



Assessing functions of movement in a Great Plains endemic fish

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Abstract Pelagic broadcast spawning cyprinids are a mobile group of fishes commonly found within semi-arid areas of the Great Plains of North America. In several species, upstream movements of 50 to 200 km have been reported and associated with reproductive migration. Long distance migrations also are associated with finding food and refuge. Goals of this study were to detect synchronous movement of Prairie Chub at specific life stages and relate movement to functions associated with migration (i.e., reproduction, feeding, and refuge). Movement was inferred by quantifying monthly occurrences of age groups using length frequency distributions among five sites in two rivers and supported with range-wide assessment of genetic structuring. Monthly occurrences of age groups among sites were related to reproductive season (i.e., gonadosomatic indices, ovarian condition) for assessing reproductive migration, to food consumption (i.e., gut content assessments) for assessing feeding migration, and to habitat associations (e.g., specific conductance) for assessing refuge migration. Spatial and temporal patterns in age-0, age-1 and age-2 fish occurrences and abundances suggested movement within only one river. Non-

synchronized movements were more consistently associated with specific conductance following a high flow event, which was more consistent with a refuge function than reproductive season or food consumption. Our findings suggest that Prairie Chubs are capable of moving long distances, but movement was inconsistently associated with reproductive efforts as previously described. Without synchronized movements, we question whether movement is migration or dispersal and provide a contrasting narrative to the drift compensation theory used to describe broadcast spawning cyprinid migrations.

Keywords Red River basin · Fish migration · Fish dispersal · Life history · Isolation by distance

Introduction

Within the semi-arid Great Plains region of North America, current fish communities are a result of historical species dispersion and isolation events, with many species possessing or evolving early maturation, frequent spawning during a protracted season, small clutch size, and rapid population turnover rates (i.e., opportunistic life history strategy; Winemiller and Rose 1992). Opportunistic life history strategy is associated with streams having variable flows and widely fluctuating turbidity, temperature, and specific conductance (Cross et al. 1986; Matthews 1988). Pelagic broadcast spawning cyprinids are a reproductive guild with an opportunistic life history strategy (Johnston 1999).

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Pelagic broadcast spawning cyprinids commonly inhabit Great Plains streams and are of increasing conservation concern largely due to fragmentation of river reaches by dams and the associated effects on pelagic broadcast spawning cyprinid life cycles, which includes large-scale (i.e., 50 to 200 km) upstream movements (Bestgen et al. 2010; Perkin and Gido 2011; Wilde 2016; Worthington et al. 2017). Movement, or a lack thereof, has been detected via a variety of means including length frequency assessments and reproductive condition (Bonner 2000), catch rates and reproductive condition (Walters et al. 2014), visible implant elastomer tags (Wilde 2016), otolith microchemistry (Chase et al. 2015), and genetic assessments (Salgueiro et al. 2003; Alò and Turner 2005; Hurwood et al. 2008; Franssen 2012). Large-scale movement is described as a migration (Walters et al. 2014) and the function is presumed to be primarily for reproduction (Worthington et al. 2017).

Migration is defined as a synchronized, round-trip, long distance movement relative to home range by many individuals of the same life stage and at the same time and direction (Endler 1977; Lucas and Baras 2001; Semlitsch 2008) with three recognized functions: 1) reproduction, 2) feeding, and 3) refuge (Northcote 1978, 1984). During reproductive migration, organisms move to complete a spawning cycle (Lucas and Baras 2001) with fish moving to spawning grounds prior to the onset of reproduction (Irving and Modde 2000; Fredrich et al. 2003). Feeding migration occurs when organisms are moving to increase resource acquisition and in fish includes horizontal movement into floodplains and other areas to access newly available resources or higher-quality food (L'Abée-Lund and Vøllestad 1987; Lucas and Baras 2001). Refuge migration takes place when organisms move from unfavorable abiotic conditions to new locations with better conditions in order to enhance survivorship and reproductive output (Lucas and Baras 2001) and in fish includes movement immediately prior to stream drying (Cambray 1990) and once physiological preferences are exceeded (Edwards 1977). Identifying and quantifying the underlying functions (i.e., reproductive, feeding, refuge) of observed upstream movements can provide greater insight into the basic behaviors of pelagic broadcast spawning cyprinids and facilitate management and threat assessments of Great Plains fishes.

The Prairie Chub *Macrhybopsis australis* (Hubbs and Ortenburger 1929) is an endemic Great Plains broadcast spawning cyprinid that occurs only in the

upper Red River drainage of Texas and Oklahoma and likely migrates similar to other *Macrhybopsis* (Wilde 2016) species within the “Speckled Chub” complex (Eisenhour 2004). The conservation status of the Prairie Chub is listed as G2G3 (G2 = imperiled; G3 = vulnerable) by NatureServe (Natureserve 2017), vulnerable by the 2008 American Fisheries Endangered Species Committee (Jelks et al. 2008), and species of greatest conservation need by both the Texas Parks and Wildlife Department (TPWD 2012) and the Oklahoma Department of Wildlife Conservation (ODWC 2005). Life history information for the Prairie Chub (i.e., reproductive season and effort, age class structure, and diet) is lacking, and information is similarly limited with respect to distribution, abundance, and habitat associations (Taylor et al. 1996; Wilde et al. 1996; Eisenhour 2004).

The goals of this study were to detect synchronous movement of Prairie Chub at specific life stages (i.e., age 0, age 1, age 2) and relate movement to functions associated with migration (i.e., reproduction, feeding, and refuge). Goals were addressed by four primary objectives. The first objective was to update current distribution, abundance, and habitat associations of Prairie Chub within its historical range in Texas and the Red River of Oklahoma. This objective was necessary in order to quantify breadth in Prairie Chub habitat associations used to assess refuge migration and to identify sites with sufficient numbers of individuals to sustain collections for population genetic, reproduction, diet, and age assessments. The second objective was to test for genetic isolation by distance (IBD) of Prairie Chub by assessing genetic differentiation (G_{ST}) across geographic river distances (rkm). Lack of IBD can identify sites with gene flow (i.e., movement of individuals among sites). The third objective was to quantify monthly age class structure, reproductive pattern, and diet of Prairie Chub at three, unimpeded sites on one river (i.e., Pease River) and two, unimpeded sites on another river system (i.e., North Wichita-Wichita River). The fourth objective was to relate monthly changes in Prairie Chub occurrences and age structure at each of the five sites (i.e., synchronized movement by specific age groups) to reproductive status (i.e., gonadosomatic index, ovarian condition), feeding (i.e., gut fullness, diet items and abundance), and habitat conditions. Based on previous findings in closely related taxa in the *Macrhybopsis* “Speckled Chub” complex, expectations were that the Prairie Chub would have life history and habitat

associations similar to congeneric species. For example, other *Macrhybopsis* species consume benthic invertebrates, have a short life span, produce multiple clutches for three to five months based on latitude, and associate with run and riffle habitats (Gotelli and Pylon 1991; Bonner 2000; Williams 2010; Perkin et al. 2013). Furthermore, a lack of IBD in Prairie Chubs would be expected if life histories are similar to other prairie stream minnows (Alò and Turner 2005) and consistent with large-scale movement of fishes. Opportunistically, we assessed if the dams on the Wichita River would affect genetic differentiation among populations of Prairie Chubs, as reported for other riverine fishes separated by dams (Hudman and Gido 2013; Gousskov et al. 2016; Sotola et al. 2017; Smith et al. 2019). Lastly, movement of Prairie Chubs is expected to correspond with one or more of the migration functions: reproductive migration–movement during gonadal recrudescence but before egg release (Tyus 1990; Fredrich et al. 2003); feeding migration–movement into areas with greater food quality or quantity (L'Abée-Lund and Vøllestad 1987); or refuge migration–movement for physiological preference or intermittent drying (Edwards 1977; Cambray 1990).

