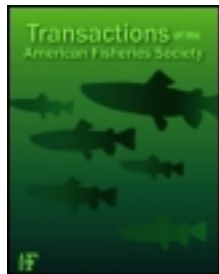


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Fragmentation and Drought Legacy Correlate with Distribution of Burrhead Chub in Subtropical Streams of North America

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ARTICLE

Fragmentation and Drought Legacy Correlate with Distribution of Burrhead Chub in Subtropical Streams of North America

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Abstract

Burrhead Chub *Macrhybopsis marconis* is a species of special concern endemic to subtropical streams in south Texas. We documented life history attributes and historical patterns in abundance and distribution to aid in understanding range-wide declines of the species among the Colorado and Guadalupe-San Antonio River systems. Life history results suggest Burrhead Chub lives for 2 years, reaches sexual maturity at age-1, and spawns multiple clutches during March–September. Review of museum vouchers revealed Burrhead Chub is now missing from 26% of its historical range, including most impounded stream segments. There was a significant difference in the size of stream fragments for which Burrhead Chub is missing or still persists. Timing of many extirpations occurred after fragmentation and coincided with a record drought (1949–1959) when range-wide stream flows were exceedingly low during the Burrhead Chub reproductive season. Furthermore, extensive historical collections taken during 1950–1961 in the Guadalupe River revealed a decline in relative abundance in upstream reaches as the drought continued. Based on these data, we hypothesize that Burrhead Chub experienced range-wide declines associated with historical drought conditions in desiccated stream fragments. Following the drought, stream flows recovered but recolonization by Burrhead Chub was blocked by impoundments in many fragments. These findings support previous linkages between stream connectivity, flow magnitude, and the persistence of fish populations while providing insight into the mechanisms driving freshwater fish declines in the plains of North America.

Stream-fish assemblages of the North American plains (plains hereafter) changed substantially during the past half-century associated with anthropogenic alterations to water availability, fragmentation of riverscapes, habitat destruction, introduction of nonnative species, and water pollution (Gido

et al. 2010; Hoagstrom et al. 2011). These changes resulted in species introductions, replacements, and extirpations, which collectively led to a general pattern of fish homogenization (Rahel 2000; Hoagstrom et al. 2010). Consequently, nearly 40% of North American fishes are listed as imperiled and require

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conservation intervention to ensure their long-term persistence (Jelks et al. 2008). Conservation approaches implemented at broad spatial extents that incorporate riverscape perspectives are most likely to be successful in terms of identifying and mitigating drivers of species decline, especially when multiple drivers of change occur (Fausch et al. 2002; Erős et al. 2012; Geheber and Piller 2012).

Broad-scale studies linking ecological attributes of declining species to environmental change provide insight into biotic and abiotic assemblage structuring mechanisms that lead to species declines (Pease et al. 2011; Perkin and Bonner 2011). For example, life history attributes are commonly used to ascribe population regulations among North American freshwater fishes (Winemiller and Rose 1992; Vélez-Espino et al. 2006) and are linked to environmental variability to describe changes in fish populations (Mims and Olden 2012). Life history attributes related to reproductive ecology predict the decline of numerous stream fishes in the plains, especially stream-dwelling cyprinids (e.g., Dudley and Platania 2007; Durham and Wilde 2009a). Among declining plains cyprinids, those belonging to the genus *Macrhybopsis* are among the most imperiled because of their unique adaptations to plains streams (Jelks et al. 2008; Hoagstrom et al. 2011). Unique adaptations include enhanced olfactory senses for inhabiting turbid water (Davis and Miller 1967), synchronized spawning during periods of elevated flows that suspend progeny and enhance survival (Wilde and Durham 2008), production of ova that passively drift downstream during development and avoid desiccated upstream reaches (Bottrell et al. 1964; Platania and Altenbach 1998), and potentially upstream migration to counter downstream transport during early life stages (Bonner 2000). Because of these unique adaptations, *Macrhybopsis* species generally respond negatively to anthropogenic environmental alterations such as reservoir construction and the associated changes in water clarity (Bonner and Wilde 2002), dewatering of stream channels (Wilde and Durham 2008), and fragmentation of riverscapes (Luttrell et al. 1999). Recent studies covering broad spatial extents synthesized drivers of decline and identified regions that might serve as habitat refuges for many *Macrhybopsis* species (Hoagstrom et al. 2011; Perkin and Gido 2011). However, despite knowledge of these mechanisms, declines among *Macrhybopsis* fishes remain poorly documented relative to the extent of anthropogenic alteration to plains streams. This is especially true of regionally endemic species such as the Burrhead Chub *Macrhybopsis marconis* for which few ecological and life history attributes are known.

The Burrhead Chub is a small-bodied cyprinid endemic to the Colorado and Guadalupe-San Antonio drainages of Texas and was described by Eisenhour (2004) during an evaluation of members of the Speckled Chub *M. aestivalis* group west of the Mississippi River. The Burrhead Chub is considered a species of special concern in Texas (Hubbs et al. 2008) owing to declines caused by flow regime alterations and fragmentation of riverscapes (Hoagstrom et al. 2011). Although stream

fragmentation was first implicated in the decline of Burrhead Chub more than half a century ago (Kuehne 1955), the extent to which fragmentation has contributed to the imperilment of the species has been insufficiently studied. Eisenhour (2004) concluded impoundments have caused Burrhead Chub extirpations in the Colorado River system and suggested a review of the species was necessary to evaluate the extent of decline. Furthermore, relationships between habitat alterations and life history attributes represent necessary information for successful conservation of rare and declining species (e.g., Lopez et al. 2010). In particular, conservation of Burrhead Chub might be enhanced by addressing research needs in terms of natural history information, the extent of habitat connectivity required for persistence, ecological relationships with streamflow components, and predicting responses to river network restoration or management (Cooke et al. 2012).

We examined the life history and distribution of Burrhead Chub in subtropical streams in south Texas. Specific objectives were to (1) assess life history attributes, (2) document the historical and contemporary distribution of Burrhead Chub throughout its native range, and (3) relate life history information to broad-scale drivers of the Burrhead Chub decline, including stream fragmentation and streamflow.

METHODS

Study area.—Subtropical river basins in the Western Gulf Slope of North America were selected for inclusion based on historical occurrence of Burrhead Chub. Documented occurrences are known from the Colorado River and Guadalupe-San Antonio river basins of Texas (Eisenhour 2004). Although the Guadalupe and San Antonio basins join upstream of the San Antonio Bay inlet, these basins were treated as independent systems for the purposes of quantifying Burrhead Chub distribution and river network connectivity. Life history attributes of Burrhead Chub were evaluated using specimens collected from the lower Guadalupe River near Cuero, Texas (29°8'59"N, 97°18'59"W). This collection site was chosen because Burrhead Chub has maintained a stable population in the area since at least 1938 based on abundance values reported among historical museum collections (Perkin and Bonner 2011).

