

The emblematic minnows of the North American Great Plains: A synthesis of threats and conservation opportunities

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Abstract

Anthropogenic changes to the Great Plains rivers of North America have had a large, negative effect on a reproductive guild of pelagic-broadcast spawning (PBS) cyprinid fishes. The group is phylogenetically diverse, with multiple origins of the PBS mode. However, because of incomplete life-history information, PBS designation often relies only on habitat and egg characteristics. We identified 17 known or candidate PBS fishes and systematically synthesized the literature on their biology and ecology in relation to major threats to persistence. Research output on an individual species was unrelated to conservation status, but positively correlated with breadth of distribution. The PBS species have opportunistic life-history strategies and are typically short-lived (generally 1–3 years) fishes. Many PBS species have truncated ranges showing declines in both distribution and abundance, especially those endemic to the Rio Grande catchment. Fundamental habitat associations are unknown for many species, particularly regarding seasonal shifts and early life stages. Critical thermal tolerances have been quantified for five PBS species and are generally >35°C. Turbidity and salinity changes are linked to responses at multiple life stages, but information is lacking on interactions between water quality and quantity. Hydrologic alteration appears to be a primary threat to PBS species, through complex interactions with landscape fragmentation, and habitat change. We highlight areas where scientific and management communities are lacking information and underline areas of potential conservation gain.

KEYWORDS

conservation, flow alteration, fragmentation, Great Plains, habitat complexity, non-native species

1 | INTRODUCTION

The loss of vertebrate species in the past century is estimated at 100 times higher than background rates during the five previous mass extinctions (Ceballos, Ehrlich, Barnosky, Garcia & Pringle, 2015). Fishes, in particular, are experiencing high levels of biodiversity loss. Local extirpations of marine fishes are the highest in recorded history (Harnik,

Lotze & Anderson, 2012), and extinction rates of North American freshwater fishes are conservatively estimated to be over 800 times higher than background rates (Burkhead, 2012). The loss of fishes undoubtedly corresponds to ecosystem degradation. In addition to their importance as a protein source, fishes provide numerous other benefits to the well-being of humans through nutrient cycling, algae control and food web stability (Holmlund & Hammer, 1999). Fishes also

make excellent vertebrate models for advancements in curing disease and slowing the ageing process (Harel, Benayoun & Machado, 2015). Finally, fishes have aesthetic and inherent conservation value beyond any benefits to humans (Holmlund & Hammer, 1999).

The prairie rivers of the Great Plains ecoregion have experienced dramatic changes over the past 100–150 years due to changing land-cover patterns, land-use practices and climatic shifts (Dodds, Gido, Whiles, Fritz & Matthews, 2004; Hoagstrom, Brooks & Davenport, 2011; Matthews, 1988; Perkin & Gido, 2011; Rabeni, 1996). Under natural conditions, these systems were characterized by highly variable flows and extremes in temperature and dissolved oxygen, yet supported a diverse native fish fauna adapted to the unique challenges of this environment (Matthews, 1988). However, anthropogenic activities have resulted in high levels of fragmentation, loss of channel complexity, reductions in stream discharge and high-flow events, and elevated temperatures, resulting in new extremes, different from those formerly characteristic of prairie rivers and streams (Dodds et al., 2004; Hall, Leavitt, Quinlan, Dixit & Smol, 1999; Hoagstrom et al., 2011; Matthews, 1988; Perkin & Gido, 2011). For example, the upper reaches of the Platte and Arkansas rivers have been transformed from shallow, wide rivers to turbid, narrow channels throughout eastern Colorado and Kansas due to irrigation pumping and wastewater treatment activities that began in the early twentieth century (Cross & Moss, 1987; Fausch & Bestgen, 1997; Perkin, Gido, Falke, Fausch & Crockett, 2017). As groundwater becomes increasingly scarce, stream flow is often diverted to municipal and agricultural water supplies (Cross & Moss, 1987; Dodds et al., 2004), leading to complete dewatering of stream channels (e.g. Arkansas River in western Kansas, Rabeni, 1996). Dewatering leads to disturbances and reductions in riparian vegetation (Rabeni, 1996), causing bank instability, loss of allochthonous energy sources, reduced insect abundance (Moring, Garman & Mullen, 1994), higher amounts of dissolved solids, increased water temperatures and critically decreased oxygen levels (Lynch, Corbett & Mussallem, 1985). The drastic physicochemical changes to Great Plains prairie streams have caused population declines, and extirpations (in some cases extinctions) in more than 80% (41 of 49) of the endemic fish fauna (Hoagstrom et al., 2011).

In this study, we present a systematic review of the biology and ecology of a group of pelagic-broadcast spawning (PBS) species, or pelagophils, comprising a reproductive guild of minnows (Cyprinidae) emblematic of Great Plains streams and particularly susceptible to losses via anthropogenic changes to in-stream characteristics. The PBS and lithopelagophilic-broadcast spawning (LPBS) modes of reproduction form a subset of broadcast spawning, which involves scattering of eggs and sperm with no prior preparation of the substrate (Johnston & Page, 1992). The PBS reproductive ecotype represents approximately 15–20 species of small-bodied (<5–6 cm total length) cyprinids that release semi-buoyant ova and potentially require substantial lengths of free-flowing river to successfully complete development (Hoagstrom et al., 2011; Perkin & Gido, 2011; Williams & Bonner, 2006). Thirteen of these species are of conservation concern (Jelks, Walsh & Burkhead, 2008; Warren, Burr & Walsh, 2000), and status of the remaining species is unclear. The rapid decline of this

reproductive guild has been attributed to a range of factors including fragmentation (Hoagstrom et al., 2011; Perkin & Gido, 2011), altered flow regimes (Hughes, 2005) and invasive species (Bonner & Wilde, 2002; Felley & Cothran, 1981; Hoagstrom et al., 2011; Pigg, Gibbs & Cunningham, 1999).

The development of a systematic review can significantly aid evidence-based decision making (Petticrew, 2001; Pullin, Knight, Stone & Charman, 2004). Our review identifies common themes across species (e.g. causes of decline), synthesizes the current understanding of life-history requirements and evaluates areas of uncertainty in ecological knowledge of Great Plains PBS species. Our purpose is to critically assess and synthesize existing knowledge for PBS species and identify knowledge gaps. The objective is to provide a basis for targeted investigations aimed at furthering the conservation of pelagic-broadcast spawning cyprinids. First, we provide an analysis of the key bibliographic attributes of papers published on PBS species. Second, we review aspects of the ecology of PBS species. The review briefly summarizes the reproductive strategy of PBS species, providing a basis for understanding how anthropogenic pressures affect these species. We describe the phylogenetic and geographical organization and the current conservation status of PBS species. The choice of life-history attributes and ecological requirements to evaluate was determined by two factors: (i) their role in explaining threats to the group and (ii) the amount of information available. The discussion is centred on the four primary threats to PBS species: flow alteration, fragmentation, habitat change and non-native species. Although each of these aspects is addressed in a separate subsection, interactions between them and aspects related to diet and water-quality requirements are examined. The final section addresses conservation opportunities and challenges, highlighting areas where the scientific and management communities are lacking information, and underlining areas of potential conservation gain.

2 | METHODS

2.1 | Study area

The species reviewed here are regarded as emblematic of the rivers of the Great Plains ecoregion of central North America. Although the core of many of these species' historic distributions are centred within the Great Plains, substantial portions of the rivers covered here flow through other Level I ecoregions (see Omernik, 1987). For instance, to the south and west of the Great Plains, a large extent of the Rio Grande basin is within the North American Deserts ecoregion; and to the east, a large portion of the Mississippi/Missouri basin is located within the Eastern Temperate Forest ecoregion. However, for brevity, we refer to the study region as the "Great Plains" hereafter.

2.2 | Species reviewed

The list of 17 taxa (one comprising two subspecies) treated in this review (Table 1) is somewhat limited by our understanding of

TABLE 1 Reproductive characteristics of pelagic-broadcast spawning (PBS) species, potential PBS (LP/P-BS) species and lithopelagophilic-broadcast spawning (LPBS) species and number of studies on PBS and LP/P-BS species. LP/P-BS = species showing eggs characteristics expected of PBS or LPBS fishes (non-adhesive, semi-buoyant), but spawning behaviour not observed. NR = Not reviewed as part of the bibliographic search as belonging to LPBS group

Genus/Species	Reproductive mode	Post-fertilization diameter.	Specific gravity eggs/larva ^a	Adhesive	Spawning	References ^b	Number of studies ^c
<i>Hybognathus</i>							
Rio Grande silvery minnow <i>H. amarus</i> , Cyprinidae	PBS	3.2	s-b/-	no	pelagic	1	87
Western silvery minnow <i>H. argyritis</i> , Cyprinidae	LP/P-BS	-	-/-	-	-	2	70
Plains minnow <i>H. placitus</i> , Cyprinidae	PBS	2.7	1.008/-	no	pelagic	1,3	229
<i>Macrhybopsis</i>							
Speckled chub <i>M. aestivalis</i> , Cyprinidae	PBS	3.4	s-b/-	no	pelagic	1	40
Prairie chub <i>M. australis</i> , Cyprinidae	LP/P-BS	-	s-b/-	no	-	4	17
Peppered chub <i>M. tetranema</i> , Cyprinidae	LP/P-BS	-	-/-	-	-	4	43
Shoal chub <i>M. hyostoma</i> , Cyprinidae	LP/P-BS	3.2	1.005/1.05	no	-	3	155
Burrhead chub <i>M. marconis</i> , Cyprinidae	LP/P-BS	-	-/-	-	-	2	14
Sturgeon chub <i>M. gelida</i> , Cyprinidae	LP/P-BS	-	s-b/-	no	-	5	86
Sicklefin chub <i>M. meeki</i> , Cyprinidae	LPBS	-	s-b/-	no	bottom	6	NR
Silver chub <i>M. storeriana</i> , Cyprinidae	LPBS	-	-/-	-	-	7	NR
<i>Platygobio</i>							
Flathead chub <i>P. gracilis</i> , Cyprinidae	LPBS	2.3	s-b/-	no	pelagic	8,9	NR
<i>Notropis</i>							
Emerald shiner <i>N. atherinoides</i> , Cyprinidae	LPBS	-	-/-	no	pelagic	2,10	NR
Red River shiner <i>N. bairdi</i> , Cyprinidae	LP/P-BS	-	-/-	no	-	4	60
Smalleye shiner <i>N. buccula</i> , Cyprinidae	PBS	2.6	1.008/1.04	no	-	3	33
Arkansas River shiner <i>N. girardi</i> , Cyprinidae	PBS	2.3	1.008/1.05	no	pelagic	1,3	82
Rio Grande shiner <i>N. jemezianus</i> , Cyprinidae	PBS	2.9	s-b/-	no	pelagic	1	54
Phantom shiner <i>N. orca</i> , Cyprinidae	LP/P-BS	-	-/-	-	-	2	15
Sharpnose shiner <i>N. oxyrhynchus</i> , Cyprinidae	PBS	~2.2	1.008/1.04	no	-	3	38
Bluntnose shiner <i>N. simus</i> , Cyprinidae	PBS	3.0	s-b/-	no	pelagic	1	50
Sabine shiner <i>N. sabinae</i> , Cyprinidae	LP/P-BS	-	-	-	-	11	41

^as-b = semi-buoyant

^bReferences: 1 Platania and Altenbach (1998); 2 Hoagstrom and Turner (2015); 3 Coleman (2015); 4 G. Wilde unpublished data; 5 Hoagstrom, Hayer, et al. (2006); 6 Albers and Wildhaber (2017); 7 Simon (1999); 8 Haworth and Bestgen (2016); 9 K. Bestgen unpublished data; 10 Flittner (1964); 11 Williams and Bonner (2006).

^cNumber of studies given only for PBS and potential PBS species (LP/P-BS).

reproductive mechanisms for many fish species. As a starting point, we used the species highlighted in Table 1 of Hoagstrom and Turner (2015) as known or potential pelagic-broadcast spawning (PBS) species. We included another member of the speckled chub complex, the shoal chub (see Coleman, 2015) and also the Sabine shiner, which was suggested as a candidate PBS species by Williams and Bonner (2007).

We use the abbreviation PBS to designate pelagic-broadcast spawners (also known as pelagophilic broadcast spawners or pelagophils). Species suspected to be either PBS or LPBS are included in this review and designated as LP/P-B (Table 1). Four species (silver chub, sicklefin chub, flathead chub and emerald shiner) belonging to a similar LPBS reproductive group are discussed in this study only in relation to phylogenetics of the focal guild and do not constitute part of the bibliographic data. Due to their phylogenetic placement and similarities in habitat and morphology, we also highlighted river shiner (*N. blennius*, Cyprinidae), chub shiner (*N. potteri*, Cyprinidae), silverband shiner (*N. shumardi*, Cyprinidae), Tamaulipas shiner (*N. braytoni*, Cyprinidae) and Texas shiner (*N. amabilis*, Cyprinidae) as warranting further reproductive investigation. This also applies to *N. megalops* (Cyprinidae), a species taxonomically re-established within the geographically overlapping and traditionally recognized *N. amabilis* (Conway & Kim, 2016). These species are only included in the phylogenetics section (*N. megalops* treated as *N. amabilis*) and do not constitute part of the bibliographic data. We use the contraction PBS to refer to all the species reviewed, regardless of uncertainty of their reproductive guild designation.

2.3 | Bibliographic review

We developed a Google Scholar search string for each of the 17 focal species treated as PBS or potential PBS species (LP/P-B; carried out during December 2015 and January 2016; Table S1). The general form of the search string consisted of terms related to the common name, the scientific name (genus and species), scientific name with genus abbreviated (e.g. *Notropis* = N) and any synonyms for the scientific name given by Gilbert (1978) and Hendrickson and Cohen (2015). The search terms were placed in double quotation marks and separated by the Boolean operator “or” to form the search string. For prairie chub and Arkansas River shiner, the Latin contraction produced multiple results not relevant to the study; therefore, these terms were omitted. The search string for each species was entered individually into Google Scholar and the options to “include patents” and “include citations” were turned off. Goggle Scholar was used because it searches the body of the text in addition to title, abstract and keywords.

