Conservation Genetics
https://doi.org/10.1007/s10592-021-01374-x

RESEARCH ARTICLE

Still time for action: genetic conservation of imperiled South Canadian River fishes, Arkansas River Shiner (*Notropis girardi*), Peppered Chub (*Macrhybopsis tetranema)* and Plains Minnow (*Hybognathus placitus*)

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Received: 10 September 2020 / Accepted: 6 May 2021

Abstract
Pelagic broadcast spawning cyprinids have declined throughout the North American Great Plains because of adverse habitat changes caused by river fragmentation and altered flow regimes. Despite losses elsewhere, a 218-river kilometer section of the South Canadian River maintains three of these imperiled species: Arkansas River Shiner, Peppered Chub and Plains Minnow. The objective of this study was to determine if species occupying the same river stretch and hence a shared environment, exhibit the same trajectory of genetic change and relative abundance over contemporary timescales. Genetic evaluation of these species is an essential precursor to conservation efforts that may include translocations and establishment of captive populations. Across the time series each species experienced substantial changes in abundance with Arkansas River Shiner consistently having the highest overall abundance. The abundance of Peppered Chub was uniformly lower but increased between 2012 and 2019, while Plains Minnow abundance declined from 2014 to 2019. Despite dramatic fluctuations in population size over the time-series, data from microsatellites and mitochondrial DNA demonstrated that the South Canadian River harbors genetically diverse populations of each of these species. With the Southwestern United States entering another period of exceptional drought, immediate intervention is necessary to ensure persistence of range restricted Arkansas River Shiner and Peppered Chub. Results of this study show that remnant populations provide a crucial resource for recovery efforts for these species.

Keywords Pelagophil · Great plains · Cyprinid fishes · Genetic monitoring

Introduction

Genetic diversity within and across populations is determined by a combination of forces including climatic and geological events that rearranged drainages such as Pleistocene climatic fluctuations. These events profoundly affected species distributions with populations of many species periodically expanding and contracting (e.g., Jones et al. 2015). Populations that served as refugia during glacial periods may be reservoirs of diversity and important for conservation (Hampe and Petit 2005). Second, contemporary landscape features may act as barriers to dispersal resulting in population structure. Finally, intrinsic traits of a species such as fecundity, reproductive strategy and migratory behavior influence standing stocks of genetic diversity within populations via their influence on genetic effective size (e.g., Waters et al. 2001; Osborne et al. 2014; Ellegren and Galtier 2016; Sousa-Santos et al. 2016). Recent habitat changes and stochastic events that cause substantial fluctuations in population size can also affect levels of diversity and its distribution among populations (e.g., Guy et al. 2008). In riverine systems, anthropogenic barriers to dispersal (e.g., dams, stream dewatering, habitat degradation) disrupt gene flow and source-sink dynamics (e.g., Fausch and Bestgen

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Published online: 15 May 2021

1997). The interaction of these factors may result in different patterns of genetic diversity among species. However, co-distributed species that share life histories and sensitivities to stochastic events may show similar patterns of genetic change over contemporary timescales. This can be assessed by tracking changes in genetic diversity and effective population size at multiple contemporary time points in co-occurring taxa. Improving our understanding of how these species respond to particular environmental conditions may allow us to make more informed decisions regarding potential conservation actions. For example, positive changes in abundance across species in response to increases in stream discharge, would lead to a different set of management recommendations than if responses varied between taxa.

The prairie rivers of the North American Great Plains have been altered significantly over the past century with changes negatively affecting pelagic broadcast spawning minnows (referred to as pelagophils) (e.g. Luttrell et al. 1999; Dudley and Platania 2007; Perkin and Gido 2011; Perkin et al. 2015a, b). This group of fishes possess life-history traits that have facilitated persistence in highly variable and harsh environments of Great Plains streams including small body size (< 100 mm total length), short generation time (1–3 years; e.g., Horwitz et al. 2018), fractional spawning in some species (e.g., Bonner 2000; Wilde and Durham 2008) and release of semi-buoyant eggs by females into the water column (Moore 1944; Bottrell 1964). In pelagophils, fertilized eggs develop over several days as they drift passively downstream in river currents (Bottrell et al. 1964). Persistence of upstream populations depends on retention of eggs and larvae and/or upstream dispersal of young-of-year individuals or adults (e.g., Fausch and Bestgen 1997; Archdeacon et al. 2018; Platania et al. 2020). Despite these adaptations, species within this guild have suffered extensive range contractions and population declines across the Great Plains as a result of river fragmentation caused by impoundments, dams and dry stream segments, reductions in stream discharge, changes to flow periodicity, and a reduction in channel complexity (e.g. Cross and Moss 1987; Larson 1991; Luttrell et al. 1999; Dudley and Platania 2007). Luttrell et al. (1999) suggested extinction-recolonization and source-sink dynamics were particularly important to the continued persistence of plains-stream fishes. More recently Perkin et al. (2019) and Archdeacon et al. (2020a) showed that pelagophils are particularly sensitive to extreme low flow events that may result in recruitment failure. Recruitment failure in short lived species mean that populations may experience order of magnitude fluctuations in population size from one year to the next. For example, Rio Grande Silvery Minnow (*Hybognathus amarus*) which inhabits the Rio Grande in New Mexico, experienced a > 99% decline in October density from 2017 to 2018 as a consequence of poor spring runoff in 2018 (Dudley et al. 2018). Likewise, Wilde and Durham (2008) reported an 80% population decline in Peppered Chub (*Macrhybopsis tetranema*) associated with periods of low flow. Declines of this magnitude have the potential to erode genetic diversity on contemporary timescales through reductions in genetic effective population size. Together, short lifespan, fragmented habitats, and limited geographic distribution may culminate in population or species extinction following a brief episode of unfavorable conditions (e.g., Perkin et al. 2015a, b; Pennock et al. 2017).

Here we focus on two imperiled members of this guild, Arkansas River Shiner (*Notropis girardi*) and Peppered Chub, as well as the more widely distributed Plains Minnow (*Hybognathus placitus*). Arkansas River Shiner is listed as a threatened species under the Endangered Species Act (U.S. Fish and Wildlife Service 1998) and is endemic to the Arkansas River basin. Historically, this species was found throughout the basin in New Mexico (NM), Kansas, Arkansas, Texas (TX), and Oklahoma (OK). Current information suggests Arkansas River Shiner is now restricted to two distinct fragments (separated by Lake Meredith TX) of the South Canadian River (between Ute Lake [NM] and Lake Eufaula [OK]) (Fig. S1). Peppered Chub is a member of the *Macrhybopsis aestivalis* complex, which includes at least nine species distributed in rivers throughout the Mississippi Valley, Gulf Slope drainages and the Rio Grande basin of NM, TX and Mexico (Eisenhour 2004; Gilbert et al. 2017). Peppered Chub has a similar historical distribution to Arkansas River Shiner, but is absent from Arkansas (Eisenhour 1999). Peppered Chub has also disappeared from the vast majority of its range and was proposed for listing as an endangered species in 2020 (U.S. Fish and Wildlife Service 2020). Extirpation of this species from the Ninnescah and Arkansas rivers during the most recent drought cycle (2011–2013; Perkin et al. 2015b; Pennock et al. 2017) leaves a single extant population located in a 218 km stretch of the South Canadian River between Ute Lake and Lake Meredith (Bonner and Wilde 2000; Pennock et al. 2017). Recent population losses of these species, as well as other Southwestern pelagophils (Osborne et al. 2021) underscores the high risk that Arkansas River Shiner and Peppered Chub face from stochastic environmental and demographic events and should act as a call to action to protect remnant populations and to actively mitigate the threats that endanger them.

Plains Minnow is still widely distributed across the Great Plains (Hubbs et al. 1991; Miller and Robison 1973) including the main tributaries of the Mississippi River including the Missouri, Platte, Arkansas rivers as well as the Gulf Coast drainages including the Brazos, Colorado and South Canadian rivers. Although more broadly distributed than Arkansas River Shiner and Peppered Chub, there have been declines within its range including in the states of Kansas (Perkin et al. 2015a, b; Osterhaus and Martin 2019) and Colorado (Propst and Carlson 1986). Both Arkansas River

Shiner and Plains Minnow have non-native populations in the Pecos River that could serve as genetic reservoirs (Bestgen et al. 1989; Hoagstrom 2003; Osborne et al. 2013).

