

RESEARCH ARTICLE

Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape

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Funding information

National Institute of Food and Agriculture, Grant/Award Numbers: HATCH Project 1017538 and 1017538; Great Plains Landscape Conservation Cooperative; Kansas Department of Wildlife, Parks and Tourism

Abstract

Dryland stream fishes are adapted to highly connected habitats with unpredictable hydrologic conditions, including frequent low flows and sometimes extreme drought. The low flow recruitment hypothesis predicts that some fishes spawn in main channel habitats during low flows when water temperatures and prey densities are high. However, extreme low flows during drought periods might be disruptive even among fishes whose life histories otherwise benefit from lower flows. We studied recruitment dynamics of six fishes (family Cyprinidae) at 15 sites in a fragmented Great Plains riverscape in Kansas, USA, during 2 years of extreme drought. We tracked the chronology of gonadal development and age 0 recruitment to test the hypothesis that recruitment by fishes that broadcast spawn planktonic ova would be less successful compared with fishes that spawn demersal or adhesive ova. We found all six taxa were reproductively active but recruitment was evident for only four. The two species for which recruitment was not evident, peppered chub (*Macrhybopsis tetranema*) and silver chub (*Macrhybopsis storeriana*), are confirmed or suspected pelagic-broadcast spawning fishes that have declined in other fragmented and dewatered Great Plains riverscapes. Our data highlight the potential for extreme low flows within isolated stream fragments to cause complete or near-complete recruitment failure for pelagic-broadcast spawning fishes, especially those with small population sizes. Failed recruitment during extreme drought may be related to spawning mode, ova characteristics, or both. Our work informs management of fish diversity in drought-prone riverscapes by establishing mechanistic linkages among extreme drought, fish recruitment, and assemblage structure.

KEYWORDS

aquatic biodiversity, flow–ecology relationships, low flows, pelagic-broadcast spawning, regulated rivers

1 | INTRODUCTION

Recruitment ecology of stream fishes is strongly linked to hydrologic processes. For example, fishes that spawn in inundated floodplains require overbank flows that connect main channel habitats and

spawning habitats (King, Humphries, & Lake, 2003). Other fishes cue on hydrologic processes such as seasonal wet periods (Agostinho, Gomes, Verissimo, & Okada, 2004), small flow pulses that synchronize spawning in main channels (Durham & Wilde, 2008), and low flow periods when main channel habitats are

simplified (Summerfelt & Minckley, 1969). For most riverine fishes, recruitment—defined as young fish surviving the first growing season and entering a population—is not possible when stream flows do not provide appropriate spawning habitats. For instance, the low flow recruitment hypotheses (LFRH) postulate that periods of low flow when water temperatures and prey densities are high can be advantageous to small-bodied fishes that produce multiple clutches of planktonic (suspended by currents) or demersal (sinking) ova during a protracted summer spawning season (Humphries, King, & Koehn, 1999). Although the LFRH has been tested and supported across a diversity of biomes (Dettmers, Wahl, Soluk, & Gutreuter, 2001; Zeug & Winemiller, 2008), studies from dryland rivers have challenged the applicability of the LFRH. Dryland river studies have found that small-bodied fish recruitment is unrelated to flow (Hoagstrom, Archdeacon, Davenport, Propst, & Brooks, 2014), recruitment is most successful at intermediate flows (Moore & Thorp, 2008), or that exceptionally low flow periods are detrimental to recruitment for some populations (Durham & Wilde, 2009; Perkin, Gido, Costigan, Daniels, & Johnson, 2015; Wilde & Durham, 2008). Conservation concerns emerge when prolonged periods of low flow, such as during extreme drought, alter population dynamics of species that are otherwise expected to recruit during typical low flows (Lake, 2003; Matthews & Marsh-Matthews, 2003).

Fishes inhabiting dryland rivers have life history adaptations that promote population maintenance in otherwise harsh environments. Hydrologic variation in dryland rivers ranges from periods of prolonged low flow brought on by little precipitation to punctuated deluge events capable of producing floods (Dodds, Gido, Whiles, Fritz, & Matthews, 2004). Given such unpredictable hydrology, most dryland river fishes have adapted opportunistic life history strategies characterized by early age at maturity, short life spans, low fecundity, and little parental care (McManamay & Frimpong, 2015; Winemiller & Rose, 1992). Opportunistic strategists also use a variety of spawning modes, including spawning adhesive ova within benthic crevices (“crevice spawners”), adhesive ova over benthic substrata such as gravel or sand (“substrate spawners”), pelagic release of demersal (sinking) ova (“pelagic-benthic spawners”), and pelagic release of neutrally buoyant (i.e., will sink without currents) ova that swell with river water immediately after spawning (“pelagic-broadcast spawners”; see descriptions and classifications by Balon, 1975, and Simon, 1999). Some pelagic-broadcast spawning species are hypothesized to engage in synchronized summer spawning during high flow pulses but fail to recruit during zero flows (e.g., Durham & Wilde, 2008), whereas crevice- and benthic-spawning populations generally benefit from extreme low summer flows (Gido & Propst, 2012; Perkin, Gido, Costigan, et al., 2015). Seemingly, extreme low flow events differentially affect the species expected to recruit during typical low flows, but comparative studies tracking recruitment among multiple species during extreme low flows are rare. This is largely because of the difficulty in predicting when extreme low flows will occur. Consequently, investigating the ecological consequences of extreme low flows is critically needed for conservation planning in regions where drought intensity and frequency are expected to increase in the future

(Hermoso & Clavero, 2011; Lake, 2003), including many dryland river systems (Seager et al., 2018).