Methods

Field collections

For objectives 1 and 2, two range-wide and longitudinal surveys, once during the non-reproductive season and once during the reproductive season, were conducted at 36 sites among 20 water bodies (i.e., named creeks, tributaries, and rivers) encompassing 730 river km (rkm) within the upper Red River drainage between September 2015 and September 2016 (Fig. 1; Appendix 1). At each site, geomorphic units (i.e., wadeable riffles, runs, pools, backwaters, and eddies; Hawkins et al. 1993) were delineated and sampled in proportion to their availability. Geomorphic units were exhaustively sampled with single to multiple seine hauls, using a standard seine (3 m × 1.8 m, mesh size = 3.2 mm) or bag seine (5 m × 1.8 m, mesh size = 3.2 mm). Seines were selected as the gear type, because they are more efficient in sampling large areas of wadeable habitats, environmental variables can be accurately quantified, and fish are obtained with limited trauma (Pierce et al. 1990). In addition, seining effectiveness,

despite bias towards pelagic fishes over benthic fishes, is increased in water bodies like the upper Red River drainage with fine substrates, shallow water depths, few snags, and slow current velocities (Parsley et al. 1989; Pierce et al. 1990; Neufeld et al. 2016). Elevated specific conductance within the upper Red River precluded electroshocking (Reynolds 1996). Length and width of each geomorphic unit were measured. Substrate (i.e., clay, silt, sand, gravel, cobble, boulder, and bedrock), woody debris, detritus, and aquatic vegetation were visually or tactilely estimated and represented as a percent coverage of the total area of each geomorphic unit. Mean water depth (m) and current velocities (m/s) were estimated from three to five-point estimates within a representative cross section of each geomorphic unit. Water temperature (°C), dissolved oxygen (mg/L), pH, and specific conductance (µS/cm) were measured at each site with a YSI 556 multi-probe sonde. Prairie Chubs were taken as available for genetic analysis, anesthetized in a lethal dose of tricane methanesulfonate (MS222), and preserved in 95% ethanol.

For objectives 3 and 4, five sites were selected for monthly collections of Prairie Chubs between February 2016 and January 2017 from three sites (i.e., FM 104, Hwy 6, and Hwy 283) on the Pease River and two sites (i.e., Hwy 6 and FM 1919) on the North Wichita-Wichita River. Sites on the Pease River and North Wichita-Wichita River were selected because 1) populations have low levels of introgression with congener Shoal Chub *M. hyostoma* Gilbert 1884 (Sotola et al. 2019), and 2) Prairie Chubs taken during range-wide surveys ($N=61$ in the Pease River, $N=270$ taken in North Wichita-Wichita River; Ruppel et al. 2017) indicated sufficient numbers to allow a monthly harvest of 10 individuals per site. Sites on the Pease River and on the North Wichita-Wichita River were similar and consisted of shallow braided channels dominated by sand and silt substrates. Pease River and North Wichita-Wichita River flow into the Red River. Sites on the Pease River are continuous with the Red River; however, sites on the North Wichita-Wichita River are discontinuous with the Red River, separated by two reservoirs (i.e., Lake Kemp and Lake Diversion) on the lower Wichita River. On the Pease River, the upper site (i.e., FM 104) was located about 60 rkm upstream from middle site (i.e., Hwy 6), and the middle site was located about 60 rkm upstream from the lower site (i.e., Hwy 283). On the North Wichita-Wichita River, the upper site (i.e., Hwy 6) was located about 90 rkm

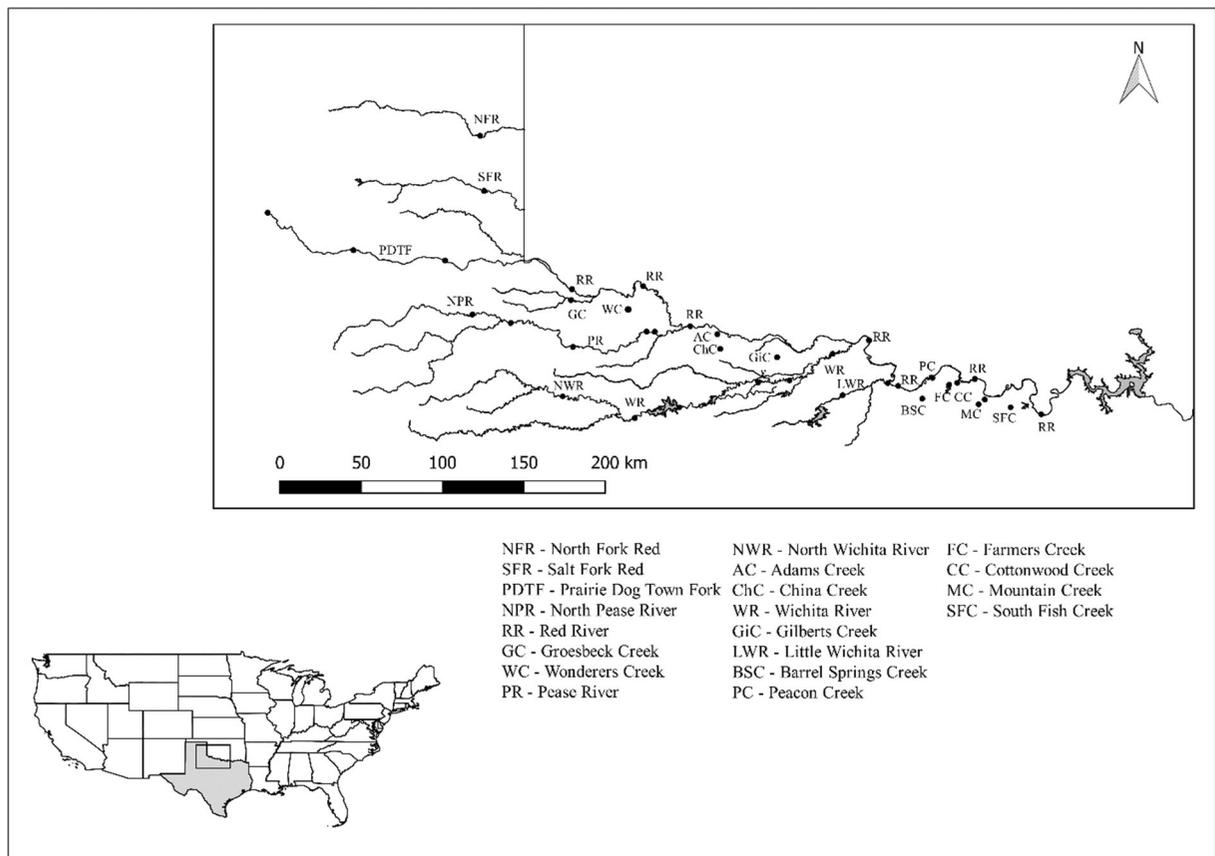


Fig. 1 Site locations ($N=36$, black dot) and water bodies ($N=20$) for longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016. See Appendix 1 for georeferenced site locations

upstream from the lower site (i.e., FM 1919). At each collection site and date, a minimum of 10 seine hauls was made to capture 10 Prairie Chubs (≥ 35 mm in total length; minimum length for sexual maturity in congeneric Peppered Chub *M. tetranema* Gilbert 1886; Bonner 2000). Total lengths (nearest mm) were measured on all Prairie Chubs captured and used for length frequency assessment. Up to 10 Prairie Chubs were retained for life history assessment, anesthetized with a lethal dose of MS222, and fixed in 10% formalin.

Laboratory techniques

Genetics

Genomic DNA was extracted from fin clips in 96-well format using Qiagen DNeasy blood and tissue extraction kits. For each individual, a reduced-complexity genomic library was prepared for genotyping by sequencing protocols modified from Meyer and Kircher

(2010), Gompert et al. (2012), Parchman et al. (2012), Mandeville et al. (2015), and described in detail in Sotola et al. (2019). DNA was digested using the enzymes EcoRI and MseI and the resulting fragments were labeled with 8–10 base pair barcodes. Two rounds of polymerase chain reaction were performed on these restriction-ligation products using Illumina primers, and all samples were pooled into a single library and sent to the University of Texas Genomic Sequencing and Analysis Facility (Austin, TX, USA). After size selection between 300 and 400 base pairs, the library was sequenced on an Illumina HiSeq 4000 SR 150 platform.

After sequencing, PhiX contaminants, MseI adapters and barcodes were removed (Sotola et al. 2019), and a de novo assembly was performed using dDocent (Puritz et al. 2014). Unique reads were identified for each individual and those with fewer than four copies and shared by fewer than four individuals were removed from the dataset. The scaffolds obtained from this de

novo assembly formed the basis of a subsequent reference-based assembly in which all sequenced reads were added (Li et al. 2009; Sotola et al. 2019). Single Nucleotide Polymorphisms (SNPs) were identified and the Bayesian posterior probabilities that individual SNPs were variable were calculated (Li et al. 2009). For contigs containing more than one SNP, a single SNP was randomly chosen for subsequent analyses. SNP genotypes were not “called,” but rather likelihood estimates were calculated for each SNP across all individuals and used to determine population allele frequencies. SNPs with minor allele frequency of <0.05 were excluded from the dataset.