Intraspecific diversity is typically the first component of biodiversity to be impacted when environments are altered (Spielman et al. 2004). Specifically, population declines and disruption of source-sink dynamics may result in decay of standing genetic diversity with a population which can ultimately increase a species' vulnerability through lowered fitness associated with inbreeding depression, and loss of evolutionary potential accelerating the path to extinction (*e.g.*, Franklin 1980; Frankham 1996; Willi et al. 2006). Blanchet et al. (2020) recently argued that intraspecific diversity should be the focal point of conservation efforts in order to maintain ecosystem function. Previous studies (Luttrell et al. 1999; Perkin et al. 2015b; Pennock et al. 2017) have proposed steps that could protect existing populations of Peppered Chub and Arkansas River Shiner including translocations to formerly occupied habitats and establishing genetically diverse captive populations to serve as refuges or source populations for repatriation efforts. Genetic data collected to evaluate potential sources of the non-native populations of Arkansas River Shiner suggested that the South Canadian River population harbored considerable genetic diversity (Osborne et al. 2013). The South Canadian River population of Plains Minnow also appears diverse as assessed using microsatellites when compared to populations at more northerly latitudes (Osborne et al. 2014). A severe range-wide drought from 2011 to 2013 (Fig. S2B) reduced densities of Arkansas River Shiner and Peppered Chub (Pennock et al. 2017) across their native range. Genetic status of Arkansas River Shiner has not been assessed since the 2011–2013 drought and there has been no evaluation of genetic status of Peppered Chub.

An essential precursor to conservation efforts is a genetic evaluation of extant populations of Arkansas River Shiner, Peppered Chub and Plains Minnow. Here, we assess temporal trends in genetic diversity (at microsatellite loci and a mitochondrial DNA gene) and consider these trends with respect to population status (measured by catch-per-unit-effort). We also use genetic data to provide insights into the historical demography of Arkansas River Shiner, Peppered Chub and Plains Minnow. Results can be used to inform future management decisions for these taxa.

Methods

Study sites and sampling

The U.S. Fish and Wildlife Service (USFWS) and New Mexico Department of Game and Fish personnel collected fin clips from Arkansas River Shiner (2012–2019), Peppered Chub (2015–2018) and Plains Minnow (2014 and 2015) by seining the fish community at seven sites along the South Canadian River and its tributary Revuelto Creek from Ute Lake to the NM-TX border. Generalized random tessellation stratified sampling was used to randomly select these sites (Kincaid and Olsen 2012) and thereafter these sites were surveyed between October and November (fall) from 2012 to 2019. Fall sampling was not conducted in 2016. Extremely low abundance of Peppered Chub between 2012 and 2014 precluded collection of sufficient samples for genetic analysis. Sampling methods were consistent with those used to collect fishes in other wadeable sand-bed rivers (Hatch et al. 1985; Bestgen et al. 1989; Hoagstrom and Brooks 2005). Fish were sampled with a 3.0×1.2 m seine with 3.2-mm mesh, with at least 12 seine hauls conducted per site. Seine hauls were made in discrete mesohabitats in proportion to their approximate frequency of occurrence. Seine haul length was measured to the nearest 0.1 m (mean length $= 10.2 \pm 3.4$ m). Samples of Arkansas River Shiner were collected in 2017 from near Byng, Oklahoma (downstream of Lake Meredith [LM]), and from Arkansas River Shiner and Peppered Chub upstream of Lake Meredith in Texas by USFWS (Fig. S1). Caudal fin clips were taken from captured fish and stored in 95% ethanol. Samples and associated field notes were deposited at the Museum of Southwestern Biology, Division of Fishes at the University of New Mexico. We included additional samples of Plains Minnow collected in 2013 near Amarillo Texas ($n = 32$ upstream of Lake Meredith) and from several sites downstream of Lake Meredith ($n = 6$) by J. Perkin in 2013 as part of another study (Osborne et al. 2014).

Molecular methods

Genomic DNA was extracted from air-dried fin clips using standard proteinase-K digestion and standard phenol/chloroform methods (Hillis et al. 1996). A portion of the mitochondrial NADH dehydrogenase subunit 4 gene (ND4) (306 and 328 base pair fragments for Arkansas River Shiner and Plains Minnow respectively) was sequenced as described in Osborne et al. (2012). For Peppered Chub, we sequenced a 580-base pair fragment of NADH dehydrogenase subunit 4L and NADH dehydrogenase subunit 4 genes using the following PCR primers (*ARGBL* and *NAP2*) and cycling conditions: initial denatured at 90 °C for 2 m, followed by 30 cycles of denaturing at 90 °C for 30 s; annealing at 50 °C for 30 s; extension at 72 °C for 45 s; and ending with a final extension at 72 °C for10 m. Unique haplotypes were sequenced in both directions and deposited in GenBank with the following accession numbers: MT856089-MT856138 for Arkansas River Shiner, MT856056-MT856088 for Peppered Chub and MT856139-MT856191 for Plains Minnow.

All species were assayed for variation at nine variable microsatellite loci. Microsatellites were amplified as 10 µL reactions, containing 1 µL diluted DNA, 1X Colorless GoTaq® Flexi Buffer, 2 mM $MgCl_2$ solution, 0.8 mM dinucleotide triphosphates (dNTPs), 0.4 µM of both forward and reverse primers, and 0.375 units of GoTaq® DNA polymerase. For Arkansas River Shiner, polymerase chain reactions (PCRs) were initially denatured at 90 °C for 2 m, followed by 30 cycles of denaturing at 90 °C for 30 s; annealing at 60 °C (*Nme* 208, Gold et al. 2004), 58 °C (*Nme232*, Gold et al. 2004), *Ppro126*, *Ppro132*, Bessert and Orti 2003), 54 °C (*Ca12*) or 49 °C (*Ca6*, *Ca8,* Dimsoski et al. 2000; *Lco3*, *Lco6* Turner et al. 2004) for 30 s; extension at 72 °C for 45 s; and ending with a final extension at 72 °C for 30 m. Arkansas River Shiner samples genotyped in a prior study (Osborne et al. 2013) were also genotyped for *Ca6*, *Ca8* and *Ca12* as these loci were not assayed previously. For Peppered Chub, PCR conditions were identical except the following annealing temperatures were used: 60 °C (*Ppro126/Ppro132/Ca3/Ca12*), 56 °C (*Lco3*), 50 °C (*Nme93/232*), or 49 °C (*Lco1/Ca6*). For Plains Minnow, annealing temperatures of 58 °C (*Ppro126/Ppro132*, *Nme93/232*), 56 °C (*Ca12*), or 49 °C (*Lco3/Lco6* and *Lco7* and *Ca6*) were used. For each sample, one microliter of PCR product was mixed with 10 µl of formamide and 0.4 µl of HD400 size standard. Samples were denatured at 90 °C for five minutes, and assayed on an ABI 3130 DNA sequencer and analyzed with Genemapper software (ABI).

Data analyses

Demographic history and genetic variability—mtDNA

Samples were pooled across temporal/spatial collections for analyses of demographic history. All sequences were translated into the amino acid code to verify they corresponded to coding genes using MEGA vers. 7 (Kumar et al. 2018). To examine demographic history for each species, we calculated: average nucleotide diversity (π; Tajima 1993), Tajima's *D* (Tajima 1989) and Fu's F_s (Fu 1997) using ARLEQUIN (Excoffier and Lischer 2010). Significance was assessed using 9999 bootstrap replicates. Significant departures from zero for both Tajima's D and Fu's F_s indicate that neutrality or population stability can be rejected. We also evaluated the mismatch distribution (Rodgers and Harpending 1992) to assess population histories using the raggedness statistic (*rg*) (Harpending et al. 1993). Demographic or spatial population expansion leave a distinctive unimodal mismatch distribution, contrasting with a *ragged* multimodal distribution exhibited by stable/equilibrium populations that have accumulated more mutations among haplotypes. Significant *rg* values are indicative of population size stability while small values are consistent with population expansion and high values are indicative of bottlenecks (Harpending et al. 1993). We calculated the R_2 statistic (Ramos-Onsins and Rozas 2002) in DNAsp vers. 5.0 and assessed significance with 999 coalescent simulations (Librado and Rozas 2009). Small values of R_2 are expected following recent extreme population growth. Fu's F_s and R_2 statistic have been shown to be more powerful than Tajima's *D* and *rg* (Ramos-Onsins and Rozas 2002). We used the program POPART (http://popart.otago.ac.nz) to visualize the relationship among haplotypes using a median joining network (Bandelt et al. 1999).