Alterations to hydrologic regimes that generally reduce stream flow are likely to disrupt spawning and recruitment dynamics of many dryland river fishes. Although drought-induced low flow is a natural phenomenon among dryland rivers (Dodds et al., 2004), natural expansion and contraction dynamics (*sensu* Stanley, Fisher, & Grimm, 1997) are influenced by human alterations to riverine landscapes (“riverscapes” hereafter; Ward, 1998). These alterations include storage of water in reservoirs (Costigan & Daniels, 2012), levee construction (Galat et al., 1998), surface water diversion (Ferrington, 1993), groundwater extraction (Falke et al., 2011; Perkin et al., 2017), and increases in total aridity (Seager et al., 2018). Dryland river fishes must contend with truncated expansions and accelerated contractions within habitat arenas that are severely fragmented by instream structures that do not allow downstream movement or upstream recolonization (Lehner et al., 2011; Perkin & Gido, 2011, 2012). Consequently, in some dryland rivers, natural patterns in fish recruitment dynamics no longer match the habitat templates that shaped fish life histories (Bunn & Arthington, 2002) and the majority of fish taxa endemic to regions such as the Great Plains of North America are now threatened with decline (Hoagstrom, Brooks, & Davenport, 2011). Previous research in the Great Plains has demonstrated fish diversity loss caused by interactions between spawning mode, habitat isolation, and low flow disturbance (Perkin, Gido, Cooper, et al., 2015; Worthington et al., 2018). These works highlight loss of pelagic-broadcast spawning fishes from highly fragmented habitats during periods of extreme drought. Perkin, Gido, Costigan, et al. (2015) presented the ecological ratcheting hypothesis (ERH) that postulates population extirpations brought on by low flow disturbances in small, isolated habitat patches are reinforced by barriers to recolonization even after drying disturbance subsides. The ERH is contingent on disturbances causing either adult mortality prior to reproduction (e.g., Durham, Wilde, & Pope, 2006) or failed recruitment after reproduction (e.g., Rodger, Mayes, & Winemiller, 2016) at a pace more rapid than the duration of the disturbance. Increases in the application of the ERH (Kerezsy, Gido, Magalhães, & Skelton, 2017; Perkin, Gido, Costigan, et al., 2015; Schumann, Haag, Ellensohn, Redmond, & Graeb, 2018) suggest that additional research on the mechanisms causing population extirpation during drought events is necessary for understanding ecological consequences of extreme low flow events in highly fragmented riverscapes.

The goal of this paper was to assess recruitment dynamics for six fishes in the family Cyprinidae during consecutive years of extreme drought in 2011 and 2012. We first characterized the chronology of gonad development to assess reproductive activity during summer months for all six species. As a second step, we measured age 0 recruitment using time series length data and length-based models to estimate age structure based on the relationship between time and fish growth (Hoagstrom et al., 2014; Shepherd, 1987). We hypothesized that among the six species studied, those that are confirmed or suspected pelagic-broadcast spawners would experience reduced recruitment during extreme drought compared with species

utilizing other spawning modes. This hypothesis is based on previous works in the Great Plains that demonstrated greater sensitivity to extreme low flows by pelagic-broadcast spawning fishes compared with crevice, benthic, and pelagic-benthic spawning fishes (Hoagstrom & Turner, 2015; Perkin, Gido, Cooper, et al., 2015; Worthington et al., 2018).

2 | METHODS

2.1 | Study area

We studied fishes and their recruitment dynamics in the Arkansas and Ninescah rivers in southcentral Kansas, USA (Figure 1). Although the Arkansas River is desiccated in the reaches upstream of Great Bend, KS (Ferrington, 1993), the Ninescah River maintains a natural longitudinal gradient characterized by a widening channel, fining substrate grain size, and increased discharge magnitude despite the existence of Cheney Reservoir on the North Fork Ninescah tributary (Costigan, Daniels, Perkin, & Gido, 2014). Stream channel sizes range from 12 to 100 m wide, from order 3 to 6 (Strahler, 1957), and tend to become braided at lower flows (see Costigan et al., 2014 for further geomorphology details). The fragments of stream we studied are isolated from the broader Arkansas River basin to the west by small dams on the South Fork Ninescah River near Pratt, Kingman, and Murdock, KS, to the north by a small dam on the Arkansas River in Wichita, KS, and to the south by Kaw Reservoir on the Arkansas River (Figure 1 a). The small dam near Murdock, KS, is a temporary barrier that is left in place during the summer spawning season and therefore likely acts as a barrier to movements associated with spawning (Costigan, Ruffing, Perkin, & Daniels, 2016). We distributed 15 fixed sampling sites along the Arkansas River ($n = 4$) and Ninescah River ($n = 11$) and repeatedly visited each site for 2 years. Repeated visits consisted

of 11 consecutive weekly samples between May 15 and August 15, 2011, one sample in November 2011, one sample in March 2012, and seven consecutive fortnightly samples between May 15 and August 15, 2012. In total, 20 sampling events were made to each site. We monitored stream flows at two United States Geological Survey (USGS) gages, one on the Ninescah River near Peck, KS (USGS gage ID 07145500), and one on the Arkansas River near Arkansas City, KS (USGS gage ID 07146500). We also tracked monthly Palmer drought severity index (PDSI) values for the study area using data from the North American Drought Monitoring Program (www.ncdc.noaa.gov).