The Google Scholar results for each PBS species were interrogated and journal articles from peer-reviewed publications were added to a database. To fully capture all publications related to PBS species, it would have been necessary to include grey literature (e.g. theses, reports, conference proceedings); however, searching unpublished literature sources in a consistent and comprehensive manner was deemed unfeasible (sensu Gates, 2002). Therefore, to ensure consistency in the

sources used to derive the bibliographic data, only peer-reviewed publications were included, but unpublished literature was incorporated in the written descriptions. We excluded articles that only mentioned a PBS species as occurring in the paper's study area or while discussing the findings of another study, or only in the reference list. As the aim of this study was to review the ecology of PBS species, studies orientated towards legal aspects of water use (generally affecting only the Rio Grande silvery minnow) were not included. Studies added to the database were given a unique identifier, and key bibliometric information was recorded. The year the study was published, the journal and the PBS species included in the study were all added to the database. For the *Macrhybopsis aestivalis* complex, studies published before Eisenhour (2004) or not adopting the new species designations were attributed to species based on study location or the use of a subspecies name (e.g. *Hybopsis aestivalis tetranemus* was assigned to peppered chub). Studies not attributable to a particular species were assigned to an overall “chub” group. Studies treating PBS species in general rather than referring to specific species were placed in their own group. The journal of publication was assigned to one of 15 broad research areas (Table S2) to examine publishing trends. To assess relationships between number of studies undertaken and the distribution extent or conservation status of PBS species, the number of U.S. catchments (U.S. Geological Survey 8-digit cataloguing unit) occupied by a species and its “global status” were accessed from NatureServe (2017). Although the distribution data underrepresent ranges of trans-international-boundary species (e.g. plains minnow, western silvery minnow and species of the Rio Grande basin), it provides a good indication of relative distributions. The monotonic relationships between distribution and conservation status and number of papers published on a species were assessed using Spearman's rank correlation (single-sided positive association).

3 | RESULTS

3.1 | Bibliographic data

A total of 551 papers across 144 journals were included in the systematic review. The earliest paper was from 1918 with numbers of papers published per year increasing exponentially through time (Figure 1a). Until the 1990s, fewer than 10 papers were published on PBS species per year, but by the early 2000s, this had increased to >15 papers per year. Eighty-five per cent of the studies were published in five of the 15 broad categories of journals: fisheries ($n = 162$), state ($n = 114$), regional ($n = 91$), freshwater ($n = 53$) or ecology ($n = 47$) journals. The journals *Copeia* ($n = 40$), *The Southwestern Naturalist* ($n = 41$), *Transactions of the American Fisheries Society* ($n = 35$) and *Journal of Freshwater Ecology* ($n = 30$) contained the most publications (Table S2). There was a temporal shift in type of journal selected (Figure 1b). Until the 1960s, studies were concentrated in fisheries, ecology, regional and state journals. Beginning in the 1970s, there was an emergence of studies in more specialized outlets (e.g. genetics, freshwater and geomorphology journals). Since the 1990s, the range of journals has increased

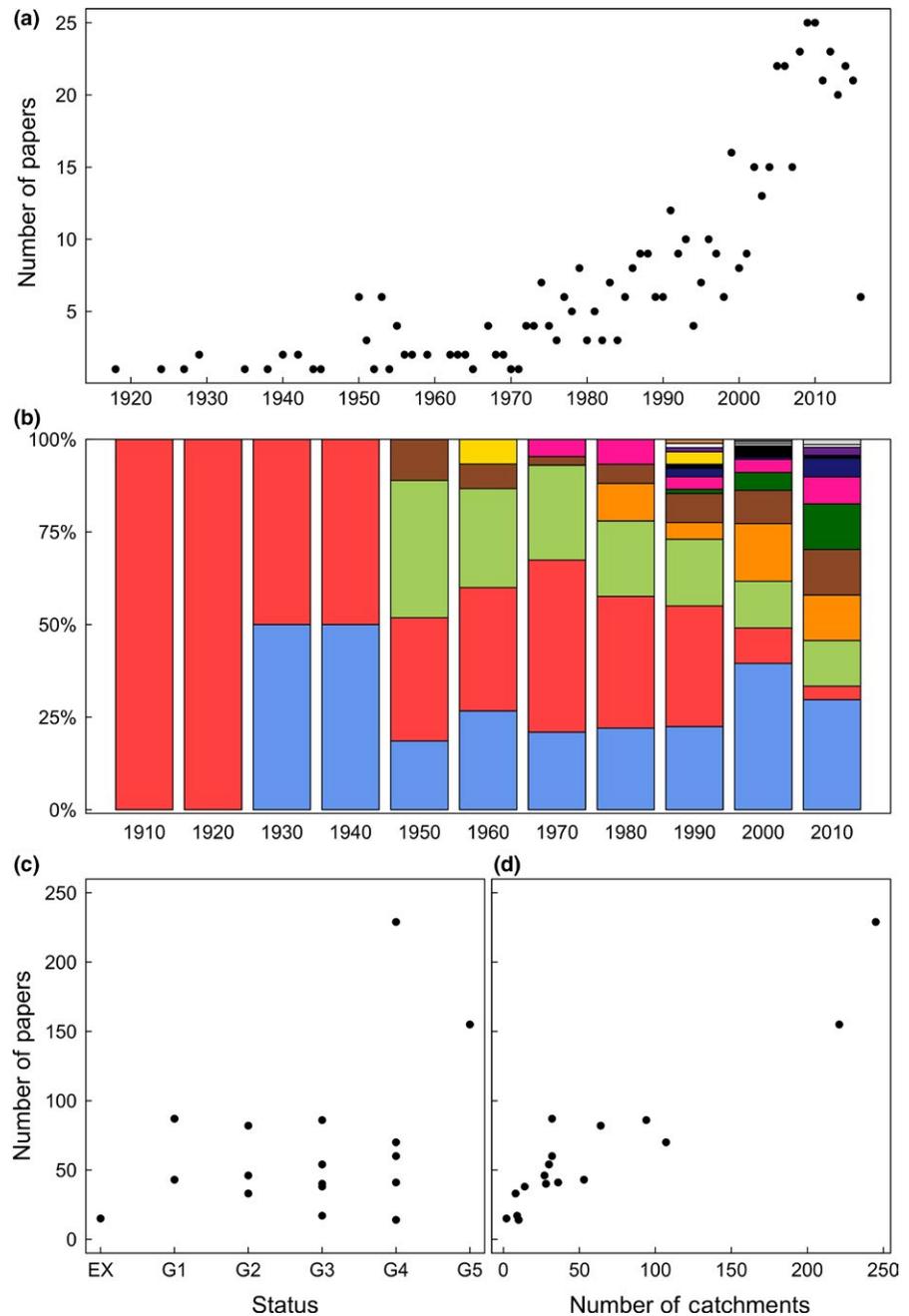


FIGURE 1 (a) Number of studies published on pelagic-broadcast spawning (PBS) species per year; (b) relative percentages of publications in 15 broad journal categories, fisheries (light blue), state (red), regional (light green), freshwater (orange), ecology (dark brown), geomorphology (dark green), genetics (pink), environmental (dark blue), water resources (black), biology (yellow), hydrology (purple), agriculture (white), general (light grey), forestry (light brown), marine (dark grey); (c) number of studies for each PBS species versus its NatureServe global status Presumed Extinct (EX), Critically Imperilled (G1), Imperilled (G2), Vulnerable (G3), Apparently Secure (G4), Secure (G5); and d) number of studies for each PBS species versus number of catchments in its US distribution

markedly, with percentage contribution of publications in regional and especially state journals decreasing.

The number of papers including a species was not significantly related to the status of the species (Figure 1c, $S = 613.3$, $P = .17$, $\rho = 0.25$), but was strongly related to number of catchments in its distribution (Figure 1d, $S = 101.6$, $P < .0001$, $\rho = 0.88$). There was a positive correlation between species status and number of catchments in the distribution ($S = 448.0$, $P = .035$, $\rho = 0.45$). Plains minnow was the subject of the most studies, with burrhead chub studied least often (Table 1). Nine studies focused on PBS species in general, and in 15 studies, species was assignable only to the *Macrhybopsis aestivalis* complex. Number of PBS species in individual studies was low (median = 1, mean = 2.07), but 14 species were considered in one broad review.

3.2 | Key aspects of reproductive biology

Pelagic-broadcast spawning species reproduce by releasing non-adhesive, semi-buoyant eggs in open water whereby they are passively transported downstream by the current (Balon, 1975). The LPBS species have a similar reproductive strategy except that eggs are released over rock or gravel and might be initially adhesive (Simon, 1999). The PBS reproductive strategy was extensively reviewed by Hoagstrom and Turner (2015); therefore, we provide a brief overview of key aspects:

- Multiple spawning events during a protracted breeding period (Durham & Wilde, 2008, 2009a, 2014; Hatch, Baltosser & Schmitt, 1985; Taylor & Miller, 1990).

- Spawning during spring to late summer, although intraspecific, spatial and temporal variation is apparent (Archdeacon, Blocker, Davenport & Henderson, 2015; Durham & Wilde, 2008; Taylor & Miller, 1990).
- Synchronous spawning coincides with periods of high flow and produces large proportions of young-of-year fish (Archdeacon, Blocker, et al., 2015; Durham & Wilde, 2008, 2009a, 2014; Lehtinen & Layzer, 1988; Taylor & Miller, 1990).
- Asynchronous spawning through the entire reproductive season (Durham & Wilde, 2008, 2014), although reproductive success is likely not achieved during periods of no flow (Durham & Wilde, 2006, 2009a).
- Spawning takes place within aggregations (Aló & Turner, 2005; Taylor & Miller, 1990).
- Eggs are non-adhesive, semi-buoyant and pelagic (Bottrell, Ingersol & Jones, 1964; Platania & Altenbach, 1998).
- Eggs are virtually neutrally buoyant and therefore held in suspension by minimal water current; larvae are denser and therefore are likely to require higher flows (Coleman, 2015; Platania & Altenbach, 1998).
- The suspended and drifting ova and larvae (ichthyoplankton) are displaced long distances downstream as they develop (Hoagstrom & Brooks, 2005), although entrainment in off-channel floodplain environments has been proposed for Rio Grande silvery minnow (Medley & Shirey, 2013).
- Rapid development of ichthyoplankton; horizontal swimming and first feeding ~three days after hatching (Bottrell et al., 1964; Moore, 1944).

For the 17 species included in the review, assignment of reproductive mode was based on imperfect information, but represented our current understanding of the species' biology. For eight PBS species, this was based on our current knowledge of combinations of their pelagic spawning behaviour and non-adhesive, semi-buoyant eggs (Table 1). Seven species were considered potential PBS species (LP/P-BS) based on our limited knowledge of their habitat (occupying Central Plains streams) and egg characteristics (non-adhesive, semi-buoyant). The Sabine shiner has been speculated as a LP/P-BS species based on its sandy-bottomed, stream habitat and the temporal, longitudinal pattern of occurrence of age-0 fish, downstream early in the breeding season, upstream later in the year (Williams & Bonner, 2006). Finally, the phantom shiner was included because it has been mentioned as a potential PBS species based on habitat and similarity to a known, co-occurring PBS species (Platania & Altenbach, 1998).

3.3 | Origins and phylogenetic distribution of pelagic spawning

The Great Plains LP/P-BS cyprinids are members of the large, multi-genera shiner clade or the closely related *Platygobio* clade (flathead chub and *Macrhybopsis*). Both clades are placed with most eastern North American cyprinids in Simons and Mayden's (1999) open posterior myodome clade (Figure 2). Reviews using a phylogenetic

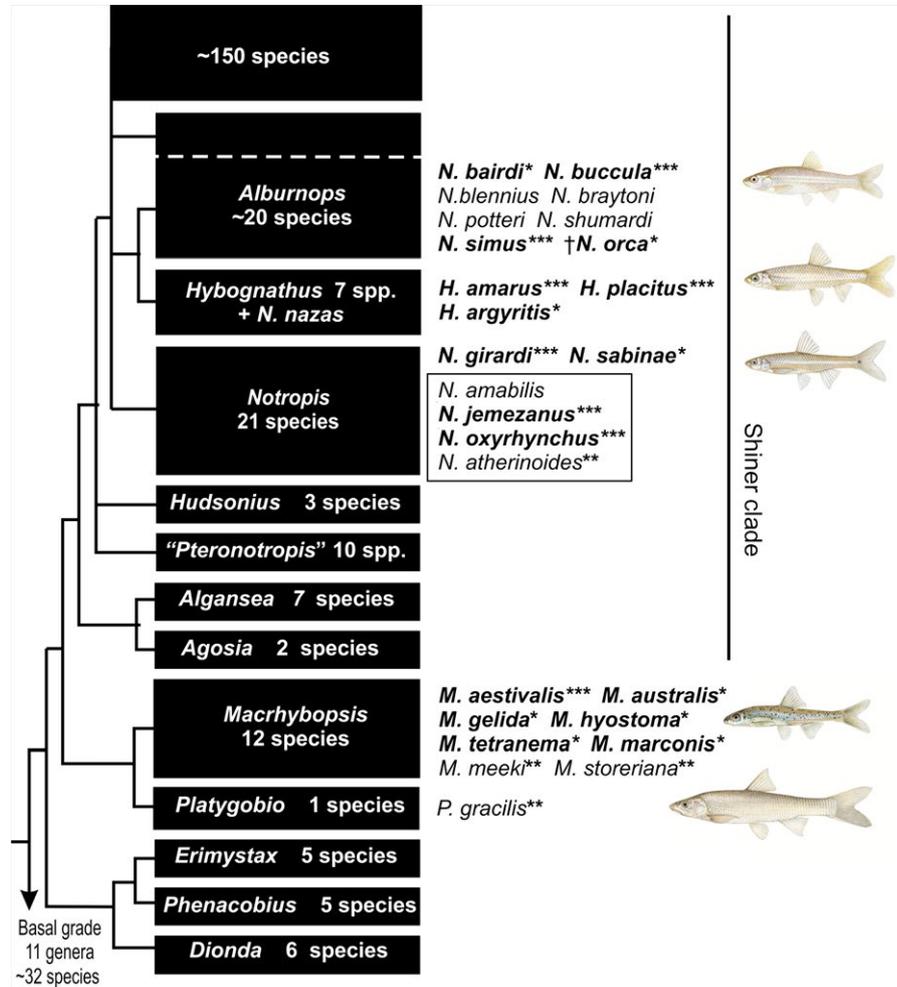
framework indicate that broadcasting is the ancestral spawning mode in cyprinids (Johnston & Page, 1992; Mayden & Simons, 2002), and that the benthic lifestyle is ancestral to the pelagic lifestyle seen in most members of the shiner clade (Hollingsworth, Simons, Fordyce & Hulseley, 2013). Therefore, the variety of lifestyles in Great Plains cyprinids are likely derived from benthic, broadcast spawning ancestors.