For each temporal collection haplotype diversity (*h*) and haplotype richness (H_R) were calculated from mtDNA data using the R package *hierfstat* (Goudet and Jombart 2015). Values of pairwise Φ_{ST} based on mtDNA data were calculated using ARLEQUIN (Excoffier and Lischer 2010) with significance assessed with 9999 bootstrap replicates.

Genetic variability- microsatellites

Within contiguous river fragments, the drifting nature of Arkansas River Shiner, Peppered Chub and Plains Minnow eggs and larvae allows opportunities for genetic mixing among sampling sites. We verified this before pooling samples across sampling sites by calculating pairwise values of F_{ST} among localities (Weir and Cockerham 1984). For Arkansas River Shiner, we also examined whether there was significant divergence among samples collected above and below Lake Meredith. We used 9999 bootstrap replicates to evaluate significance using GenoDiv vers. 3.0 (Meirmans 2020). We did not detect significant divergence between sites in any species (results not shown). For this reason, calculations of genetic diversity statistics and genetic effective size are based on temporal collections (pooled across localities).

Genepop'007 (Rousset 2008) was used to conduct modified exact tests to determine whether observed genotype frequencies conformed to Hardy–Weinberg expectations in each temporal sample (analyzed separately). This program was also used to conduct the global test for linkage disequilibrium among loci. Sequential Bonferroni correction (Rice 1989) was applied to account for multiple comparisons. Since all measures of diversity (number of alleles, Nei's gene diversity [Nei 1987] and heterozygosity) are dependent on sample size, we used a resampling procedure to calculate diversity measures. For each species 1000 random subsamples were drawn without replacement from each temporal sample. Diversity measures and 95% Confidence Intervals (CIs) were calculated for each locus and temporal sample and a mean was obtained across loci for each statistic (corrected number of alleles [N_{AC}] reflects allelic diversity, gene diversity [H_{EC}], heterozygosity [H_{OC}]). This analysis was conducted in the R statistical package (www.r-project.org; R script available on request). Minimum samples sizes used

for this analysis was based on the smallest temporal collection for each species (Peppered Chub n = 87; Arkansas River Shiner n = 97; Plains Minnow n = 38). As different minimum sample sizes are used, estimates are not directly comparable among species. Average inbreeding co-efficients (F_{IS}) were calculated across loci using the R package *hierfstat* (Goudet and Jombart 2015).

Genetic effective size and relative abundance

The single sample linkage disequilibrium method (Hill 1981) was used to estimate the effective population size (N_{eD}) from microsatellite DNA data for Arkansas River Shiner, Peppered Chub and Plains Minnow using the program NeEstimator Vers. 2.0 (Do et al. 2014). We used $P_{crit} = 0.02$ to exclude low frequency alleles as suggested where the number of individuals sampled is greater than 25 (Waples and Do 2010). Confidence intervals for N_{eD} were calculated using the jackknife approach (Jones et al. 2016). Variance genetic effective size (N_{eV}) and 95% CIs were estimated from temporal changes in microsatellite allele frequencies using two temporal method estimators (Nei and Tajima 1981; Jorde and Ryman 2007) implemented in NeEstimator. For all taxa, generation time of one year was used (Taylor and Miller 1990; Wilde and Durham 2008) and N_c was set to 100,000. We also used $N_c = 10{,}000$ and N_{eV} estimates were virtually identical (not reported). Female effective size (N_{ef}) was calculated using the temporal method (Waples 1989) implemented in NeEstimator. Upper- and lower-bound 95% CIs for N_{eV}/N_{ef} were calculated using the parametric approach (Waples 1989).

Catch-per-unit-effort (CPUE), a measure of relative abundance, was used to track the population trends of each species. CPUE was calculated as number of fish per m^2 seined. To determine the area seined, seine haul length was multiplied by width for each seine haul. Site was selected as our sampling unit, thus the total area sampled at each site was divided by the total of each species collected to calculate CPUE by site. To account for over-dispersion in the counts, we followed the approach described in Archdeacon et al. (2020b) that uses a generalized linear model with a negative binomial distribution to model fish count data (O'Hara and Kotze 2010). This approach gives mean expected count of fish per unit area sampled ($\widehat{E}[CPUE]$). Finally, we visually compared trends in effective size estimates (N_{eV} and N_{eD}) for each species to trends detected in CPUE estimates.

Results

Demographic history and genetic variation- mtDNA

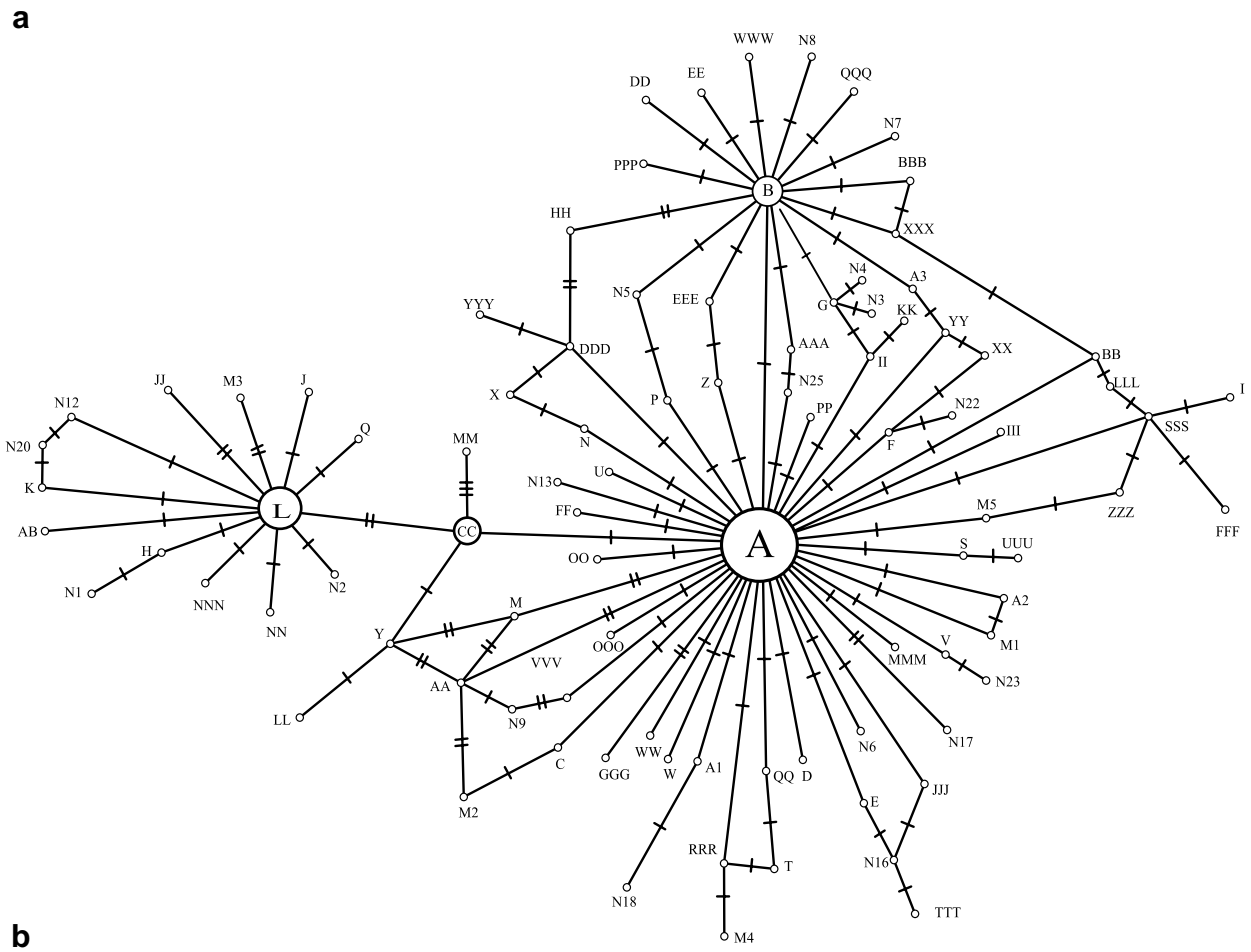
Across all collections of Arkansas River Shiner, 94 ND4 haplotypes were identified. Of the 69 substitutions between haplotypes, four were transversions. The relationship between the structure of the haplotype network and the shape of the mismatch distribution is shown in Fig. 1. Haplotype A and B are the most common haplotypes (present in 15–37% of individuals) and other haplotypes are rare (0.1%–6%) and separated from haplotype A by few mutations. The modal number of difference among haplotypes was one (Fig. 1b). Tajima's *D* was significantly negative indicative of an excess of rate haplotypes. Fu's F_s was also significantly negative (Table 1). Raggedness (*rg*) was small and not significant however, R_2 was significant.