Life history attributes.—Collections of Burrhead Chub were conducted once per month using a seine (2.4 × 1.8 m, 3.2-mm mesh) beginning in October 2007 and extending through September 2008. Total lengths of all Burrhead Chub collected were recorded and up to 12 individuals of various sizes were retained to assess reproductive ecology. Fish retained for laboratory analysis were euthanized in a lethal dose of tricaine methanesulfonate (MS-222) at 80 mg/L of water before being preserved in a 10% formalin solution.

In the laboratory fundamental aspects of reproductive ecology were assessed, including longevity (age in years), population age structure (number of age-classes), reproductive season timing and length, age at maturation, occurrence of fractional

spawning, and clutch size. All TL data collected from Burrhead Chub at the Cuero site were used to conduct modal progression analysis in the program Fish Stock Assessment Tools, version 2 (FiSAT II; Gayanilo et al. 2005) to determine the occurrence and distribution of length modes during each month. This approach, which was developed for data-sparse contexts in particular, uses time series length frequency data to identify modes associated with sizes-classes and allows for following growth of size-classes through time. Consequently, FiSAT II is useful when sample sizes are relatively small (e.g., <30 fish per month) and has been applied to other imperiled, small-bodied cyprinids to document age-classes (Perkin et al. 2012). Modal progression results were plotted by month to illustrate longevity and age-classes. To determine reproductive activity, gonads of all individuals were removed and used to calculate a gonadosomatic index (GSI), where $GSI = (\text{gonad weight}/\text{somatic weight}) \times 100$. The left ovary of reproductively mature females was also removed and teased apart in a Petri dish. To assess occurrence of fractional spawning, 100 oocytes from the left ovary were indiscriminately selected for measurement (mm) using a stage micrometer; those data were used to construct frequency histograms based on a bin width of 0.04 mm (Perkin et al. 2012). Reproductive season of Burrhead Chub was defined using the presence of vitellogenic oocytes in ovaries combined with the corresponding elevated monthly mean GSI values of >6.0% for females and >1.0% for males. We used this approach rather than highly detailed histological techniques because we were interested specifically in estimating reproductive season timing and length, rather than individual spawning bouts (Brewer et al. 2008). Consequently, the GSI values used in this study are not likely to be useful for defining the reproductive season of fish other than Burrhead Chub; however, the occurrence of vitellogenic oocytes is evidence of fish reproductive activity. Vitellogenic oocytes were identified as yellow and nontransparent, which differed from developing oocytes that were translucent to opaque and immature oocytes that were transparent with a visible nucleus. Minimum age at maturation was estimated by comparing the TL of the smallest female in which vitellogenic oocytes occurred with age structure results from FiSAT II. Finally, all vitellogenic oocytes in the left ovary of mature females were enumerated and multiplied by 2 to estimate clutch size.

Historical and contemporary distribution.—Published and unpublished information on the historical and contemporary distribution of Burrhead Chub was reviewed to assess spatial patterns in declines and extirpations. To date, only one publication has documented detailed information on Burrhead Chub distribution (Eisenhour 2004), and that was combined with museum vouchers housed in the Texas Natural History Collections (TNHC) to assess distribution and status of the species. Additional surveys of the Guadalupe and San Antonio river networks were available in published (Kuehne 1955; Perkin and Bonner 2011) and unpublished (Runyan 2007; SARA 2011) forms. We chose 1970 as the year in which collections transitioned between historical and contemporary strata because this repre-

sented a period of habitat change related to completion of most large reservoirs in the plains (Gido et al. 2010) and other Western Gulf Slope drainages (Perkin and Bonner 2011). Timing of extirpation for areas between impoundments was estimated (methods of Luttrell et al. 1999) using the last reported voucher specimen from the river reach among collections housed in the TNHC. Although such an approach might suffer from type II error (i.e., Burrhead Chub undetected when present), we stress this approach is similar to previous works documenting the historical decline of other *Macrhybopsis* species (Luttrell et al. 1999). Museum records were sparse for areas between immediately adjacent impoundments, so we combined available data with the date of impoundment for the downstream reservoir to estimate Burrhead Chub extirpation because the species does not persist within reservoirs (Eisenhour 2004).

Broad-scale drivers of decline.—Stream fragmentation and flow alteration are identified as the primary drivers of Burrhead Chub decline (Hoagstrom et al. 2011). Temporal changes in habitat connectivity were quantified at the basin scale using the Dendritic Connectivity Index (DCI; Cote et al. 2009). Quantifying longitudinal connectivity in river networks requires the use of measures that incorporate the effects of multiple barriers arranged throughout dendritic (branching) lines of habitat. The DCI measures connectivity by dividing the longitudinal length of stream into sections that are isolated by barriers, then computing a weighted average of the probability of movement within and among all sections (see Cote et al. 2009 for additional details). As such, the DCI is a measure of connectivity that is sensitive to fish response to barriers (Perkin and Gido 2012). Isolated sections of habitat were defined based on the construction of large-stream impoundments documented in the National Inventory of Dams (U.S. Army Corps of Engineers) in each river network assuming the permeability of such barriers was zero (Luttrell et al. 1999). The potamodromous component of the DCI (DCI_p) was calculated using georeferenced data for dams and the stream layer from the National Hydrography Dataset (NHD) produced by the U.S. Geological Survey (USGS) using a GIS approach in ArcView 9.3 (ESRI 2009). Specifically, we used GIS to determine the adjacency of all fragments (i.e., areas between dams), quantify the length of each fragment, and import these data into Program R via source code available from Cote et al. (2009). Because the DCI is based on the longitudinal length of stream in each fragment, determining the appropriate spatial scale at which to measure stream length is necessary for developing ecologically meaningful connectivity measures (Perkin et al. 2013). Consequently, because Burrhead Chub distribution is limited to fifth-order (Strahler 1957) streams (see Whiteside and McNatt 1972), as supported by museum collection data, only fifth-order and greater streams were included in connectivity measures. The only small stream (i.e., less than fifth-order) in which we found Burrhead Chub to occur was the upper spring-fed reach of the San Marcos River, where discharges from the Edwards Aquifer contribute to disproportionately high streamflows relative to the

assigned stream order (Perkin and Bonner 2011). Consequently, we only consider fifth-order and greater streams (plus the upper San Marcos River) in habitat connectivity measures. A retrospective approach was used to calculate the DCI for each river system after the construction of each impoundment to document changes in basin connectivity through time.