2.2 | Fish collections

We sampled fishes with a seine (4.6 × 1.8 m, 3.2-mm mesh). At each site and date, we seined all available habitats for a period of 2 hr and worked from a fixed starting point at the downstream extent of the site to a fixed ending point at the upstream extent of the site. We chose sites that spanned the longitudinal lengths of the Ninescah and Arkansas rivers. The length of stream sampled at each site ranged 85–250 m, with longer sites on wider reaches of streams. Sampling of all sites occurred over the course of 3 days, and we alternated the starting positions so that sites were equally sampled during morning or afternoon across surveys. We identified and enumerated all fish species collected and measured total length (TL; mm) of up to 30 randomly selected individuals of each species in each seine haul. After measurement, up to five individuals for each of six target species (see next section) were euthanized in a lethal dose of MS-222 (80 mg L⁻¹) and stored in 10% neutrally buffered formalin until laboratory dissection. All other fishes were released back to the site of capture. We reduced the frequency of collections during 2012 because occurrences of two species notably declined as an extreme drought event persisted.

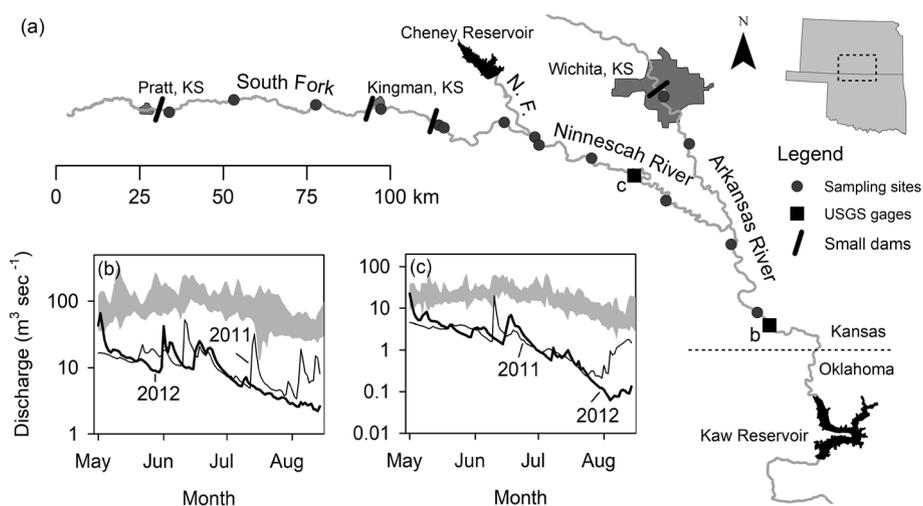


FIGURE 1 (a) Map of the study area showing 15 sampling sites and two United States Geological Survey (USGS) stream flow gages distributed along the Arkansas and Ninescah rivers of Kansas, USA. Inset hydrographs for (b) the Arkansas River and (c) the Ninescah River USGS gages show discharge ($\text{m}^3 \text{s}^{-1}$) for 2011 (thin line), 2012 (thick line), and 1980–2010 (95% confidence bounds; grey area) during the months that fishes reproduce

2.3 | Target species

Species were selected for inclusion based on known or suspected reproductive modes and ova characteristics. Peppered chub (*Macrhybopsis tetranema*) is a pelagic-broadcast spawning species that produces nonadhesive and neutrally buoyant ova that swell with stream water shortly after spawning (Bottrell, Ingersol, & Jones, 1964; Wilde & Durham, 2008). Silver chub (*Macrhybopsis storeriana*) life history is poorly studied. Simon (1999) classified the species as belonging to the pelagic-benthic spawning guild, though Williams (1962) and Auer (1982) report pelagic spawning with production of nonadhesive and apparently neutrally buoyant ova. Consequently, we consider silver chub a suspected member of the pelagic-spawning guild (Perkin & Gido, 2011). Emerald shiner (*Notropis atherinoides*) is a pelagic-benthic spawning species that produces nonadhesive and demersal (sinking) ova (Flittner, 1964). Sand shiner (*Notropis stramineous*) is a benthic-spawning species that produces demersal and adhesive ova (Platania & Altenbach, 1998). Red shiner (*Cyprinella lutrensis*) and bullhead minnow (*Pimephales vigilax*) are crevice-spawning species that produce adhesive and demersal ova (Gale, 1986; Parker, 1964). Among these six species, all spawn during summer months (Frimpong & Angermeier, 2009).

2.4 | Reproductive investment

Adult individuals (>40-mm TL) of target species that were obtained during 2011 were used to assess gonadal development. In the laboratory, we measured total mass (g), TL (mm), and dissected each individual to remove organs. Gonads (testes for males and ovaries for females) were then separated from remaining organs and measured to the nearest 0.1 mg. We also measured body mass after removal of the viscera (i.e., eviscerated mass) to the nearest 0.1 mg and calculated the gonadosomatic index (GSI; Nikolsky, 1963) using the equation

$$\text{GSI} = \frac{\text{gonad mass}}{\text{eviscerated mass}} \times 100.$$

We calculated the median GSI value for all individuals collected from a site on a particular date. This approach allowed for estimation of reproductive investment across the 11 sample periods during summer 2011, which corresponded with the spawning season for all species selected for inclusion in the study. We did not continue reproductive investment analyses during 2012 because two species became too rare to remove individuals from the population.

2.5 | Statistical analyses

We described reproductive investment for each species using GSI values and generalized additive models (Wood, 2011). A smoothing function was used to predict median GSI values as a function of time for each sampling period for the first 11 samples (i.e., weekly time step). We fit models to each species independently using the “gam”

function from the “mgcv” package (Wood, 2017) and a quasipoisson error distribution because GSI distributions are constrained to non-negative values. We fit models to males and females separately given differences in GSI values between sexes for cyprinid fishes (e.g., Perkin, Shattuck, & Bonner, 2012). This approach provided insight into the timing and magnitude of reproductive investment for each species during the first year of extreme drought.

