

VARIATION IN ABUNDANCE IN THE BARTON SPRINGS SALAMANDER ASSOCIATED WITH FLOW REGIME AND DROUGHT

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Abstract.—The Barton Springs Salamander (*Eurycea sosorum*) is an endangered species of neotenic salamander endemic to Barton Springs, a cluster of springs along the Balcones Fault Zone of the Edwards Aquifer in central Texas, USA. Anthropogenic threats to this species include habitat loss and fragmentation caused by modification of natural flow regimes by impoundment and flow diversion. Additionally, groundwater withdrawal threatens the quantity and quality of water emanating from Barton Springs. Evaluating the effects of anthropogenic threats on this species requires an understanding of the relationship between local flow regime and salamander abundance, and the influence of aquifer discharge. In this paper, we use 10 y of salamander census and flow regime data to examine variation in abundance, density, and flow regime within and among four springs during drought and non-drought. Salamander density and abundance differed significantly among sites. Abundance was associated with sediment cover, water depth, and flow velocity. Associations among flow regime characteristics differed among sites and reflect the influence of impoundments. Flow regimes also changed within sites as aquifer discharge declined. During drought, flow velocity and water depth were lower, and sediment cover was higher. There were significantly fewer juveniles, young adults, and adults during drought, and reproduction appeared to be curtailed. Local flow regime appeared to exert a dominant influence on habitat quality during non-drought, while aquifer discharge appeared to dominate during drought. Altered flow regimes and groundwater withdrawal magnify detrimental effects of droughts on *E. sosorum*. Restoration of natural flow regimes could help mitigate effects of drought on salamanders and their habitat.

Key Words.—conservation; Edwards Aquifer; endangered species; *Eurycea sosorum*; groundwater withdrawal; flow regime

INTRODUCTION

Recovery of endangered species is often difficult. Although large-scale factors driving the march to extinction are known (e.g., habitat loss, pollution), scientific information on evolutionary ecology and natural history in the wild is often lacking (Foin et al. 1998; Stearns and Stearns 2000; Bury 2006). Management can become a balance of triage to avoid immediate extinction, and collection of data on a wide range of potential factors to determine and ameliorate the causal factors. Consequently, management and recovery strategies can require drawing inferences from a broad array of disciplines and related, more common species. An example of this type of challenge is conservation of *Eurycea sosorum*, the Barton Springs Salamander (Fig. 1), in Austin, Texas, USA.

Eurycea sosorum is a solely aquatic, neotenic, epigeic species of salamander (Sweet 1982; Chippindale et al. 2000; Bendik 2006). It was added to the U.S. Endangered Species List in 1997 because of degradation of water quality and decrease in quantity

of groundwater discharge (U.S. Fish and Wildlife Service [USFWS] 1997). Typically, endangered species have small population sizes or small ranges (Terborgh and Winter 1980; Munton 1987; Mace and Kershaw 1997; Abrams 2002), both of which are true for *E. sosorum*. Since 1995, maximum observed abundance (approximately 1,900 individuals; City of Austin, unpubl. data) is small enough for this species to be considered at risk of extinction by several rules-of-thumb for population size (Muller 1950; Bell 1982; Lynch and Gabriel 1990; Lynch 1996; Maynard Smith 1998). The species also has a small range (Chippindale et al. 1993; International Union for the Conservation of Nature [IUCN] 2012; Devitt and Nissen 2018). The area of known occurrence is roughly 400 km² (McDermid et al. 2015). Recorded continuous residence is limited to the Barton Springs complex, which comprises four springs located within 350 m of one another, adjacent to or within Barton Creek, in Zilker Park, Austin, Texas (Fig. 2). Its entire range lies within a metropolitan area with a rapidly growing human population (1,299,207 Travis + Hays County; U.S. Census data 2015; <https://>



FIGURE 1. Photograph of a gravid female Barton Springs Salamander (*Eurycea sosorum*) taken in April 2008 in Eliza Spring, Austin, Texas. (Photographed by Laurie A. Dries).

factfinder.census.gov/faces/nav/jsf/pages/index.xhtml [Accessed 31 January 2017]), which is driving an increase in urban development within Austin and in the outlying catchments of the Barton Springs Segment of the Edwards Aquifer. Urban development threatens persistence of *E. sosorum* by contributing to degradation in the quality and quantity of groundwater feeding Barton Springs (Mahler and Lynch 1999; Mahler et al. 1999; Lynch et al. 2004; Mahler et al. 2004; Wong et al. 2012).

In addition, since the 19th Century, human activities in and around Barton Springs have modified salamander habitats (e.g., dams, amphitheaters, creek water bypass systems, concrete channelization, plugging of spring outlets; Fig. 2) to enhance commercial and recreational uses (Pipkin 1993. Austin History Center archive photographs <https://texashistory.unt.edu/explore/partners/ASPL/browse/> [Accessed 15 May 2016]). These modifications have resulted in incremental loss and fragmentation of habitat where these salamanders reside. Moreover, these modifications have altered the natural local flow regimes from the stream conditions under which the species evolved, to pond-like habitats (Fig. 3). While aquifer-wide water quality and quantity degradation have been recognized as major threats to the persistence of this species (USFWS 1997, 2005), local flow regime modification and its potential interaction with catchment-based environmental degradation have not been explicitly considered.

There are no published studies describing variation in average annual abundance of *E. sosorum* in each site of the Barton Springs complex over a multi-year period. Nor are there studies of the potential relationships among salamander abundance, local flow regime characteristics (e.g., flow velocity, sediment deposition,