Spatial patterns in Burrhead Chub extirpation and persistence were illustrated using a patch-based graphic approach as outlined by Erős et al. (2012). This approach included illustrating stream segments between confluences as habitat patches using nodes (circles) in proportion to the size of the patch (i.e., heterogeneous node resolution). Longitudinal stream lengths were used to define patch size because of the relationship between stream length and persistence of other *Macrhybopsis* species (Perkin and Gido 2011). Dispersal linkages were illustrated with lines linking unfragmented nodes (i.e., homogeneous link resolution), and linkages were disconnected when an impoundment occurred (Perkin et al. 2013). Fragmentation of river basin networks resulted in subnetworks in which Burrhead Chub were missing (extirpated or undetectable), still present, or naturally absent. Subnetworks were color coded to illustrate spatially explicit patterns in Burrhead Chub population status, and subnetwork size (i.e., total stream length in the subnetwork) was quantified for either missing or present populations and compared using a two-tailed *t*-test ($\alpha = 0.05$).

Patterns in flow regime were analyzed using USGS streamflow gages distributed throughout Burrhead Chub range. Retrospective analysis of the Guadalupe River system suggested declines in abundance of numerous stream fishes, including Burrhead Chub, during the drought of record for the region (1949–1959; Perkin and Bonner 2011). Furthermore, pelagic-broadcast spawning fishes, including Peppered Chub *M. tetranema* (Wilde and Durham 2008) and Smalleye Shiner *Notropis buccula* (Durham and Wilde 2009), are known to decline when streamflow magnitude is reduced during the reproductive season. Since preliminary results suggested the timing of most extirpations of Burrhead Chub occurred during the drought of record, we tested the hypothesis that Burrhead Chub populations declined or became extirpated because of reduced flows during reproductive seasons during the drought (as with other regions of the plains; Aguilar 2009; Perkin and Gido 2011). Abundant historical collections during the drought were available for the Guadalupe River system because of efforts by the late Clark Hubbs (University of Texas; Perkin and Bonner 2011). We first regressed Burrhead Chub relative abundance (dependent variable) against time (independent variable) in three sections of the Guadalupe River: (1) the Guadalupe River upstream of the location of Canyon Lake Reservoir, (2) the San Marcos River main stem between San Marcos and Gonzales, Texas, and (3) the Guadalupe River main stem downstream of the confluence with the San Marcos River near Gonzales. These three sections represent distinct regions of the Guadalupe River system with various streamflow magnitudes during the drought of record. We then considered the relationship between Burrhead

TABLE 1. U.S. Geological Survey (USGS) streamflow gages distributed throughout Burrhead Chub range in the Colorado, Guadalupe, and San Antonio river networks of Texas. Gage identification letters correspond with locations shown in Figure 3.

Gage	Description	USGS number
Colorado River network, Texas		
A	Colorado River near San Saba	08147000
B	Llano River near Junction	08150000
C	Colorado River at Austin	08158000
D	Colorado River at Wharton	08162000
Guadalupe River network, Texas		
E	Guadalupe River near Spring Branch	08167500
F	Guadalupe River at New Braunfels	08169500
G	San Marcos River at Luling	08172000
H	Guadalupe River at Victoria	08176500
San Antonio River network, Texas		
I	Medina River at San Antonio	08181500
J	San Antonio River near Falls City	08183500
K	Cibolo Creek near Falls City	08186000
L	San Antonio River at Goliad	08188500

Chub relative abundance and discharge magnitude during the reproductive season for the previous year, which was estimated using the statistical program Indicators of Hydrologic Alteration (IHA) developed by Richter et al. (1996). Streamflow data from 12 USGS gages (Table 1) were loaded into IHA and used to calculate flow regime properties for the period 1940–2011. Magnitude of discharge from April to August were calculated for each year using IHA and averaged to illustrate interannual variability in discharge during the core reproductive season for Burrhead Chub. Average streamflow for these months during the drought was regressed against Burrhead Chub relative abundance among museum records collected for the following year (i.e., a 1-year time lag) because Burrhead Chub population dynamics closely followed that of other cyprinids for which population fluxes are expected to occur on an annual basis (Wilde and Durham 2008; Durham and Wilde 2009b). For analyses, we $\log_{10}(n + 1)$ -transformed relative abundance and discharge data to address skewed distributions. We then assessed the potential for similar patterns in flow regime across the Burrhead Chub range by analyzing long-term (1940–2011) data at 12 USGS gages (Table 1).

RESULTS

Life History Attributes

Size structure and modal distribution of length groups based on 199 measurements made at the FM-766 crossing on the Guadalupe River suggested Burrhead Chub lived 2 years, i.e., age-0 to age-2 individuals (Figure 1). Age-0 fish ranged 25–35 mm TL, age-1 fish ranged 35–55 mm TL, and age-2 fish ranged 55–75 mm TL. The GSI values were elevated for females (i.e., >6%) and males (i.e., >1%) from late March through

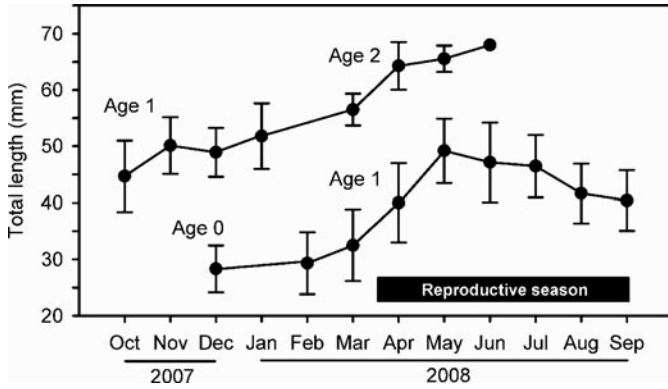


FIGURE 1. Monthly mean (\pm SD) total lengths for age-0, age-1, and age-2 Burrhead Chub collected from the Guadalupe River at FM-766 crossing near Cuero, Texas, during 2007 and 2008.

early September, during which time, mean monthly GSI values ranged 6.4–16.1% for females and 1.1–1.8% for males. There was evidence for reproductive activity during October of 2007 when female GSI values averaged 5.5%, four females with mature ovaries (i.e., contained vitellogenic oocytes) were collected, and male GSIs averaged 0.8%. Thus, October likely represents the period of onset in gonadal quiescence when reproductive activity slows to dormancy during the winter. Reproductive activity during the months of late March through early September was supported by patterns in oocyte size distributions and vitellogenic oocytes. Multiple modes were apparent during these months and were generally characterized by a single, large cohort of vitellogenic oocytes ranging 0.8–1.1 mm in diameter (Figure 2). Comparisons between occurrence of vitellogenic oocytes and TL suggested the minimum size of a mature female was 40 mm, or age-1. Clutch size ranged from 88 to 300 among 21 females examined (three during each month of reproductive activity, excluding October of 2007).