One apparently independent origin of LP/P-BS lifestyles began with the evolution of the LPBS mode in the most recent common ancestor for the *Platygobio* + *Macrhybopsis* clade. The LPBS mode characterizes *Platygobio* and the two earliest branching events in *Macrhybopsis* (Figure 3), indicating that LPBS preceded the evolution of PBS in the clade. The LPBS common ancestor likely arose from a lithophilic broadcast spawner because this reproductive mode characterizes nearly all genera of the open posterior myodome clade that, like the *Platygobio* clade, are outside the shiner clade. The known exceptions are the phytophilic Oregon chub (*Oregonichthys crameri*, Cyprinidae) and splittail (*Pogonichthys macrolepidotus*, Cyprinidae) which broadcast their eggs in vegetation (Moyle, Baxter, Sommer, Foin & Matern, 2004; Pearsons, 1989), and the speleophilic loach minnow (*Rhinichthys cobitis*, Cyprinidae) whose adhesive eggs are deposited on the underside of flattened rocks in areas of sufficient velocity to ensure oxygenation and submergence during low flows (Propst & Bestgen, 1991).

The PBS mode is best documented for speckled chub because it is assigned based on both spawning behaviour and egg characteristics (Platania & Altenbach, 1998). Three other members of the *Macrhybopsis aestivalis* complex, prairie chub, shoal chub and peppered chub, have not been studied for spawning behaviour, but are probable PBS species given they closely resemble speckled chub in egg characteristics (Table 1), body form (Eisenhour, 2004) and habitat. A fourth *Macrhybopsis aestivalis* complex species, burrhead chub, has been the subject of few ecological studies, but was suggested a potential PBS by Hoagstrom and Turner (2015). The phylogenetic placement (Figure 3) of the south-eastern species of *Macrhybopsis* (Gulf chub, *M. tomellerii*, Cyprinidae; Mobile chub, *M. boschungii*, Cyprinidae; Coosa chub, *M. etneiri*, Cyprinidae; and pallid chub, *M. pallida*, Cyprinidae) in streams associated with the northern Gulf Coastal Plain (Eisenhour, 2004; Mayden & Powers, 2004) makes them potential PBS species.

Within the shiner clade, LP/P-BS reproductive modes occur in three clades recognized as genera by Mayden, Simons, Wood, Harris and Kuhajda (2006) and Gidmark and Simons (2014): *Notropis* (*sensu stricto* (*s.s.*)), *Alburnops* (traditionally in *Notropis*) and the genus *Hybognathus* (Figure 4). Hollingsworth et al. (2013) resolved a sister relationship between *Hybognathus* (+ Nazas shiner, *Notropis nazas*, Cyprinidae) and a clade conforming to part of *Alburnops* (Figure 2). The other species of *Alburnops* formed a separate clade with unresolved relationships within the shiner clade (Figure 4). The sister clade to *Hybognathus* (+ Nazas shiner) includes two known PBS species (small eye shiner and bluntnose shiner) and a LP/P-BS species (Red River shiner) within *Alburnops*. This suggests the most recent common ancestor of the two clades had the pelagic reproductive

FIGURE 2 Phylogenetic hypothesis for the species treated in this study. Topology based on the review by Gidmark and Simons (2014). Exceptions are based on Hollingsworth et al. (2013), including the indicated paraphyly for *Alburnops* (dashed line, see text). Names in black boxes follow Mayden et al. (2006) and Gidmark and Simons (2014). Bold-font names outside black boxes are species reviewed in this study. The generic abbreviation “N.” = *Notropis*. One asterisk = LP/P-B; two asterisks = LPBS; three asterisks = PBS; † = extinct. Species with no asterisks = possibility of PBS or LPBS based on phylogenetic placement (see text). Open box shows a four-species clade (Hollingsworth et al., 2013). Placement of the extinct phantom shiner is from comments by Chernoff et al. (1982) on morphological similarities to *N. simus*. Drawings show representative species of the four groups of PBS and LP/P-B species (top to bottom: Red River shiner, Rio Grande silvery minnow, Arkansas River shiner, shoal chub) and one LPBS species (flathead chub). Drawings by J. Tomelleri



mode, but inferences regarding the evolution of PBS in these two clades are confounded by a lack of data on reproductive mode for most species of *Alburnops*. Five *Alburnops* species (redlip shiner, *N. chiliticus*, Cyprinidae; saffron shiner, *N. rubricroceus*, Cyprinidae; rainbow shiner, *N. chrosomus*, Cyprinidae; greenhead shiner, *N. chlorocephalus*, Cyprinidae; rough shiner, *N. bailey*, Cyprinidae; Figure 4) are known to be broadcast spawners that deposit their eggs in nests built by other fishes, and are not likely to be LP/P-B species. Reproductive mode is relatively well known for *Hybognathus*. Three of the four species occurring primarily in sandy-bottomed plains stream habitat (Rio Grande silvery minnow, western silvery minnow and plains minnow) are known or suspected PBS. The fourth broadcasts eggs in vegetation (Mississippi silvery minnow, *H. nuchalis*, Cyprinidae; Becker, 1983). The remaining three species either broadcast adhesive or at least demersal eggs in quiet, non-riverine environments (Falke, Bestgen & Fausch, 2010; Raney, 1939) or occupy quiet backwaters and oxbows (Cypress minnow, *H. hayi*, Cyprinidae; Robison & Buchanan, 1988) where LP/P-B modes are not expected.

Various species of *Alburnops* are PBS candidates because of similarities in habitat (sandy-bottomed plains streams) and morphology to the three PBS or LP/P-B species (Red River shiner, small-eye shiner, and bluntnose shiner) and the extinct phantom shiner.

These include three Great Plains species: river shiner, chub shiner and silverband shiner. Their breeding habits are poorly understood, although the river shiner is said to be a broadcast spawner (Cross, 1967). A fourth candidate for LP/P-B reproduction is Tamaulipas shiner. This species inhabits large-stream habitats of the Rio Grande system, which supported six other cyprinid PBS species (Haworth & Bestgen, 2016; Platania & Altenbach, 1998). To our knowledge, Tamaulipas shiner previously has not been considered a LP/P-B candidate, but a recent phylogenetic analysis placed it in *Alburnops* as sister to the LP/P-B species, Red River shiner (Hollingsworth et al., 2013).

The genus *Notropis* (sensu Mayden et al., 2006) includes four LP/P-B species. These include Arkansas River shiner (PBS) and three species in a clade of four with the following mtDNA relationships (Hollingsworth et al., 2013; Mayden et al., 2006): Rio Grande shiner (PBS), Texas shiner, sharpnose shiner (PBS) and emerald shiner (LPBS). The reproductive habits of Texas shiner are unknown, but owing to its phylogenetic placement and large-river habitat, further research is warranted to establish whether it belongs to the LP/P-B group. This also applies to the geographically overlapping *N. megalops*, a species recently re-established within the traditionally recognized *N. amabilis* (Conway & Kim, 2016). Most members of *Notropis* (s.s.) appear to be broadcast spawners (Johnston &

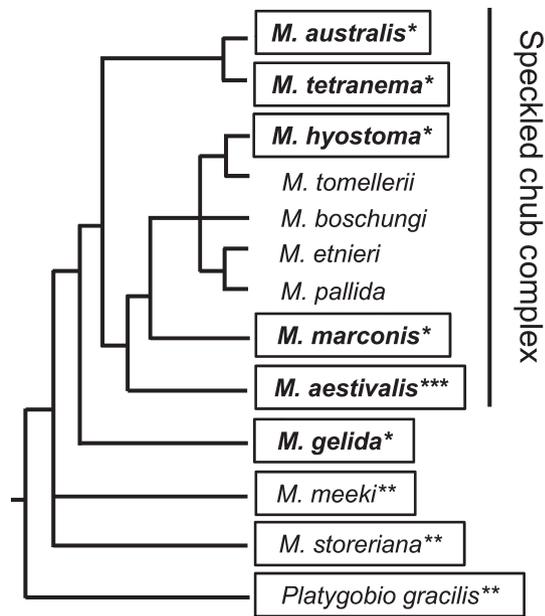


FIGURE 3 Phylogeny for *Macrhybopsis* and *Platygobio*. Branching pattern for *Macrhybopsis* is from Eisenhour's (2004) morphological analysis, except for *M. tomellerii*, which he grouped with *M. hyostoma* (Gilbert, Mayden & Powers, 2017). Placements of *P. gracilis*, *M. storeriana*, *M. meeki* and *M. gelida* are based on a molecular analysis by A.A. Echelle et al. (in preparation). Names in boxes signify species in Great Plains streams; *LP/P-BS; **LPBS; ***PBS spawning mode

Page, 1992; Mayden & Simons, 2002). Hollingsworth et al. (2013) resolved Arkansas River shiner in a clade with seven other species. Of these, and excepting Arkansas River shiner, breeding behaviour is known only for Tennessee shiner (*N. leuciodus*, Cyprinidae), a broadcast spawner that uses the nests of other species (Mayden & Simons, 2002).

In summary, the plains stream LP/P-BS cyprinids comprise a phylogenetically diverse group, suggesting multiple origins of the pelagic reproductive mode. The potential for LP/P-BS has not been evaluated for many plains stream cyprinids. This reflects the general lack of data on reproductive mode for many cyprinids (Johnston, 1999; Johnston & Page, 1992; Mayden & Simons, 2002). The phylogenetic placement of a variety of plains stream species suggests that they should be assessed for LP/P-BS reproductive modes.

3.4 | Population genetics

Most information on the genetic structure of pelagic spawning cyprinids is from four species in the middle Rio Grande and Pecos River drainages of New Mexico. These include two species endemic to the Rio Grande system, the endangered Rio Grande silvery minnow and Pecos bluntnose shiner and two introduced species, plains minnow and Arkansas River shiner. Information on the endemic species is presented here, with the genetic aspects of the introduced species discussed in the context of threats from non-native species in the discussion.

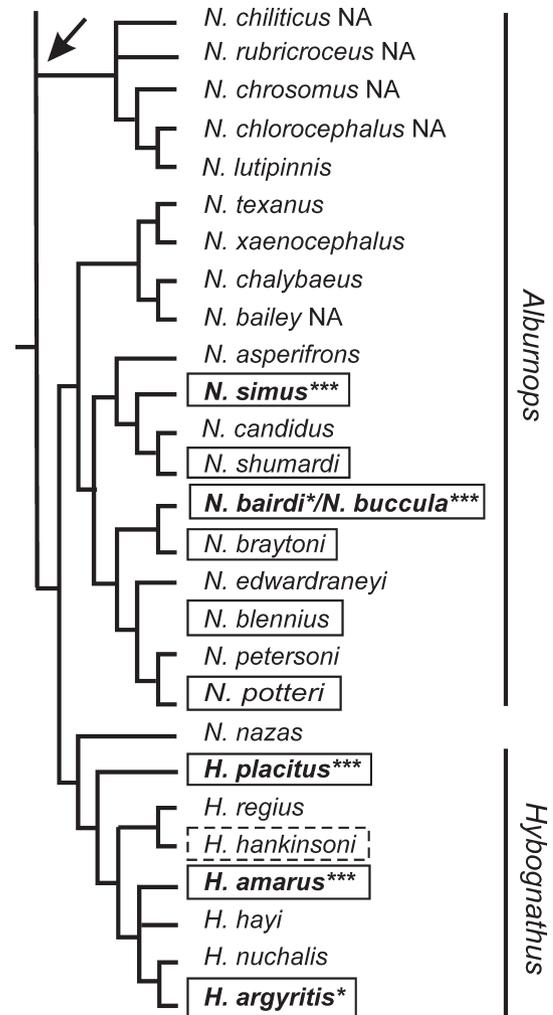


FIGURE 4 Hypothesis of relationships in *Hybognathus* and *Alburnops* and the distribution of LP/P-BS spawning modes. Arrow at top points to a node that includes the two primary nodes in a polytomy with remaining lineages of the shiner clade. Tree topology from Hollingsworth et al. (2013), except smalleye shiner (*N. buccula*) which was not included in the phylogenetic analysis, but is highly similar to Red River shiner (Cross, 1953). Names in boxes = plains stream species. Bold font = species included in this review: *LP/P-BS; ***PBS spawning mode; non-bold names in boxes = potential PBS species; see text). Dashed-line box = plains stream dweller that broadcasts eggs into vegetation (Falke et al., 2010). NA = nest associates, broadcast spawners using nests of other cyprinids or sunfish (Goldstein, Harper & Edwards, 2000)

3.4.1 | Genetic status of Rio Grande silvery minnow

The last wild remnant of Rio Grande silvery minnow, excluding the potentially repatriated population in the lower Rio Grande (Edwards, 2013), occupies a 280-river-km (rkm) section of the Rio Grande between Cochiti and Elephant Butte reservoirs in New Mexico. This section is fragmented by three diversion dams (maximum fragment length 90 rkm) that are impassable in the upstream direction. In most years since 2003, the wild populations of Rio Grande silvery minnow have been augmented, primarily with fish reared from captive broodstock or from wild-caught eggs hatched

and reared in captivity before transfer to the wild (Osborne, Carson & Turner, 2012). Genetic monitoring of wild and captive stocks occurred in 1987 and annually since 1999. Using variation in mtDNA (ND4 gene) and microsatellite loci, this work centres on estimates of genetic diversity and genetically effective population sizes (N_e). The following are some key outcomes from genetic monitoring of wild Rio Grande silvery minnow:

1. Estimates of N_e are small relative to abundances of the adult population (Aló & Turner, 2005; Osborne et al., 2012). Normally, N_e is smaller than N_c , the census population size (Palstra & Ruzzante, 2008), but this is exaggerated in Rio Grande silvery minnow in which some estimates of variance effective population size ($N_{eV} < N_e$ estimated from temporal variation in N_c) are <100 at times when N_c is 10,000s. When $N_{eV} < 100$, there are immediate concerns regarding inbreeding effects and, via losses of genetic diversity, short- and long-term concerns regarding resistance to environmental change.
2. The low N_e/N_c ratio likely reflects an interaction between the breeding biology of Rio Grande silvery minnow and the modified hydrology of the Rio Grande (Turner, Osborne, Moyer, Benavides & Aló, 2006). Individual spawning groups, each with a different subset of genetic diversity, show high variance in contribution to the next generation of offspring because of variation in the hydrodynamics associated with local habitats where eggs are released. High reproductive variance among spawning groups is equivalent to high variance in reproductive success of individuals, which reduces N_e .
3. A test of this hypothesis showed (i) drifting eggs are divergent in allele/haplotype frequencies from the adult gene pool and (ii) drifting eggs taken during different spawning days or at different hours of the same day are heterogeneous in genetic structure (Osborne, Benavides & Turner, 2005). This patchiness is expected if spawning occurs in relatively small local groups, a critical prediction if spawning-group variance in reproductive success explains the low N_e/N_c ratio.
4. The species has low genetic diversity compared with other plains stream fishes (Osborne et al., 2012). This reflects the small N_{eV} , as well as the historical decline in distribution and subsequent orders-of-magnitude fluctuations in population densities due to natural and human-induced variation in water flows. The present diversity clearly represents a severe decline, a factor of concern for the long-term evolutionary adaptability of the species.
5. Estimates of N_{eV} were consistently lower than inbreeding effective population size (N_{eI}), as predicted for a declining population. This interpretation was confounded, however, by unknown effects of the augmentation programme on the relationship between N_{eV} and N_{eI} (Osborne et al., 2012).

3.4.2 | Genetic status of Pecos River populations

In contrast to Rio Grande silvery minnow, none of the surveyed Pecos River populations showed mtDNA or microsatellite evidence of

reduced diversity. This includes the endemic Pecos bluntnose shiner and the non-native, plains minnow and Arkansas River shiner, all of which have moderate to high levels of mtDNA and microsatellite DNA diversity (Moyer, Osborne & Turner, 2005; Osborne, Benavides, Aló & Turner, 2006; Osborne, Davenport, Hoagstrom & Turner, 2010; Osborne, Diver & Turner, 2013). This likely reflects hydrologic differences between the inhabited sections of the Rio Grande and the Pecos River. Osborne et al. (2010) suggested that refugia during periods of river intermittency are larger (330 rkm), better connected and more suited to sustaining populations in the Pecos River than those in the middle Rio Grande.

3.4.3 | *Macrhybopsis aestivalis* complex

Allozyme analyses of the genetic structure of *Macrhybopsis* in the Red and Arkansas rivers are consistent with the hypothesis from morphology (Eisenhour, 1999, 2004) that the endemic Red and Arkansas river forms, prairie chub and peppered chub, respectively, are sister species, both of which intergrade with downstream populations of the widespread shoal chub (Underwood, Echelle, Eisenhour, Jones & Echelle, 2003). Based on allele frequencies, shoal chub from the Red and Arkansas rivers cluster with the respective endemic species and separately from shoal chub populations from other basins. Differences between species accounts for only 2% and 5% of the total genetic diversity, respectively, in the Arkansas and Red river populations of *Macrhybopsis*. Allozyme similarity in the face of morphological differentiation might be explained by (i) extensive genetic introgression for neutral (or effectively neutral) genetic markers and (ii) selection favouring one set or the other set of distinguishing morphological traits in different ecological contexts (Underwood et al., 2003). Ecological differences between shoal chub and the two endemics are evident in the distributions of the three species, with shoal chub primarily in larger, downstream reaches and the endemics primarily in more upstream reaches.

A genomic sequencing analysis of structure in three populations of shoal chub from the upper Mississippi River basin found weak genetic variation among populations, indicating high levels of gene flow (Gaughan, 2016). Within-population genetic diversity was low (i.e. high homozygosity), potentially representing reduced capacity to respond to anthropogenic disturbance. High existing similarities in gene frequencies can reflect either ongoing gene flow or a legacy of past gene flow prior to fragmentation. For example, among-population differences accounted for only ~1% of total allozyme diversity in peppered chub separated by hundreds of stream kilometres and several dams (Underwood et al., 2003).

3.5 | Distribution

Pelagic-broadcast spawning species are generally distributed in the larger rivers of the central United States, Canada and Mexico, with large portions of the rivers falling within the Great Plains ecoregion (Figure 5a). Their overall extent is described by five main areas (Figure 5b). Most of the individual species were historically confined

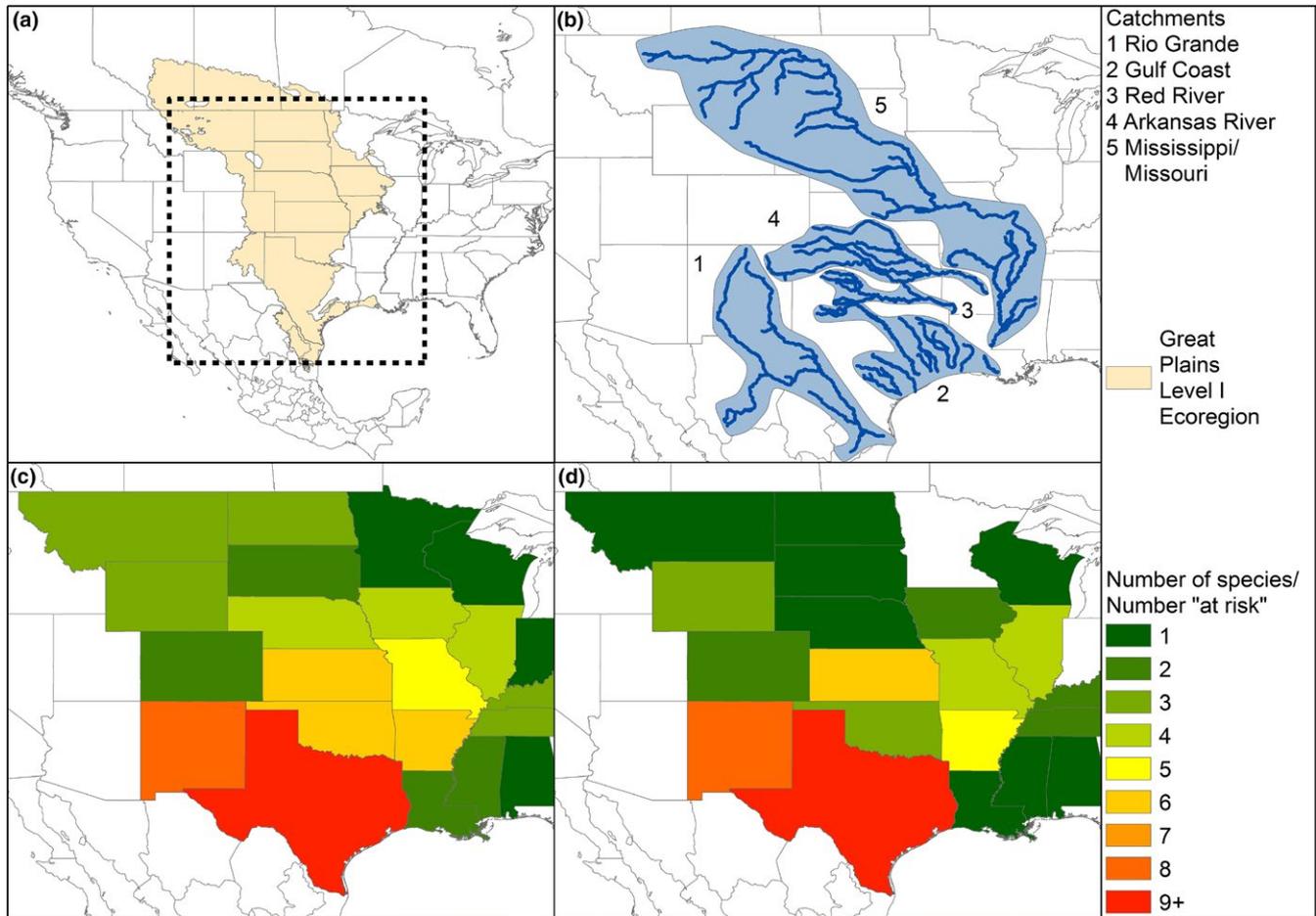


FIGURE 5 Maps of (a) extent of study area and Great Plains Level I ecoregion, (b) major catchments supporting pelagic-broadcast spawning cyprinids, (c) number of pelagic-broadcast spawning cyprinid present in each state and (d) number of pelagic-broadcast spawning cyprinids species considered "at risk" (either listed at the state level or given NatureServe rankings ranging from vulnerable to presumed extinct)

to a single drainage, with the Rio Grande supporting five endemics, the Mississippi/Missouri two and the Gulf Coast, Red River and Arkansas River basins two each. Three species were found across multiple areas: the Sabine shiner in the Gulf Coast rivers and the Mississippi/Missouri river system, and the plains minnow and shoal chub in all areas except the Rio Grande (Bestgen, Platania, Brooks & Propst, 1989; Hoagstrom, Zymonas, Davenport, Propst & Brooks, 2010; Sublette, Hatch & Sublette, 1990). Given four of the five broad areas are found within the state, Texas historically supported the most species ($n = 15$), followed by New Mexico, Kansas, Oklahoma and Arkansas (Figure 5c).

All five PBS species endemic to the Rio Grande basin have undergone major range contractions (Figure 6). The phantom shiner, formerly widely distributed in the mainstem Rio Grande, is considered extinct (Chernoff, Miller & Gilbert, 1982; Hoagstrom, Remshardt, Smith & Brooks, 2010; Hubbs, Edwards & Garrett, 1991, 2008; Miller, Minckley & Norris, 2005; Miller, Williams & Williams, 1989; Platania, 1991; Propst, Burton & Pridgeon, 1987). The Rio Grande silvery minnow (Figure 6a), speckled chub (Figure 6b) and Rio Grande shiner (Figure 6c) once occurred throughout the Rio Grande basin from the mouth of the river to northern New Mexico and within

major tributaries, such as the Pecos River (Bestgen & Platania, 1991; Contreras-Balderas, Edwards, Lozano-Vilano & Garcia-Ramirez, 2002; Edwards & Contreras-Balderas, 1991; Edwards, Garrett & Marsh-Matthews, 2002; Hubbs, 1957; Hubbs, Edwards & Garrett, 1991; Miller et al., 2005; Miller, 1986; Sublette et al., 1990; Thomas, Bonner & Whiteside, 2007; Treviño Robinson, 1959). Speckled chub and Rio Grande shiner were extirpated from the upper Rio Grande (Bestgen & Platania, 1990; Hoagstrom, Remshardt, et al., 2010; Propst et al., 1987) and are now confined to the lower river in Texas and the Pecos River (Edwards et al., 2002; Heard, Perkin & Bonner, 2012; Hoagstrom & Brooks, 2005; Hubbs, Edwards & Garrett, 2008; Sublette et al., 1990). Conversely, the Rio Grande silvery minnow (now confined to only 5% of its historic range) has been extirpated from the Pecos River and the Rio Grande in Texas/Mexico (Bestgen & Platania, 1991; Contreras-Balderas, Almada-Villela, Lozano-Vilano & Garcia-Ramirez, 2003; Sublette et al., 1990; Thomas et al., 2007). The bluntnose shiner has two subspecies, one endemic to the upper portion of the Rio Grande and one endemic to the upper Pecos River (Figure 6d). The declines of the Rio Grande subspecies mirror those of the speckled chub and Rio Grande shiner, with the subspecies considered extinct (Hoagstrom, Remshardt, et al., 2010; Hubbs et al., 2008; Miller et al.,