We described age structure for each species using length-based models to evaluate recruitment success. We first plotted time series length-frequency histograms for the 11 sampling weeks in summer 2011 to show change in population-level size distribution concurrent with change in GSI data. We expected that small individuals would appear in the collections following periods of gonadal development. To evaluate the growth dynamics of these populations, we used the “fishmethods” package in R (Nelson, 2018) to fit age models based on Shepherd's (1987) decomposition of seasonal length frequencies into age classes based on the von Bertalanffy growth model:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right),$$

where L_t is length at age t (in years), L_∞ is asymptotic length or the maximum attainable length, k is the Brody growth coefficient or the rate at which fish approach their maximum size, and t_0 is the theoretical age at which fish have a length of zero. Fitting this model to seasonal length frequency data followed a two-step process. The first step was an exploratory analysis in which ranges of von Bertalanffy model parameters k and L_∞ were selected from a table of goodness-of-fit measures. Once the best k and L_∞ values were selected, the second step involved selecting the corresponding t_0 parameter and using the function “slca” from the “fishmethods” package to assign proportions of annual age classes within the population for each sampling week. We fit models and selected parameter values using 2011 data and then fit the same model to 2012 (i.e., using parameter estimates from 2011) because fish abundances were higher in 2011 compared with 2012. When data were available, we compared the selected von Bertalanffy parameters with estimates from the broader literature using the “FishLife” package in R (Thorson, Munch, Cope, & Gao, 2017). Life history estimates from “FishLife” were derived through phylogenetically constrained analyses of life history data housed in the online database FishBase as described in detail by Thorson et al. (2017).

3 | RESULTS

3.1 | Drought-induced reductions in flow

Monthly drought conditions for the study area during 2011 included moderate drought ($-2 > \text{PDSI} > -3$) in May, severe drought ($-3 > \text{PDSI} > -4$) in June, extreme drought ($-3 > \text{PDSI} > -4$) in July, and exceptional drought ($\text{PDSI} < -5$) in August. During 2012, drought conditions included abnormally dry ($-1 > \text{PDSI} > -2$) in May, moderate drought in June, severe drought in July, and extreme drought in

August. Daily flow values during May through August of 2011 and 2012 fell below the historical (1980–2010) range of flows in the Arkansas and Ninescah rivers. Arkansas River flows were already below the long-term range by the beginning of May 2011 and continued a near-linear decline interrupted by small spikes in flow (Figure 1 b). The flow conditions observed during 2011 were repeated during 2012 except that fewer pulses occurred during the second half of summer 2012. Ninescah River flows were below the long-term range at the beginning of May 2011 and declined over the course of the summer (Figure 1c). Drought-induced low flow conditions were essentially replicated in the Ninescah River during 2012, except that August 2012 flows were lower compared with 2011.

3.2 | Fish collections

We collected and measured 63,472 total individuals across the six target species over the course of the study (Table 1). Red shiner was the most abundant species ($n = 26,106$), followed by sand shiner (17,232), emerald shiner (16,145), bullhead minnow (3,519), silver chub (422),

and peppered chub (48). Total effort was less in 2012 compared with 2011, owing to fewer site visits and less water volume to sample during 2012 (Table 1). Retention of up to five individuals per site and date for assessment of reproductive investment resulted in 943 individuals. This included 251 red shiner (124 males; 127 females), 227 sand shiner (113; 114), 181 emerald shiner (87; 94), 201 bullhead minnow (92; 109), 68 silver chub (35; 33), and 15 peppered chub (8; 7).

3.3 | Reproductive investment

Reproductive investment varied by species and across the 11 sample weeks of summer 2011 (Figure 2). Peppered chub GSI values did not significantly differ through time but peaked at 26.0% in mid-June for females ($F = 0.66$, 0.57, deviance explained = 24.8%) and 1.2% on June 21 for males ($F = 1.39$, 0.33, deviance explained = 35.8%). Silver chub GSI peaked at 48.3% in early June for females ($F = 10.28$, $P < .01$, deviance explained = 89.1%) and 0.85–0.88% between June 1 and June 21 for males ($F = 4.92$, $P < .01$, deviance explained = 68.8%). Emerald shiner GSI peaked at 35.6% in late May for females ($F = 7.85$,

TABLE 1 Dates of sampling and number of specimens measured and life history estimates for individual growth (k), asymptotic length (L_{∞}), and time at zero length (t_0) for six fish species surveyed during 2011 and 2012, in the Arkansas and Ninescah rivers of Kansas, USA