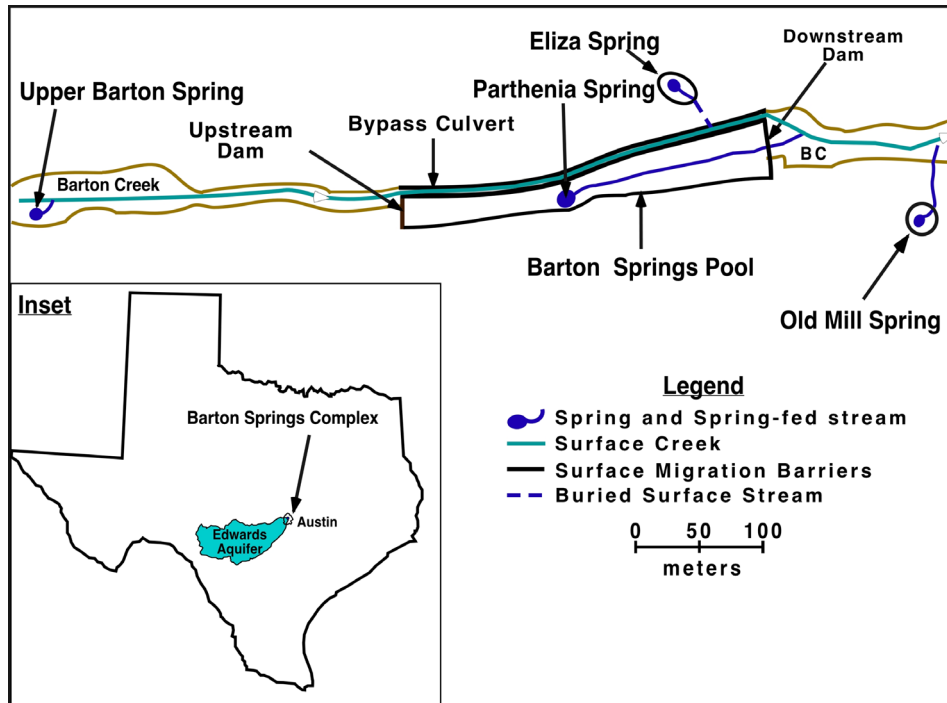


FIGURE 2. Geographic locations of the Edwards Aquifer, City of Austin, and Barton Springs (inset), and spring site locations and surface water flow paths of the Barton Springs Complex in central Texas, USA. Parthenia Spring is within Barton Springs Pool. Surface habitats among sites are fragmented by concrete obstructions that include dams separating Barton Springs Pool from the three other springs and Barton Creek except during large floods, and a bypass culvert separating Barton Creek and Eliza Spring from Barton Springs Pool. The outflow stream from Eliza Spring is buried in a concrete pipe (shown as blue dashed line) that joins Barton Creek inside the box culvert. Predatory fishes and human recreational activities render surface aquatic habitat between Old Mill, Eliza, and Upper Barton springs largely unsuitable for salamanders.

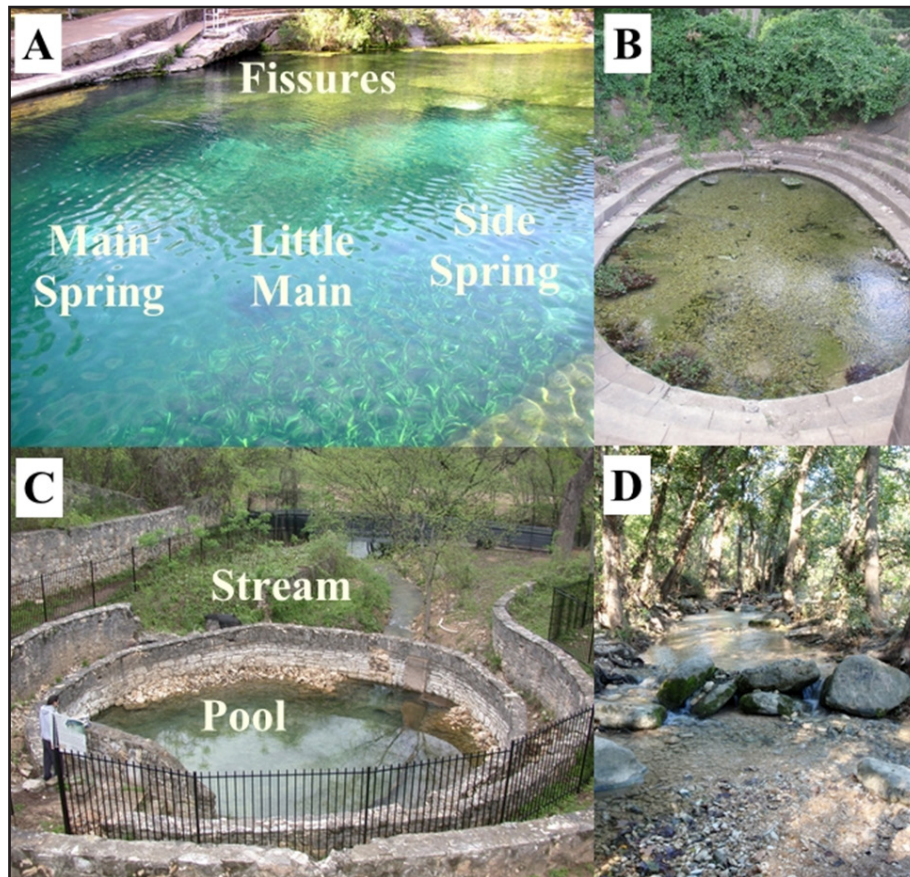


FIGURE 3. Spring sites of the Barton Springs Complex: A) The deep (foreground) and shallow (background) survey areas of Parthenia Spring. The spring is bounded by upstream and downstream dams (not shown), and thereby submerged beneath several feet of water. B) Eliza Spring has a concrete bottom with overlying rock and is surrounded by an amphitheater. The outflow stream enters the buried pipe at the far end of the spring pool. C) Old Mill Spring is surrounded by amphitheater walls that obstruct free water flow to the outflow surface stream. D) Upper Barton Spring is in the basin of Barton Creek and has no un-natural impoundments.

water depth), and aquifer conditions. An examination of these factors would improve our understanding of what constitutes good habitat and would contribute to a greater understanding of how we expect natural and anthropogenic environmental variation to affect *E. sosorum* and over what time frames.

Our objective here is to identify abiotic habitat characteristics of flow regimes that influence salamander abundance, and whether those factors vary among sites and aquifer conditions. We use data from 10 y of monitoring to ask the following questions about *E. sosorum* and its habitat: (1) does the density of salamanders in surface habitat vary among spring sites; (2) does salamander abundance vary within spring sites; (3) do flow regime characteristics vary among and within sites; (4) are flow regime characteristics associated with salamander abundance within sites; and (5) do salamander abundance and flow regime vary with aquifer discharge condition (drought versus non-drought)? We use this information to discuss variation in abundance among populations of *E. sosorum*, and

how anthropogenic modifications of local flow regime and anthropogenically driven depletion of groundwater may affect the fate of this species.