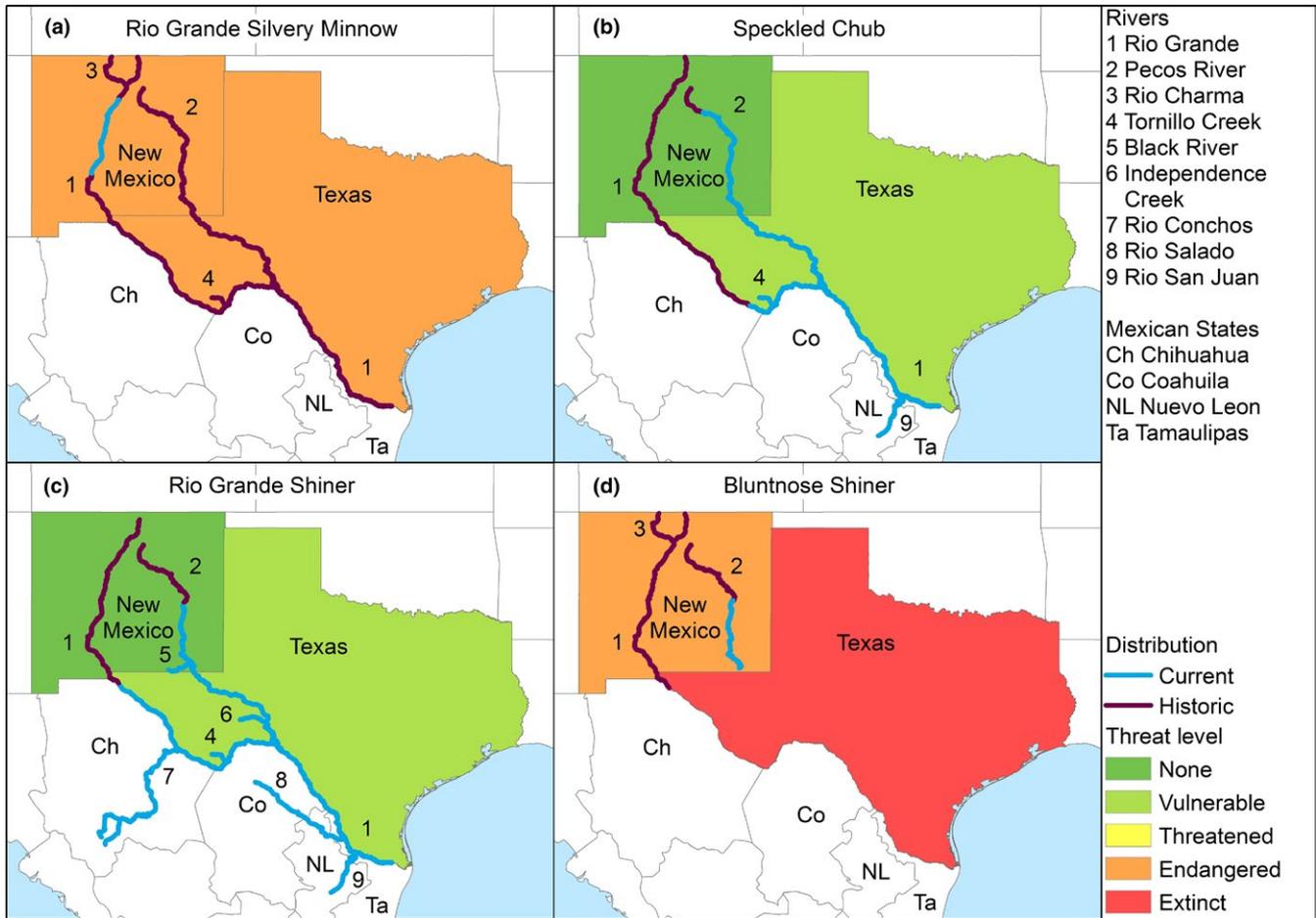


FIGURE 6 Estimated current and historic (in combination with current distribution) distributions and state-level status of (a) Rio Grande silvery minnow, (b) speckled chub, (c) Rio Grande shiner and (d) bluntnose shiner. State-level status from Table S3. Species listed as special concern (SC) equated to vulnerable on the figure. Distribution maps were constructed using multiple sources (see Supplemental Information). Ch = Chihuahua, Co = Coahuila, NL = Nuevo León, Ta = Tamaulipas

2005). The Pecos bluntnose shiner persists in the Pecos River, New Mexico (Chernoff et al., 1982; Hatch et al., 1985; Sublette et al., 1990); however, it has declined dramatically since the 1940s and is now confined to the central portion of its distribution (Furlow, 1996; Hatch et al., 1985).

Four PBS species are generally confined to smaller catchments in Texas that drain into the Gulf of Mexico. The burrhead chub is endemic to the Colorado and Guadalupe-San Antonio rivers (Eisenhour, 2004; Perkin & Bonner, 2011; Thomas et al., 2007). River fragmentation by reservoir construction is implicated in the species being extirpated from over 25% of its historic range (Figure 7a; Perkin & Bonner, 2011; Perkin, Shattuck, Gerken & Bonner, 2013). The small eye shiner and sharpnose shiner once were widespread in the Brazos River (Figure 7b,c; Durham & Wilde, 2009b; Hubbs et al., 1991; Hubbs, 1957; Ostrand & Wilde, 2002; Wilde & Urbanczyk, 2013), but are now thought to have been extirpated from the lower and middle Brazos River, with present distributions restricted to the upper third of the basin (Ostrand & Wilde, 2002). Sharpnose shiner has apparently been extirpated from the North and South Wichita rivers of the Red River basin (Wilde & Urbanczyk, 2013); we follow

Cross, Mayden and Stewart (1986) in treating this as a native population although introduction of individuals from the Brazos River basin as bait bucket fish has also been postulated (Hall, 1956; Miller, 1953). The Sabine shiner comprises three disjunct populations (Figure 7d), relatively stable populations in a number of rivers in the Gulf Coast lowlands, from the San Jacinto of south-eastern Texas to the Sabine basin in south-western Louisiana (Heins, 1981; Hubbs, 1957; Hubbs et al., 1991; Schaefer, Duvernell & Kreiser, 2011; Thomas et al., 2007; Williams & Bonner, 2006). The species has been recorded irregularly and apparently uncommonly in the White, Black and St. Francis drainages of north-central Arkansas and south-east Missouri (Bounds, 1977; Matthews & Harp, 1974; McAllister, Starnes, Raley & Robison, 2010; Robison & Beadles, 1974). In Arkansas, the species has not been recorded in the St. Francis River drainage after 1900 (H. Robison, personal communication). A third population is found east of the Mississippi River in the Big Black drainage and the Yalobusha and Yazoo basins (Hashim & Jackson, 2009; Pezold, Douglas & George, 1993; Ross & Breneman, 2001). Populations in Missouri, Arkansas and Mississippi are of conservation concern given their restricted ranges (Williams & Bonner, 2007), although

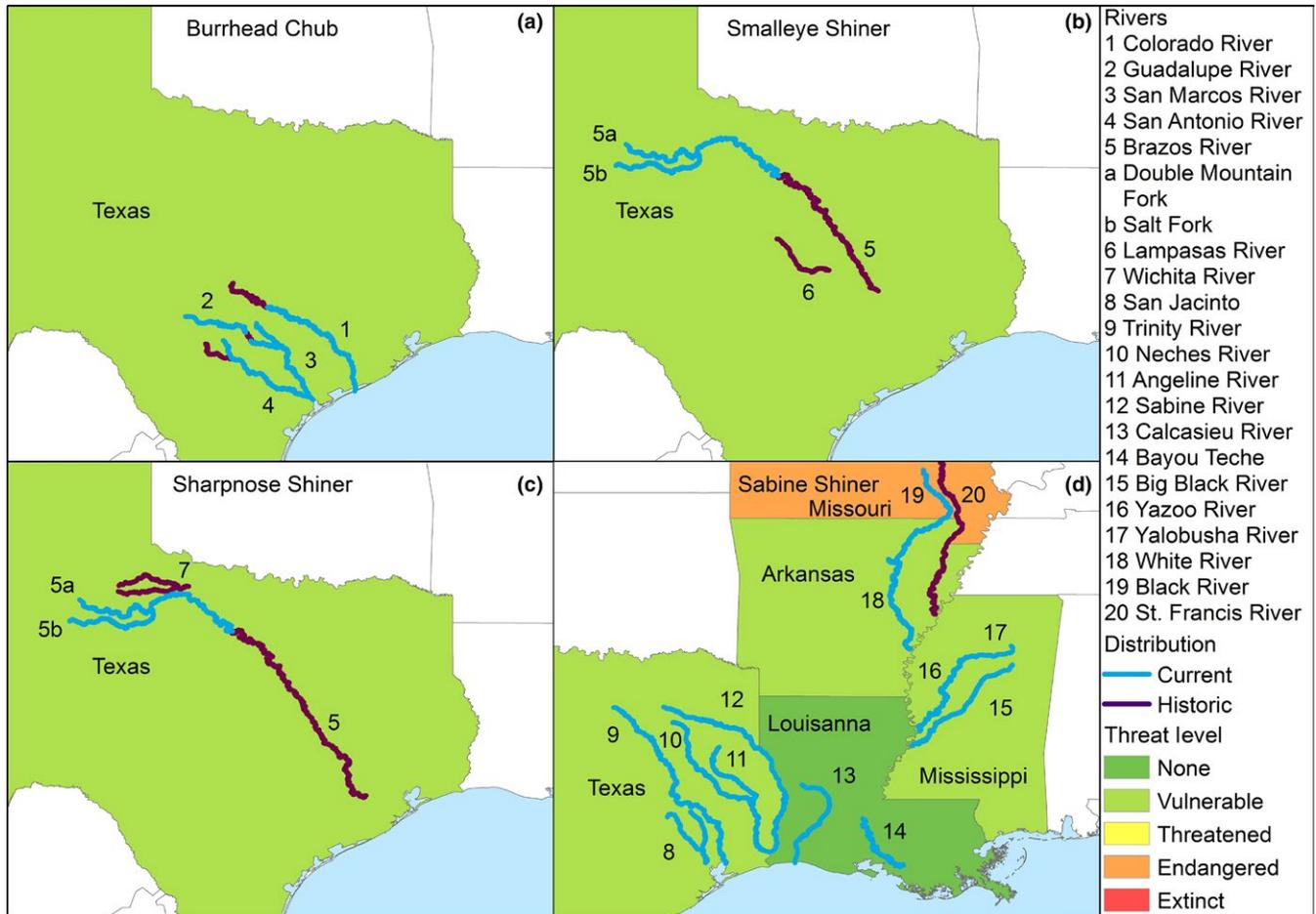


FIGURE 7 Estimated current and historic (in combination with current distribution) distributions and state-level status of (a) burrhead chub, (b) smalleye shiner, (c) sharpnose shiner and (d) Sabine shiner. State-level status from Table S3. Species listed as special concern (SC) equated to vulnerable on the figure. Distribution maps were constructed using multiple sources (see Supporting information)

periodically monitoring in the lower Black River, Missouri, suggests the population is secure (R.A. Hrabik, personal communication).

The Red and Arkansas river basins each have an endemic species of *Notropis* (Red River shiner and Arkansas River shiner, respectively) and an endemic species of *Macrhybopsis* (prairie chub and peppered chub, respectively), along with populations of the wide-ranging plains minnow and shoal chub. The prairie chub, which is endemic to the upper Red River basin (Eisenhour, 2004; Hubbs et al., 2008; Miller & Robison, 2004; Taylor, Winston & Matthews, 1993, 1996; Wilde, 2015), has been extirpated from the North Fork of the Red River (Figure 8a; Miller & Robison, 2004; Perkin & Gido, 2011; Winston, Taylor & Pigg, 1991). The Red River shiner, which was historically more widely distributed in the Red River basin than the prairie chub (Figure 8b; Buchanan, 1973; Hubbs et al., 2008; Miller & Robison, 2004; Wilde, 2015), is known in Arkansas from only two collections (Robison, 1974b) and none since impoundment of Lake Texoma in 1944 (Buchanan, Wilson, Claybrook & Layher, 2003). The peppered chub was historically found in the middle and upper reaches of the Arkansas River catchment (Figure 8c; Cross & Collins, 1995; Eisenhour, 1999; Luttrell, Echelle, Fisher & Eisenhour, 1999), but since the mid-20th century, has undergone large-scale

declines and is extirpated from 90% of its historic range (Cross & Collins, 1995; Eberle, Ernsting, Tomelleri & Wells, 1993; Luttrell et al., 1999; Pigg, 1987). The species until recently was confined to two disjunct areas, a relatively stable population in the South Canadian River between Ute Lake, New Mexico and Lake Meredith, Texas (Bonner & Wilde, 2000), and a second potentially declining population in the Arkansas River in south-central Kansas (Luttrell et al., 1999; Perkin & Gido, 2011; Perkin, Gido, Costigan, Daniels & Johnson, 2015). However, intensive sampling in 2015 in the Ninescah and Arkansas rivers following two years of drought conditions (2011 and 2012) resulted in no collection of peppered chub, suggesting the species may be extirpated (Pennock, Gido, Perkin, Weaver & Davenport, 2017). The historic range of the Arkansas River shiner was similar to that of the peppered chub, except for extending into Arkansas (Figure 8d; Robison, 1974b). Like the peppered chub, since the middle of the 20th century, severe declines have been observed across much of its historic range (Cross, Moss & Collins, 1985; Hubbs et al., 2008; Wilde, 2002). The Arkansas River shiner is now thought to be confined to two fragments of the Canadian River between Ute Lake, New Mexico, and Lake Eufaula, Oklahoma (Parham, 2009; Wilde, 2002; Worthington, Brewer,

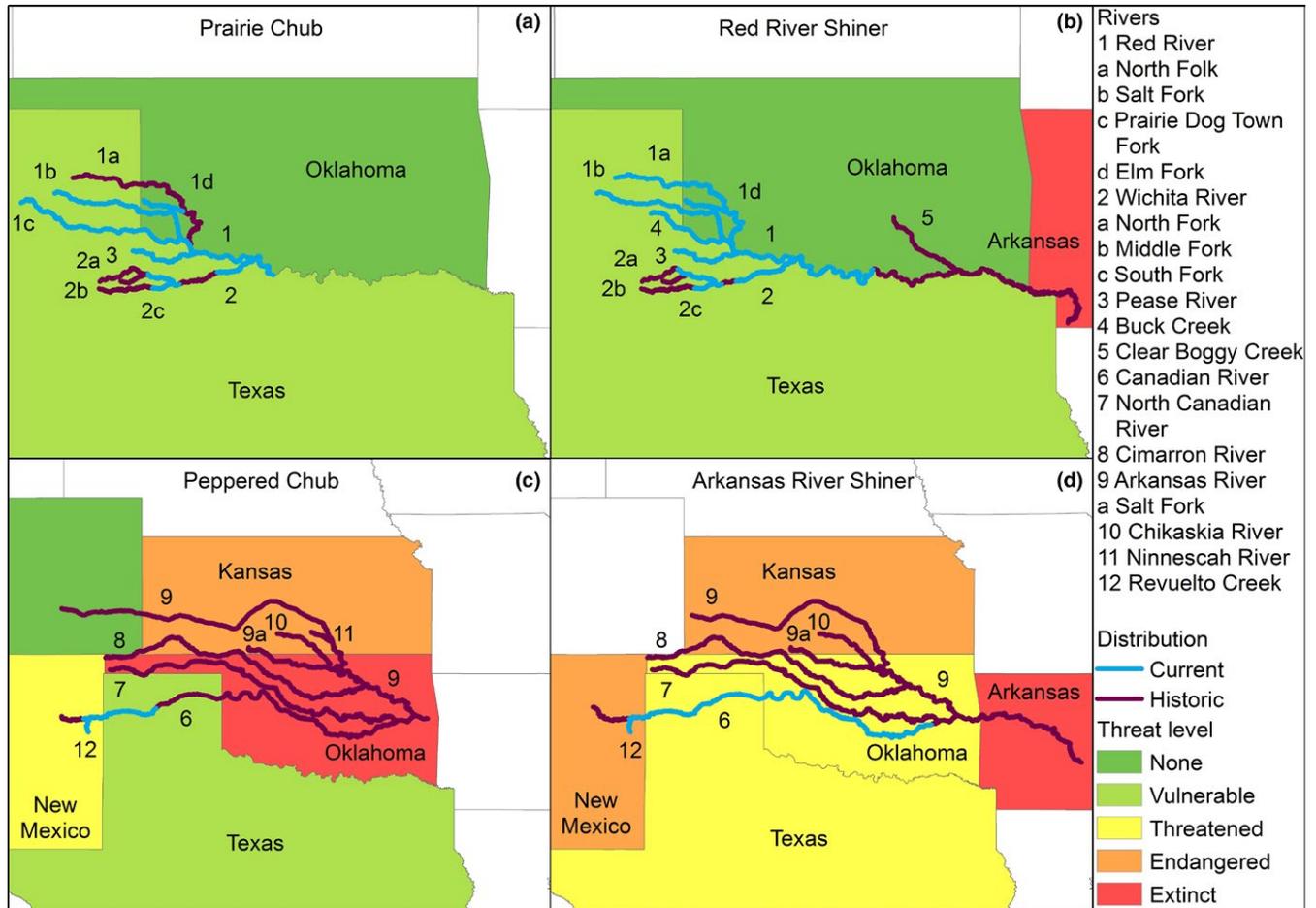


FIGURE 8 Estimated current and historic (in combination with current distribution) distributions and state-level status of (a) prairie chub, (b) Red River shiner, (c) peppered chub and (d) Arkansas River shiner. State-level status from Table S3. Species listed as special concern (SC) equated to vulnerable on the figure. Distribution maps were constructed using multiple sources (see Supporting information)

Grabowski & Mueller, 2014), although population declines are apparent (Bonner & Wilde, 2000; Pigg et al., 1999).