Sampling date	Area seined (m ²)	Peppered chub	Silver chub	Emerald shiner	Sand shiner	Red shiner	Bullhead minnow
5/16–5/18, 2011	9,550	2	15	668	642	897	194
5/23–5/27, 2011	8,162	0	58	728	533	1,401	183
5/31–6/2, 2011	6,985	6	19	759	444	1,510	193
6/6–6/8, 2011	6,839	6	86	716	603	1,466	386
6/13–6/15, 2011	6,913	6	13	766	840	1,533	192
6/21–6/23, 2011	6,839	6	34	627	931	1,387	257
6/27–6/29, 2011	7,005	7	37	899	1,063	1,502	213
7/6–7/8, 2011	8,039	3	48	789	1,201	1,418	303
7/12–7/15, 2011	5,096	1	44	833	881	1,317	269
7/18–7/20, 2011	5,045	7	12	781	1,018	1,330	306
8/8–8/10, 2011	5,597	2	33	1,016	860	1,390	280
11/18–11/22, 2011	7,584	1	0	645	1,208	673	150
Total	83,654	47	399	9,227	10,224	15,824	2,926
3/31–4/6, 2012	4,423	0	1	880	773	944	47
5/15–5/17, 2012	4,615	0	2	1,021	826	1,289	66
5/28–5/29, 2012	2,746	0	0	445	484	1,101	30
6/12–6/16, 2012	4,875	0	0	1,019	919	1,439	89
6/25–6/27, 2012	5,932	0	2	927	976	1,429	89
7/9–7/11, 2012	5,362	1	7	1,048	1,033	1,235	62
7/23–7/25, 2012	4,420	0	11	905	1,027	1,490	155
8/7–8/9, 2012	4,512	0	0	673	1,061	1,355	55
Total	36,885	1	23	6,918	7,099	10,282	593
Grand total	120,539	48	422	16,145	17,232	26,106	3,519
Life history parameter estimates	k	0.9	0.4	0.7	0.77	1.2	1
	L_{∞}	90	230	130	90	80	80
	t_0	0.42	0.42	0.38	0.25	0.4	0.41

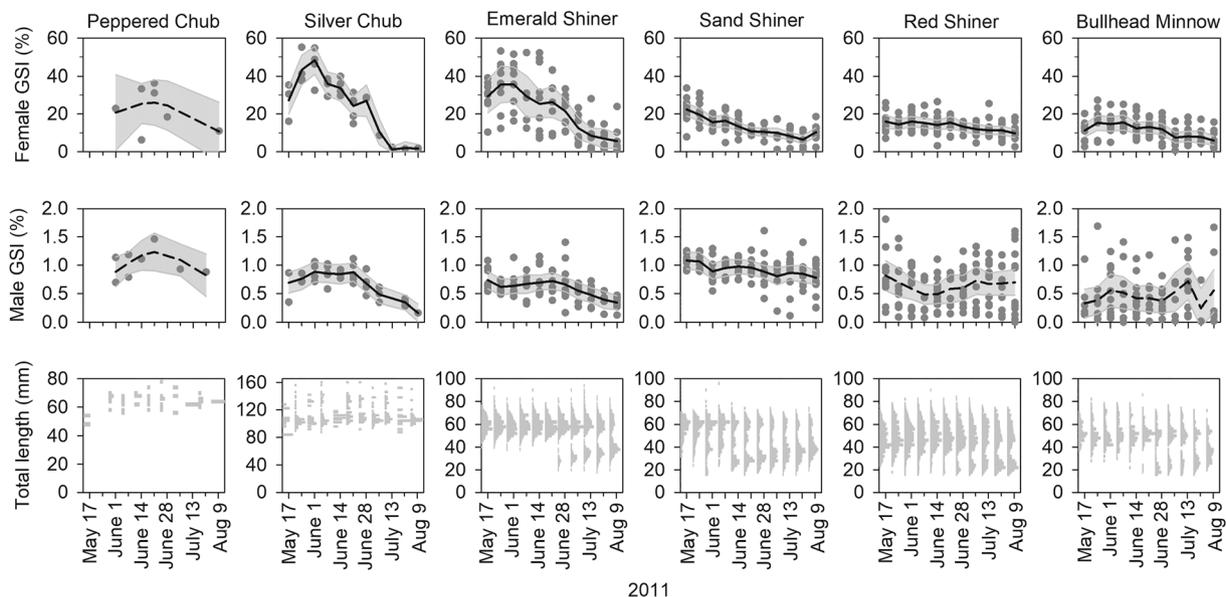


FIGURE 2 Temporal patterns in gonadosomatic index (GSI) for females (top row) and males (middle row) as well as length-frequency plots for the sizes (total length, mm) of individuals captured (bottom row) for six fish species collected during 11 samples in the summer of 2011 (see Table 1 for all dates). Raw GSI data are summarized with generalized additive models (GAMs), and model fits (black lines) with 95% confidence intervals (grey areas) are shown. Nonsignificant changes in GSI through time (i.e., nonsignificant GAMs) are shown as dashed lines whereas significant changes in GSI are shown as solid lines. Length data were binned by 2-mm categories for length-frequency plots and relative frequencies are shown

$P < .01$, deviance explained = 52.8%) and 0.62–0.73% between mid-May and late June for males ($F = 3.09$, $P < .01$, deviance explained = 28.8%). Sand shiner GSI declined nearly linearly after a maximum of 22.4% on May 17 for females ($F = 13.24$, $P < .01$, deviance explained = 51.8%) and 1.08% for males ($F = 2.07$, $P = 0.04$, deviance explained = 13.9%). Red shiner GSI ranged 14.1–16.2% from mid-May to the end of June before declining for females ($F = 3.66$, $P < .01$, deviance explained = 24.8%) but did not vary for males ($F = 1.19$, $P = 0.31$, deviance explained = 8.5%). Bullhead minnow GSI ranged 14.7–15.5% from late May to early June before declining for females ($F = 3.99$, $P < .01$, deviance explained = 28.3%) but did not vary for males ($F = 0.79$, $P = 0.63$, deviance explained = 8.4%).