MATERIALS AND METHODS

Study sites.—*Eurycea sosorum* inhabits four springs of the Barton Springs complex, Parthenia Spring in Barton Springs Pool, Eliza Spring, Old Mill/Sunken Garden Spring, and Upper Barton Spring (Chippindale et al. 1993), Texas, USA. These springs are in close proximity to one another (Fig. 2) and hydrologically connected via the subterranean conduits of the underlying karst aquifer (Brune 1975, 1981; Slade et al. 1986; Hauwert 2009). In the past, there were surface connections among springs via outflow streams that converged with Barton Creek. Although subterranean connections remain, surface habitats are fragmented by dams, amphitheaters, a creek water diversion culvert, and interment of outflow streams (Fig. 3). No surface migration routes from Parthenia Spring to the other

springs exist today. Although surface migration routes exist between Eliza, Old Mill, and Upper Barton springs (Fig. 2), habitat along those routes is inhospitable (e.g., overabundance of predatory fishes, high amount of human recreation). In addition, we found no evidence of salamander movement among sites over the period of this study (Dries et al. 2013; Nathan Bendik, pers. comm.), which suggests salamander populations are partially or completely isolated. Records indicate that water flow from Parthenia and Eliza springs is perennial, while Old Mill Spring occasionally goes dry during severe drought (Brune 1975, 1981). In Upper Barton Spring, water flow at the surface is intermittent; it disappears when discharge from Barton Springs, as measured by the U. S. Geological Survey, drops below 1.13 m³/s.

The spring sites differ in size and extent of modification to flow. Parthenia Spring is the largest (approximately 557 m²) and most altered site. It is bounded by two large dams and has the deepest water (0.9–5.2 m; Fig. 3A). Eliza Spring is a small spring pool (74 m²) with a concrete floor overlain by rocky substrate and a buried outflow stream leading to Barton Creek (Figs. 2, 3B). Furthermore, the spring is surrounded by a concrete amphitheater. The flow regime of the spring pool is stream-like and water depth is managed to keep it at about 0.3 m. Old Mill Spring is composed of a spring pool (61.7–133 m²) and an outflow stream during non-drought (0–49.7 m²). The spring pool is pond-like and surrounded by an amphitheater, but the stream, when present, has more natural flow (Fig. 3C). Upper Barton Spring is the smallest site and has the most natural flow regime (Fig. 3D). The average size of the surface habitat is 45.9 m² and can be as large as 81.8 m² under high aquifer conditions (> 2.54 m³/s). No artificial impoundments or permanent structures surround this spring; however, the upstream dam of Barton Springs lies approximately 82 m downstream of the spring and human recreational activity includes hand-built temporary rock dams across the outflows. Upper Barton and Parthenia springs are open to human recreation, while Eliza and Old Mill springs are not, but were until the 1950s and 1998, respectively.

Salamander abundance surveys.—The staff of the City of Austin, including the authors, collected *Eurycea sosorum* abundance data from July 2003 through December 2013 from all spring sites. We conducted surveys monthly in accordance with USFWS permits and Habitat Conservation Plan (City of Austin 1998). If circumstances in a particular month prevented conducting a survey, it was skipped until the next month, which resulted in some survey intervals of 30, 60, or 90 d. The number of surveys per site, therefore, varied over the years (Fig. 4). Because Upper Barton Spring

flows intermittently, low sample sizes correspond with years that included periods of dry surface habitat. We conducted all surveys during daylight hours of one day. Depending on the water depth at each site, we waded, snorkeled, or used SCUBA to conduct surveys. We did not survey Parthenia and Upper Barton springs when they were inundated by floodwater from Barton Creek because underwater visibility was typically < 0.3 m and current velocity was too swift to ensure safety of surveyors. Generally, floodwater did not inundate Eliza and Old Mill springs.

We estimated salamander abundance in all spring sites using a modification of the drive survey method (Rasmussen and Doman 1943; Gilbert and Grieb 1957). We searched all wetted surface habitat in Eliza, Old Mill, and Upper Barton springs, and a large, contiguous area of Parthenia Spring where groundwater issues from the aquifer. The modified drive method consisted of observers oriented in a line perpendicular to the current, moving in concert from downstream to upstream, removing all loose substrate and replacing it behind the line. This creates a moving, 15–25.4-cm strip of coverless habitat that salamanders are reticent to cross (Cecala 2012). We added each salamander that crossed coverless habitat from upstream to downstream to the cumulative number. Furthermore, we subtracted from the cumulative number any salamander returning to upstream habitat from behind the line. When surveyors were near aquifer openings, we added salamanders observed moving forward and retreating into the aquifer to the total. We divided salamander abundance by survey area to obtain density.

We measured total area surveyed for each spring site and each survey. The survey area of Eliza Spring was constant. We chose the area surveyed at Parthenia Spring based on available staff, time, and SCUBA safety. We always surveyed the large spring mouths (Main Spring, Little Main and Side Spring; Fig. 3A) because data collected prior to 2003 indicated that most salamanders were found in these areas (City of Austin, unpubl. data). When feasible, we also surveyed the upstream fissures (Fig. 3A). Our surveys included all of wetted habitat in Old Mill and Upper Barton springs, but the total wetted area expanded or contracted with changes in aquifer discharge. When aquifer discharge was < 1.13 m³/s Upper Barton Spring was dry, while at < 0.71 m³/s, the Old Mill Spring Stream was dry.

We assigned salamanders encountered during abundance surveys to one of three categories based on total length (TL; < 25.4 mm, 25.4–50.0 mm, and ≥ 50 mm). These are thought to represent juvenile (< 6 mo), young adult (6–12 mo), and adult (> 12 mo) life stages, respectively. We verified the suitability of these categories using the following procedure. We captured 114 salamanders from Eliza Spring on November 19