Two PBS species were generally confined to the Missouri basin and the mainstem of the Mississippi. The western silvery minnow was historically distributed throughout the Missouri River and major tributaries, south from southern Canada (Figure 9a; Houston, 1998; Hrabik, Schainost, Stasiak & Peters, 2015; Neebling & Quist, 2010). The species was also previously recorded in the Mississippi mainstem from the confluence of the Missouri River to the mouth of the Ohio River (Houston, 1998; Smith, 1979), although it is rarely collected nowadays (Schramm, Hatch, Hrabik & Slack, 2016). The species was formerly common in a number of the northern states (Cunningham, Olson & Hickley, 1995; Hesse, 1994; Hoagstrom, DeWitte, Gosch & Berry, 2006; Hoagstrom, Wall, Duehr & Berry, 2006; Hoagstrom, Wall, Kral, Blackwell & Berry, 2007); however, widespread declines have been observed (Berry & Young, 2004; Eberle, 2014; Hesse, 1994; Patton, Rahel & Hubert, 1998; Smith, Fischer & Quist, 2014). Sturgeon chub has been recorded in a number of the major tributaries of the Missouri (Figure 9b; Everett, Scarnecchia & Ryckman, 2004; Reigh & Elsen, 1979). The species has been recorded in the mainstem of the Mississippi from the mouth of the Missouri River south to Louisiana

(Lee, Gilbert, Hocutt, Jenkins & McAllister, 1980); however, the only current known population south of the Ohio River confluence is at Wolf Island, near Columbus, Kentucky (R.A. Hrabik, unpublished data). The distribution and abundance of sturgeon chub has declined dramatically (Berry & Young, 2004; Dieterman, Roberts, Braaten & Galat, 2006; Everett et al., 2004; Hesse, 1994; Hoagstrom, Hayer, Kral, Wall & Berry, 2006), with the species believed to have gone extinct in several areas (Figure 9b; Gido, Dodds & Eberle, 2010; U.S. Fish & Wildlife Service, 2001). In Kansas, for example, the species is thought to have been extirpated from several rivers including the Wakarusa, Republican, Smoke Hill and lower Kansas (Albers, 2014).

Two species, plains minnow and shoal chub, had historic distributions across much of the study area. The plains minnow occurs in the major western tributaries of the Mississippi including the Missouri (Kelsch, 1994; Patton et al., 1998; Pegg & Pierce, 2002; Steffensen, Eder & Pegg, 2014), Niobrara (Hrabik et al., 2015), Platte (Hrabik et al., 2015; Lynch & Roh, 1996; Scheurer, Bestgen & Fausch, 2003; Yu & Peters, 2003), Republican (Hrabik et al., 2015), Kansas (Eberle, Wenke & Welker, 1997), Arkansas (Branson, 1967; Eberle et al., 1993; Kilgore & Rising, 1965) and Red River (Hubbs & Ortenburger, 1929; Pigg, 1977) basins. The species is also present in the Gulf Coast drainages of the

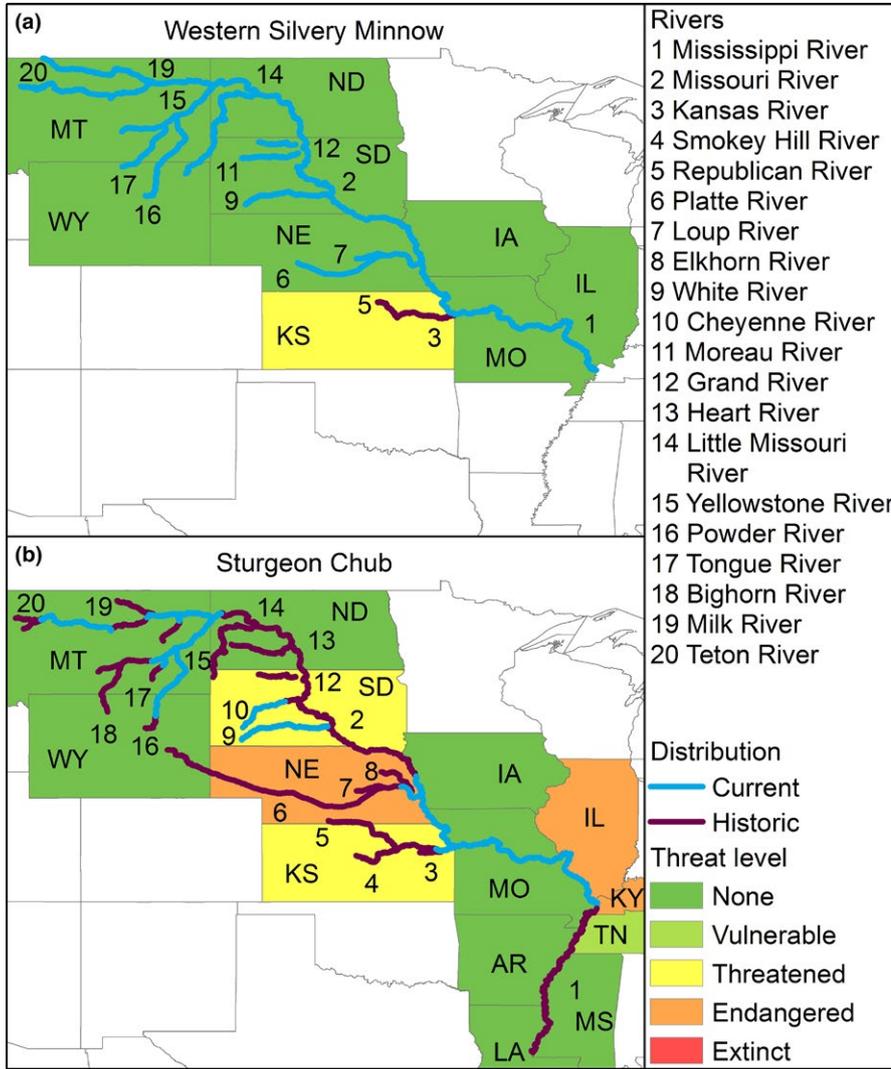


FIGURE 9 Estimated current and historic (in combination with current distribution) distributions and state-level status of (a) western silvery minnow, (b) sturgeon chub. State-level status from Table S3. Species listed as special concern (SC) equated to vulnerable on the figure. Distribution maps were constructed using multiple sources (see Supporting information). AR = Arkansas, IA = Iowa, IL = Illinois, KS = Kansas, KY = Kentucky, LA = Louisiana, MO = Missouri, MS = Mississippi, MT = Montana, ND = North Dakota, NE = Nebraska, SD = South Dakota, TN = Tennessee, WY = Wyoming

Colorado and Brazos rivers (Al-Rawi & Cross, 1964; Ostrand & Wilde, 2002; Ostrand, Wilde, Strauss & Young, 2001; Thomas et al., 2007). Despite historically being one of the most abundant species across its extensive distribution, the plains minnow has declined across much of its range (Eberle et al., 1997; Eberle, Ernsting, Stark, Tomelleri & Wenke, 1989; Haslouer, Eberle & Edds, 2005; Hesse, 1994; Hoagstrom et al., 2011; Smith et al., 2014; Taylor & Eberle, 2014), particularly in the southern portion of its range (Hrabik et al., 2015). Shoal chub is distributed extensively in the central United States from Missouri to West Virginia in the east, and Texas as the south and west boundaries (Hrabik et al., 2015). The species occurs in the larger streams of the Mississippi and Ohio River basins and the western gulf slope south to the Lavaca River in Texas (Burr, 1980; Eisenhour, 2004; Pearson & Pearson, 1989; Starrett, 1950a, 1951; Underwood et al., 2003). Shoal chub is sympatric with other members of *Macrhybopsis aestivalis* complex in the Colorado River (burrhead chub), Red River (prairie chub) and Arkansas River (peppered chub) basins (Eisenhour, 1999, 2004). Although common across much of its distribution (Eisenhour, 2004), river fragmentation is associated with extirpation in parts of the range (Gido, Guy, Strakosh, Bernot & Hase, 2002; Hesse, 1994; Luttrell, Echelle & Fisher, 2002; Luttrell

et al., 1999), including portions of the Arkansas River, Big Blue River and Republican River basins (Hrabik et al., 2015; Perkin, 2014).

3.6 | Status

Five of the 18 taxa treated in this review (17 species, one with two subspecies) are federally listed as “threatened” or “endangered” in the United States (Table S3), and two others (phantom shiner and Rio Grande bluntnose shiner) were extinct before federal listing was proposed. All of the PBS species with distributions extending into Canada (two species) or Mexico (five species) are considered threatened or endangered within those countries (Contreras-Balderas et al., 2002; Miller et al., 2005), although two of those in Mexico, phantom shiner and Rio Grande bluntnose shiner, are generally considered extinct (Jelks et al., 2008; Miller et al., 1989; Williams & Miller, 1990). The NatureServe global rankings categorized 11 of the 17 species as “vulnerable” or worse (Table S3), with only shoal chub categorized as “secure”.

The conservation status of North American freshwater and diadromous fish compiled by the American Fisheries Society’s

Endangered Species Committee points to a worsening situation (see also Hoagstrom et al., 2011). In the first edition (Deacon, Kobetich, Williams & Contreras, 1979), only bluntnose shiner and Rio Grande shiner were categorized as Special Concern/Vulnerable or worse (Table S3). The number expanded to seven in the second edition (Williams, Johnson & Hendrickson, 1989) and to 12 in the most recent edition (Jelks et al., 2008), though these numbers exclude the extinct phantom shiner, which was not removed from synonymy with bluntnose shiner until 1982.

At the state level, Texas has the most ($n = 13$) "at-risk" PBS species (either listed at the state level or given NatureServe rankings ranging from Vulnerable to Presumed Extinct). All PBS species historically present in New Mexico (eight species) and Kansas (six) are considered at risk (Figure 5d). Both PBS species recorded in Colorado, peppered chub and plains minnow, have been extirpated from the state (although plains minnow has been recorded in the Platte River basin close to the Colorado border; Hrabik et al., 2015), and there have been multiple extirpations of species from Arkansas ($n = 3$) and Texas ($n = 3$). Only Indiana and Minnesota have no at-risk PBS species (Figure 5d). Status varies widely across the range for certain species (Table S3). For example, NatureServe rankings for wide-ranging species such as western silvery minnow, plains minnow and shoal chub range from threatened or endangered (rankings SX, SH, S1 and S2) in some states to unlisted (S4 and S5) in others.

3.7 | Age and growth

Pelagic-broadcast spawning species exhibit an opportunistic life-history strategy (Hoagstrom & Turner, 2015), a strategy characterized by small adult body sizes and rapid growth rates of early life stages (Winemiller & Rose, 1992). The small body size might provide advantages such as efficient foraging and predator avoidance, increased number of spawning sites and higher population densities (Hoagstrom et al., 2011). However, in the Pecos River, non-native, larger-bodied, PBS species (plains minnow) were speculated as having a competitive advantage over native, smaller-bodied PBS species (Rio Grande silvery minnow; Hoagstrom, Zymonas, et al., 2010). The authors postulate that larger plains minnow may be more fecund, producing larger eggs with a greater survival rate (Hoagstrom, Zymonas, et al., 2010). Rapid growth rates of age-0 fish and early maturation are likely essential to the long-term persistence of PBS populations given the observation that age-0 fish are more sensitive to environmental change than older stages (Durham & Wilde, 2009b; Wilde & Durham, 2008).

The bet-hedging strategy (multiple spawning events in a protracted reproductive season) of PBS species results in juvenile fish being exposed to considerable variation in physicochemical conditions in Great Plains streams. Durham and Wilde (2005) compared trends in age-0 growth rates for four LP/P-BS species. A later hatch date resulted in slower age-0 growth for three of the four species: Arkansas River shiner, plains minnow and flathead chub (Durham & Wilde, 2005). Slower growth was attributed to smaller eggs and larvae, and summertime water temperatures exceeding the thermal

maximum for these species. Interestingly, faster growth was observed for age-0 peppered chub that hatched later in the season (Durham & Wilde, 2005).