Historical and Contemporary Distribution

Distribution of Burrhead Chub indicated a decline during the period for which museum vouchers were available (1925–2009), and patterns in decline matched patterns in subnetwork isolation. Burrhead Chub was historically absent in the Colorado River network upstream of the location of Lake Buchanan Dam, and this section was excluded from analysis of Burrhead Chub distribution. In the remainder of the Colorado River network, Burrhead Chub was not detected (i.e., missing) in 47.7% of stream lengths in which the species historically occurred (Figure 3). Just downstream of Lake Buchanan Dam, Burrhead Chub is now missing from reaches bound by Roy Inks, Alvin Wirtz, Max Starcke, Mansfield, Tom Miller, and Longhorn dams (Figure 4). In the Guadalupe River network, Burrhead Chub is now missing from 5.1% of stream lengths in which the species historically occurred, including reaches bound by Canyon Lake, Lake Dunlap, and Lake McQueeney dams. In the San Antonio River network, Burrhead Chub is now missing from 12.6% of

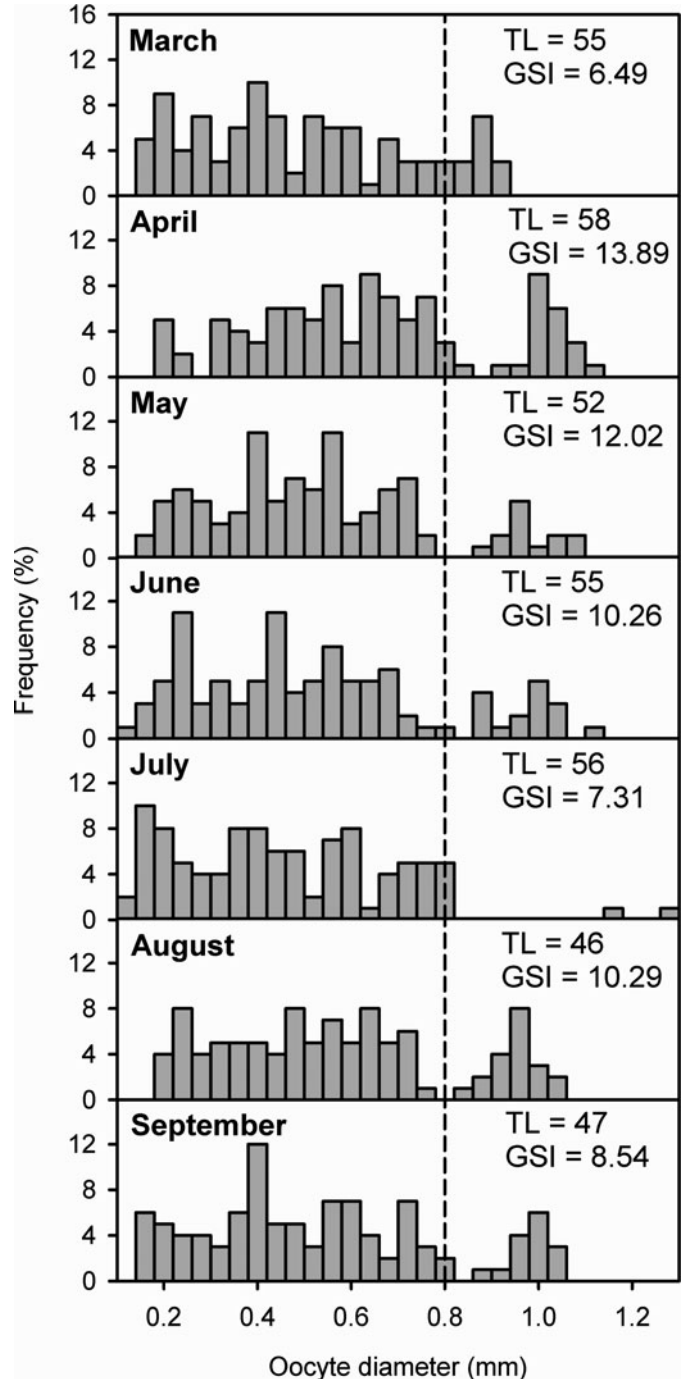


FIGURE 2. Oocyte size distributions for reproductively mature female Burrhead Chub collected from the Guadalupe River during 2007 and 2008. Total length (mm) and gonadosomatic index (GSI) of representative individuals are presented. The vertical dashed line represents the minimum observed size of vitellogenic oocytes (0.8 mm).

stream lengths in which the species historically occurred. Burrhead Chub is missing in fragmented upstream reaches near Medina Lake but persisted among multiple sites along the lower San Antonio River (SARA 2011).

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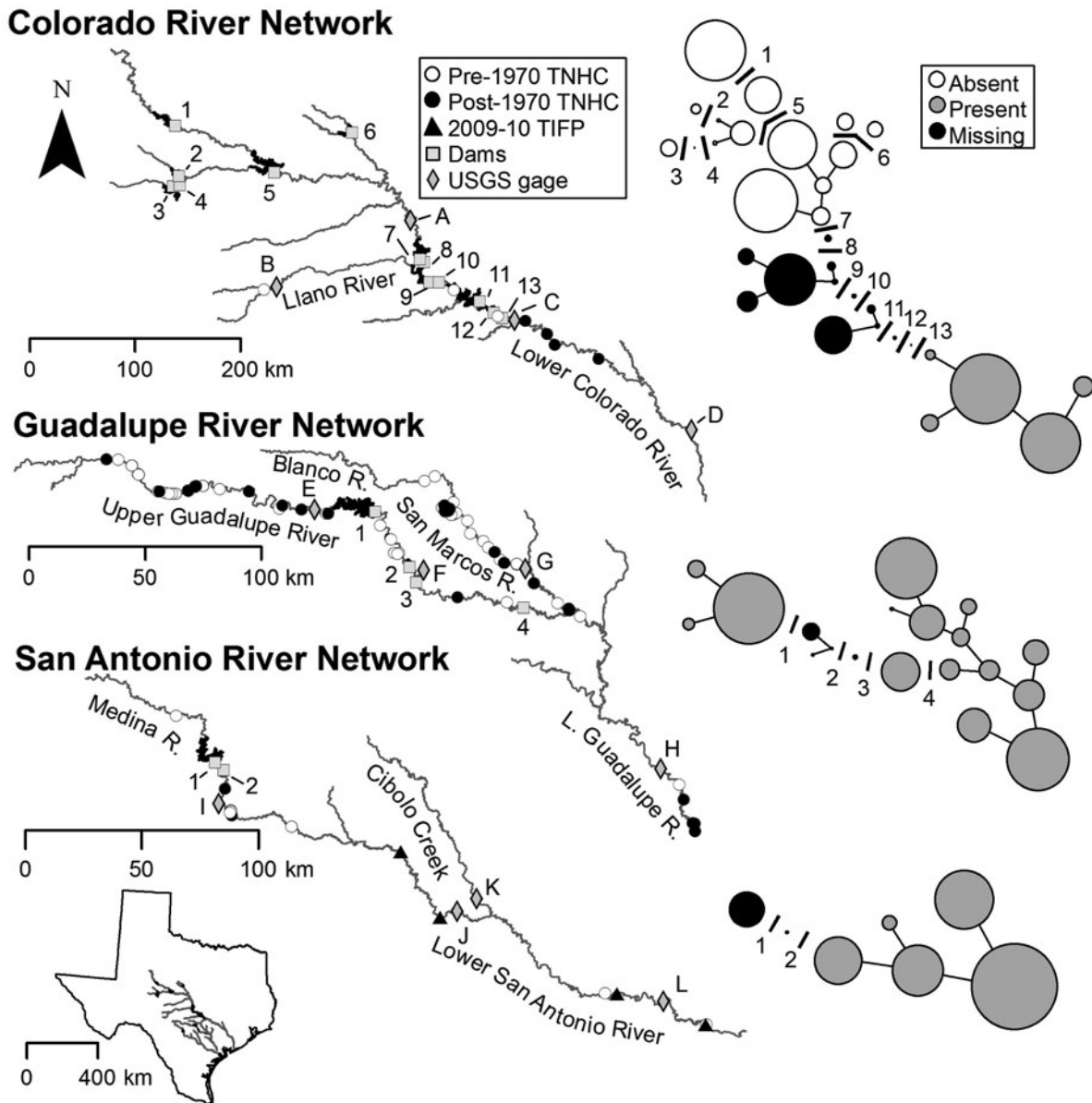