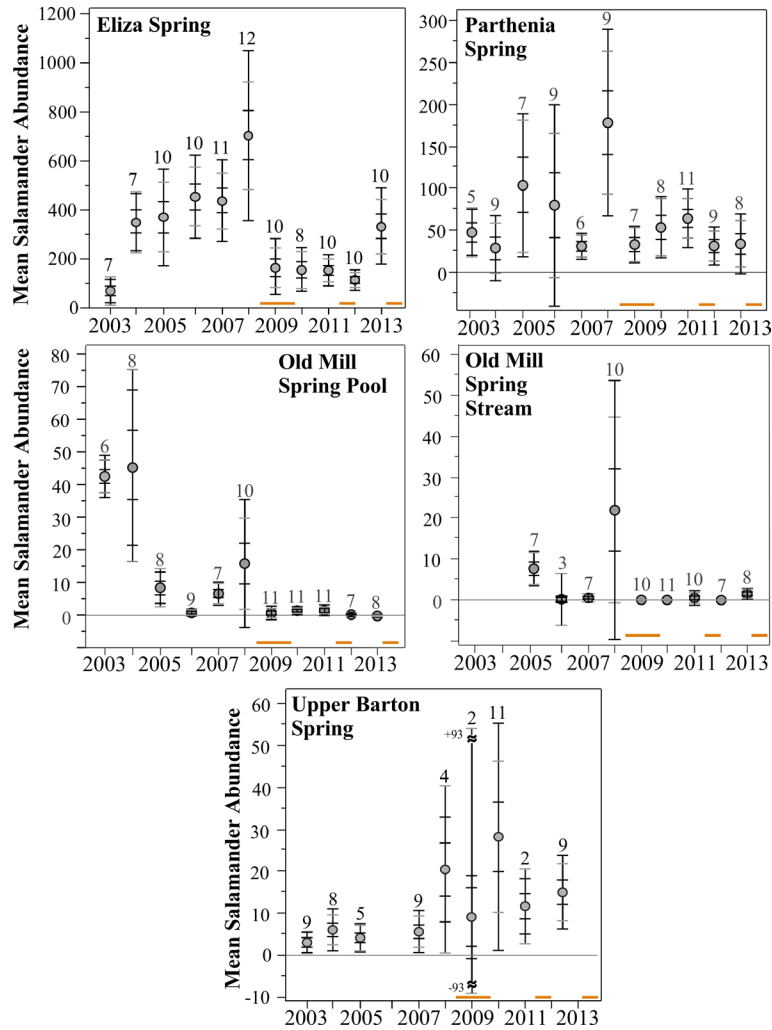


FIGURE 4. Mean yearly abundance of the Barton Springs Salamander (*Eurycea sosorum*) by spring site. Standard error and standard deviation bars are shown in black, 95% confidence interval bars shown in gray. Sample size (n) for each year is shown above each annual mean. Old Mill Spring Pool and Old Mill Spring Stream are shown separately because many aspects of the habitats differ significantly (see Fig. 5). Drought periods (≤ 0.71 m³/s) are indicated by brown bars on the abscissa. Vertical axis scale differs among sites. Upper Barton Spring was dry for all of 2006 and 2013 (see Fig. 6 for all dry periods).

and December 19, 2003 and measured total length (TL) and snout-vent length (SVL) with Vernier calipers. We used these data in a linear regression to develop the following equation:

$$SVL \text{ (mm)} = 2.397 + 0.501 \times TL \text{ (mm)}; (P < 0.001, r^2 = 0.934).$$

We used this equation to convert chosen total length categories into snout-vent length (SVL) categories (juvenile < 15.1 mm SVL, young adult 15.1–27.5 mm, and adult ≥ 27.5 mm SVL). These categories are consistent with information on life-stage/size relationships for juvenile and sexually mature *E. sosorum* museum specimens (Chippindale et al. 1993), captive-bred *E. sosorum* (Chamberlain and O'Donnell 2003), *E. nana*, the San Marcos Salamander (Najvar

2001), and *E. neotenes*, the Texas Salamander, of Lamb and Turtle Creek springs (Bruce 1976), now recognized as the Valdina Farms Salamander, *E. troglodytes* (Chippindale et al. 2000).

Flow regime characteristics.—We divided survey area of each spring site into sections of known size at the beginning of the study. Defined section sizes differed among and within spring sites but remained the same throughout the study. Within each section, we then measured or estimated habitat characteristics associated with flow regime. We estimated visually the percentage of each section with wet habitat and percent of substrate area covered with an overlying layer of sediment. We photographed each section before each survey; we verified visual habitat composition estimates using a

grid overlain on the overhead photograph. We used percentage wetted habitat to calculate square meters of wetted habitat from known section sizes and summed for total survey area. We averaged percentage sediment cover values from all sections within a spring to obtain a single value per site. We measured sediment depth to the nearest millimeter in five randomly chosen locations in each section of each spring. We measured water depth to the nearest mm in five randomly chosen locations in three of the springs. Because water in Parthenia Spring was unnaturally deep (1.5–6.1 m), we measured water depth to the nearest foot using SCUBA depth gauges and converted those measurements to cm. We averaged water and sediment depth values within a section and then averaged section means to obtain a grand mean value for each survey date at each site. From 2008 through 2013, we used a Marsh-McBirney Flo-Mate 2000® (Hach Company, Loveland, Colorado, USA) flow meter to measure flow velocity at the substrate during each survey at Eliza, Old Mill, and Upper Barton springs. We measured flow velocity in Eliza Spring at 15 locations where groundwater entered the spring pool and flowed roughly parallel to the substrate. We recorded similar measurements at five locations in the Old Mill Spring Pool and the Old Mill Spring Stream, and at five locations in the three outflow streams of Upper Barton Spring. We did not measure flow velocity at Parthenia Spring.

Aquifer condition and discharge.—We used U.S. Geological Survey (USGS) estimates of discharge from the Barton Springs complex (all four springs combined). Personnel of the USGS calculated these values using a rating curve based on the gauge of water level in Barton Springs Pool near Parthenia Spring, and verified with periodic physical discharge measurements of Barton Creek downstream of all four springs. We used the data to categorize climatic condition as drought (≤ 0.71 m³/s) or non-drought (> 0.71 m³/s; http://waterdata.usgs.gov/tx/nwis/dv/?site_no=08155500&agency_cd=USGS&referred_module=sw). There were three drought periods during this study, June 2008 to September 2009, July 2011 to January 2012, and March to September 2013.

Statistical analyses.—We tested all data for adherence to assumptions of typical parametric statistics (Zar 1984; Sokal and Rohlf 1995). Our data did not meet the assumptions of normality and homogeneity of variances. In addition, there was evidence of serial autocorrelation at 1-mo intervals. We tried a variety of data transformations to eliminate these problems, but we were unsuccessful. Therefore, we used non-parametric tests with a significance threshold of $\alpha = 0.05$ (Zar

1984), except where noted. Although the probability of Type II error is increased with non-parametric tests, their power and reliability are more robust to violations of assumptions than parametric tests (Tukey 1962; Seaman and Jaeger 1990; Potvin and Roff 1993).