Several studies indicate that PBS species typically live only 2–3 years (Bestgen & Platania, 1990; Braaten & Guy, 2002; Durham & Wilde, 2014; Hatch et al., 1985; Heins, 1981; Hoagstrom, Brooks & Davenport, 2008b; Perkin, Williams & Bonner, 2009; Williams & Bonner, 2006); however, age 4 sturgeon chub have been recorded (Stewart, 1981). Historical variation might be expressed, with Cowley, Shirey and Hatch (2006) suggesting that Rio Grande silvery minnow from the late 1800s survived to at least age 5. In general, studies indicate that number of individuals declines sharply with increasing age class. Few individuals older than age-1 were observed for Sabine shiner (Williams & Bonner, 2006), bluntnose shiner (Hatch et al., 1985; Hoagstrom, Brooks & Davenport, 2008b) and sharpnose shiner (Durham & Wilde, 2014). However, Everett et al. (2004) found that age 2 was the most abundant age class for sturgeon chub.

3.8 | Key ecological aspects

3.8.1 | Habitat

Fundamental habitat associations are missing for several PBS species (Table 2), and of those species for which information is available, very little is documented for life stages other than adults (but see Magana, 2012). Data generally are available only from a single study, making ontogenetic, seasonal or regional variation in habitat use difficult to assess. Depth of occurrence was the most commonly recorded microhabitat variable (Table 2). PBS species were generally recorded at depths of <1 m, as expected from the shallow, braided habitat typical of Great Plains rivers, the exception being *Macrhybopsis* spp. in the larger Mississippi and Missouri rivers. PBS species were observed using a range of substrates, although silt, sand and gravel were the most common (Table 2).

At the mesohabitat scale, PBS species appear to be most often associated with either swift-main channel or slow-slackwater environments. Western silvery minnow, plains minnow and Red River shiner were reported from backwaters, side channels, mainstream borders and depressional environments (Hesse, 1994; Houston, 1998; Kilgore & Rising, 1965; Welker & Scarnecchia, 2004). Conversely, sturgeon chub and Pecos bluntnose shiner were reported in swift velocity mainstem habitats (Kehmeier, Valdez, Medley & Myers, 2007; Ridenour, Starostka, Doyle & Hill, 2009; Welker & Scarnecchia, 2004). Despite the commonalities in mesohabitat, habitat partitioning between western silvery minnow and plains minnow has been observed at finer spatial scales. In undisturbed streams of Nebraska and South Dakota, western silvery minnow generally occupies areas of harder or slightly larger substrates (coarse sand and small gravel) associated with deeper and faster flowing areas, compared to plains minnow (R.A. Hrabik and G.R. Cunningham, personal observation). However, these broad associations may be a sampling artefact with seasonal shifts between main river and backwater habitats, as reported for the plains minnow and the Arkansas River shiner (Matthews & Hill, 1980).

TABLE 2 Habitat variables associated with PBS cyprinids in the Great Plains

Species	Habitat Variable	Measure	Value	References ^a
Rio Grande silvery minnow	Depth	Occurrence	<0.40 m	1
	Velocity	Occurrence	<0.30 m/s	1
	Substrate	Dominant	Silt, sand	1
Western silvery minnow	Depth	Occurrence	<1 m	2
	Velocity	Occurrence	<0.5 m/s	2
		Occurrence	<0.03 m/s	3
	Substrate	Dominant	Sand	3
Plains minnow	Depth	Maximum	0.43 m	4
		Range	0.2–0.9 m	5
	Velocity	Maximum	0.05 m/s	4
	Substrate	Observed	Mud, sand, gravel	5
Speckled chub	Depth	Maximum	0.3 m	6
		Range	0.1–0.7 m	7
	Velocity	Maximum	1 m/s	6
		Range	0–1.2 m/s	8
			0.05–0.6 m/s	7
	Substrate	Dominant	Sand	9
		Gravel	8	
Prairie chub	-	-	-	-
Shoal chub	Depth	Maximum	1.2 m	10
		Range	0.7–17.2 m	11
	Velocity	Range	0.2–0.4 m/s	12
	Substrate	Dominant	Gravel	12
		Range	Sand, small gravel	13
Burrhead chub	-	-	-	-
Peppered chub	Depth	Mean	0.3 m	5
Sturgeon chub	Depth	Mean	2.36 m	10
		Range	0.31–0.74 m	14
			2–5 m	2
	Velocity	Range	0.4–0.9 m/s	14
			0.5–1.0 m/s	2
	Substrate	Observed	Silt, sand, gravel	14
			Sand, fine gravel	15
		Range	Gravel	13
Rio Grande shiner	Depth	Range	0.1–0.7 m	7
	Velocity	Range	0.05–0.6 m/s	7
	Substrate	Dominant	Gravel	8
Bluntnose shiner	Depth	Range	0.17–0.41 m	16, 17
			0.1–0.5 m	7
	Velocity	Range	0.05–0.4 m/s	7
	Substrate	Range	Sand	17
Phantom shiner	-	-	-	-
Sharptnose shiner	Depth	Range	0.04–0.64 m	18
	Velocity	Range	0–0.75 m/s	18
	Substrate	Dominant	Silt, gravel	18

(Continues)

TABLE 2 (Continued)

Species	Habitat Variable	Measure	Value	References ^a
Smalleye shiner	Depth	Maximum ^b	0.35 m	19
		Range	0.03–0.65 m	18
	Velocity	Mean ^b	0.35 m/s	19
		Range	0–0.64 m/s	18
	Substrate	Dominate	Silt	18
Sabine shiner	Depth	Maximum	0.25 m	20
	Velocity	Range	0–0.2 m/s	20
	Substrate	Observed	Sand	20
Red River shiner	–	–	–	–
Arkansas River shiner	Depth	Maximum	0.3 m	6
		Range	0.2–0.6 m	7
			0.3–0.9 m	5
			0–0.5 m	21
	Velocity	Maximum	1.0 m/s	6
		Range	0.05–0.2 m/s	7
			0–1.0 m/s	21
	Substrate	Dominate	Mud, sand, gravel, rock	5

^aReferences: 1 Dudley and Platania (1997); 2 Welker and Scarnecchia (2004); 3 Pollard (2003); 4 Harrel, Davis and Dorris (1967); 5 Kilgore Jr. and Rising (1965); 6 Bonner, Wilde, Jimenez and Patiño (1997); 7 Kehmeier et al. (2007); 8 Heard et al. (2012); 9 Gido et al. (2002); 10 Ridenour et al. (2009); 11 Miranda and Killgore (2014); 12 Luttrell et al. (2002); 13 Hesse (1994); 14 Hampton and Berry Jr (1997); 15 Herzog, Ostendorf, Hrabik and Barko (2009); 16 Hatch et al. (1985); 17 Furlow (1996); 18 Wilde (2007); 19 Wilde and Durham (2013); 20 Williams and Bonner (2006); 21 Polivka (1999).

^bLow flow months only.

3.8.2 | Temperature

Pelagic-broadcast spawning species in the Great Plains are capable of surviving wide fluctuations in temperature (Matthews, 1987). Great Plains streams are especially prone to abiotic fluctuation due to their wide, shallow channels and anthropogenic reductions in groundwater input and riparian shading (Matthews & Zimmerman, 1990). Thermal tolerances of PBS species have rarely been studied, and the critical thermal maximum (CTM) has only been determined for five species (Table 3). However, for these species, CTMs were higher than most other cyprinids (Matthews, 1987). The seasonal abundance of PBS species seems dependent on temperature. With rising summer temperatures, the abundance of Arkansas River shiner declines as that of plains minnow increases, likely because the latter has higher thermal tolerance (Matthews & Maness, 1979; although the effect of sampling detection is likely to be a factor).

Future climate change might negatively affect PBS species as their thermal tolerances are close to maximum summer temperatures. Temperature also alters habitat use, swimming speed (Bestgen, Mefford, Bundy, Walford & Compton, 2010) and parasite susceptibility (Marcogliese, 2001). Climate change may act synergistically with other anthropogenic stressors, for example reduced base flows in the spawning season (Matthews & Zimmerman, 1990) and contaminants, to further impact PBS and other Great Plains species. For example, the preferred temperature of plains minnow was 30°C at O₂ concentrations above 4.8 mg/l and 17°C at 2.0 mg/l O₂ (Bryan, Hill & Neill, 1984).

3.8.3 | Water quality

Turbidity and salinity undoubtedly influence many aspects of PBS life history, although our ability to predict responses is limited by a lack of information for many of the focal taxa (Table 3). Pelagic-broadcast spawning species have varying morphological adaptations to the range of turbidity conditions encountered in the Great Plains. These include cutaneous taste buds and certain aspects of brain morphology (reduced optical brain lobes) particularly pronounced in some species of *Macrhybopsis* and PBS species of *Notropis* (Davis & Miller, 1967; Gidmark & Simons, 2014; Huber & Rylander, 1992; Moore, 1950), centred on non-sight feeding in turbid conditions. However, within the *Macrhybopsis aestivalis* complex, Davis and Miller (1967) described a variety of body types such as large-eyed forms (shoal chub, burrhead chub, speckled chub) inhabiting generally clearer waters, with prairie chub and peppered chub displaying small eyes, reduced optic lobes and a corresponding increase in cutaneous taste buds in the more turbid Arkansas and Red River basins. Perhaps reflecting such adaptations, sturgeon chub and sicklefin chub abundances increased as turbidity increased in the Missouri and Yellowstone rivers (Everett et al., 2004). Under historic conditions in Great Plains streams, this adaptation provided a competitive advantage compared to visual feeders (Bonner & Wilde, 2002). However, construction of barriers within the catchments is thought to have reduced turbidity, shifting the advantage to sight-feeding fish (Clark, 1979; Dieterman & Galat, 2004; Everett et al., 2004; Griffith, 2003; Haslouer et al., 2005). Sicklefin chub (LPBS species) populations in altered systems with clearer

water have changed morphologically towards fewer taste buds and shorter olfactory brain lobes, presumably in response to the increased advantage of visual feeding (Dieterman & Galat, 2005). In experimental trials, reduced prey consumption at elevated turbidity was greater in species characteristic of less turbid environments than in species adapted to elevated turbidity, including peppered chub and Arkansas River shiner (Bonner & Wilde, 2002).

Levels of turbidity and salinity have been linked to species responses at multiple life stages (e.g. Mueller, Grabowski, Brewer & Worthington, 2017). Decreased turbidity and increased salinity were associated with decreased abundances of plains minnow, smalleye shiner and sharpnose shiner in isolated pools in the Brazos River (Ostrand & Wilde, 2004). Mortality of the three species was 100% at salinities greater than 22‰ (Ostrand & Wilde, 2001). Increased salinity

TABLE 3 Water-quality values associated with Great Plains PBS species

Species	Water Quality Variable	Measure ^a	Value	References ^b
Rio Grande silvery minnow	Salinity	Egg Survival	<3 PSU	1
Western silvery minnow	Temperature	Occurrence	18–22°C	2
	Turbidity	Occurrence	<250 NTU	2
Plains minnow	Diss. Oxygen	Mean Time ^{2,7}	118.5 min	3
		Minimum ²	2.08 mg/L	4
	Salinity	Range	1.2–2.17 ppt	5
		LC50 ^{1,2}	16 ppt	4
		Temperature	Preference ³	30°C
		Preference ⁴	17°C	6
		CTmaxima ⁵	31.8°C	7
		CTmaxima ²	40.0°C	3
		CTmaxima ²	37.9–36.5°C	4
	CTmaxima ⁶	39.7°C	4	
Speckled chub	–	–	–	–
Prairie chub	Salinity	Range	1.2–19.6 ppt	5
Shoal chub	–	–	–	–
Burrhead chub	–	–	–	–
Peppered chub	Conductivity	Range	0.7–14.0 µS/cm	8
	Diss. Oxygen	Range	4.6–16.3 mg/L	8
	Temperature	Range	0.1–31.6°C	8
	Turbidity	Successful Forage	>4000 NTU	9
		Range	4.3–7750 NTU	8
Sturgeon chub	Temperature	Occurrence	18–22°C	2
	Turbidity	Occurrence	<250 NTU	2
Rio Grande shiner	–	–	–	–
Bluntnose shiner	–	–	–	–
Phantom shiner	–	–	–	–
Sharpnose shiner	Diss. Oxygen	Minimum ²	2.66 mg/L	4
	Salinity	LC50 ^{1,2}	15 ppt	4
	Temperature	CTmaxima ²	37.9–36.5°C	4
		CTmaxima ⁶	39.2°C	4
Smalleye shiner	Diss. Oxygen	Minimum ²	2.11 mg/l	4
	Salinity	LC50 ^{1,2}	18 ppt	4
	Temperature	CTmaxima ²	37.9–36.5°C	4
		CTmaxima ⁶	40.6°C	4
Sabine shiner	–	–	–	–
Red River shiner	Salinity	Range	0.4–21.7 ppt	5
	Temperature	CTmaxima ⁸	41.6°C	10

(Continues)

TABLE 3 (Continued)

Species	Water Quality Variable	Measure ^a	Value	References ^b
Arkansas River shiner	Conductivity	Range	0.7–14.4 μ S/cm	8
		Diss. Oxygen	Range	3.4–16.26 mg/L
		Mean ^{2,7}	1.2–1.5 ppm	3
		Survival ⁹	17.3%	11
		Survival ¹⁰	65%	11
		Preference	6.16–7.4 ppm	11
	Temperature	Range	0.4–31°C	8
		CTmaxima ²	38.64°C	3
		CTmaxima ²	35.92°C	11
		Preference	18.2°C	11
	Turbidity	Range	4.3–10,390 NTU	8

PSU, practical salinity units; NTU, Nephelometric Turbidity Units; ppt, parts per thousand; ppm, parts per million; μ S/cm, micro Siemens per cm.

^a1Per cent sodium chloride; ²Acclimation temperature 25°C; ³Dissolved oxygen at 4.8 mg/l; ⁴Dissolved oxygen at 2.0 mg/l; ⁵Acclimation temperature 10°C; ⁶Acclimation temperature 30°C; ⁷Dissolved oxygen at 1.2–1.5 ppm; ⁸Acclimation temperature 35°C; ⁹Dissolved oxygen 0.2–0.9 for 10 h; ¹⁰Dissolved oxygen 0.2–0.9 for 35 h.