Reproduction and diet

Up to five females fixed in formalin were randomly selected, measured to the nearest mm, and weighed to the nearest mg from Pease River and North Wichita-Wichita River sites by month. An incision was made from the urogenital opening to isthmus. The esophagus was severed, and the stomach, intestine, and ovaries were removed. Ovaries were weighed, and gonadosomatic index (GSI; [mass of ovaries / mass of fish] × 100) was calculated for each fish. Ovaries were macroscopically categorized as 1) immature or resting ovaries with small, translucent oocytes; 2) developing ovaries with small (< 0.2 mm in diameter), translucent oocytes and small (< 0.5 mm) opaque oocytes indicating early stages of yolk deposition; 3) mature ovaries with small translucent oocytes, small opaque oocytes, and large (> 0.5 mm in diameter) vitellogenic oocytes (Williams and Bonner 2006). The left ovary of up to three females with mature ovaries was selected, and individual oocytes were separated by teasing oocyte mass apart and redistributing in a petri dish with a gentle swirl. Diameters were measured for oocytes >0.2 mm to the nearest 0.01 mm for the first 100 oocytes encountered in multiple fields of view with a dissection microscope fitted with an ocular micrometer. Oocyte diameters were plotted by percent frequency of occurrence to estimate modalities of clutch production (i.e., single spawning or multiple batch spawning). The stomach was separated from the intestine at the pyloric sphincter muscle. The stomach wall was cut longitudinally from the sphincter muscle to the esophagus, carefully exposing the gut contents. Stomach fullness (i.e., percent of stomach filled by contents) was determined by two independent observers, assigning a number from 0%

(empty) to 100% (full) in increments of 10% (Childs et al. 1998). Inconsistencies in stomach fullness between the two observers were resolved by averaging the two assigned numbers. Stomach contents were sorted and identified. Percent volume was defined as the volume of algae, animal materials, substrates, and plastics comprising the total volume of stomach fullness. Percent occurrence was defined as the number of fish with a food item identified to the lowest practical taxonomic level. Animal materials were counted per lowest practical taxonomic level, and relative abundance was calculated for each item.

Data analysis

Physical and chemical habitat associations

Habitat associations were quantified from physical and chemical habitat variables taken during range-wide surveys with principal component analysis (PCA; SAS Institute, Cary, NC). Geomorphic units were denoted as dummy variables. Quantitative habitat variables (i.e., percent substrate, percent woody debris, percent detritus, percent aquatic vegetation, water depth, current velocity, pH, and specific conductance) were z-transformed (Krebs 1999). Resulting PCA loadings of axes I and II were plotted to express similarities and differences in physical and chemical habitat variables among geomorphic units. Principal component axes I and II scores with Prairie Chub occurrences were compared to PC scores without Prairie Chub occurrences using t-tests ($\alpha = 0.05$). Numbers of Prairie Chubs were $\log_{10}(N + 1)$ transformed and regressed with PC axes I and II scores (i.e., independent variables) to assess relationship between abundance and habitat gradients with linear regression. Loadings were averaged among each experimental unit (a geomorphic unit with corresponding physical and chemical habitat variables) within a water body. Mean PC axes I and II scores for water bodies with Prairie Chub occurrences were compared to mean PC scores for water bodies without Prairie Chub occurrences using t-tests. We additionally tested Prairie Chub distributions among geomorphic units with Chi-Square and among depth, current velocity, and specific conductance gradients with Kolmogorov-Smirnoff (KS), because these variables were identified as factors associated with fish distributions within upper Red River drainage (Ruppel et al. 2017).

Genetics

Genetic differentiation, Nei's G_{ST} (Nei 1987), was calculated using Program R (R Core Team 2017) with allele frequency estimates calculated from the mean genotype posterior probabilities from Entropy (Gompert et al. 2014; Mandeville et al. 2015; Sotola et al. 2019). Bayesian linear regressions were used to determine the degree to which linearized pairwise genetic differentiation ($G_{ST}/(1-G_{ST})$) could be explained by pairwise geographic distance (measured as the river km [rkm] difference between two sites, scaled and centered prior to analysis). A positive linear relationship between G_{ST} and rkm indicates IBD exists in Prairie Chubs, suggesting genetic structure and consistent with limited gene flow and short, frequent movements, whereas lack of a relationship between G_{ST} and rkm indicates the lack of IBD, suggesting lack of genetic structure and consistent with gene flow and longer movements (Wright 1943; Slatkin 1985, 1993). Program R and the RJAGS package were used to run MCMC models using the JAGS language (Plummer 2003). Because the Prairie Chub is hybridizing with the Shoal Chub (Sotola et al. 2019), only sites and individuals with >95% assignment probability to Prairie Chub clusters in Entropy were used (Gompert et al. 2014; Mandeville et al. 2015; Sotola et al. 2019). This included individuals from the Pease River, Wichita River, and upper Red River. Two separate linear regression models were assessed. The first regression model used pairwise G_{ST} estimates taken from sites not separated by dams. The model consisted of 15 pairwise estimates among six, unimpeded sites on the Pease River and upper Red River, and one pairwise estimate between the two Wichita River sites separated from all other sites by a dam as the dependent variable. The second regression model used pairwise G_{ST} estimates taken from all sites. The model consisted of 28 pairwise estimates including 12 pairwise estimates between sites separated by dams as the dependent variable. In total for each regression, four independent chains each were ran with 1000 iterations, a 500 iteration burn-in and a thinning interval of 10. We specified vague Gaussian priors on the standardized scale for the regression coefficients ($\mu = 0$, $\sigma^2 = 0.01$). Significance was assessed via the 95% credible intervals of the slope estimate; if the 95% credible intervals overlapped zero it was considered a non-significant slope (estimate did not differ from zero) estimate. Chains were checked for convergence

using diagnostic plots and Gelman and Rubin's scale reduction factor to verify adequate chain mixing was calculated (value between 1 and 1.1 was acceptable; Gelman and Rubin 1992; Plummer et al. 2006).

Age groups

Length frequency histograms were constructed from monthly collections using 2-mm bin increments combined across sites to assess number of age groups and life span. Modal progression analysis (Bhattacharya's Method, Fish Stock Assessment Tools II, FiSAT II) was used to estimate the number of age groups from their lengths monthly between February 2016 and January 2017. Birth date follows conventional standard of January 1 (Jearld 1983). Age-0 fish were spawned in 2016, age-1 fish were spawned in 2015, and age-2 fish were spawned in 2014.

Results

Habitat associations — longitudinal surveys

Prairie Chubs ($N=486$) were taken from 51 (13%) of 400 geomorphic units, 16 (44%) of 36 sites, and six (30%) of 20 water bodies sampled within the upper Red River drainage. Relative abundance of Prairie Chub among all habitats, sites, and water bodies was 1.3% and ranged between 0.1% and 9.6% among sites where they occurred. Density of Prairie Chub among all geomorphic units, sites, and water bodies was 0.009 fish/m² and ranged between <0.01 fish/m² and 0.28 fish/m² among sites where they occurred. Geomorphic units ($N=400$) consisted primarily of runs (70%) and pools (12%). Geomorphic units were generally shallow (mean depth ± 1 SE: 0.3 m \pm 0.01) with moderate current velocities (0.21 m/s \pm 0.009) and predominantly sand (57%), silt (30%), and gravel (9%) substrates. Mean woody debris, detritus, and aquatic vegetation ranged from 0.7% (\pm 0.14) to 1.1% (\pm 0.22). Water temperatures ranged between 5 °C and 37 °C, dissolved oxygen ranged between 2.6 to 15 mg/l, and pH ranged between 6.9 and 8.9. Specific conductance ranged between 115 and 49,968 μ S/cm with greater specific conductance observed in western water bodies of the Red River drainage and lower specific conductance observed in eastern water bodies.

Principal component axes I and II explained 24% of the total variation among 400 geomorphic units sampled. Axis I explained 13% of the total variation and represented a geomorphic unit and substrate gradient. Strongest loadings for PC axis I were pool (0.33), silt (0.30), run (−0.46), and sand (−0.45) (Fig. 2a). PC Axis II explained 11% of the variation and represented a geomorphic unit, substrate, and current velocity gradient. Strongest loadings for PC axis II were riffle (0.42), gravel (0.40), current velocity (0.39), and silt (−0.37). Prairie Chub occurrences were not associated with PC axis I (t-test; $t_{0.05(2), 398} = 0.42$, $P = 0.67$) or PC axis II ($t_{0.05(2), 398} = 0.37$, $P = 0.67$). Likewise, Prairie Chub abundances were not associated with PC axis I (linear regression; $F_{1398} = 0.14$, $P = 0.71$) or PC axis II ($F_{1398} = 0.13$, $P = 0.72$) (Fig. 2b). Six water bodies with Prairie Chub did not differ among 14 water bodies without Prairie Chub for PC axis I (t-test; $t_{0.05(2), 398} = 1.80$, $P = 0.07$) but differed for PC axis II (t-test; $t_{0.05(2), 398} = 3.25$, $P < 0.01$) (Fig. 2c). Water bodies with Prairie Chub generally consisted of swifter waters with sand substrates in the western portion of the drainage, whereas water bodies without Prairie Chub consisted of slow-moving pools with silt substrates within the eastern portion of the drainage. However, Prairie Chub was not taken from several water bodies with swift waters and sand substrates (i.e., negative water body averages on PC axis I), such as Prairie Dog Town Fork, Salt Fork Red River, North Fork Red River, Adams Creek, or Cottonwood Creek.