FIGURE 3. Channel topologies (for fifth-order and greater streams) and patch-based graphical representation of Colorado, Guadalupe, and San Antonio river networks illustrating the distribution of dams (numbered blocks) and Burrhead Chub collections during pre-1970 (Texas Natural History Collections; TNHC), post-1970 (TNHC), and 2009–2010 (SARA 2011; TIFP). For graphic representations, habitat nodes (circles) represent stream segments between confluences sized in proportion to the length of stream in each segment, and nodes are connected by dispersal links (lines) in the absence of dams (blocks). White nodes indicate subnetworks composed of patches in which Burrhead Chub are naturally absent, gray nodes indicate persistent populations, and black nodes indicate missing populations (i.e., locations from which they were historically collected). Lettered diamonds represent U.S. Geological Survey streamflow gages listed in Table 1.

Broad-Scale Drivers of Decline.—Habitat connectivity measured at the basin scale using the DCI indicated variable levels of fragmentation among river networks inhabited by Burrhead Chub. Thirteen dams were constructed in the Colorado River network between 1930 and 1989, four in the Guadalupe River network between 1928 and 1964 and two in the San Antonio River network in 1913. The timing and distribution of these dams contributed to declining DCI values among basins, ultimately resulting in contemporary connectivity values of 17 for

the Colorado, 49 for the Guadalupe, and 78 for the San Antonio River networks. The majority of fragmentation occurred during the 1930s (Figure 5). Timing of Burrhead Chub extirpations suggested the greatest magnitude in decline occurred between 1949 and 1955, after major fragmentation of riverscapes. Among all subnetworks isolated by large impoundments, Burrhead Chub was missing from 26.3% of historical stream length (775 km missing/2,947 km historical; or 10 of 15 subnetworks) and patterns in extirpation were associated with upstream or small

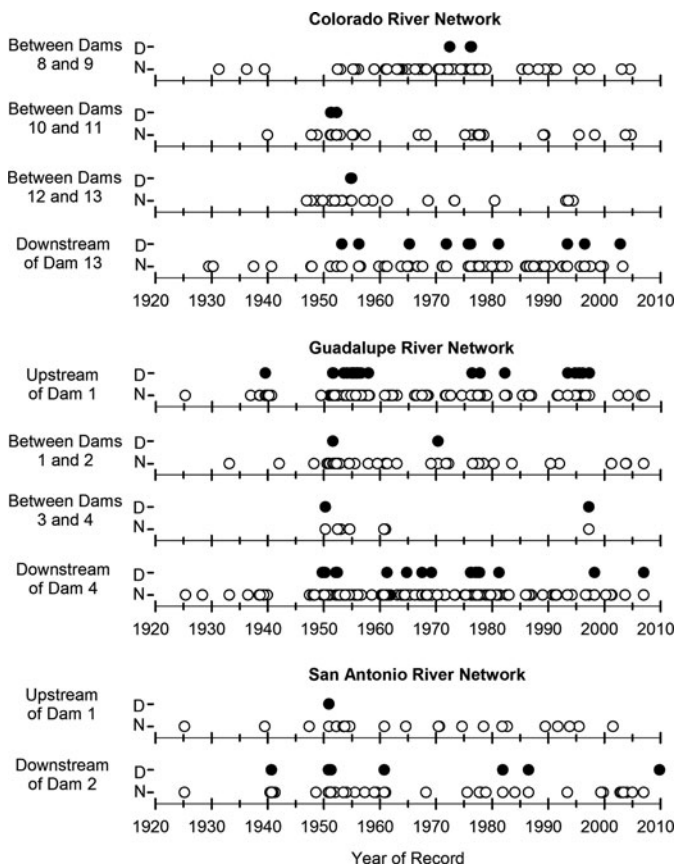


FIGURE 4. Historical collections taken in the Colorado, Guadalupe, and San Antonio river networks, Texas, in which Burrhead Chub were detected (D, black circles) or not detected (N, white circles). Collection data are from the Texas Natural History Collections and represent georeferenced voucher specimens. Dam locations by number are presented in Figure 3.

subnetworks. Subnetworks from which Burrhead Chub was missing ranged 2.4–333.9 km in total length and averaged 68.9 km (SD, 106.3), and subnetworks in which Burrhead Chub was present ranged 86.1–716.4 km in total length and averaged 451.6 km (SD, 278.7). Distributions of subnetwork lengths differed for missing versus present populations ($t_{13} = 3.9$, $P < 0.01$).