We used Mann-Whitney U and Kruskal-Wallis tests (Zar 1984; Sokal and Rohlf 1995) to look for differences in salamander density and flow regime characteristics among sites. We used these results to evaluate whether to pool data from all sites. We found significant differences among sites in salamander density and some flow regime characteristics. Consequently, we chose to analyze each site separately for relationships among flow regime characteristics, salamander abundance, and aquifer condition.

We used Pearson Rank correlations to examine relationships among flow regime characteristics and associations with salamander abundance (Zar 1984; Sokal and Rohlf 1995). We examined potential differences among drought versus non-drought conditions within sites using a threshold of 0.71 m³/s discharge from all Barton Springs sites combined. We used this threshold because we thought it was more biologically relevant to *E. sosorum* than a geological or climatically based threshold. This discharge threshold is correlated with contracting surface habitats and with dissolved oxygen concentrations (Mahler and Bourgeais 2013) that compromise survival and growth of *E. sosorum* (Woods et al. 2010).

We tested for difference in abundance of salamanders between drought and non-drought within sites using Mann-Whitney U tests. We analyzed juvenile, young adult, and adult abundance separately to determine if drought affects all size classes equally because adults may be more resilient to physiological stress than younger salamanders (Duellman and Trueb 1986). We used StatView software (SAS Institute Inc., Cary, North Carolina, USA) for analysis of all data. For all tests, $\alpha = 0.05$.

RESULTS

Salamander density and abundance.—Abundance and density of *E. sosorum* differed significantly among sites ($H = 236.9$, $P < 0.001$, $H = 141.8$, $P < 0.001$, respectively). Average annual abundances ranged across several orders of magnitude, reaching highs in Old Mill Spring Pool in 2004, in Eliza, Parthenia, and Old Mill Spring Stream in 2008, and in Upper Barton Spring in 2010 (Fig. 4). Highest to lowest average densities over the 10-y period occurred in Eliza Spring ($4.32/\text{m}^2 \pm 3.4$ SD), Parthenia Spring ($0.25/\text{m}^2 \pm 0.3$), Upper Barton Spring ($0.24/\text{m}^2 \pm 0.3$), and Old Mill Spring ($0.093/\text{m}^2 \pm 0.2$). There was a significant difference in salamander

TABLE 1. Summary of significant results from Spearman Rank Correlation tests of flow regime and salamander abundance of the Barton Springs Salamander (*Eurycea sosorum*) in each spring site in central Texas, USA. For all other variables, there were no significant correlations ($\rho = -0.001$ to 0.529 , $P_s = 0.150$ – 0.990). The theoretical expected direction of association among variables in a naturally flowing, shallowly sloped stream is indicated in parentheses. Sites are indicated by the abbreviations ES (Eliza Spring), PS (Parthenia Spring), OMSP (Old Mill Spring Pool), OMSS (Old Mill Spring Stream), and UBS (Upper Barton Spring). Variable abbreviations are Sediment Depth (SD), Sediment Cover (SC), and Salamander Abundance (SA). The direction of observed association follows each site abbreviation; items in bold are consistent with expectations. Rho (ρ) values are provided following each site abbreviation. Statistical significance is denoted with one (*), two (**), or three (***) asterisks for $P \leq 0.05$, $P \leq 0.005$, or $P \leq 0.001$, respectively.

	Flow Velocity	Non-drought H ₂ O Depth	% Sediment Cover	Flow Velocity	Drought H ₂ O Depth	% Sediment Cover
SD	(-) ES 0.303*	(+)	(+) ES 0.271* OMSS 0.367* PS -0.261*	(-)	(+) OMSP -0.521*	(+)
% SC	(-) ES 0.563*** OMSP 0.447*	(+) ES 0.468*** PS 0.457* UBS 0.418*		(-) OMSS -0.808***	(+)	
H2O Depth	(-) ES 0.368* OMSP 0.627***		(+)	(-)		(+)
SA	(+)	(-) ES -0.367** OMSP 0.513***	(-) ES -0.436*** OMSP -0.411** PS -0.329*	(+) OMSP 0.458* OMSS 0.521*	(+) ES 0.442*	(-) ES -0.386* OMSS -0.575*

density in the Old Mill Spring Pool versus the Old Mill Spring Stream ($U = 3685.5$, $z = -2.081$, $P = 0.038$).

Flow regime.—Flow regime characteristics varied among sites, and within sites between drought and non-drought. Within Old Mill Spring, flow regime characteristics differed significantly between the Pool and the Stream (flow velocity: $U = 333.0$, $z = -7.319$, $P < 0.001$; sediment depth: $U = 1284.0$, $z = -4.857$, $P < 0.001$; percentage sediment cover: $U = 559.5$, $z = -8.824$, $P < 0.001$; water depth: $U = 483.0$, $z = -7.873$, $P < 0.001$; Fig. 5). Therefore, we analyzed these two locations separately.

Among sites, flow velocity, sediment depth, percent sediment cover, and water depth differed significantly (Fig. 5). Within Eliza Spring, mean flow velocity, sediment depth, percentage sediment cover, and water depth were all significantly lower during droughts than non-droughts (flow velocity: $U = 110.5$, $z = -6.056$, $P < 0.001$; sediment depth: $U = 702.0$, $z = -2.820$, $P = 0.005$; sediment cover: $U = 690.0$, $z = -2.829$, $P = 0.005$; water depth: $U = 587.0$, $z = -2.687$, $P = 0.007$; Fig. 5). In Old Mill Spring Pool, flow velocity and water depth were significantly lower during drought versus non-drought ($U = 41.0$, $z = -5.693$, $P < 0.001$; $U = 87.0$, $z = -5.920$, $P < 0.001$, respectively), while sediment cover was higher ($U = 560.5$, $z = -2.352$, $P = 0.019$). There was no significant difference in sediment depth ($U = 718.0$, $z = -0.224$, $P = 0.823$). In the Old Mill Spring Stream, flow velocity and water depth were

lower during drought ($U = 82.0$, $z = -4.503$, $P < 0.001$ and $U = 68.0$, $z = -5.127$, $P < 0.001$, respectively), while sediment cover was higher ($U = 105.5$, $z = -4.920$, $P < 0.001$). There was no significant difference in sediment depth ($U = 364.0$, $z = -0.226$, $P = 0.821$). There were no significant differences in any variable between drought and non-drought in Parthenia Spring (sediment depth: $U = 581.5$, $z = -0.112$, $P = 0.911$; sediment cover: $U = 621.0$, $z = -0.579$, $P = 0.562$; water depth: $U = 196.5$, $z = -0.476$, $P = 0.634$; Fig. 4). Upper Barton Spring is dry during drought.