Prairie Chub distributions differed from expected for geomorphic units, current velocity, depth, and specific conductance. Prairie Chub was taken more often in run (76%) and riffles (10%) than available (70% runs, 9% riffles) and less often in pools (8%) and backwaters (6%) than available (12% pools, 9% backwater; Chi-square, $\chi^2 = 16.8$, $P < 0.01$). Prairie Chub occurrences among current velocities ranged between 0 and 0.6 m/s with 66% of Prairie Chub captured between 0 and 0.2 m/s. Use of current velocities did not differ from expected for Prairie Chub occurrences (KS = 0.12, $P > 0.05$), but differed for abundances (KS = 0.24, $P < 0.01$) (Fig. 3). Prairie Chub occurrences among water depths ranged between 0.04 and 1.2 m with 88% of Prairie Chub captured between 0.1 and 0.4 m. Use of shallow water depths differed from expected for Prairie Chub occurrences (KS = 0.22, $P < 0.05$) and abundances (KS = 0.20, $P < 0.01$). Prairie Chub

occurrences among specific conductance ranged between 2215 and 26,408 $\mu\text{S}/\text{cm}$ with 77% of Prairie Chub captured between 10,000 and 20,000 $\mu\text{S}/\text{cm}$. Use of moderately high specific conductance differed from expected for Prairie Chub occurrences (KS = 0.19, $P < 0.05$) and abundances (KS = 0.28, $P < 0.01$).

Genetics — longitudinal surveys

A total of 32,122 SNPs was generated in our dataset of 166 individuals from eight sites. Pairwise G_{ST} ($N = 16$) among sites not separated by dams and pairwise G_{ST} ($N = 28$) among all sites were low and ranged from 0.004 to 0.035. Relationships between G_{ST} and rkm were not detected for sites not separated by a dam (slope: 0.015, 95% CI: −0.006 – 0.036) (Fig. 4a) or among all sites including sites separated from another by a dam (slope: 0.002, 95% CI: −0.004 – 0.007) (Fig. 4b).

Reproduction, diet, and age— Pease and North Wichita-Wichita rivers

A total of 193 female Prairie Chubs was taken for reproductive assessments from Pease River ($N = 87$) and North Wichita-Wichita River ($N = 106$). Mean monthly GSIs were < 2% from October through February, corresponding with females having immature or resting ovaries ($N = 80$ females; 39–63 mm in TL) (Fig. 5). Mean monthly GSIs were > 2% from March through September, corresponding with females having developing ovaries between March and September ($N = 27$ females; 37–62 mm in TL) and with females having mature ovaries between May and September ($N = 64$ females; 38–66 mm in TL). Individual GSIs ranged between 0.9 to 8.8% for females with developing ovaries and ranged between 6.0 to 23% for females with mature ovaries. Oocyte diameters ranged from 0.3 mm to 1.2 mm in females with mature ovaries taken monthly from May through September (Fig. 6). Non-vitellogenic and early vitellogenic oocytes occurred continuously among mature ovaries from May through September.

A total of 197 male and female Prairie Chubs was taken for gut content assessments from the Pease River ($N = 89$) and North Wichita-Wichita River ($N = 108$). Gut content by volume consisted primarily of animal

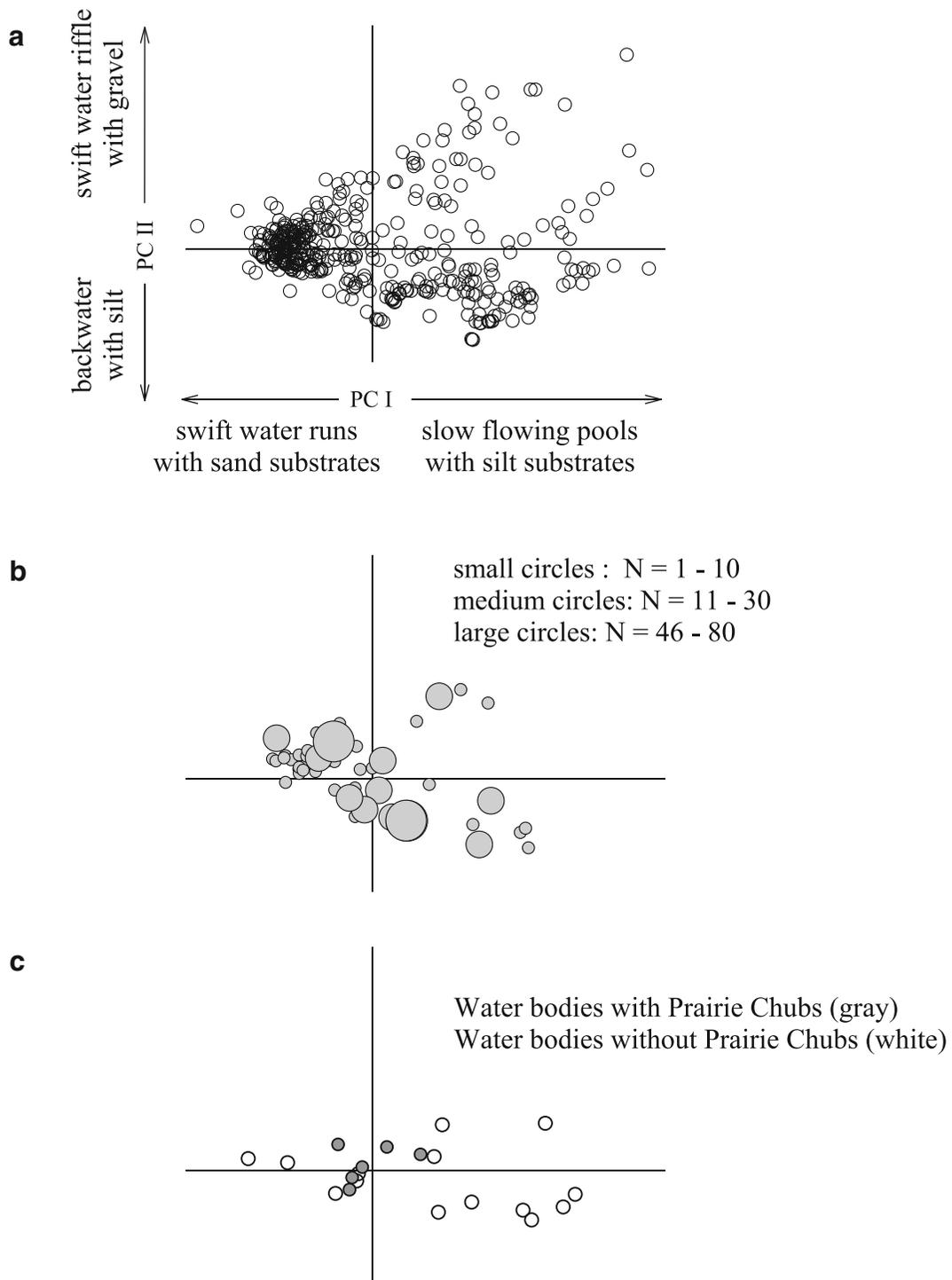


Fig. 2 Principal component analysis from the longitudinal surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016. Circles represent all geomorphic units ($N=400$) along PC I and PC II gradients

sampled during the longitudinal surveys (a). Shaded circles represent the number of Prairie Chub taken from each geomorphic units (b) and water bodies with Prairie Chub occurrences (c) from the upper Red River drainage