3.4 | Recruitment

Weekly length-frequency plots between May 17 and August 9, 2011, illustrated emergence of small fishes during the latter half of the spawning season for all fishes except peppered chub and silver chub (Figure 2). Age 0 fishes appeared or increased in number during June 2011 approximately after peak GSI, including emerald shiner (June 28), sand shiner (June 14), red shiner (June 28), and bullhead minnow (June 14). Breakdown of seasonal length-frequency data revealed no evidence of age-0 recruitment for pepper chub or silver chub during 2011 or 2012, though all other species studied successfully recruited during this time (Figure 3). During 2011, the peppered chub population was dominated by age 1 individuals, but by 2012, only a single age 2 individual was captured. Similarly, in 2011, the silver chub population was split by age 1 and age 2 individuals with a few age 3

individuals, and by the end of 2012, the population was dominated by age 2 individuals. The emerald shiner population was dominated by age 1 individuals, but recruitment was evident as early as June 28, 2011, when age 0 individuals emerged. During both 2011 and 2012, age 0 emerald shiner increased in prevalence across the second half of the summer. Sand shiner, red shiner, and bullhead minnow populations consisted of age 0, age 1, and age 2 individuals, and during both 2011 and 2012, the proportion of age 2 individuals was replaced by age 0 individuals as the fraction of the population composed of age 0 individuals increased.

4 | DISCUSSION

Our results provide empirical evidence for recruitment failure among some, but not all, Great Plains fishes during extreme drought. Reproductive investments measured as GSIs indicated that all fishes studied were at minimum preparing for spawning during summer months of 2011. However, only four of six species showed indication of successful spawning and recruitment. Emerald shiner, sand shiner, red shiner, and bullhead minnow populations were increasingly dominated by age 0 individuals during July through August of 2011 and 2012. Peppered chub and silver chub populations were dominated by age 2 fish during early summer 2011, but age 2 fish were replaced by age 1 fish by July and August. These population dynamics are consistent with other life history studies on Great Plains *Macrhybopsis* spp. (Albers & Wildhaber, 2017; Albers, Wildhaber, & Green, 2018; Perkin, Shattuck, Gerken, & Bonner, 2013; Wilde & Durham, 2008), except that no age 0 individuals were detected in our study. By 2012, only a single age 2 peppered

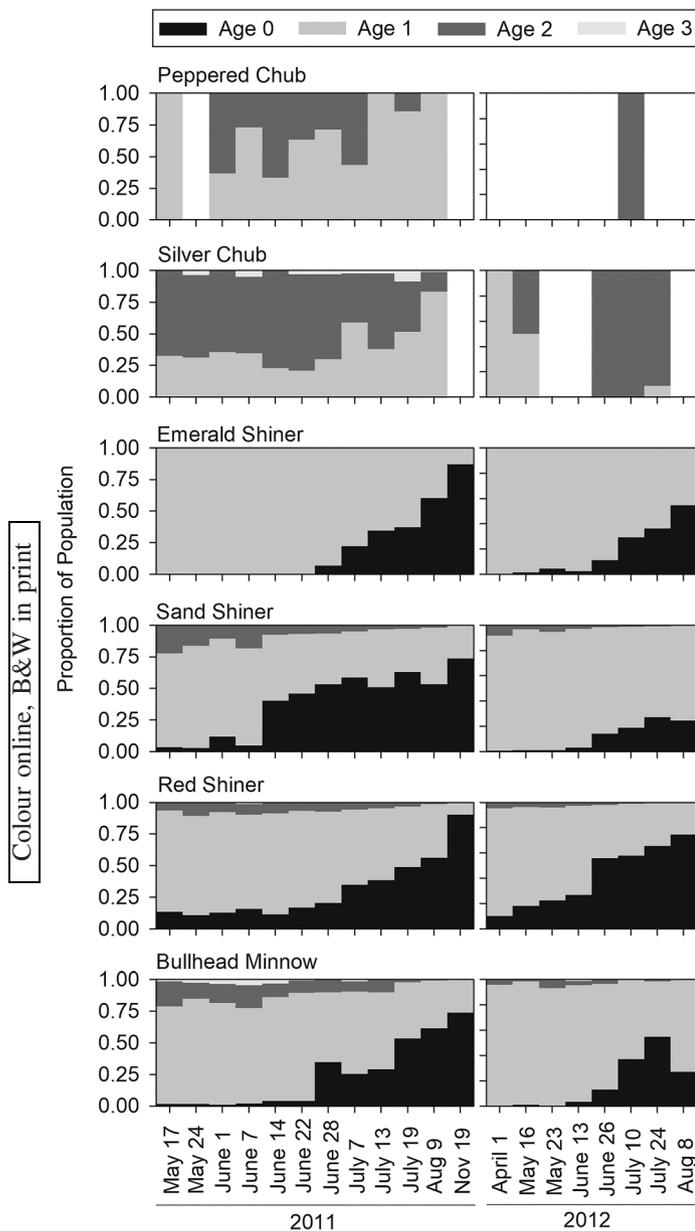


FIGURE 3 Temporal change in the proportions of populations assigned to age classes across 20 samples for six fish species collected in the Arkansas and Ninescah rivers of Kansas, USA, during 2011 and 2012. See Table 1 for the number of individuals measured in each sampling occasion

chub and mostly age 2 silver chub were collected, indicating that the existing stocks were likely hold-overs from the previous year. A single age 1 silver chub was collected in late 2012, suggesting that limited recruitment must have happened during 2011, but was not widely evident in our sampling. We also note that both species of *Macrhybopsis* have smaller apparent population sizes (based on catch rates) compared with the other four species. However, the existence of an age 3 group for silver chub in 2011 might explain why peppered chub but not silver chub ultimately suffered extirpation during the extreme drought of 2011 and 2012 (Pennock et al., 2017; Pennock et al., 2018). These results highlight recent calls for greater investigation of linkages between environmental fluctuations and dynamics of early

life stages to promote conservation of imperilled fishes (Wilde & Durham, 2008; Worthington et al., 2018).