We found significant associations among flow regime variables within sites during both drought and non-drought (Table 1). In Eliza Spring, during non-drought, flow velocity is significantly positively associated with sediment depth, percent sediment cover, and water depth (Table 1). Water depth was positively associated with sediment cover, and sediment cover is positively associated with sediment depth (Table 1). There were no significant relationships among these variables during drought.

In Old Mill Spring Pool during non-drought, flow velocity was positively associated with sediment cover and water depth (Table 1). During drought, water and sediment depth were negatively associated. In Old Mill Spring Stream during non-drought, percentage sediment cover was positively associated with sediment depth. During drought, flow velocity was negatively associated with percentage sediment cover. In Parthenia Spring during non-drought, water depth and sediment cover

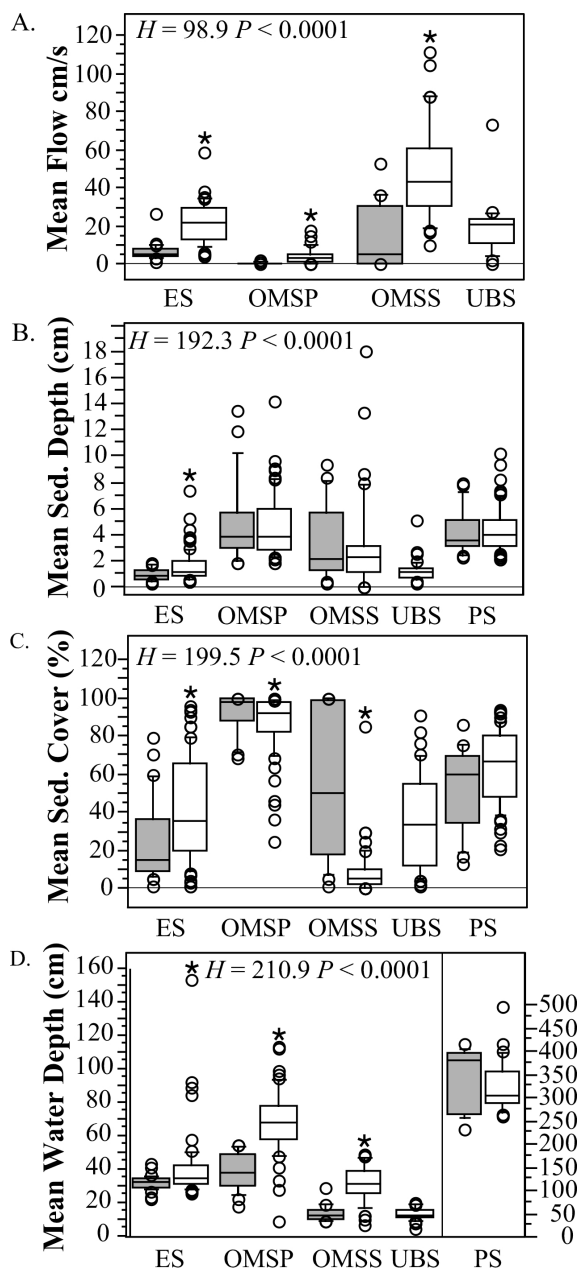


FIGURE 5. Flow regime characteristics of the Barton Springs Complex in Austin, Texas, USA, with medians, quartiles, and ranges of (A) flow velocity, (B) sediment depth, (C) percentage sediment cover, and (D) water depth in Eliza Spring (ES), Old Mill Spring Pool (OMSP), Old Mill Spring Stream (OMSS), Parthenia Spring (PS), and Upper Barton Spring (UBS). Gray shading indicates drought data. Upper Barton Spring is dry during drought. The statistical result of analysis of difference among sites is listed on each graph. An asterisk indicates a significant difference between drought and non-drought within a site (statistics in text). There are no velocity data for Parthenia Spring and the water depth scale for Parthenia Spring is indicated on the right y-axis.

were significantly positively associated, and sediment cover was negatively associated with sediment depth (Table 1). There were no significant associations during droughts in this site. Upper Barton Spring flowed during non-drought only and the significant result was a positive association between water depth and sediment cover (Table 1).

Flow regime and salamander abundance.—Salamander abundance was negatively associated with sediment cover during non-drought and drought in Eliza Spring, during non-drought only in Parthenia and Old Mill Spring Pool, and during drought only in Old Mill Spring Stream (Table 1). During non-drought, salamander abundance and water depth were negatively associated in Eliza Spring, and positively associated in Old Mill Spring Pool. In Eliza Spring this association was significantly positive during drought (Table 1). During drought, salamander abundance was positively associated with flow velocity in Old Mill Spring Pool and Stream (Table 1). Salamander abundance in Upper Barton Spring was not associated with any flow regime variable.

Salamander abundance and drought.—Salamander abundance within sites was significantly lower during drought compared with non-drought in Eliza Spring, Parthenia Spring, and Old Mill Spring (Table 2). There were significantly fewer adults during drought in Eliza, Parthenia, and Old Mill springs (Table 2). There were fewer young adults in Old Mill Spring, and fewer juveniles in Eliza Spring and Old Mill Spring (Table 2, Fig. 6). Upper Barton Spring was dry during droughts; consequently, there were no salamanders in surface habitat to compare with non-drought.

Discharge of Barton Springs was significantly associated with total salamander abundance in Old Mill Spring ($\rho = 0.467, z = 4.645, P < 0.001$), and Upper Barton Spring ($\rho = 0.451, z = 3.930, P < 0.001$), but not in Eliza Spring ($\rho = -0.123, z = -1.276, P = 0.200$) or Parthenia Spring ($\rho = -0.162, z = -1.536, P = 0.120$). However, the discharge of Barton Springs was significantly positively associated with salamander abundance six months later in Parthenia Spring ($\rho = 0.453, z = 3.536, P < 0.001$) and Old Mill Spring ($\rho = 0.373, z = 3.056, P = 0.002$).