Haplotype diversity ranged from 0.787 to 0.863 in the temporal collections of Arkansas River Shiner (Table 2). Values of pairwise Φ_{ST} among temporal samples of Arkansas River Shiner were not significantly different from zero (supplementary material Table S1). Likewise, values of pairwise Φ_{ST} among samples collected from above and below Lake Meredith in 2017 were not significantly different from zero.

Across the time series for Peppered Chub 32 haplotypes were detected. Haplotypes were separated from each another by one to eight nucleotide substitutions (Fig. 2). Five haplotypes included transversions. Translation to the amino acid code did not identify any internal stop codons and the sequences aligned to previously sequenced *Macrhybopsis* sequences on GenBank. In Peppered Chub, there were four moderately common haplotypes (A, D, I and S) (> 10% of individuals) and most other haplotypes are rare (< 10% of individuals). These were separated from the core haplotypes by a few mutations. The modal number of differences among haplotypes was three (i.e., the mismatch distribution is shifted to the right indicative of a slightly older population expansion). Fu's F_s was significantly negative consistent with population expansion, however the value of F_s indicated fewer rare alleles compared to both Arkansas River Shiner and Plains Minnow. Tajima's *D, rg* and R_2 were not significant.

Haplotype diversity was high in Peppered Chub ranging from 0.884 to 0.922 in the temporal collections. Values of Φ_{ST} among temporal samples of Peppered Chub were not significantly different from zero (supplementary material Table S2).

Plains Minnow had high mitochondrial diversity with 54 haplotypes detected from 234 individuals. Haplotypes E and I were present at frequencies > 10% while the others were rare. The corresponding mismatch distribution



◂**Fig. 1** **a** Median joining haplotype network for Arkansas River Shiner haplotypes detected across the time series. Bars between circles represent nucleotide substitutions. Letters within or adjacent to circles refer to unique haplotypes. Circle size reflects haplotype frequency. **b** Mismatch distribution for Arkansas River Shiner

shows a weakly multi-model shape with a mode of two and a smaller secondary peak at seven, indicative of several more divergent haplotypes (Fig. 3). However, a non-significant value of *rg* indicates that the observed mismatch distribution did not differ from expectations under a model of population expansion. Mean nucleotide diversity was 0.008. Tajima's *D*, Fu's F_s and R_2 were significant indicative of population expansion.

In Plains Minnow haplotype richness varied from 15.55 (2014) to 19.42 (2015) and haplotype diversity ranged from 0.822 (2014) to 0.916 (2015). Following Bonferroni correction, values of pairwise Φ_{ST} between collections were small and not significantly different from zero (supplementary material Table S3).

Genetic diversity-microsatellites

We assessed genetic variation at nine microsatellites for 969 Arkansas River Shiner. Three loci (*Ca6*, *Nme232*), *Ppro132* conformed to HardyWeinberg expectations (HWE) in all collections and there were single departures from expectations at two loci (*Ppro126* and *Ca12* in the 2009). Multiple departures from HWE were detected at four loci (*Lco3*, *Lco6*, *Nme208*, *Ca8*). All departures were explained by an excess of homozygotes. Significant linkage disequilibrium was detected between *Nme208* and *Ca6* and between *Ppro126* and *Ppro132*. Allelic diversity ranged from 21.92 to 24.70, H_{EC} ranged from 0.766 to 0.788 and F_{IS} was between 0.061 and 0.176 (Table 2). Values of pairwise F_{ST} among temporal samples were very small (F_{ST} = 0.001-0.007) but nine comparisons were significantly different from zero following Bonferroni correction (supplementary material Table S4). Pooling samples collected up and downstream of Lake Meredith for 2009 and 2017 did not change this result (Table S4).

We characterized genetic variation at nine microsatellite loci for 533 Peppered Chub collected annually between 2015 and 2018. There was an excess of homozygotes in 14 of 36 comparisons after Bonferroni correction for multiple comparisons. Three loci (*Ca3*, *Ca6* and *Lco3*) conformed to HWE in all populations and three loci (*Ppro118*, *Ppro126* and *Lco1*) departed in half of the samples (2015, 2016 and 2018). Linkage disequilibrium was not detected among any pairs of loci. Allelic diversity ranged from 20.67 to 21.84, H_{EC} was virtually identical across temporal collections and F_{IS} ranged from 0.081 to 0.123. All values of F_{ST} calculated between temporal collections were very small (F_{ST} = − 0.0002–0.004) but the 2016–2017 comparison was significantly different from zero following Bonferroni correction.

For Plains Minnow, we assayed variation in 247 individuals sampled across three consecutive years. We detected departures from HWE in 12 of 27 total comparisons after Bonferroni correction. *Nme232* and *Lco7* departed from expectations in three collections, *Ppro126* and *Ca12* departed in two temporal samples, and *Nme93* and *Ppro132* departed in a single temporal sample. Allelic diversity, gene diversity and heterozygosity were virtually identical between temporal samples. F_{IS} ranged from 0.141 to 0.204. Values of F_{ST} among years were small (F_{ST} = − 0.001 to 0.009) but the 2013–2014 comparison was significantly different from zero (Table S6).

Genetic effective size and relative abundance

For Arkansas River Shiner, estimates of N_{ef} were 1395 (2009–2012) and 970 for the 2017–2019 comparison. In the intervening period estimates of N_{ef} were very large. Finite estimates of N_{eD} were obtained for temporal collections made between 2014 and 2017 and ranged from 2446 (2017) to 39,689 (2014). Variance effective size ranged from 38 (2014 to 2015) — 290 (125–1866) across the time series. Small N_{eV} estimates between 2014 and 2017 are indicative of substantial genetic drift between sampling periods. Although confidence intervals overlap between 2014 and 2015, the substantial decrease in relative abundance in 2017 is consistent with correspondence between demographic and genetic data.

For Peppered Chub, female effective size was indistinguishable from infinity for the 2015–2016 comparison. For the 2016–2017 N_{ef} was 268 and N_{ef} was 178 for 2017–2018 (Table 3). Point estimates of N_{eD} were at least an order of magnitude larger than N_{eV} estimates and ranged from 1386 to 2793 (Table 2). Variance effective size estimated obtained using the method of Nei and Tajima (1981) ranged from 80 to 153. Estimates obtained using the Jorde and Ryman method (2007) were uniformly lower but the trend was the same. A single estimate (2016) was negative indicative of a very large effective size. From 2012 through spring 2014, relative abundance of Peppered Chub was uniformly low when compared to Arkansas River Shiner (Fig. 4). Relative abundance increased from fall of 2014 through 2019; consistent with marginal increases in N_{eV}.

For Plains Minnow, female effective size ranged from 69 (2013–2014) to 81 (2014–2015) (Table 3). Estimates of N_{eD} obtained for Plains Minnow ranged from 4907 (2013) to indistinguishable from infinity (2014) (Table 1). Variance effective size calculated between 2013 and 2014

Table 1 Sample size (n), nucleotide diversity (π), Harpending's raggedness statistic (*rg*), R_2 and Fu's F_s and Tajima's *D* calculated from mitochondrial ND4 sequences for Arkansas River Shiner, Peppered Chub and Plains Minnow

Species	n	π	*rg*	R_2	F_S	*D*
Arkansas River Shiner	941	0.006	0.036	0.014*	−25.870***	−2.158***
Peppered Chub	478	0.005	0.019	0.040	−12.358*	−1.215
Plains Minnow	234	0.008	0.033	0.028*	−26.373***	−1.632*

Significantly negative values for Fu's F_s, Tajima's *D* are indicative of population expansion. Significant values for *rg* are indicative of population stability. *p 0.05–0.01, p ** 0.01—0.001, *** $p < 0.0001$

samples of Plains Minnow was also small ($N_{eV\ NT} = 32$) but was indistinguishable from infinity for the 2014 to 2015 comparison (Table 3). In contrast, relative abundance has been trending downward since 2014 but confidence intervals were wide (Fig. 4).