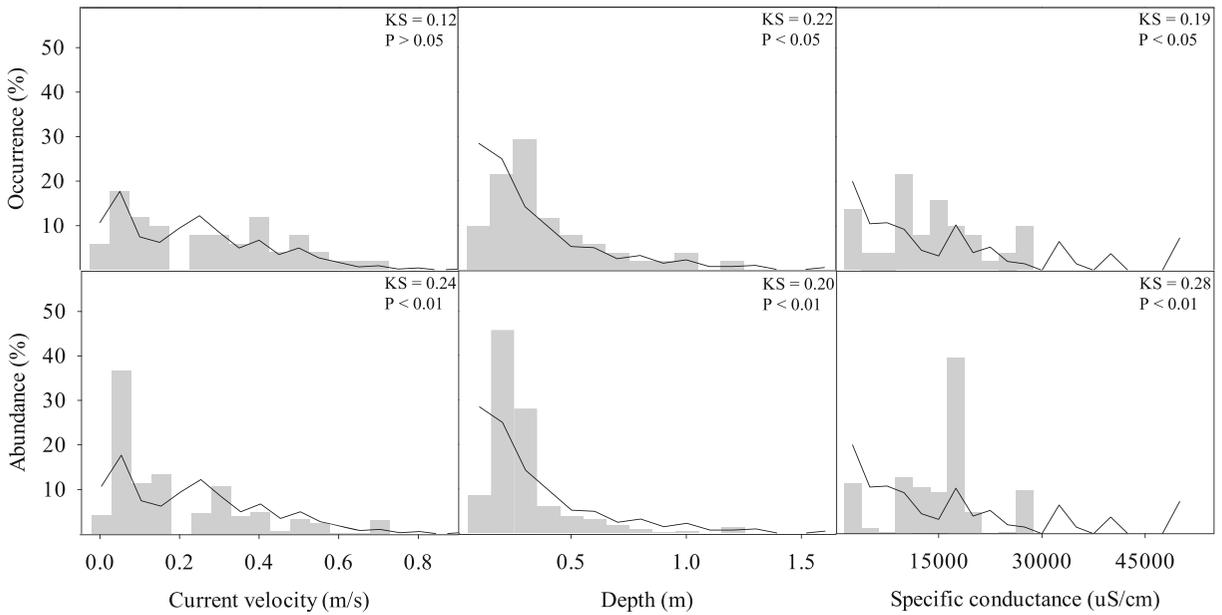


Fig. 3 Frequency of occurrences and abundances of available habitats (line) and used habitats (bars) by Prairie Chub for current velocity, depth, and specific conductance from the longitudinal

surveys within the upper Red River basin of Texas and Oklahoma, September 2015 through September 2016. Kolmogorov-Smirnov (KS) test statistic and associated *P* value are provided

materials (99%) (Table 1). Mean (\pm 1 SD) monthly gut fullness ranged from 4.6% (\pm 7.6) in November 2016 to 65% (\pm 41.1) in May 2016. Frequency of empty stomachs was 4.5%. The most frequently occurring items were Chironomidae (88% occurrence), sand

(37%), clay or silt (14%), and unknown Diptera pupa (11%). Chironomidae occurred in Prairie Chub stomachs year-round with monthly occurrences ranging from 70% in December 2016 to 100% in July 2016. Among animal material, Chironomidae was the most

Fig. 4 Scatter plot of linear genetic differentiation ($G_{ST}/(1-G_{ST})$) values among collection sites versus river distance between sites (rkm) not separated by dams (a) and between sites separated and not separated by dams (b) from three sites on the Pease River, two sites on the North Wichita-Wichita River, and three sights on the Red River of Texas and Oklahoma, September 2015 through September 2016

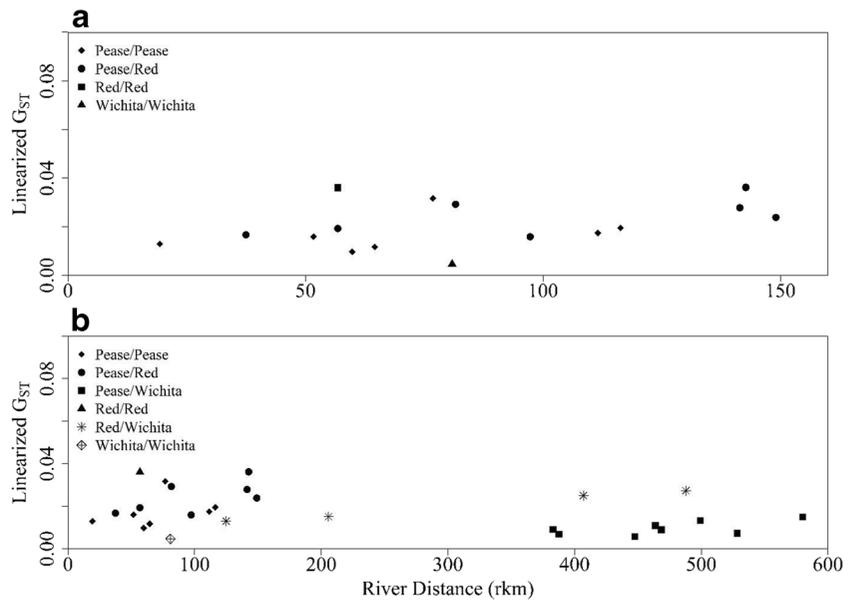
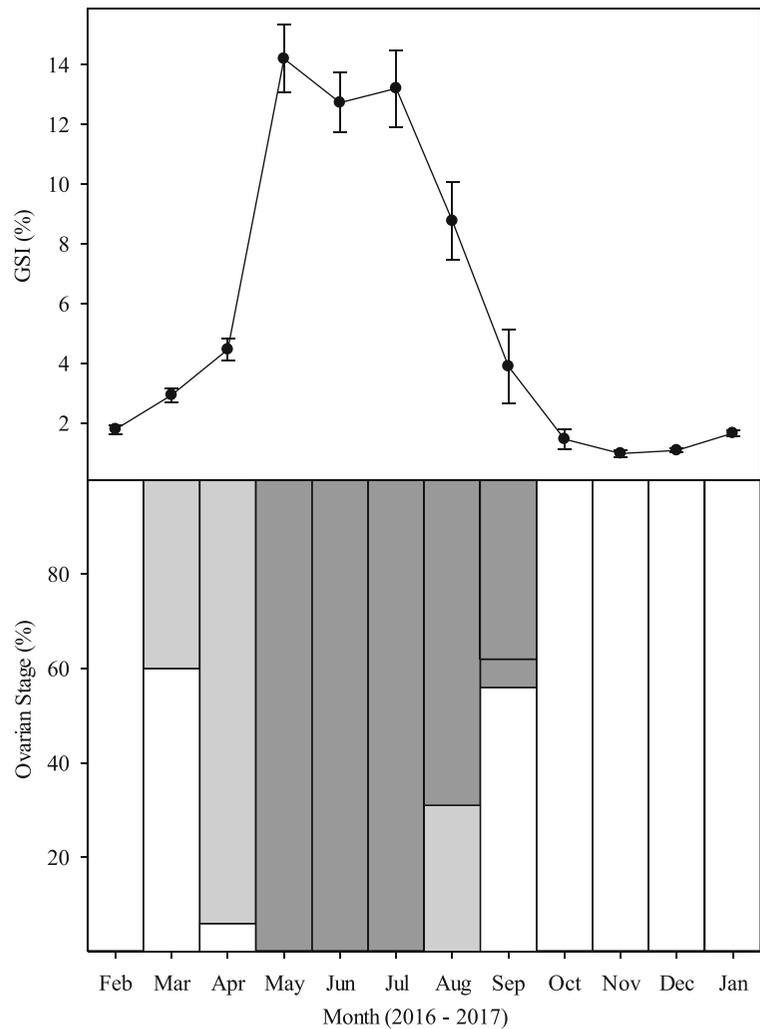


Fig. 5 Mean (± 1 SE) monthly gonadosomatic index (GSI) for Prairie Chub taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017, and corresponding ovarian stages (%) by month for immature (white), developing (light gray), and mature (dark gray) females



abundant food item (95%) followed by unknown Diptera pupa (2%). Other aquatic invertebrate taxa were consumed but at low ($\leq 0.1\%$) relative abundance. Likewise, terrestrial invertebrates and parts of vertebrates (i.e., fish scales and gills) were consumed but at low relative abundances.