DISCUSSION

Salamander density and abundance.—Abundance and density of *E. sosorum* in surface habitat is widely variable among and within spring sites, with episodes of many salamanders interspersed by periods of few. Periods of high and low abundance are generally

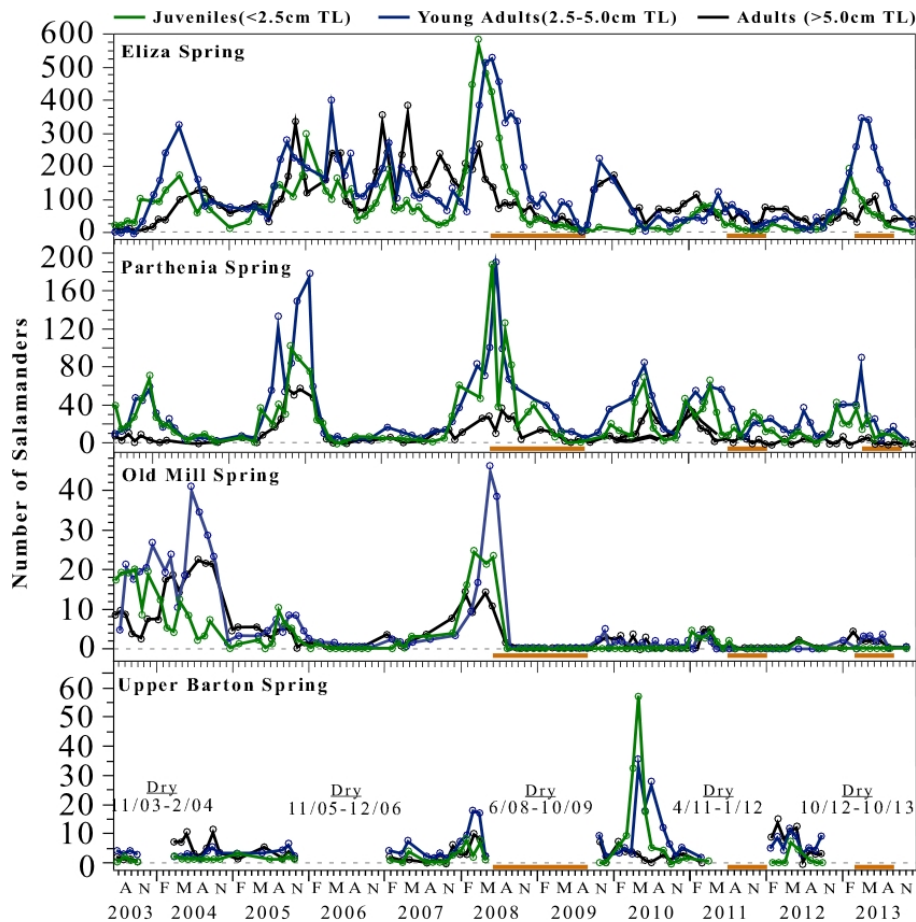


FIGURE 6. Variation in abundance of the Barton Springs Salamander (*Eurycea sosorum*) by size class. Green lines show change in abundance of juveniles, blue lines, of young adults, and black lines, of adults. Brown lines along the abscissa represent periods of drought ($\leq 0.71 \text{ m}^3/\text{s}$). Dashed line represents zero. Dots indicate data points. Note the differences in y-axis scale among plots.

concordant among spring sites. While the ranges in salamander abundance and density differ among sites, perhaps surprisingly, they are not concordant with size of surface habitat. Eliza Spring, the second smallest site, generally has the highest abundance and density. Parthenia Spring, with roughly 10 times the surface habitat, has half as many salamanders and far lower density. Abundances in Upper Barton and Old Mill springs are lower still, although density in Upper Barton Spring is similar to Parthenia Spring. This suggests that local surface habitat condition exerts an influence on salamander abundance.

Flow regime.—Our data indicate that under a given aquifer condition flow regimes differ among sites and that flow regimes differ within sites among aquifer conditions. Some sites are more stream-like while others are more pond-like. Many of the associations among flow regime characteristics documented here confound our expectations (See Table 1) of characteristics of

natural spring-fed streams. In a naturally flowing stream, we expect shallower water to flow faster, and faster water to flush out excess sediment and help prevent its deposition (Leopold et al. 1992). Further, we expect sediment depth and cover to decrease with increasing flow velocity (Leopold et al. 1992). In the absence of impoundments, we expect these relationships to be consistent among all sites (Leopold et al. 1992). Almost half of the significant associations we found were contrary to these expectations. In addition, drought diminishes or reverses expected relationships among flow regime characteristics. The deviations can be explained, in part, by the impoundment of water flow and other human activities (Wetzel 2001). Impoundment affects flow velocity, water depth, and accumulation and distribution of sediment that enters surface habitats from the aquifer or floods (Leopold et al. 1992). The influence of impoundments can be magnified under drought conditions (Leopold et al. 1992).

Dries and Colucci.—Flow regime and abundance of *Eurycea sosorum*.

TABLE 2. Mean \pm standard deviation, and standard error (se) of abundance of each life stage of the Barton Spring Salamander (*Eurycea sosorum*) in Eliza, Parthenia, and Old Mill Spring during drought ($\leq 0.71\text{m}^3/\text{s}$) and non-drought ($> 0.71\text{m}^3/\text{s}$) periods from 2003–2013. Drought periods are June 2008 to September 2009, July 2011 to January 2012, and March 2013 to September 2013. Bold text indicates a significant difference between drought and non-drought.

	Juvenile	Young Adult	Adult
Eliza Spring			
Non-Drought (n = 66)	101.9 \pm 131.7 (16.2)	148.1 \pm 116.3 (14.3)	117.2 \pm 800.8 (9.9)
Drought (n = 31)	46.2 \pm 48.6 (8.7)	153.5 \pm 111.8 (20.1)	58.5 \pm 37.3 (6.7)
Mann-Whitney <i>U</i>	<i>U</i> = 770.5, <i>P</i> = 0.019	<i>U</i> = 1036.0, <i>P</i> = 0.67X	<i>U</i> = 673.0, <i>P</i> = 0.002
Parthenia Spring			
Non-Drought (n = 67)	25.4 \pm 31.5 (3.9)	34.4 \pm 40.0 (4.9)	10.0 \pm 13.6 (1.7)
Drought (n = 24)	19.6 \pm 25.4 (5.1)	25.7 \pm 25.8 (5.3)	4.6 \pm 7.4 (1.5)
Mann-Whitney <i>U</i>	<i>U</i> = 704.5, <i>P</i> = 0.370	<i>U</i> = 722.5, <i>P</i> = 0.46X	<i>U</i> = 521.5, <i>P</i> = 0.010
Old Mill Spring			
Non-Drought (n = 67)	4.0 \pm 6.5 (0.8)	6.7 \pm 10.3 (1.2)	4.2 \pm 6.0 (0.7)
Drought (n = 29)	1.0 \pm 4.3 (0.8)	1.6 \pm 7.0 (1.3)	0.8 \pm 2.0 (0.4)
Mann-Whitney <i>U</i>	<i>U</i> = 610.0, <i>P</i> = 0.001	<i>U</i> = 456.0, <i>P</i> < 0.001	<i>U</i> = 568.0, <i>P</i> < 0.001