Discussion

We evaluated demographic history, trajectory of genetic change and population trends in co-distributed pelagophilic taxa: Arkansas River Shiner, Peppered Chub and Plains Minnow from the South Canadian River using genetic monitoring time series and population survey data. Across the contemporary time-series, each species experienced substantial changes in relative abundance with Arkansas River Shiner having the highest abundance. Relative abundance of Peppered Chub was uniformly lower but increased between 2012 and 2019, while abundance of Plains Minnow declined from 2014 to 2019. Results demonstrate that although these species share key life-history traits, they respond differently to shared environmental conditions; hence detailed investigations are warranted to inform conservation decisions. Despite fluctuations in relative abundance and recurrent drought conditions over the past decade, the South Canadian River harbors genetically diverse populations of these species. Analysis of historical demography suggests that this region may have served as a refuge for these species during Pleistocene climatic fluctuations (Osborne et al. 2014). The immediate risk to these range-limited species is not a loss of genetic diversity, but rather regional stochastic environmental and demographic events which endanger Peppered Chub and Arkansas River Shiner.

Demographic history

Pleistocene climatic oscillations resulted in glacial and interglacial cycles that impacted rivers of the Great Plains and their inhabitants (e.g., Pazzaglia 2005; Hoagstrom and Berry 2006; Repasch et al. 2017). Likewise, changing environmental conditions (e.g., temperatures, precipitation regimes; Cross 1970) during these periods strongly influenced distribution of aquatic species. Such profound events leave genetic signatures in affected species (e.g. Bernatchez and Wilson 1998; Inoue et al. 2015; Osborne et al. 2016). The focal taxa of this study all show genetic patterns consistent with past population expansions although each species had a unique mismatch distributions (i.e., left and right shifted modal values for Arkansas River Shiner and Peppered Chub respectively, and weakly multimodal pattern for Plains Minnow) implying slight differences between species. Right-shifted modal value for Peppered Chub suggests older population expansion in this species. In the Canadian River valley, successive glacial and interglacial periods resulted in cyclic incision and alluviation (Dolliver 1984; Wisniewski and Pazzaglia 2002). These changes may have gradually allowed conditions to develop that were suitable for periodic population expansions of Peppered Chub, Plains Minnow and Arkansas River Shiner exhibiting different ecological requirements.

Latitudinal gradients in genetic diversity (i.e., higher diversity at southern latitudes) have been observed in various minnows found across the Great Plains including Plains Minnow, Red Shiner (*Cyprinella lutrensis*) (Osborne et al. 2014) and Sand Shiner (*Notropis stramineus*, Pittman 2011) suggesting southern populations of these species survived in situ during Quaternary climatic oscillations where conditions were more favorable and less impacted by climatic variability and river rearrangements compared to northern populations (e.g., Bernatchez and Wilson 1998). Unfortunately, we do not have data from populations of Peppered Chub and Arkansas River Shiner from the northern part of their historical range as these populations have been extirpated. However, South Canadian River populations of the focal taxa have high haplotype diversity and low nucleotide diversity; consistent with findings in other Great Plains fishes. The South Canadian River is far from the continental glaciers and only directly affected by the relatively minor glaciations of the Southern Rockies. Hence this area may have served as a refugia able to support relatively large (high N_e) populations with subsequent spatial expansions when conditions became favorable (Wang et al. 2013; Bagley et al. 2013). The data for Arkansas River Shiner and Plains

Table 2 Genetic diversity and effective size estimates for Arkansas River Shiner, Peppered Chub and Plains Minnow from the Canadian River

	Microsatellites								mtDNA			
	n	N_{AC}	H_{EC}	H_{OC}	F_{IS}	N_{eD}	− 95%	+95%	n	N haps	*h*	H_R
Arkansas River Shiner												
2009	196	24.29	0.774	0.653	0.151	∞	1101	∞	194	38	0.821	22.99
2012	145	23.67	0.786	0.703	0.099	∞	694	∞	135	27	0.787	22.51
2014	97	23.44	0.788	0.731	0.061	39,689	335	∞	96	26	0.818	25.84
2015	98	24.70	0.766	0.679	0.123	2481	292	∞	94	31	0.841	31.00
2017	207	21.92	0.771	0.656	0.142	2446	538	∞	196	52	0.842	32.59
2019	225	22.48	0.787	0.653	0.176	∞	890	∞	226	49	0.863	30.65
Peppered Chub												
2015	87	20.67	0.830	0.760	0.081	1386	265	∞	87	23	0.917	23.00
2016	122	21.84	0.841	0.753	0.110	∞	510	∞	102	22	0.884	20.50
2017	125	21.72	0.828	0.748	0.100	1894	384	∞	101	27	0.922	24.64
2018	199	21.70	0.829	0.729	0.123	2793	457	∞	188	25	0.896	19.70
Plains Minnow												
2013	38	12.22	0.700	0.563	0.204	4907	115	∞	32	17	0.903	19.00
2014	115	11.58	0.696	0.581	0.141	∞	382	∞	111	29	0.822	15.55
2015	94	11.68	0.690	0.575	0.168	1748	235	∞	91	34	0.916	19.42

Values shown are: sample sizes (n), genetic diversity metrics from microsatellites including allelic diversity [N_{AC}], gene diversity [H_{EC}], and heterozygosity [H_{OC}] and inbreeding coefficient [F_{IS}], genetic effective size estimates (N_{eD}) and upper and lower 95% confidence intervals. Negative estimates of N_{eD} are shown as infinity (∞). Genetic diversity measures from mitochodrial DNA include number of haplotypes [N haps], haplotype diversity [*h*] and haplotype richness [H_R]

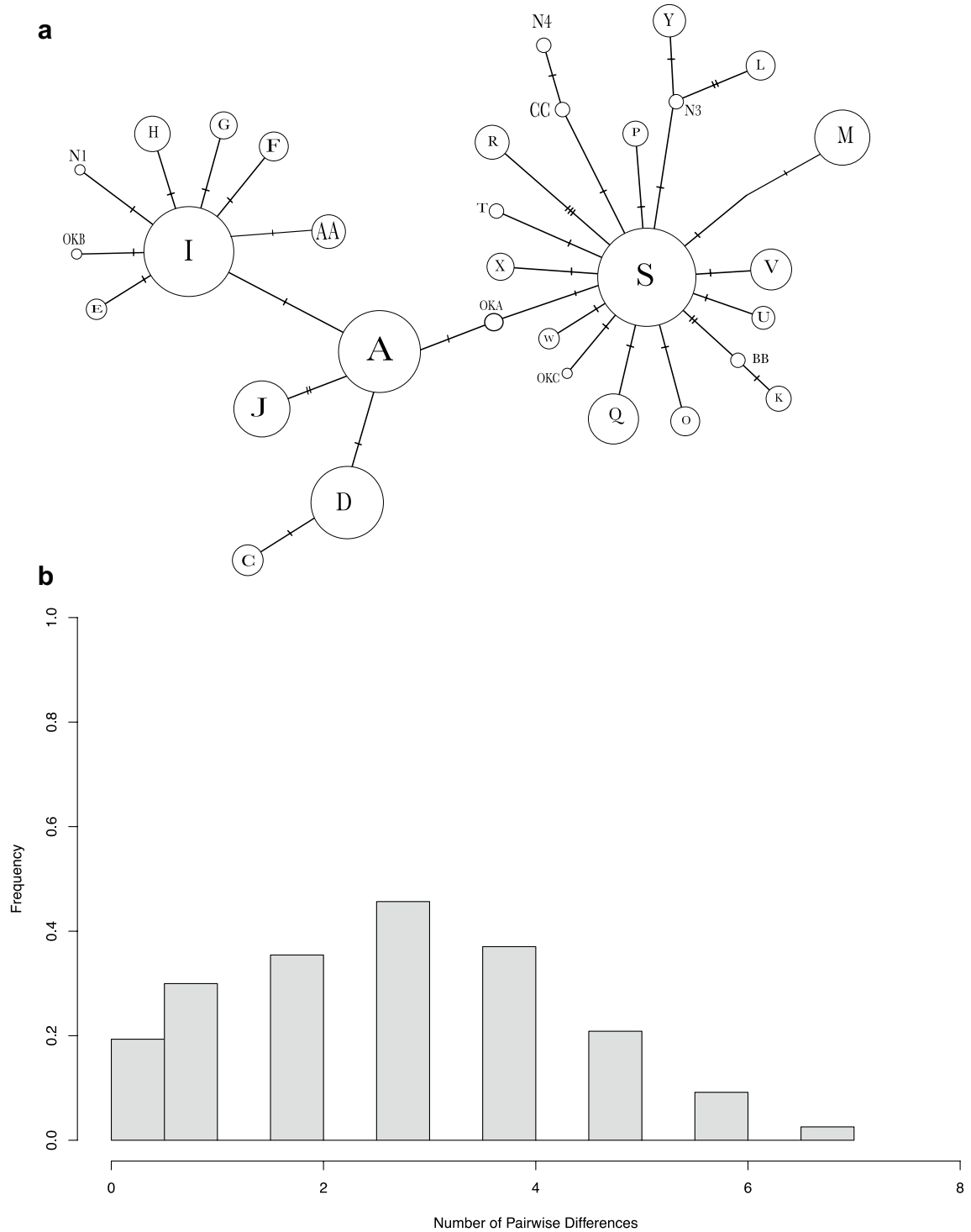


Fig. 2 **a** Median joining haplotype network for Peppered Chub haplotypes detected across the time series. Bars between circles represent nucleotide substitutions. Letters within or adjacent to circles refer to unique haplotypes. Circle size reflects haplotype frequency. **b** Mismatch distribution for Peppered Chub