Relative abundance of Burrhead Chub reported among historical collections in the Guadalupe River network suggested declines occurred during the drought of record, including 1950 through 1961 (Figure 6). Burrhead Chub relative abundance declined through time in the Guadalupe River upstream of the location of Canyon Lake Reservoir ($F_{1,79} = 13.89$, $P < 0.01$; $b_1 = -9.89$; $R^2 = 0.15$; Figure 6A) and in the main-stem San Marcos River ($F_{1,37} = 5.04$, $P = 0.03$; $b_1 = -6.63$; $R^2 = 0.12$; Figure 6B) but showed no change through time in the lower Guadalupe River ($F_{1,9} = 0.29$, $P = 0.61$; $b_1 = -14.48$; $R^2 = 0.03$; Figure 6C). Additionally, Burrhead Chub relative abundance was positively correlated with discharge during the previous reproductive season in the upper Guadalupe River ($F_{1,6} = 6.33$, $P = 0.04$; $b_1 = 0.59$; $R^2 = 0.56$; Figure 6A insert), but was

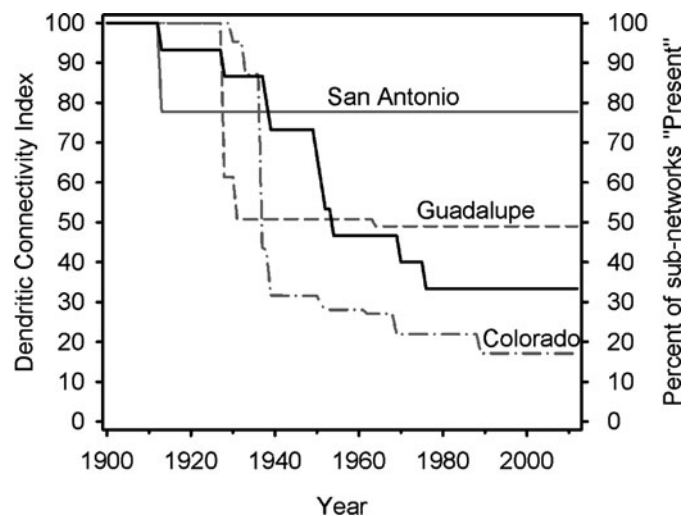


FIGURE 5. Relationship between time, extirpations of Burrhead Chub (solid black line; shown as percent of 15 subnetworks with present populations) and Dendritic Connectivity Index (DCI) for the Colorado, Guadalupe, and San Antonio River systems in Texas. Sequential addition of impoundments was used to calculate the DCI through time assuming impoundments do not allow fish passage (i.e., barrier permeability = 0).

not in the San Marcos River ($F_{1,4} = 0.91$, $P = 0.37$; $b_1 = 1.11$; $R^2 = 0.18$; Figure 6B insert) nor the lower Guadalupe River ($F_{1,4} = 0.01$, $P = 0.93$; $b_1 = -0.03$; $R^2 < 0.01$; Figure 6C insert). Among river networks, mean monthly streamflow during the Burrhead Chub core reproductive season declined during the drought of record, and declines were most notable in the San Antonio River network, followed by the Guadalupe and the Colorado river networks (Figure 7). Upstream streamflow gages documented greater declines in discharge magnitude relative to downstream gages, though a general pattern of dewatering during the drought was detectable among all gages.

DISCUSSION

Our findings suggest Burrhead Chub in the Guadalupe River live approximately 2 years, senesce during the second summer of life, reach sexual maturity at age 1, and spawn multiple clutches of 88–300 ova per spawning event during a protracted spawning season ranging March through September. These findings resemble life history attributes of Peppered Chub in the Canadian River (Bonner 2000) and Shoal Chub *M. hyostoma* in the Brazos River of Texas (Williams 2010). Similarities in population structure between Burrhead Chub and Peppered Chub include maturation at age-1, senescence during the second summer of life, and decline in abundance during periods of attenuated streamflow (Wilde and Durham 2008). The protracted spawning season for Burrhead Chub in the Guadalupe River resembles that of Shoal Chub in the Brazos River (April to October; Williams 2010). Eisenhour (1997) suggested prolonged reproduction of Burrhead Chub in the Guadalupe River system might be related to stenothermal influences from large springs

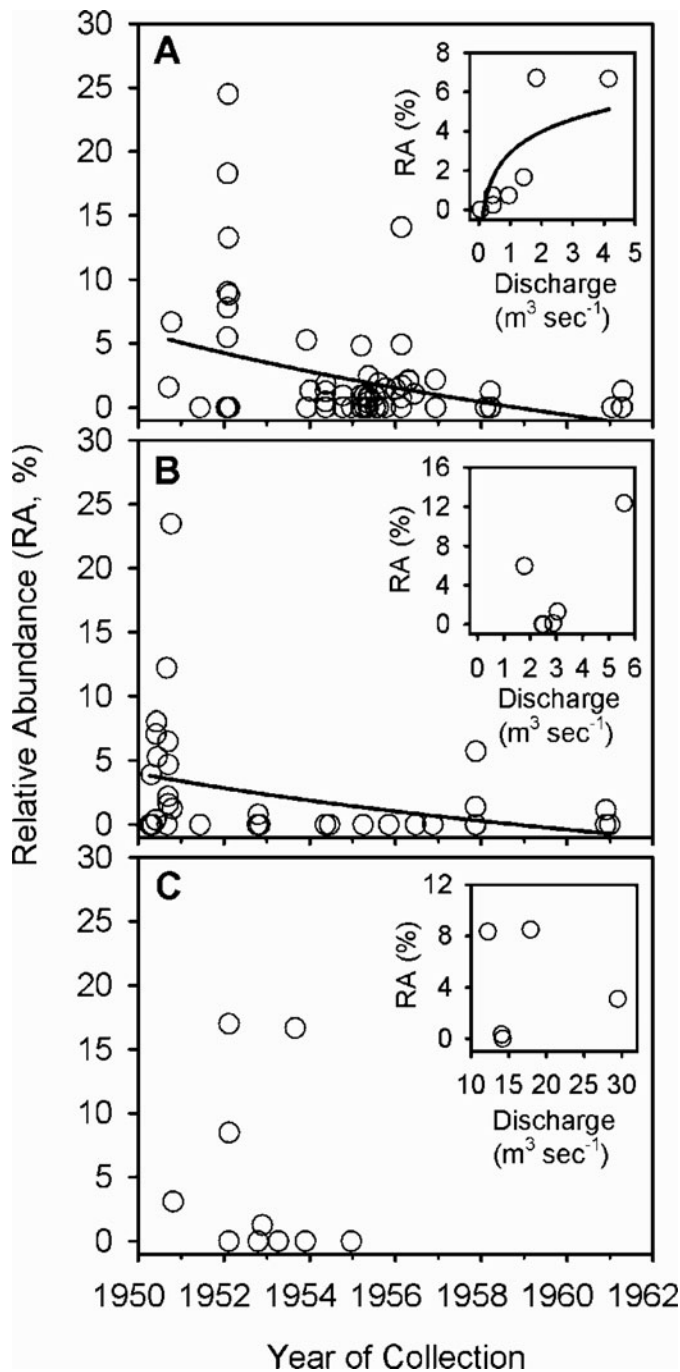


FIGURE 6. Relationship between time and relative abundance of Burrhead Chub in historical collections reported from (A) the Guadalupe River upstream of the location of Canyon Lake Reservoir, (B) the San Marcos River between San Marcos and Gonzales, and (C) the Guadalupe River downstream of Gonzales, Texas, during the drought of record (1949–1959). Inserts illustrate relationships between mean annual flow during Burrhead Chub core reproductive season (April–August) and relative abundance of the species the following year. Relative abundance and discharge data were $\log_{10}(n + 1)$ -transformed for analyses; axes are shown untransformed for clarity.