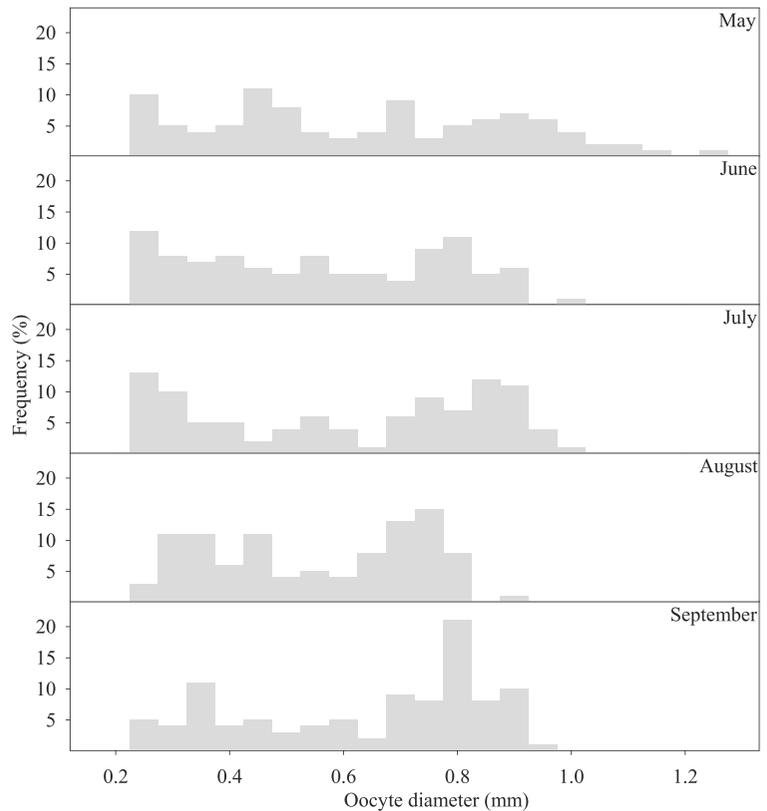
Length measurements were taken from 1295 Prairie Chubs ($N=569$ from Pease River, $N=726$ from North Wichita-Wichita River). Prairie Chub population consisted of three estimated age groups: Age 0, Age 1, and Age 2 (Fig. 7). Age-0 fish were taken July through December 2016 and reached a mean total length (± 1 SD) of 40 mm (± 4). Age-1 fish represented 89% of the adult population, were taken year-round, and reached a

mean total length (± 1 SD) of 57 mm (± 2). Age-2 fish represented 11% of the adult population, were taken February through August 2016, and reached a maximum total length of 67 mm.

Age group distributions among sites — Pease and North Wichita-Wichita rivers

Sexually mature fish (i.e., age 1 and age 2) were less homogeneously distributed among sites on the Pease River from March 2016 through January 2017 and more homogeneously distributed between sites on the North Wichita-Wichita River from February 2016 through January 2017. Within the upper site of the Pease River,

Fig. 6 Frequency of oocyte size distributions in mature ovaries of Prairie Chub taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, May 2016 through September 2016



adult fish were present only June through August and in January (Fig. 8). Within the middle site, adult fish were present every month, except in June. Within the lower site, adult fish were present March through May and October through January. Age-0 fish were first detected in July and found at all sites from August through December, except at the upper site from October through December. Within the upper site of the North Wichita-Wichita River, adult fish were present every month except in October (Fig. 9). Within the lower site, adult fish were present every month, except in June. Age-0 fish were first detected in July and found consistently at both sites from August through December.

Associations with age group distributions among sites

Heterogeneity in adult fish occurrences by site and month within the Pease River corresponded consistently more with a water quality (i.e., specific conductance) than with reproductive effort or with feeding. Adult fish were not detected at the upper Pease River site during or

soon after periods of elevated specific conductance (>26,408 $\mu\text{S}/\text{cm}$, maximum levels for Prairie Chub observed in this study). Specific conductance decreased following elevated flows from precipitation events, April through June. With lower specific conductance in May and June, adult fish were observed at the upper site but not at the middle or lower site. As specific conductance increased >26,408 $\mu\text{S}/\text{cm}$, adult and age-0 fish were no longer present at the upper site. Occurrences of adult fish at the upper site June through September corresponded with reproductive season (March–September) and spawning season (May – September), but after reproductive and spawning seasons were underway. Occurrences of adult fish in January did not correspond with the reproductive season. Occurrences of adult fishes at the upper site were not related to food quality or availability, given that mean ($\pm\text{SD}$) gut fullness was 15% (± 10) and the dominant diet item of adult Prairie Chub at the upper site was Chironomidae (97%) and only consumed three food items. Gut fullness, dominant food items, and number of food items consumed

Table 1 Percent volumes, occurrences, and relative abundances of food items in stomachs of Prairie Chubs taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017

Food items	Volume (%)	Occurrence (%)	Relative abundance (%)
Plant			
Algae	0.2	8	
Animal	99		
Aquatic invertebrates			
Crustacea		0.5	< 0.1
Copepoda		0.5	0.1
Isopoda		0.5	< 0.1
<i>Daphnia</i>		0.5	0.1
Trombidiformes		0.5	< 0.1
Diptera			
Chironomidae		88	95
Pupa		11	2
Ephemeroptera		2	< 0.1
Odonata			
Gomphidae		0.5	< 0.1
Trichoptera		1	< 0.1
Hydropsychidae		0.5	< 0.1
Unidentifiable		3	< 0.1
Pupa		4	< 0.1
Invertebrate egg		1	1
Terrestrial invertebrates			
Diptera		1	< 0.1
Unidentifiable		0.5	< 0.1
Vertebrates			
Scales		0.5	< 0.1
Gill filaments		0.5	< 0.1
Substrate			
Clay/Silt	0.7	14	
Sand	0.1	37	
Plastic	< 0.1	2	
Total N	197		

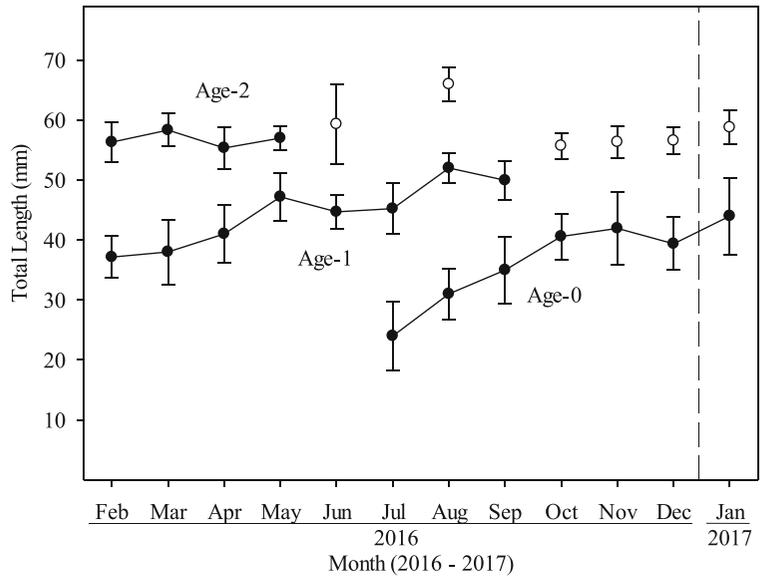
was not noticeably different at the middle site (19% (\pm 27); Chironomidae, 95%; three food items) and lower site (11% (\pm 28); Chironomidae, 99%; two food items).

Discussion

Life history and habitat associations of the Prairie Chub were similar to those reported for other congeners within the *Macrhybopsis* “Speckled Chub” complex

(Eisenhour 1997; Bonner 2000; Heard 2008; Perkin et al. 2013; Wilde 2016). Similarities include benthic invertivore (i.e., primarily chironomids), short-lived (i.e., up to age 2), multiple batch spawner over a 5-month period, inhabit run and riffle geomorphic units with sand to gravel substrates, and mobile (i.e., moving \leq 60 km). As expected, G_{ST} was not related to geographic river distances. Patterns in age group distributions indicated movement within the Pease River but not in the North Wichita-Wichita River. Movement was

Fig. 7 Mean \pm 1 SD total lengths (black circles) for Age-0, Age-1, and Age-2 Prairie Chub taken from three sites on the Pease River and two sites on the North Wichita-Wichita River, February 2016 through January 2017. White circles represent mean and \pm 1 SE of total lengths taken from ≤ 3 individuals within an age group per month. Dashed line indicates transition into the next age class



consistent with expectations of refuge migration, somewhat consistent with expectations of reproductive migration, and inconsistent with expectations of feeding migration.

Prairie Chub were not homogeneously distributed among available habitat variables or water bodies within upper Red River drainage. Prairie Chubs were detected in runs and riffles of braided, sand-bed prairie streams comprised of shallower depths, moderate current velocities, sand and silt substrates, and specific conductance $< 26,408 \mu\text{S}/\text{cm}$ in the western extent of the study area. Prairie Chubs were not detected in more entrenched, slower flowing, and relatively deep water bodies in the eastern extent of the study area. Absence from entrenched, slower flowing, deeper water bodies in the eastern extent of the study area could be linked to specialization for braided sand-bed streams (Kehmeier et al. 2007) or driven by competition and predation (Echelle et al. 1972; Gido et al. 1999). Prairie Chub was not detected in five braided, sand-bed water bodies in the western extent of the drainage (i.e., North Fork, Prairie Dog Town Fork, Salt Fork of the Red River, Adams Creek, Cottonwood Creek). Extirpation of Prairie Chub in the North Fork was reported previously, attributed to predation and reproductive failures related to construction of Lake Altus (Winston et al. 1990). In Prairie Dog Town Fork, Prairie Chub were inconsistently reported since the 1920s (Wilde et al. 1996; Hendrickson and Cohen 2015), and this lack of occurrence could be attributed to specific conductance

$> 40,000 \mu\text{S}/\text{cm}$ during the time of our surveys. In the Salt Fork of the Red River, specific conductance was $3350 \mu\text{S}/\text{cm}$ during time of our surveys, but Prairie Chub was not detected. Last record of Prairie Chub in Salt Fork was in 1999 (Hendrickson and Cohen 2015). Reasons for lack of occurrence in Adams and Cottonwood creeks are unknown, but both systems are small sand-bed water bodies, prone to drying into isolated pools, and therefore likely ephemeral.