Minnow suggest expansions have been relatively recent as insufficient time has passed to accumulate many mutations between haplotypes. Furthermore, star-like radiations from multiple common haplotypes implies that population bottlenecks have not been a recent dominant force (i.e., bottlenecks would eliminate rare haplotypes) in these species. Lack of substantial divergence among most haplotypes is consistent with high gene historical flow. High

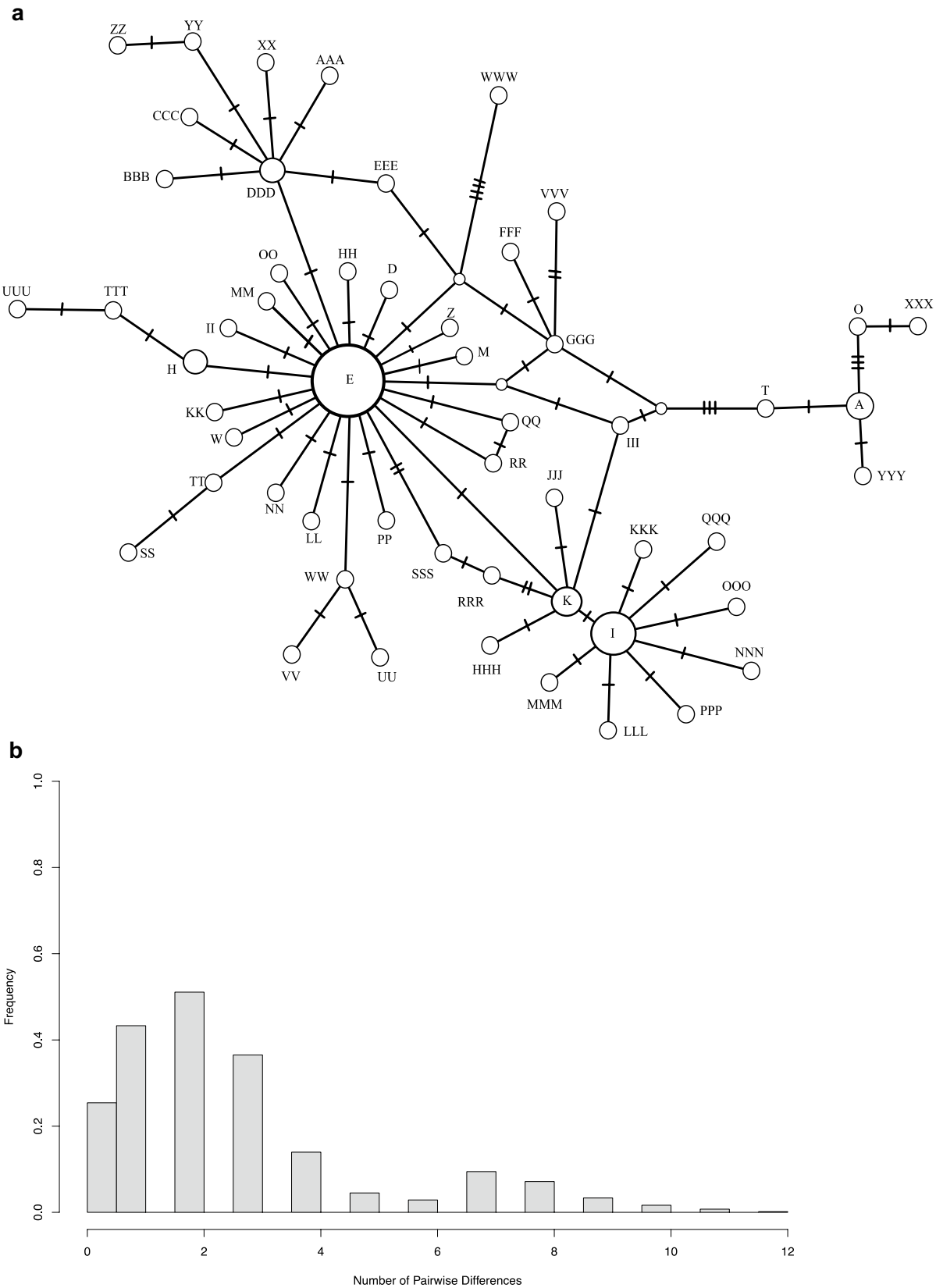


Fig. 3 **a** Median joining haplotype network for Plains Minnow haplotypes detected across the time series. Bars between circles represent nucleotide substitutions. Letters within or adjacent to circles refer to unique haplotypes. Circle size reflects haplotype frequency. **b** Mismatch distribution for Plains Minnow

Table 3 Genetic effective size estimates for Arkansas River Shiner, Peppered Chub and Plains Minnow

Species	N_{ef}	$N_{eV\ NT}$	$N_{eV\ JR}$
Arkansas River Shiner			
2009–2012	1395 (167–∞)	285 (160–586)	404 (297–528)
2012–2014	50,820 (80–∞)	290 (125–1866)	145 (106–190)
2014–2015	∞ (51–∞)	38 (23–67)	23 (17–31)
2015–2017	∞ (173–∞)	262 (124–904)	177 (130–232)
2017–2019	970 (182–∞)	173 (103–310)	121 (89–159)
Peppered Chub			
2015–2016	∞ (29–∞)	80 (39–261)	55 (41–71)
2016–2017	268 (29–∞)	131 (53–771)	69 (51–89)
2017–2018	178 (32–∞)	153 (71–694)	135 (100–174)
Plains Minnow			
2013–2014	69 (12–∞)	32 (16–79)	22 (13–80)
2014–2015	81 (23–∞)	∞ (271–∞)	∞ (218–∞)

N_{ef}- female effective size estimated from mitochondrial DNA haplotype data, variance effective size estimated using the method of Nei and Tajima (1981) ($N_{eV\ NT}$) and Jorde Ryman (2007) ($N_{eV\ JR}$). Lower and upper 95% confidence intervals are given in parentheses

gene flow is achieved partly by drifting eggs/larvae of the focal taxa and this trait would allow swift colonization of unoccupied habitats as they became suitable (Hoagstrom and Turner 2015). Fewer haplotypes (including low frequency variants) were recovered from Peppered Chub. A similar finding was reported for Speckled Chub found in the Pecos River (Osborne et al. 2021) and suggests smaller historical population sizes in these species.