in the basin. Stenothermal influences from springs are known to extend the spawning season of other cyprinids in the Guadalupe River basin by removing the cue to return to gonadal quiescence (Perkin et al. 2012), but this does not explain the equally protracted spawning season of Shoal Chub in the lower Brazos River. These similarities are most likely related to the influences of photoperiod and water temperature that occur along latitudinal gradients, so that fractional spawning species in southern regions tend to reproduce for greater periods of the year when warmer waters persist longer (Gotelli and Pyron 1991). Disruption of the reproductive cue provided by water temperature downstream of Canyon Lake Reservoir caused by hypolimnetic water releases might explain why Burrhead Chub became extirpated downstream of the reservoir after its completion (Edwards 1978). Furthermore, disappearance of Burrhead Chub from the middle Colorado River system was apparently also related to the spatial distribution of reservoirs with hypolimnetic releases (Eisenhour 2004); however, this pattern does not explain the upstream extirpation of the species from portions of each river network included in this study. Instead, extirpation from upstream reaches generally corresponded with a period of drought that caused prolonged low stream flows during Burrhead Chub reproductive season. Because of these patterns, we hypothesize that interactions between stream fragmentation and low streamflow during a historical drought have contributed to a legacy effect regarding Burrhead Chub contemporary distribution.

Reservoirs and the associated effects on water availability are known to disrupt the natural extinction and recolonization dynamics of cyprinids in plains streams. These streams exhibit longitudinal fluctuations in environmental conditions, including desiccations in upstream reaches but relatively less hydrologic variability in downstream reaches (i.e., downstream reaches tend to desiccate less often; Dodds et al. 2004). Schlosser (1987) described a process by which temporal variability in shallower upstream habitats contributed to colonizing fish communities that were maintained by recolonization from stable communities downstream. Consequently, when barriers fragment plains riverscapes and disrupt recolonization, local extirpations occur among colonizing communities. Winston et al. (1991) provided example of this dynamic by documenting the upstream extirpation of four cyprinids, including the Prairie Chub *M. australis*, following completion of a reservoir that blocked upstream movement. This mechanism has apparently contributed to declines in Peppered and Shoal chubs in the Arkansas River basin (Luttrell et al. 1999), Shoal Chub in the Big Blue River basin (Gido et al. 2002), as well as a number of other *Macrhybopsis* species throughout the Great Plains (Perkin and Gido 2011). Downstream extirpations also occur because of fragmentation by reservoirs. Impoundments that regulate streamflow regimes contributed directly to Speckled Chub declines by transforming lotic habitats into lentic habitats that contributed to downstream channelization and attenuated habitat

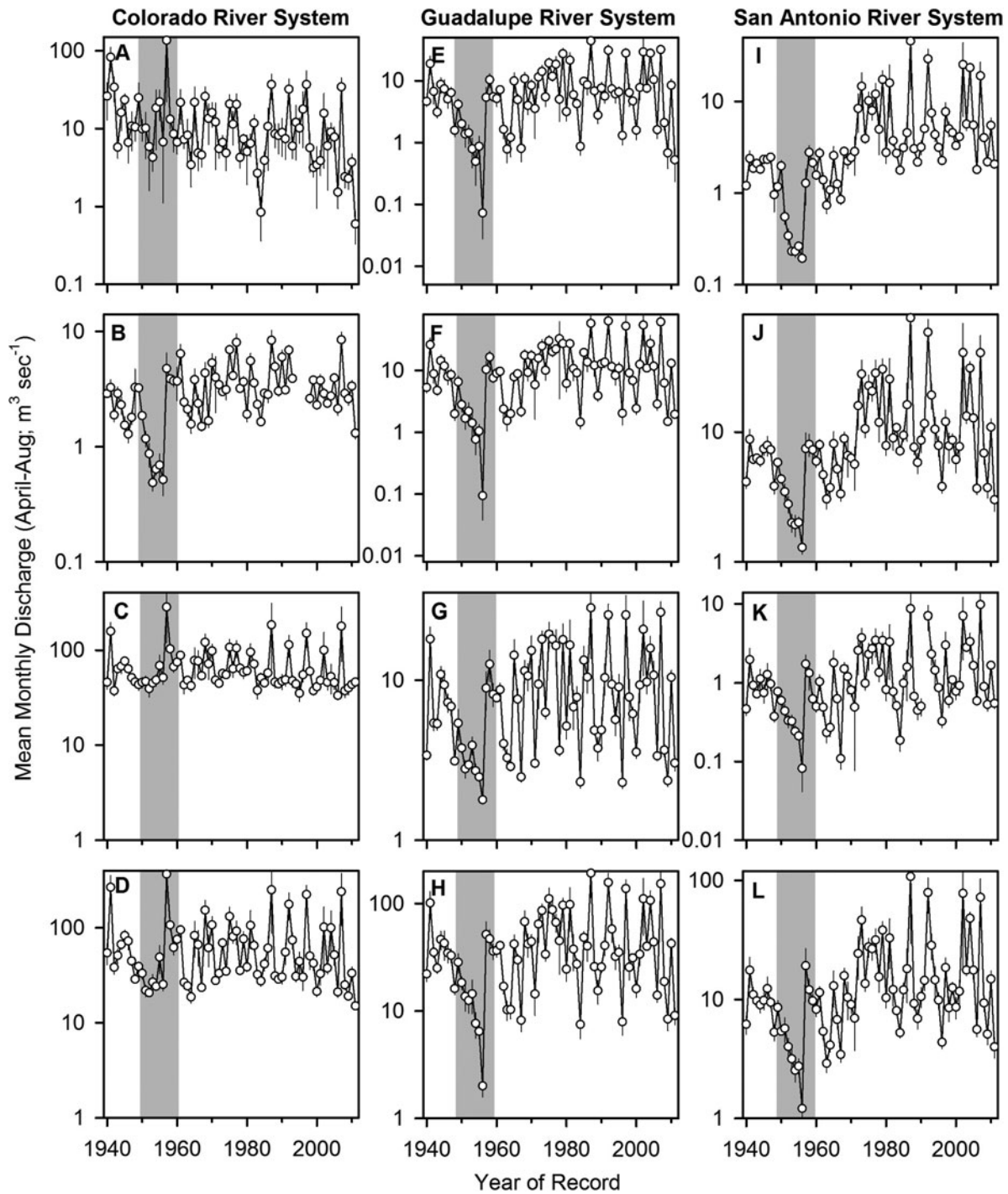


FIGURE 7. Hydrographs illustrating longitudinal variability in mean (\pm SD) monthly discharge during Burrhead Chub core reproductive season (April–August) for the (A–D) Colorado, (E–H) Guadalupe, and (I–L) San Antonio River systems. The gray shaded area represents the drought of record (1949–1959). Panel letters correspond with gage letters in Table 1 and locations in Figure 3. Note y-axes are log-scaled and change among panels.

