Conversely, barriers were rare or absent in western subwatersheds where small-stream fish capture probabilities were greatest or increased most rapidly, and where large-stream fish capture probabilities were least or decreased most rapidly. Large-stream fish capture probabilities were initially low or declined rapidly among upstream, western subwatersheds where extinction and colonization are naturally high for such fishes (35), and long-term declines attenuated in a downstream direction to the east (Fig. 4 C–F). These patterns collectively illustrate accelerated fish assemblage transformation along a natural stream size gradient initiated by the decoupling of surface streams from groundwater sources and ultimately resulting in the permanent loss of large-stream fishes.

Spatial patterns in historical (pre-1950) and more recent (post-1950) hydrologic alterations contributed to the observed patterns in fish assemblage change. The greatest area of increased depth to groundwater occurred in the North Fork Republican River subwatershed, and larger streams of fourth order generally dried over this area. Streams that remained were small second- and third-order channels near the westward extent of the subwatershed in areas where depth to groundwater is projected to approach the surface and create more small-stream habitat. This pattern explains the dominance by small-stream fishes in this subwatershed. In contrast, the rates of decline in coupled stream lengths and minimum flows were similar among Frenchman Creek, the Arikaree River, and the South Fork Republican River subwatersheds although Frenchman Creek did not experience the same fish assemblage transformation as the Arikaree River and South Fork Republican River subwatersheds. However, Frenchman Creek

had a large number of barriers that fragmented habitat before 1950 so it is possible that the fish assemblage was altered earlier than 1950. For example, among the large-stream fishes excluded from analysis because of rare occurrences (Table S5), four were last reported from the region by 1940 (*Hiodon alosoides*, *Macrhybopsis gelida*, *Macrhybopsis hyostoma*, and *Macrhybopsis storeniana*), and declines among three of these (all *Macrhybopsis*) have been linked to fragmentation (26). Fragmentation of Great Plains riverscapes began before 1950 (23), and recent work suggests that widespread groundwater extraction may have begun about 1930 instead of 1950 in some portions of the Great Plains (5). More historical information might be necessary for a complete understanding of the ecological consequences of groundwater extraction. Furthermore, declines in minimum flows cannot be attributed to groundwater extraction alone because surface diversions and extractions also reduce water availability in the Great Plains (10, 36), suggesting that the effects of surface barriers on assemblage transformation cannot be ignored.

The mechanisms driving differential responses to groundwater pumping by large- and small-stream fishes are reinforced by permanent water loss and barriers that fragment habitats. Larger streams contain more predictable habitats characterized by greater flows, deeper channels, longer longitudinal connectivity, and higher autochthonous energy production (37). Examples of adaptations of large-stream fishes to this environmental template include migratory behavior, flow-induced synchronized spawning, and spawning within the water column (38, 39). As groundwater pumping shortens the length of stream coupled with the aquifer and surface structures store or divert water, flows decline, channels become shallower, longitudinal connectivity is fragmented, and instream (autochthonous) energy production decreases. Collectively, these processes shift large streams into habitat templates that no longer match the evolutionary history of large-stream fishes. Rather, habitats become characteristic of those that shaped the ecology and life history of small-stream fishes, thus providing increased opportunities for expansion (40). In our study area, eastern subwatersheds with relatively stable depths to groundwater maintained large-stream fish assemblages, but western subwatersheds with increasing depths to groundwater experienced permanent reduction in large-stream fish assemblages. Unfortunately, western assemblages of large-stream fishes that decline or collapse have no opportunity for rebounding (e.g.,



estimated annual lengths of stream coupled with the aquifer. We calculated the mean and 95% confidence interval across all species classified as small-stream or large-stream inhabitants (*SI Methods*) to illustrate fish assemblage response to spatiotemporal variability in stream lengths coupled with groundwater. Although fish distributions in relation to stream size formed a continuum (Fig. S1), we used the designation of first- to third-order streams as “headwaters” (37) to facilitate comparison of how fishes in small and large streams might be affected by groundwater depletion. Fish collection methods were consistent with protocols approved by the Tennessee Technological University Institutional Animal Care and Use Committee (permit TTU-IACUC-14-15-001 to J.S.P.).

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