Population Structure

Although extant native populations of Arkansas River Shiner exist in two sections of the South Canadian River separated by Lake Meredith, significant divergence was not detected between them. Additional sampling of Arkansas River Shiner and Plains Minnow downstream of Lake Meredith should be conducted to increase sample sizes and geographic coverage. As movement between population above and below Lake Meredith is unlikely to have occurred since the completion of the lake in 1960's we predict that genetic drift would eventually cause divergence

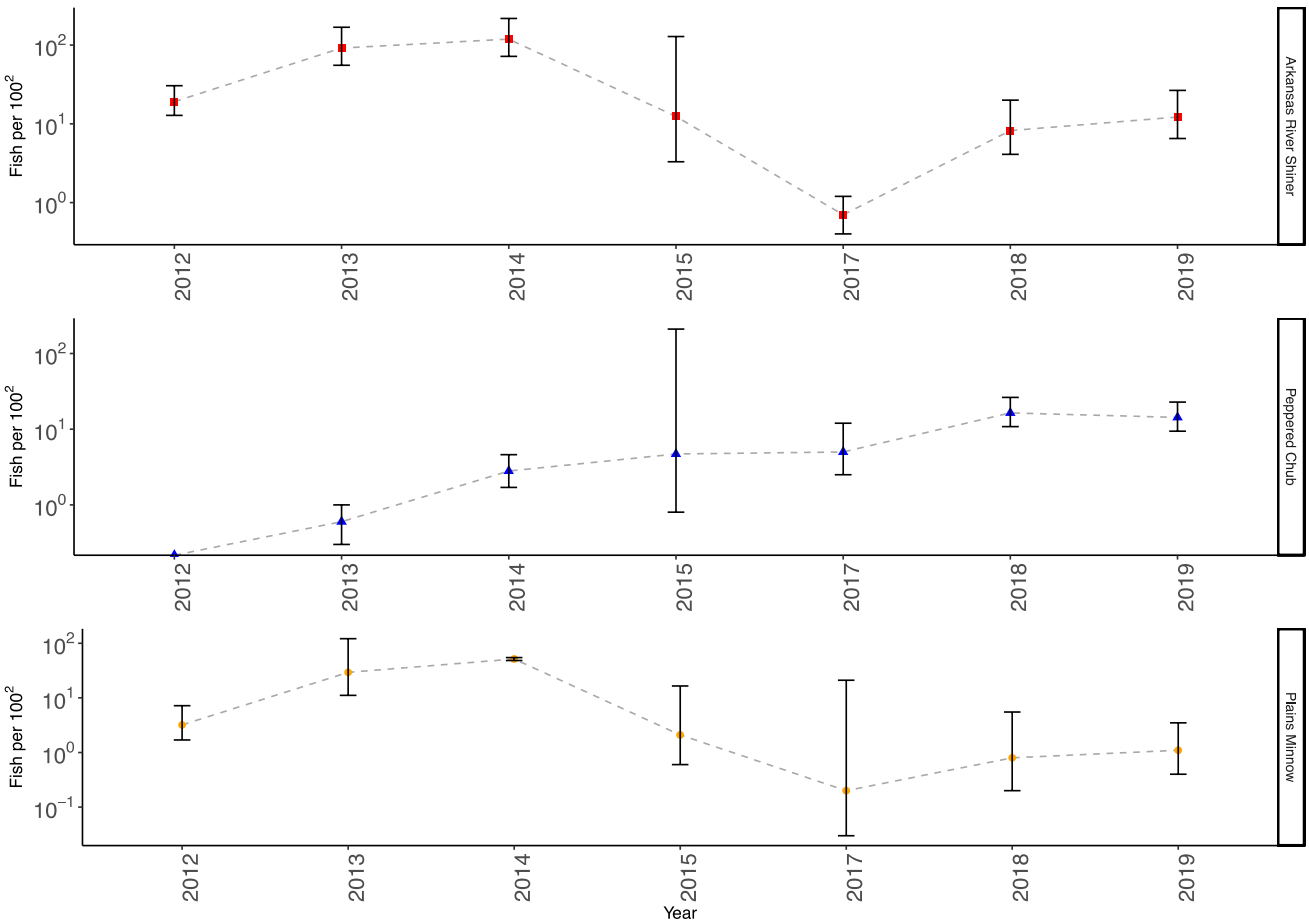


Fig. 4 Expected catch-per-unit-effort (number of fish 100 m^2) ($\widehat{E}[CPUE]$) for Arkansas River Shiner, Peppered Chub and Plains Minnow by year from 2012 to 2019 presented on a log scale

between these populations particularly if either population experiences a significant population bottleneck. For example, in the Rio Grande Basin, there is significant genetic divergence between populations of Rio Grande Shiner and Speckled Chub found in the Rio Grande in Texas and the Pecos River in New Mexico. These populations are now separated by numerous dams and degraded habitats that preclude movement between them (Osborne et al. 2021). In contrast, within contiguous fragments, drifting eggs and larvae of Arkansas River Shiner, Peppered Chub and Plains Minnow provide ample opportunity for genetic mixing. Genetic data collected across sites from other pelagophils including Pecos Bluntnose Shiner (*Notropis simus pecosensis*) (Osborne et al. 2010), Rio Grande Shiner, Speckled Chub (Osborne et al. 2021) and Rio Grande Silvery Minnow (Osborne et al. 2012) also failed to find population structure within contiguous habitats. Arkansas River Shiner, Peppered Chub, Plains Minnow and other members of this reproductive guild (Chase et al. 2015; Wilde 2016; Archdeacon et al. 2018; Platania et al. 2020) are capable of substantial movements; enabling genetic mixing and persistence provided that barriers to movement are absent. Dispersal ability is critical to persistence of these species as it allows fish to move to and from wetted refugium. Dispersal also facilitates recolonization following environmental disturbance, or from downstream segments to compensate for displacement of propagules.

Like Plains Minnow, Arkansas River Shiner and Peppered Chub were until recently distributed across multiple river drainages (Ninnescah, Cimmaron, Salt Fork, Arkansas and North Canadian rivers) and it is possible that there was divergence between these populations and those in the South Canadian River. For example, Eisenhour (1999) described geographic variation in morphological characters across the range of Peppered Chub indicative of adaptation to local environmental conditions. Specifically, Southwestern populations of Peppered Chub had physical traits including sharply sloping head and more embedded scales, considered more suitable to the swifter currents and shifting sands of the South Canadian, North Canadian and Cimarron rivers compared to populations from northeastern localities including the clear waters of the Ninnescah (Eisenhour 1999). Observations of phenotypic variability across the species former range suggests that loss of Peppered Chub from these sites may equate to a loss of adaptive variation. DNA sequence data from the S7 gene however is indicative of a close relationship between the Arkansas and South Canadian populations (Echelle et al. 2018). Genetic data also suggests a close relationship between populations of Plains Minnow from the Arkansas and South Canadian rivers but divergence between Arkansas-Canadian populations and those in the Platte and the Red River basins (Osborne et al. 2014). Although, understanding the relationship between populations is often used to evaluate suitability of source and recipient populations for translocation efforts, this is moot for both Arkansas River Shiner and Peppered Chub, as remnant populations of these species are now confined to the South Canadian River. However, analysis of historical demography shows that large populations of these species at more southerly latitudes likely persisted through the tumultuous Quaternary period and as such, are important reservoirs of diversity for conservation (Hampe and Petit 2005).

The evolutionary capacity of species to adapt to long-term environmental/anthropogenic change can be measured by evaluating the extent of standing genetic variation (within and between populations) within a species (Frankham 1996). Therkildsen et al. (2019) demonstrated that large populations with high levels of standing genetic diversity have greater scope for adaptive change. As such, an important criterion for evaluating whether a population is suitable as a source, is whether it contains sufficient genetic diversity. Reestablishing populations with a genetically diverse founding stock would maximize chances of successful establishment. Demographic monitoring data demonstrates that each of the study species can rebound quickly when environmental conditions are favorable; minimizing losses of diversity. Maintenance of genetic diversity despite substantial declines in relative abundance has also been recorded in Pecos Bluntnose Shiner; a pelagic spawning minnow endemic to a 330 km unfragmented stretch of the Pecos River (NM). In the Pecos, flows are regulated by inputs from tributaries and groundwater seepage that preserves base flows in some river segments (Mower et al. 1964; Mourant and Shomaker 1970). Hoagstrom et al. (2008b) recognized a 151 km 'relict ecosystem' reach in the Pecos River that harbors high densities of pelagophilic minnows because of its broad river channel and high base flows. This river section also retains eggs and larvae (Dudley and Platania 2007). The presence of good habitat may allow sufficient individuals to persist in high quality wetted refugium during periods of river intermittency (Osborne et al. 2010). The South Canadian River shares some of these features with the Pecos River including (1) maintenance of base flows through seepage from Ute Dam, (2) provision of flow variability by periodic inputs from the unregulated Revuelto Creek (Fig. S2) and Rana Arroyo, (3) relatively unaltered and complex habitat, and (4) a moderately long unfragmented river reach. These features likely explain the presence of an intact fish assemblage; including all of the pelagic spawning minnows, and may also explain why Arkansas River Shiner, Peppered Chub and Plains Minnow maintain genetic diversity despite substantial changes in population densities.