heterogeneity and enhanced downstream transport of progeny into reservoirs via sustained high-flow pulses (Dudley and Platania 2007). Water held within reservoirs or withdrawn from surface and groundwater sources has contributed to species declines

in portions of the Arkansas (Luttrell et al. 1999), North Canadian (Pigg 1991), South Canadian (Wilde and Durham 2008), and Cimarron (Cross et al. 1985) River systems in the plains. Though the causes for upstream or downstream extirpations may

include dewatering, pollution, introduction of nonnative species, or other forms of habitat destruction, interactions between stream fragmentation and these drivers pose a broad-scale threat to plains fishes (Hoagstrom et al. 2011). In fact, habitat fragmentation has contributed, at least in part, to the decline of 65% of the endemic fish species in the plains and therefore poses a threat to the successful conservation of declining fish biodiversity (Hoagstrom et al. 2011).

Barriers that preclude fish dispersal and colonization of fragmented stream reaches include road crossings, low-head dams, diversion dams, sections of stream that become desiccated following water withdrawal, and large impoundments (Cote et al. 2009; Fullerton et al. 2010; Perkin and Gido 2011; Perkin and Gido 2012). This study focused on large impoundments that are known to block dispersal of *Macrhybopsis* species (Luttrell et al. 1999), but the influence of smaller barriers on Burrhead Chub distribution merits additional research. For example, the Blanco River, a tributary to the San Marcos River in the Guadalupe River network, is now extensively fragmented by low-head dams that alter fish community structure (Bean et al. 2007). Burrhead Chub was historically common throughout the Blanco River (TGFC 1957); however, four individuals collected by Bean et al. (2007) were taken from downstream reaches where connectivity to the San Marcos River has not been severed by low-head dams. The effects of low-head dams on the distribution of Burrhead Chub in systems such as the Blanco River might be empirically tested as availability of data pertaining to smaller dams not documented by the National Inventory of Dams become available in the future (Chin et al. 2008). Additional research of Burrhead Chub distribution at finer spatial scales is also merited in the Colorado River network (Eisenhour 2004). Shoal Chub was recently collected in the Llano River (Curtis 2012) where the species was once thought extirpated because of isolation by the Alvin Wirtz Dam and Lyndon B. Johnson Reservoir (Eisenhour 2004). The documented occurrence of a *Macrhybopsis* species where the genus was once thought extirpated supports occurrence of Shoal Chub in stream fragments > 100 river kilometers in length (Perkin and Gido 2011) and suggests the closely related Burrhead Chub might also persist in the largest subnetwork for which extirpation is now reported. Regardless, patterns in extirpation of Burrhead Chub revealed population persistence where fragmentation was least and discharge magnitude was greatest, especially during the drought of record.

Data indicate that Burrhead Chub have maintained long-term population stability in the lower Colorado (Eisenhour 2004), lower Guadalupe (Perkin and Bonner 2011), and lower San Antonio (Runyan 2007) river networks. Each of the most downstream subnetworks in these systems retains large sections of unfragmented stream and relatively high discharge magnitudes. Despite flow regimes being modified and controlled by upstream reservoirs, these stream segments support refuge populations of Burrhead Chub and probably represent strongholds for the species in each basin. Of greater conservation concern is the management of populations isolated in the upper portions of the

Guadalupe River network, including the San Marcos and upper Guadalupe River where Burrhead Chub has declined in association with streamflow alterations and drought (Perkin and Bonner 2011; this study). Declines in Burrhead Chub relative abundance during the drought of record in these subnetworks were similar to declines observed for Peppered Chub in the South Canadian River during years of low flow (Wilde and Durham 2008). The apparent mechanism for decline of Peppered Chub was related to attenuated survival of age-0 individuals when discharge was < 11.9 m³/s, below which population growth rate declined precipitously. Although our approach did not include demographic modeling such as that used by Wilde and Durham (2008), we found evidence for declining relative abundance of Burrhead Chub when streamflow was low in the upper Guadalupe and San Marcos rivers. We also found potential for similar patterns in most upstream portions of Burrhead Chub range based on USGS streamflow gage data, although museum records were limited and did not allow analysis as with the Guadalupe River system. Because of the strong relationship between cyprinid reproductive success and streamflow magnitude (Luttrell et al. 1999; Wilde and Durham 2008; Durham and Wilde 2009b) and the timing of extirpations, we hypothesize that Burrhead Chub declined during the drought of record when discharges during the reproductive season were exceedingly low for consecutive years. Outside of these upstream peripheries of Burrhead Chub range (e.g., in the middle Guadalupe and Colorado River networks), extirpations were probably related to the effects of reservoirs that extensively fragmented habitat and altered flow regimes (Eisenhour 2004; Dudley and Platania 2007; Perkin and Gido 2011).

Our analysis revealed some potential mechanisms that might influence the long-term persistence of Burrhead Chub and require additional research related to conservation approaches. Captive propagation and repatriation are emerging techniques used to re-establish populations of previously extirpated species (Luttrell et al. 2002; Marsh et al. 2005). A central concern with such approaches is the identification of source populations that minimize loss of genetic diversity while maximizing conservation of unique evolutionary lineages (Osborne et al. 2006). Furthermore, attempts to reestablish populations following extirpations require knowledge of the cause of original extirpation to avoid a similar demise for newly reestablished populations (Minckley et al. 2003). Our findings suggest populations from the downstream subnetworks of drainages within Burrhead Chub range might be used as source populations for repatriation efforts in upstream subnetworks where the species is now missing. The greater challenge will ultimately be ensuring the repatriated populations do not become extirpated for the same reasons as the original populations. Based on our findings, upstream subnetworks of greater size in which streamflow magnitude is greater than the period of historical drought might serve as starting points for investigating the feasibility of population reintroductions. However, we stress that our approach here is only one of many research endeavors

necessary for the investigation and successful conservation of imperiled riverine fish species (Cooke et al. 2012).

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