Flow regime and salamander abundance.—Our results suggest that flow regimes exert an influence on salamander abundance. Higher salamander abundance was associated with lower sediment cover in all sites. Other flow regime characteristics that influenced salamander abundance varied among sites depending on the degree of impoundment. Despite the variation among sites, it appears that overall, *E. sosorum* fared better in habitats with more freely flowing water and less sediment. This is consistent with inferences from previous reports on this species (USFWS 2005) and other neotenic species of *Eurycea* (Bonett and Chippindale 2006; Bowles et al. 2006; Bonett et al. 2014).

The benefits of flowing water to *E. sosorum* are not surprising considering the evolutionary history of central Texas neotenic *Eurycea*. The entire clade consists of species that evolved and reside in spring-fed streams (Sweet 1982; Wiens et al. 2003, Hillis et al. 2001; Petranka 1998; Bowles et al. 2006). Higher flow velocities of streams and rivers influence every part of the aquatic ecosystem (Liss 1973; Leopold et al. 1992; Giller and Malmqvist 1998; Sabor et al. 1999; Wetzel 2001). Natural flow regimes help create silt-free interstitial spaces in rocky substrate that can be inhabited by aquatic flora and fauna (Nowell and Jumars 1984; Poff and Ward 1989; Poff et al. 1990; Vogel 1994; Bunn and Arthington 2002), including *Eurycea* salamanders (Tupa and Davis 1976; Randolph 1978; Tumilson and Cline 2003; Bowles et al. 2006; Martin et al. 2012). Faster, unidirectional water flow has long been known to favor growth of tightly attached algae (Fritsch 1929; Blum 1960; Stevenson 1983; Korte and Blinn 1983; Reiter and Carlson 1986) and promote greater diversity of stream-adapted invertebrates (Hynes 1972; Vogel

1994; Bunn and Arthington 2002). Water flow also helps maintain high water quality in rivers and streams (Spellman and Drinan 2001). Periodic disturbance imposed by natural variation in water flow also plays a critical role in stream ecosystems (Resh et al. 1988).

Therefore, flow regime alterations can have detrimental effects on resident fauna. Alteration of flow regime in the San Marcos River of central Texas has decreased the frequencies of small and large floods, resulting in a shift in the dominant species from endemic specialists to generalists (Perkin and Bonner 2011). River channelization and impoundment has restricted the distribution of *E. junaluska* (Junaluska Salamander) to a smaller portion of its natural range (Chattin et al. 2007). Likewise, this study suggests that impoundments of three of the four springs in the Barton Springs complex inhibit the ability of endangered *E. sosorum* to thrive and recover by altering natural flow regimes.

Finally, the apparent decoupling of flow velocity with other flow regime factors during drought at nearly all sites highlights the interaction between these two habitat determinants. During drought, low aquifer discharge has a more dominant effect than flow regime on local habitat conditions. While the reverse is apparently true during non-drought; local flow regime is the more dominant force driving habitat condition.

Salamander abundance and drought.—Drought has detrimental effects on abundance and reproduction of *E. sosorum* in surface habitats. There were significantly fewer salamanders during drought in all three perennial spring sites. The very low numbers of juveniles that we observed suggests that adult reproduction is curtailed when a drought lasts more than a few months. This is

consistent with theoretical and empirical demonstrations of resource allocation for long-lived animals (Pianka 1983; Harris and Ludwig 2004; Takahashi and Pauley 2010). Adults that will have more than one lifetime opportunity to reproduce are expected to allocate metabolic energy to survival alone when environmental conditions are poor (Pianka 1983). *Eurycea sosorum* are long-lived (> 12 y in captivity) and reproduce more than once in a lifetime (Chamberlain and O'Donnell 2003); consequently, the lack of constant, year-round reproduction and low abundance of juvenile *E. sosorum* at the surface suggests that in the wild, these salamanders curtail reproduction during droughts.

Alternatively, reproduction could occur at rates similar to those during non-drought but be confined to subsurface habitat during drought, with juveniles suspending growth (Gillespie 2011). We have no evidence that juveniles can suspend growth for the 7–13 mo of drought observed in this study. Furthermore, post-drought, small juveniles and hatchlings (8–10 mm TL, partial or fully developed limbs, sparse pigmentation; USFWS 2005; Chamberlain and O'Donnell 2003) appear in surface habitat within a month or two of the appearance of adults.

It is also apparent that salamander abundance and reproduction can increase when environmental conditions are good, but the proximate factors that trigger juvenile growth, onset of movement into surface habitat, or bouts of reproduction are not clear. During this study, changes in abundance of salamanders of all size classes did not occur immediately after cessation of drought; they lagged months behind increases in discharge. Therefore, direct and indirect effects of drought on salamanders may persist for some time after the return of higher aquifer discharge. The effects on the long-term persistence of *E. sosorum* of the frequent, repeated, and extended droughts that are expected in the future (Smith and Hunt 2010) may depend on not only the duration and frequency of drought, but also the duration of intervening non-drought conditions.

Conservation of *Eurycea* at Barton Springs requires consideration of the evolutionary adaptations of each species and how anthropogenic alterations of habitat impose selection countering those adaptations (contemporary evolution *sensu* Stockwell et al. 2003). Limiting the severity of drought by protecting aquifer groundwater supply is an important catchment-scale conservation goal; depletion of the aquifer is occurring at a rate faster than this species can adapt. Given that the effects of drought are magnified by impoundments (Giller and Malmqvist 1998), that impoundments change local flow regimes, and that *E. sosorum* abundance is associated with local flow regimes, a second worthy conservation goal is to reverse flow regime alterations.

Such efforts could not only improve habitat, they could potentially help mitigate the effects of drought.

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