Isolation by distance was not detected among sites, indicating gene flow and a lack of genetic structure among sites (Wright 1943; Slatkin 1993; Hutchinson and Templeton 1999). Gene flow and lack of genetic structure are consistent with large-scale movements of propagules and individuals throughout the upper Red River drainage, although shorter movements following local extirpations and recolonization events could also increase gene flow among sites (Slatkin 1985). Increased genetic differentiation (e.g., G_{ST} , G''_{ST} , and F_{ST}) is often observed between upstream and downstream populations separated by dams in other fishes (Neraas and Spruell 2001; Hudman and Gido 2013; Gousskov et al. 2016; Sotola et al. 2017; Smith et al. 2019), including in a system where time of separation was about a decade (Yamamoto et al. 2004). Dams in the North Wichita-Wichita River were constructed in the 1920s. We expected but did not detect increased G_{ST} between discontinuous populations upstream of the Wichita River dams (North Wichita-Wichita River) and those in the Pease and Red rivers. Lack of increased

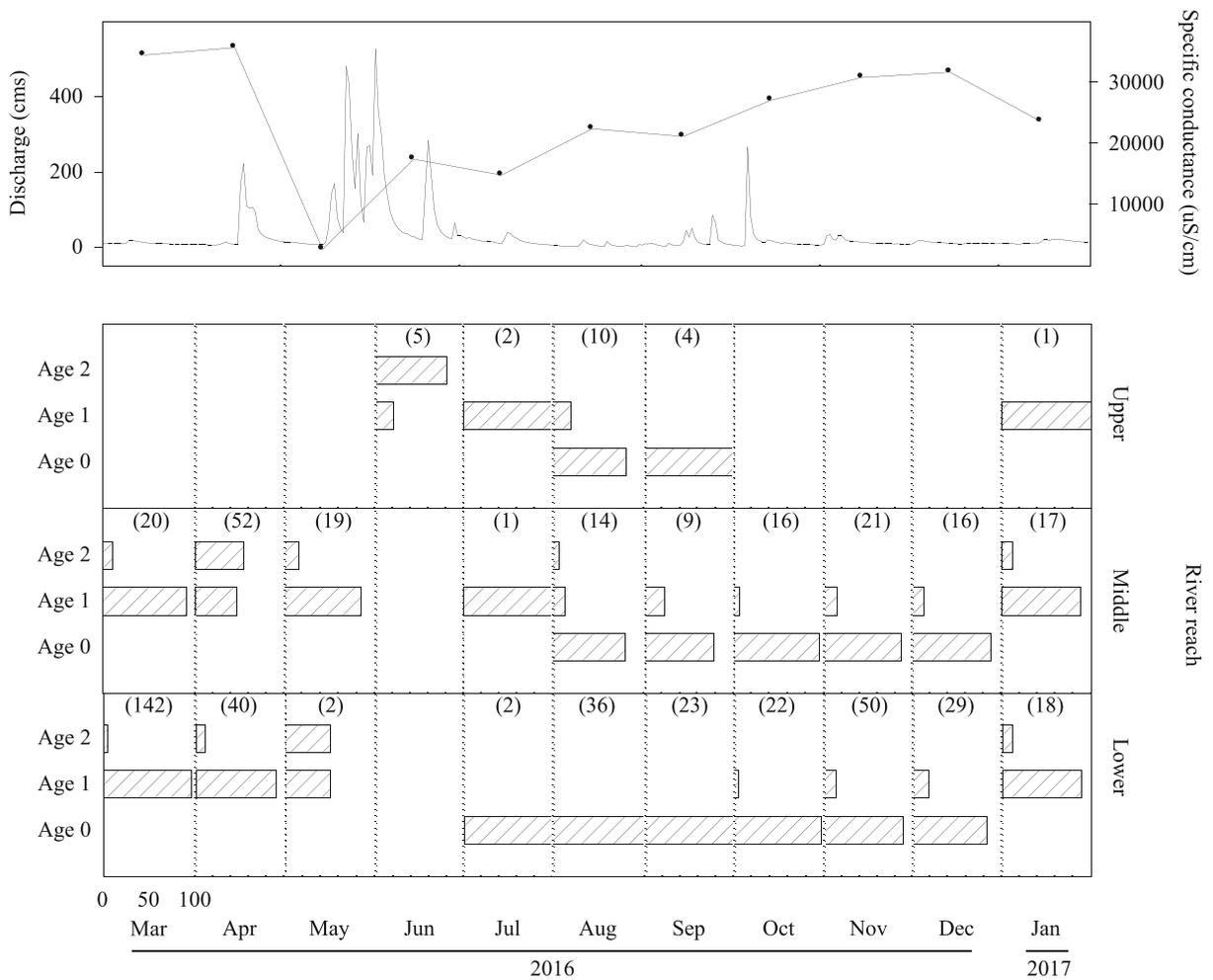


Fig. 8 Daily flow (line; USGS Station 07308200) taken near Hwy 283 crossing on the Pease River, and monthly estimates of specific conductance (symbol and line) taken from FM 104 crossing on the Pease River. Bottom panels represent relative abundances of

Prairie Chub age groups (denoted with shaded bars) among months within the upper site (FM 104), middle site (Hwy 6), and lower site (Hwy 283), March 2016 through January 2017

G_{ST} suggests that active upstream and downstream or passive downstream movement occurs between populations. Active or passive movement is unlikely given the height (i.e., 16 m for Lake Diversion Dam, 35 m for Lake Kemp Dam) and breadth (2.1 km for Lake Diversion Dam, 2.7 km for Lake Kemp Dam) of the dams, although large flow events could conceivably move propagules, juveniles, or adults downstream. Lack of increased G_{ST} could also suggest that effective population sizes upstream of the dams have remained sufficiently robust to maintain their standing genetic variation and reduce the impacts of genetic drift on population differentiation (Denier et al. 2007; Blanchet et al. 2010; Osborne et al. 2012; Gido et al. 2015). This is supported by densities of Prairie Chub in our field

surveys in the North Wichita-Wichita River (Prairie Chub densities: 0.08–0.28 fish/ m^2) were greater relative to Pease and Red rivers (<0.01–0.05 fish/ m^2). Additionally, genetic diversities reported in a previous study (Sotola et al. 2019) were similar for the populations in the North Wichita-Wichita River, relative to other Prairie Chub populations.

We attributed heterogeneity in age-1 and age-2 fish among Pease River sites to upstream movement. If spatial patterns were wholly or partially attributed to fish movement in the Pease River, movement of age-1, age-2, and potentially age-0 fish, occurred within a period of a month, during reproductive and non-reproductive seasons, while having similar gut fullness and consuming similar food items as previous months,