Life histories of the dryland stream fishes studied here are consistent with the life history parameter estimates reported elsewhere. Estimates derived from “FishLife” for the *Macrhybopsis* genus (i.e., $k = 0.42$, $L_{\infty} = 226$) were very consistent with estimates selected for the silver chub model (i.e., $k = 0.40$, $L_{\infty} = 230$). Although peppered chub is in the same genus, the fitted model parameters showed a faster growth rate (i.e., $k = 0.90$) but smaller overall size (i.e., $L_{\infty} = 90$) compared with the “FishLife” parameter estimates for the genus. However, our results for peppered chub were consistent with the life history model Wilde and Durham (2008) developed for the species, including maximum life span at age 2, maximum size 77-mm TL, and age 0 sensitivity to low flow. “FishLife” estimates for emerald shiner showed a slower growth rate (i.e., $k = 0.54$) but consistent overall size (i.e., $L_{\infty} = 139$) compared with values from our fitted model (i.e., $k = 0.38$, $L_{\infty} = 130$). Previous works on emerald shiner life history were largely conducted in northern latitudes (Campbell & MacCrimmon, 1970; Fuchs, 1967), and given known latitudinal variations in *Notropis* spp. life histories (Gotelli & Pyron, 1991; Taylor & Gotelli, 1994), slower growth rates might be expected in northern latitudes where water temperatures are cooler compared with the Great Plains. Fitted model parameters for sand shiner (i.e., $k = 0.77$, $L_{\infty} = 90$) and bullhead minnow (i.e., $k = 1.2$, $L_{\infty} = 80$) both included faster growth rates but smaller asymptotic lengths compared with “FishLife” estimates for *Notropis* (i.e., $k = 0.39$, $L_{\infty} = 203$) and *Pimephales* (i.e., $k = 0.43$, $L_{\infty} = 141$). Summerfelt and Minckley (1969) studied the life history of sand shiner in the Smoky Hill River, Kansas, and estimated maximum age and age distributions consistent with our findings, including 3-year life span, populations dominated by age 1 individuals, and a prolonged reproductive season peaking during early summer. Bullhead minnow life history attributes are known to vary along water temperature gradients, including faster growth rates and greater spawning success in warmer water temperatures (Troia & Gido, 2014). Finally, red shiner is described as the most successful fish in the Great Plains region and a “jack-of-all-trades ... [and] master of all” (Marsh-Matthews & Matthews, 2000). Red shiner can spawn within their first year of life (Marsh-Matthews, Matthews, Gido, & Marsh, 2002), reproduce during a 6-month-long season (Farringer, Echelle, & Lehtinen, 1979), and exhibit indeterminate fecundity (Gale, 1986). We found that the red shiner population in the Arkansas and Ninescah rivers was composed of three age classes (0, 1, and 2) with age 0 fish already present by May during both summers, and red shiner had the strongest recruitment across the 2 years of extreme drought. Although our study focused on a subset of species in a single riverscape, these consistencies in life history parameters suggest that our findings have application beyond the Arkansas and Ninescah rivers.

Reproductive investments varied among the six Great Plains stream fishes we studied. Some of the fishes studied here are known fractional (“serial”) spawners, meaning multiple cohorts can be produced within a single reproductive season (Frimpong & Angermeier, 2009; Simon, 1999). Known fractional spawners included red shiner (Gale, 1986) and peppered chub (Wilde & Durham, 2008), and

evidence from congeners suggests that fractional spawning is possible for sand shiner and emerald shiner (Heins & Rabito, 1986) as well as bullhead minnow (Gale & Buynak, 1982). The reproductive ecology of silver chub requires considerable additional research given this species is so unique among *Macrhybopsis* spp. (Kinney, 1954). Greater magnitude but more volatile weekly GSI values, particularly for female peppered chub, silver chub, and emerald shiner, contrasted the smaller magnitude but more stable weekly GSI values for female sand shiner, red shiner, and bullhead minnow. Other researchers have found that low flow years benefit species such as sand shiner (Summerfelt & Minckley, 1969), red shiner (Gido & Propst, 2012; Propst & Gido, 2004), and bullhead minnow (Perkin & Bonner, 2011). Moreover, occurrences of these fishes are increasing where long-term declines in flow have occurred (Gido, Dodds, & Eberle, 2010). Fractional spawning of demersal or adhesive ova is likely a more successful strategy during low flow periods compared with pelagic-broadcast spawning of neutrally buoyant ova that may require drift for survival. Population declines have occurred for peppered chub (Wilde & Durham, 2008), silver chub (Steffensen, Shuman, & Stukel, 2014), and even emerald shiner (Taylor, Knouft, & Hiland, 2001) where flows are highly modified and homogenized. Our findings revealed some consistencies in recruitment among fishes with similar reproductive modes and ova characteristics, suggesting that these attributes likely interact to determine recruitment during extreme low flows.