Despite the genetic variation maintained in the South Canadian River populations of Arkansas River Shiner, Peppered Chub and Plains Minnow, the rate of loss of genetic diversity is dependent on the genetic effective size of these

populations, and over time, population fluctuations can reduce diversity (Wright 1938; Waples 2002). Temporal estimates of effective size were consistently small for Peppered Chub ($\overline{N}_{e\ NT)} = 121$ and Arkansas River Shiner = $\overline{N}_{e\ NT} = 210$) suggesting that there is a risk of erosion of genetic diversity in these species. Small values of N_{eV} have been reported in other Southwestern pelagophils (Turner et al. 2006) and may be partly explained by sweepstakes reproductive success ([SRS] Hedgecock 1994; Hedgecock and Pudovkin 2011). The SRS hypothesis was proposed to explain the discrepancy observed in some marine taxa in which effective population size was often orders of magnitudes less than the census size (Hedgecock 1994). Southwestern pelagohils share life-history features with these species including high fecundity and low parental investment and hence high mortality of early life stages. When propagules are released into heterogeneous environments there maybe high variance in reproductive success among adults (Hoagstrom and Turner 2015) manifested by small N_e.

Estimates of effective size obtained using the linkage disequilibrium methods were an order of magnitude larger than N_{eV} but it is important to note that N_{eV} and N_{eD} do not apply to the same generation and they are calculated using difference aspects of the data. Specifically, N_{eV} measures change in allele frequencies between two samples, due to genetic drift. N_{eD} provides a measure of the inbreeding effective size (increase in homozygosity due to common ancestry) and provides the effective population size of the parental generation. However, the signature of linkage from prior generations persists; declining by a factor of two each generation (Jones et al. 2016). Although N_{eV} and N_{eD} should be identical under ideal/equilibrium conditions (Crow and Denniston 1988), there are differences between these estimators when population size fluctuates dramatically (Wang and Ryman 2001) as demonstrated by relative abundance data. Hence, population fluctuations explain the discrepancy in N_e estimates for Arkansas River Shiner and Peppered Chub. Although estimates differ, they also provide information about genetic risks these species may face. Specifically, N_{eD} provides information about reduction of fitness of the population including risks posed by inbreeding effects (Rieman and Allendorf 2001). In contrast, N_{eV} describes the rate of loss of adaptive variation and hence provides information regarding a species' potential to respond to environmental change (Rieman and Allendorf 2001). Results suggest that both Arkansas River Shiner and Peppered Chub are at greater risk of loss of adaptive variation, rather than risks imposed by increased homozygosity due to common ancestry (i.e., inbreeding) (Crow and Denniston 1988). Estimates of female effective size may be unreliable because they may be impacted by small sample size (i.e., Plains Minnow) and high numbers of rare alleles (Arkansas River Shiner and Plains Minnow) (Turner et al. 2001).

Theoretical and empirical studies demonstrate that populations with restricted geographical distributions face higher extinction risks than more broadly distributed taxa (e.g. Simberloff 1998). This is particularly true of species such as many Great Plains fishes that rely on recolonization of habitat patches following disturbances (Luttrell et al. 1999). Peppered Chub exists as a single genetically panmictic population confined to a single watershed. Likewise, there is no apparent genetic structure (evaluated by F_{ST}) between populations of Arkansas River Shiner above and below Lake Meredith; however movement between this fragments is unlikely. Under current conditions both species are vulnerable such that a regional event could eliminate the remaining populations (including the nonnative population of Arkansas River Shiner in the Pecos River). Environmental stochasticity reduces a population's resiliency through loss of available habitat (Covich et al. 1997), increased competition among taxa for limited resources, and fragmentation of available habitat (i.e., through creation of dry river segments). Perkin et al. (2019) and Archdeacon et al. (2020a) showed that pelagic broadcast spawning minnows are particularly sensitive to extreme low flow events (i.e., absence of significant rainfall and associated runoff) as these events can result in recruitment failure; which is catastrophic for short-lived species. Low flow events and coincident increases in water temperature may also make populations susceptible to parasites and other diseases (e.g. McNab and Barber 2012).

Extirpation events have occurred for all the focal taxa, as well as other pelagophils, with intensive surveys documenting the relatively rapid decline and disappearance of both Peppered Chub and Plains Minnow from the Ninnescah and Arkansas Rivers during the most recent drought cycle (Perkin et al. 2015b; Pennock et al. 2017). Prior to this event, Arkansas River Shiner was extirpated from this system with no collections in either the Ninnescah or Arkansas Rivers since 1983. These extirpations highlight the importance of the South Canadian River populations, and indicate that populations of Arkansas River Shiner, Peppered Chub and Plains Minnow are particularly susceptible to stochastic environmental events that could reduce reproduction and recruitment. Interestingly, relative abundance estimates for Peppered Chub in the South Canadian River reveal a trend of increasing abundance. The observed increase in abundance may have been a consequence of a large stream flow event in September 2017 through release of water from Ute Dam (Fig. S2). This sustained flow may have reorganized habitat such that it was more favorable to Peppered Chub. Peppered Chub has morphological traits (e.g., flattened head, large falcate fins) more suited to occupying swifter currents than

either Arkansas River Shiner or Plains Minnow (Bonner 2000). The high flows may have temporarily displaced Arkansas River Shiner and Plains Minnow which prefer slower velocity habitats. Unlike Arkansas River Shiner and Peppered Chub, Plains Minnow with populations in multiple states and drainages (including a robust non-native population in the Pecos River) is less vulnerable because a catastrophic event is unlikely to simultaneously impact all populations.

Conservation and management recommendations

Results presented here indicate that all species remain genetically diverse despite experiencing periods of low relative abundance and small N_{eV}. At least three immediate actions could be taken to protect these species particularly Peppered Chub and Arkansas River Shiner: (1) Development of an emergency response plan that may include providing environmental flows to maintain wetted instream habitat, and collection of fish from the wild and provision of temporary refuge if adverse conditions appear imminent. (2) Establishment of captive refuge populations to develop breeding protocols and husbandry practices. Founding of genetically diverse captive populations of both Arkansas River Shiner and Peppered Chub could supply fish for repatriation efforts without depleting wild populations while also serving as a safe harbor when drought conditions return to the Southwestern United States. Many captive breeding programs are not established until all but a few individuals remain. Consequently, the founding size of the population may be extremely small and not reflective of the species' former genetic diversity. Likewise, establishment of captive populations is often an emergency measure taken when the wild population is already heavily stressed which may compromise the captive population from the outset because of disease pressures triggered by poor environmental conditions (e.g. Hammer et al. 2013). (3) Reestablishment of populations in suitable locations within the historic range to increase the number of populations and their geographic spread. This measure would increase resiliency of these species. Luttrell et al. (1999) and Perkin et al. (2015b) have both advocated repatriating Peppered Chub to the upper Cimarron River and the upper Salt Fork where habitat conditions may be suitable to survival. Pennock et al. (2017) identified four locations across the Cimarron and Arkansas Rivers that have both maintained average flows predicted to support stable populations of Peppered Chub. Fragment lengths of these streams are sufficient for this species to complete its life-history. Fishes occupying streams of the Great Plains have adaptations to allow them to periodically face adverse environmental conditions but other traits (short lifespan) make them extremely vulnerable to stochastic environmental events (e.g., Pennock et al. 2018; Archdeacon et al. 2020a, b). In the longer term therefore, addressing fragmentation issues to re-establish extinction recolonization dynamics (e.g. Pennock et al. 2018; Archdeacon et al. 2018; Archdeacon and Remshardt 2012) and providing variability in flows (i.e., a natural hydrograph) will be key to securing the future of the pelagic broadcast spawning fishes of the Great Plains and elsewhere.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10592-021-01374-x.

Acknowledgements We gratefully acknowledge the assistance with sample collection provided by A. Monie, J. Caldwell (UDWR), D. C. Kitcheyan and D. Fenner (USFWS). We also acknowledge T. Turner, A. Sanchez, B. Fitzgerald, M. Paulk, S. McKitrick, C. Bell, A. Cameron (UNM) and technical staff at UNM Biology Molecular Core Facility, T. Archdeacon (USFWS) and C. Hoagstrom (Weber State University) and expert curatorial services of A. Snyder, E. DeArmon and staff of UNM's Museum of Southwestern Biology Division of Fishes.

Funding This study was funded by New Mexico Department of Game and Fish Share with Wildlife Program and State Wildlife Grant Program (Award Numbers: F11AF00075, F12AF00124, F15AP01004, F17AP00041, F18AP00129).

Data availability Genetic data are available on Dryad:https://doi.org/10.5061/dryad.9cnp5hqhn. DNA sequences have been deposited in Genbank. Field notes associated with collections are available from the University of New Mexico's Museum of Southwestern Biology, Division of Fishes.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Samples were collected under UNM IACUC protocol MSC10-100492-MCC.

Consent for publication All authors consent to publication.

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