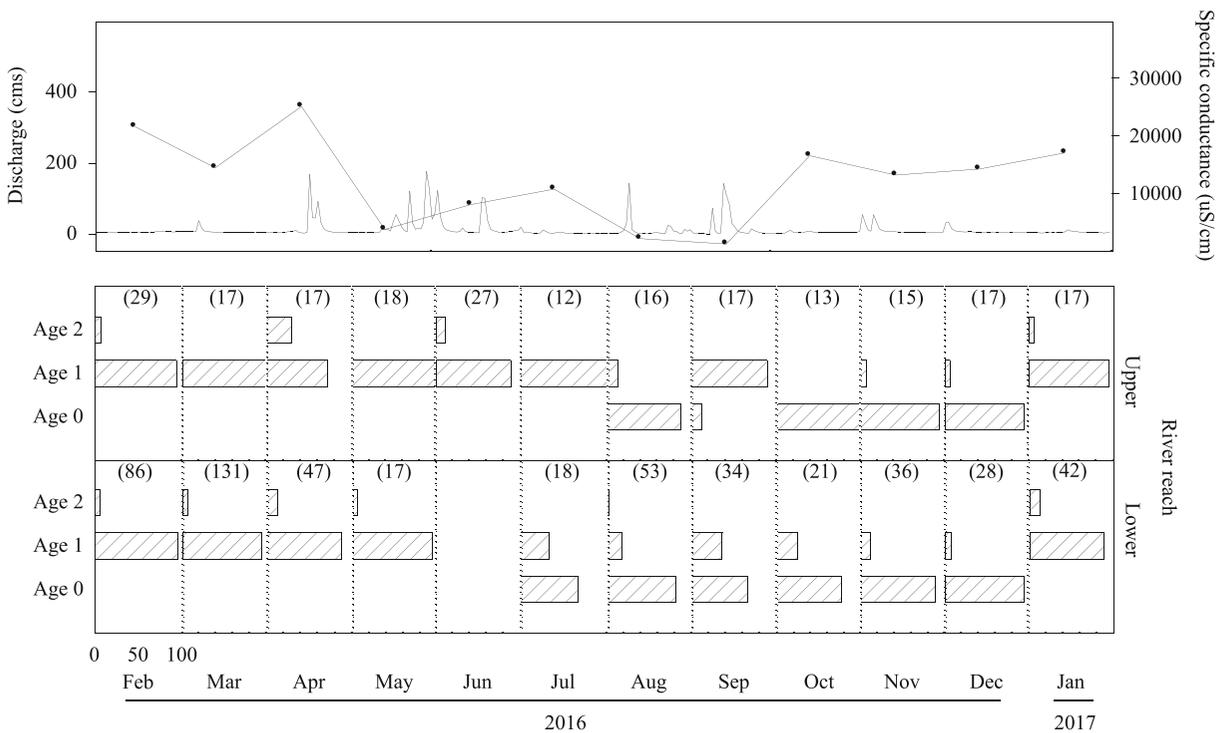


Fig. 9 Daily flow (line; USGS Station 07311700) and monthly estimates of specific conductance (symbol and line) taken near Hwy 6 crossing on the North Wichita River. Bottom panels represent relative abundances of Prairie Chub age groups (denoted

with shaded bars) among months within the upper site (North Wichita River, Hwy 6) and lower site (Wichita River, FM 1919), February 2016 through January 2017

and once specific conductance at the upper site was <26,408 µS/cm. Adult riverine fishes, including broadcast spawning cyprinids, are reported to move upstream 30 to 200 km, including congener Peppered Chub moving at least 50 km (Wilde 2016) during the reproductive season (Fredrich et al. 2003; Walters et al. 2014) or over a period of a year (Wilde 2016). Age-0 broadcast spawning cyprinids are also reported to move upstream >50 km during the summer (e.g., Speckled Chub *M. aestivalis*, Archdeacon et al. 2018) or during the fall (e.g., Pecos Bluntnose Minnows *Notropis simus pecosensis* Chernoff et al. 1982; Chase et al. 2015), which could explain age-0 Prairie Chub summer occurrences within the upper site of the Pease River. Alternatively, summer occurrences of age-0 Prairie Chub could be attributed to age-0 fish remaining in the upstream sites after egg release and by resisting downstream drift (Hoagstrom and Turner 2013; Hoagstrom 2014). Without notable changes in diet quality or quantity among adult fish during the period of perceived movement, movement was not consistent with feeding migration. Prairie Chub diet was dominated by chironomids across

all sites (i.e., range: 95% - 99%), and gut fullness was similar among all sites (i.e., range: 11% - 19%). This is contrasted by L'Abée-Lund and Vøllestad (1987), which found a shift in the diet of a European minnow from predominately detritus and vegetation (73% of gut volume) before migration to predominately chironomids (80% of gut volume) at the end of migration. Upstream movement, in part, was consistent with reproductive migration as age-1 and age-2 fish moved upstream during spawning season, but also inconsistent with reproductive migration since one age-1 fish in January was taken at the upper Pease River site. Upstream movement was most consistent with refuge migration with all age groups observed at the upper Pease River site during months where specific conductance was within their presumed tolerance (< 26,408 µS/cm).

Although patterns in age groups among Pease River sites suggest upstream movement and movement was more consistent with a type of refuge migration, we question whether movement was migratory or dispersal, which has been questioned and discussed previously (Hawkes 2009; Archdeacon

et al. 2018). Migration, as defined previously herein, is the synchronized, round-trip, long distance movement relative to home range by many individuals of the same life stage and at the same time and direction (Endler 1977; Lucas and Baras 2001; Semlitsch 2008). Dispersal, in contrast, is a one-way movement, by individuals independently (i.e., not synchronized) and not in the same direction (Endler 1977; Semlitsch 2008), but the term is often generalized and not well-defined because dispersing organisms show a gradient of movement behaviors (Hawkes 2009). Radinger and Wolter (2014) quantified dispersal patterns in 62 non-migratory freshwater stream fishes and found that fish populations consisted of core and straying individuals, surmising that long distances traveled by straying individuals contributed to gene flow within metapopulations. In this study, Prairie Chub movement was not synchronized (age-1 and age-2 fish remained in the lower two sites on the Pease River; movement was not detected in the North Wichita-Wichita River), and movement occurred among all age groups within and outside of reproductive season. In other studies, populations of Flathead Chub *Platygobio gracilis* Richardson 1836 in Fountain Creek of the Arkansas River drainage only exhibited 18% of individuals moved either upstream or downstream during the reproductive season while 82% remained within 1 km of the release site (Walters et al. 2014). Likewise, movement of Arkansas River Shiners *N. girardi* Hubbs and Ortenburger 1929 (24% remained near release site) and Plains Minnow (64% remained near release site) in the Canadian River of Texas and New Mexico showed lower range of turnover rates (i.e., percentage of fish straying from an area; Schrank and Rahel 2006) during a period of a year (Wilde 2016). Non-synchronized movements and fish populations consisting of core and straying individuals seem to support dispersal rather than migratory for broadcast spawning cyprinids. If dispersal, our finding of Prairie Chub movement being more consistent with a type of refuge migration than reproduction migration is still informative to the functions of the movement involved with dispersal (e.g., “primary triggers for mobility”; Radinger and Wolter 2014).

The life-history cycle of broadcast spawning cyprinids, specifically upstream movement of fishes to compensate for larval drift downstream (drift compensation

theory; Fredrich et al. 2003), is explicably linked to the declines of pelagic broadcast spawning cyprinids related to river fragmentation that disrupt part or all of the life-history cycle (Dudley and Platania 2007; Perkin and Gido 2011; Wilde and Urbanczyk 2013). Fitness aspects of upstream movement and propagule drift is debated (Hoagstrom 2014; Wilde and Urbanczyk 2014), and along with findings of our work, identifies an alternative mechanism for upstream movement in addition to presumed reproductive migration (Worthington et al. 2017). As such, we envision two contrasting narratives on the life-history cycle of broadcast spawning cyprinids: 1) upstream movement and downstream drift are necessary, and fragmented rivers disrupt this cycle (Perkin and Gido 2011; Wilde and Urbanczyk 2014), 2) upstream movement is a consequence of movement towards suitable abiotic conditions (suggested by this study) and downstream drift is not necessary to maintain viable upstream populations (i.e., a sink in source-sink dynamics; Pulliam 1988; Hoagstrom 2014). At this time, we do not promote one narrative over the other given the results of this study. Instead, we use the results of this study and the perspectives of Hoagstrom (2014) to support the consideration of two contrasting narratives when contemplating processes that might explain collective patterns observed in broadcast spawning cyprinids life histories: movement by age-0 fish (Chase et al. 2015; Archdeacon et al. 2018), adults (Wilde 2016) and sexually active adults (Walters et al. 2014); movements of adults occurring with equal frequency upstream and downstream (Walters et al. 2014); variable turnover rates among species (18% - 76%; Walters et al. 2014; Wilde 2016) similar to those reported for resident populations of stream salmonids (15% - 78%; Rodríguez 2002); and, estimates of downstream drift distances of propagules (Dudley and Platania 2007), while accounting for diel patterns in larvae exiting the drift (Robinson et al. 1998; Reichard et al. 2002; Reeves and Galat 2010).

Managers face a daunting task with future conservation efforts in semi-arid climates and with prairie stream fishes because current predictions of expanding aridity throughout the southern Great Plains region (Jones and Gutzler 2016). Future predictions of reduced precipitation and increased groundwater harvest are projected to further deplete aquifer levels (Milly et al. 2005; Taylor et al. 2013) resulting in the reduction of water quality and quantity (Ficke et al. 2007; Rahel and Olden 2008), which in turn, threaten existing fish

communities (Perkin et al. 2017). Therefore, development of accurate life-history models through testing of contrasting narratives (i.e., dispersion versus migration; refuge function versus reproductive function) will aid in determining processes regulating populations of broadcast spawning cyprinids, which will enable conservation strategies (i.e., removal of barriers to increase longitudinal connectivity; Perkin et al. 2014) to be more supported and focused (Hoagstrom 2014).

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