Although drought is a natural feature in dryland riverscapes, the effects of drought on populations are magnified when habitats are highly fragmented. Research from the Great Plains suggests that fishes with planktonic ova are much more sensitive to low flows compared with fishes with demersal ova (Perkin, Gido, Costigan, et al., 2015; Perkin, Gido, Cooper, et al., 2015; Worthington et al., 2018). Great Plains pelagic-broadcast spawning fishes are frequently extirpated from stream fragments <100 km in TL, especially those fragments in which stream flows are reduced by anthropogenic modifications (Dudley & Platania, 2007; Perkin & Gido, 2011; Perkin, Gido, Cooper, et al., 2015; Wilde & Urbanczyk, 2013; Worthington, Brewer, Grabowski, & Mueller, 2014). Although pelagic-broadcast spawning fishes do spawn during periods of no stream flow, recruitment is generally unsuccessful (Durham & Wilde, 2009). Temporal fluxes in GSI values we observed for peppered chub and silver chub suggest that these species were at least prepared to spawn during 2011, though ovarian and testicular resorption rather than release of gametes cannot be ruled out (Hunter & Macewicz, 1985). We also emphasize that silver chub is only a suspected member of the pelagic-spawning guild (suspected by the authors) and has previously been treated as a member of the pelagic-benthic guild (Perkin, Gido, Costigan, et al., 2015; Perkin, Gido, Cooper, et al., 2015; Simon, 1999). Still, inference from taxonomy suggests that *Macrhybopsis* spp. are sensitive to extreme low flows affecting fragmented riverscapes (Kelsch, 1994; Pennock et al., 2017; Perkin et al., 2013; Wilde & Durham, 2008). Pelagic-benthic spawning fishes such as emerald shiner (and perhaps silver chub) are extirpated from reaches upstream of dams in the Arkansas and Ninescah rivers (Pennock et al., 2018; Perkin, Gido, Costigan, et al., 2015) and are frequently absent from the same fragments of river as

pelagic-broadcast spawning fishes (Perkin, Gido, Cooper, et al., 2015; Starks, Rodger, King, & Skoog, 2018). These patterns suggest that pelagic-spawning species in general, both pelagic broadcast and pelagic benthic, are sensitive to fragmentation. In fact, even benthic-spawning species such as red shiner and sand shiner that successfully recruited in the Arkansas and Ninescah rivers during 2011 and 2012 are extirpated in other regions of the Great Plains where habitat isolation and drought jointly affect riverscapes for one or more years (Falke et al., 2011; Matthews & Marsh-Matthews, 2007). Because most opportunistic species in Great Plains riverscapes have short generation times, even short-duration drought disturbance for a single year can be problematic. Exceptions are species such as silver chub that live up to age 3 (based on our data) and thus might be able to persist despite the loss of a single year class. Our work supports recent findings that pelagic-broadcast spawning fishes likely recruit most strongly during some system-specific intermediate flow magnitude compared with extreme low flows (e.g., Pennock et al., 2017; Rodger et al., 2016), whereas crevice- and substrate-spawning fishes benefit from prolonged low flows (Perkin, Gido, Cooper, et al., 2015).

Our work has implications for predicting fish responses to future changes in flow and drought cycles in other river systems. In their derivation of the LFRH, Humphries et al. (1999) cautioned biologists against ascribing significance of floods/droughts to fish biology given limited understanding of fish ecology. Our findings help to fill previous knowledge gaps by demonstrating that recruitment during low flows is not a universal principle even among fishes that might be expected to recruit based on life history attributes alone. Unfortunately, spawning modes and ova characteristics are unknown for many species (Johnston, 1999; Worthington et al., 2018) and a clear research need exists concerning predicting these ecological attributes, either through laboratory studies (e.g., Platania & Altenbach, 1998) or phylogenetic analyses (e.g., Thorson et al., 2017). For some species, such as peppered chub that is now missing from >95% of its historical range and is relegated to a single population isolated between two reservoirs (Pennock et al., 2017), conservation actions must happen soon to avoid extinction. Outside of the Great Plains, there is emerging evidence that reduced water availability directly threatens fishes (Poff & Zimmerman, 2010; Xenopoulos et al., 2005), including arid and semiarid river systems in Australia (Baumgartner, Wooden, Conallin, Robinson, & Thiem, 2017; Humphries et al., 1999), Spain (Bernardo, Ilhéu, Matono, & Costa, 2003; Sánchez-Hernández & Nunn, 2016), South America (Fabr e, Castello, Isaac, & Batista, 2017), and the United States (Ruh , Olden, & Sabo, 2016). Given expectations of declining future water security for humans (V r smarty et al., 2010), there is a need to predict how such changes will affect fishes and inform fish conservation actions now and in the future (Closs, Krkosek, & Olden, 2015; Jaeger, Olden, & Pelland, 2014; Whitney, Whittier, & J. D., & Strecker, A. L., 2017). Theoretical frameworks such as the ERH and life history theory provide clear avenues for advancing our understanding of how fishes might be conserved in Earth's altered riverscapes; these theories only need be applied, refined, and integrated in conservation management regimes (e.g., Perkin et al., 2016; Wellemeyer, Perkin, Costigan, & Waters, 2019). The work presented here highlights the

species and ecological traits that might be targeted by comprehensive conservation planning in fragmented, drought-prone riverscapes (Baumgartner et al., 2014; Baumgartner et al., 2017; Crook et al., 2010; Lennox, Crook, Moyle, Struthers, & Cooke, 2019).

ACKNOWLEDGEMENTS

This project was funded by the Kansas Department of Wildlife, Parks and Tourism, the Great Plains Landscape Conservation Cooperative, and USDA National Institute of Food and Agriculture, HATCH Project 1017538. We thank D. Shaw and J. Edmonds for assistance with field sampling, and R. Webber, T. Davis, and T. Slagle for assistance with laboratory dissections and data entry. We thank R. Waters (Kansas Department of Wildlife, Parks and Tourism), E. Johnson (Westar Energy), and J. Luginbill (U.S. Fish & Wildlife Service) for assistance with sampling site identification, and S. Silliman (Chaplin Nature Center), Byron Walker Wildlife Management Area, the City of Kingman, the City of Pratt, the City of Wichita, and numerous private landowners for sampling site access. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Perkin JS, Starks TA, Pennock CA, Gido KB, Hopper GW, Hedden SC. Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. *Ecohydrology*. 2019;e2120. <https://doi.org/10.1002/eco.2120>