^bReferences: 1 Cowley et al. (2009); 2 Welker and Scarnecchia (2004); 3 Matthews and Maness (1979); 4 Ostrand and Wilde (2001); 5 Echelle, Echelle and Hill (1972); 6 Bryan et al. (1984); 7 Lutterschmidt and Hutchison (1997); 8 Bonner et al. (1997); 9 Bonner and Wilde (2002); 10 Offill (2003); 11 Matthews (1987).

can cause elevated mortality of Rio Grande silvery minnow eggs by reducing the diameter and increasing the specific gravity of the eggs, thereby changing transport dynamics (Cowley, Alleman, Sallenave, McShane & Shirey, 2009). Further, Rio Grande silvery minnow eggs remain in suspension longer at higher turbidities than at lower turbidities (Medley & Shirey, 2013).

Many landscape alterations and toxicants can degrade stream water quality and negatively influence fish assemblages. Sewage discharge into the Rio Grande River, New Mexico, has increased unionized ammonia to toxic levels in some areas, which could negatively influence the Rio Grande silvery minnow population (Passell, Dahm & Bedrick, 2007). Coalbed natural gas development has the potential to influence species in Great Plains streams due to increases in salinity, alkalinity, magnesium and sulphate (Davis, Bramblett & Zale, 2010), with plains minnow only present at undeveloped sites. The interaction of reduced water quality with other stressors, for example flow-regime change, has also been highlighted. Reduced flows due to dams on the Pecos River, Texas, have contributed to blooms of golden algae (*Prymnesium parvum*, Prymnesiaceae), resulting in multiple fish kills, that have included speckled chub (Rhodes & Hubbs, 1992).

3.8.4 | Diet

Detailed diet studies were available for certain PBS species (Marks, Wilde, Ostrand & Zwank, 2001; Wilde, Bonner & Zwank, 2001; Williams & Bonner, 2006), with Rio Grande silvery minnow subject of the greatest amount of research (Table 4). A general pattern is that species of *Hybognathus* are herbivores/detritivores, whereas species of *Macrhybopsis* and *Notropis* are more insectivorous. For those species with limited direct information, trophic identity can be somewhat inferred by jaw, pharynx and gut morphologies (Gidmark & Simons,

2014). For example, the inferior mouth position in *Hybognathus* suggests benthic feeding (Cowley et al., 2006; Felley, 1984; Magana, 2009), including filtering organic matter (e.g. diatoms; Hlohowskyj, Coburn & Cavender, 1989). A diet composed mainly of plant material, algae or detritus is inferred for *Hybognathus* (and borne out by gut analyses), based on its long, coiled gut and lack of a defined stomach (Cowley et al., 2006; Etnier & Starnes, 1993). The presence of sand and silt in the gut contents of several PBS species of *Macrhybopsis* and *Notropis* indicates bottom feeding (Marks et al., 2001; Wilde et al., 2001). The presence of terrestrial organisms suggests that drift feeding might be important (e.g. Davenport, Mull & Hoagstrom, 2013).

The response to anthropogenic disturbance of the natural flow regime has generally focussed on effects during the reproductive phase; however, effects on feeding opportunities are also of potential importance. Reduced high flows due to river regulation are likely to diminish the availability of important diet items such as allochthonous organic material and terrestrial invertebrates (Cowley et al., 2006; Davenport et al., 2013; Wilde et al., 2001). For example, gut contents of shoal chub from the Brazos River showed an increased percentage contribution of algae and decreased contribution by terrestrial plants and grasses during moderate-flow compared to high-flow periods (Roach & Winemiller, 2015). In addition, periods of low flow, where species are confined to isolated pools, are associated with a gut contents switch from insects to detritus, plant material and sand/silt (Marks et al., 2001; Wilde et al., 2001), which may affect nutritional intake. Changes in the identity of diatoms consumed by Rio Grande silvery minnow are indicative of a switch from species found in shallow silted habitats to those found in shallow sandy areas (Shirey, Cowley & Sallenave, 2008). This change suggests a reduction in nutrient availability in the Rio Grande, associated with a decline in sediment transport due to the presence of impoundments and a reduction in lateral connectivity with the floodplain (Shirey et al., 2008).

Species	Diet	References ^a
Rio Grande Silvery minnow	Detritus, pine pollen, cyanobacteria, algae, diatoms, Chironomidae	1–4
Western silvery minnow	Believed to similar to other <i>Hybognathus</i>	5
Plains minnow	Detritus, diatoms, algae	6–7
Speckled chub	Insect larvae, organic debris, plant material (benthic feeder)	9
Prairie chub	–	–
Shoal chub	Invertebrates, terrestrial, aquatic; Diptera, plant materials	10–12
Burrhead chub	–	–
Peppered chub	Invertebrates, terrestrial (Coleoptera, Hymenoptera), aquatic (Coleoptera); Diptera, detritus, plant materials, sand silt	13
Sturgeon chub	Invertebrates, aquatic	14
Rio Grande shiner	Carnivorous–omnivorous (similar to most other <i>Notropis</i>)	9
Rio Grande bluntnose shiner	Invertebrates, terrestrial (Diptera) and aquatic (Trichoptera, Coleoptera); detritus, filamentous algae, seeds, woody debris	15
Pecos bluntnose shiner	Believed to be similar to <i>N. s. simus</i> including terrestrial invertebrates, algae, detritus	16–17
Phantom shiner	–	–
Sharpnose shiner	Invertebrates, terrestrial (Coleoptera, Corixidae, Orthoptera, Arachnida), aquatic (Ostracoda, Trichoptera, Coleoptera, Odonata); Diptera (Chironomidae, Ceratopogonidae), detritus, plant materials, sand silt	18
Smalleye shiner	Invertebrates, terrestrial (Coleoptera, Corixidae, Orthoptera, Arachnida), aquatic (Ostracoda, Trichoptera, Coleoptera); Diptera (Chironomidae, Ceratopogonidae), fish, detritus, plant materials, sand silt	18
Sabine shiner	Invertebrates, terrestrial (Diptera, Coleoptera, Hemiptera), aquatic (Diptera, Ephemeroptera, Odonata, Plecoptera, Trichoptera); detritus, plant materials, sand silt	19
Red River shiner	Invertebrates (Chironomidae, Coleoptera, Lepidoptera), detritus	6, 20
Arkansas River shiner	Invertebrates, terrestrial (Coleoptera, Hymenoptera), aquatic (Megaloptera, Odonata, Plecoptera, Trichoptera); detritus, plant materials, algae, sand silt	13, 21

^aReferences: 1 Cowley et al. (2006); 2 Magana (2009); 3 Magana (2013); 4 Caldwell, Barrows, Ulibarri and Gould (2010); 5 Houston (1998); 6 Echelle et al. (1972); 7 Franssen and Gido (2006); 8 Gido and Franssen (2007); 9 Sublette et al. (1990); 10 Starrett (1950b); 11 Pflieger (1997); 12 Roach and Winemiller (2015); 13 Wilde et al. (2001); 14 Stewart (1981); 15 Bestgen and Platania (1990); 16 Furlow (1996); 17 Davenport et al. (2013); 18 Marks et al. (2001); 19 Williams and Bonner (2006); 20 Felley (1984); 21 Wilde (2002).

TABLE 4 Items reported from the gut contents of the 18 taxa (17 species, one with two subspecies) treated in this review

4 | DISCUSSION

4.1 | Threats

It is clear from the PBS life history that anthropogenic disturbance in the form of river fragmentation and its effect on natural hydrology

and habitat complexity are a primary threat to the persistence of Great Plains PBS species. Alterations to the flow regime and, as a consequence, stream connectivity and habitat complexity pose threats that are intuitively obvious for species with life histories dependent on egg and larval drift and, because of the resulting downstream

displacement, upstream dispersal allowing exploitation of favourable habitat and migration prior to reproduction. Finally, appropriately timed peak flows likely serve as cues triggering physiological and behavioural (upstream migration, spawning activity) mechanisms that have evolved in response to the natural hydrology of the Great Plains environment. These factors, which emphasize longitudinal aspects of stream dynamics, likely are particularly critical for PBS species. However, lateral and vertical aspects of an altered hydrology (e.g. effects on side-channels and wetlands, and hyporheic flow and connections to shallow and deep aquifers) affect the integrity of the biotic community in general, including PBS fishes.

4.2 | Flow alteration

Discharge directly affects the physicochemical spatial pattern (habitat template; Southwood, 1977) of riverine systems, thereby influencing fish distributions. For PBS species, there might be thresholds of mean annual flow, below which they do not persist. For example, an assemblage including three PBS species (plains minnow, Arkansas River shiner, peppered chub) in the Texas Panhandle remains intact in the Canadian River downstream of Ute Reservoir, NM, where mean annual discharge decreased by 38% of historical records, but the assemblage is virtually absent downstream of the next reservoir in the sequence (Lake Meredith, TX) where the discharge has been reduced by 76% (Bonner & Wilde, 2000). The present distribution of Arkansas River shiner suggests that the probability of presence is greatest where mean annual discharge is $>10 \text{ m}^3/\text{s}$ and $<110 \text{ m}^3/\text{s}$ (Worthington, Brewer, Grabowski, et al., 2014).

Pelagic-broadcast spawning species are especially susceptible to flow alteration because eggs and larvae drift passively in suspension for several days until they become free swimming (Balon, 1975; Battle & Sprules, 1960; Platania & Altenbach, 1998). Some water movement is thought necessary to keep the ichthyoplankton in suspension during development, though the velocity needed is likely greater for larvae than eggs, because larvae are more dense (Coleman, 2015). An altered flow regime can lead to stream fragmentation, reducing drift distance (or time) for eggs and larvae to complete development (Perkin, Gido, Cooper, Turner & Osborne, 2015; Worthington, Brewer, Grabowski, et al., 2014). Some evidence suggests that entrainment by slackwater habitats (Dudley, 2004; Hoagstrom, Brooks & Davenport, 2008b; Robertson, 1997) or other habitat features (Worthington, Brewer, Farless, Grabowski & Gregory, 2014) might increase the drift time, thereby promoting retention in the stream and reducing losses to reservoirs or irrigation canals.

Pelagic-broadcast spawning species are thought to migrate upstream to allow appropriate drift distance for their propagules (Cross et al., 1985; Fausch & Bestgen, 1997), as well as to allow non-spawning exploitation of suitable upstream habitat. Most of the evidence for the assumed spawning migrations has been based on discrete sampling. For example, after spawning, the highest densities of small Pecos bluntnose shiner are in downstream reaches, whereas larger adults are more abundant upstream (Bonner, 2000; Hoagstrom & Brooks, 2005; Hoagstrom, Brooks & Davenport, 2008b), and a similar pattern

is indicated for Sabine shiner (Heins, 1981). However, recent analysis for Pecos bluntnose shiner appears to support the upstream movement of PBS species, with otolith microchemistry data indicating that 82% of the population migrates upstream while the remaining fish are local residents throughout their lives (Chase, Caldwell, Carleton, Gould & Hobbs, 2015; Wilde, 2016). Based on limited understanding of PBS species movements, connectivity through periods of suitable discharge prior to or during the spawning season is anticipated to be important to a large proportion of these populations.

When flow becomes intermittent, PBS fishes are periodically forced into isolated pools where survival is compromised over time (Hoagstrom, Brooks & Davenport, 2008a; Ostrand & Wilde, 2001). Recolonization of habitat occurs when water returns to previously dry locations (Hoagstrom, Brooks & Davenport, 2008b); however, repeated drying may preclude recolonization, resulting in truncated distributions and extinctions (Perkin, Gido, Costigan, et al., 2015). Flow alteration can also disrupt the magnitude, duration of spawning cues and the timing of those cues. These available data suggest that PBS species are multiple-batch spawners breeding over a protracted period (e.g. sharpnose shiner, spawns April–September, Durham & Wilde, 2014). Spawning generally appears synchronous with increasing discharge (Bestgen et al., 1989; Dudley, 2004; Propst, 1999; Robertson, 1997), although some individuals spawn regardless of environmental conditions (Durham & Wilde, 2008, 2014; Urbanczyk, 2012). A general consensus is lacking among researchers regarding the importance of asynchronous versus synchronous spawning in PBS species, though both may be important to population persistence given the harsh stream conditions in the region.

4.2.1 | Fragmentation

Stream habitat fragmentation threatens PBS species through multiple mechanisms, including fragmentation acting alone and in concert with other threats (e.g. flow, see above). Habitat fragmentation, or isolation of formerly connected inhabitable patches, is generally coupled with habitat loss, or the transformation of patches from inhabitable to uninhabitable (Lindenmayer & Fischer, 2006). In Great Plains streams, populations of PBS species are fragmented by barriers such as diversion structures and other small dams that generally cause little habitat loss (e.g. Perkin, Gido, Costigan, et al., 2015), as well as by large impoundments and desiccated stream reaches representing large amounts of lost habitat (Dudley & Platania, 2007; Luttrell et al., 1999). Habitat fragmentation without habitat loss also occurs when streams are isolated upstream of impoundments (Gido et al., 2002; Wilde & Ostrand, 1999; Winston et al., 1991). In this case, the effects of impoundments are transmitted upstream because resident populations are isolated without the potential for recolonization following extirpation or demographic and/or genetic bottlenecks in population size (Allendorf, Luiken & Aitken, 2012; Pringle, 1997; Winston et al., 1991), as might occur during drought or harsh winters (Schlosser, 1987, 1990). Such upstream effects of impoundments appear less intense in fish assemblages not containing PBS species (Herbert & Gelwick, 2003). Similarly, isolated stream reaches shorter than the threshold length required for PBS are

correlated with population crashes and extirpations because recolonization and rescue effects are precluded in small fragments (Dudley & Platania, 2007; Perkin & Gido, 2011; Wilde & Urbanczyk, 2013).

Isolating fragmentation effects from background landscape changes causing habitat loss can be challenging and has caused contention regarding the threat posed by fragmentation acting alone (Hoagstrom, 2014; Wilde & Urbanczyk, 2014). Given the PBS lifestyle, there is little doubt concerning the need for longitudinal connectivity sufficient for the drift and development of eggs through the larvae stage (Bottrell et al., 1964; Chase et al., 2015; Moore, 1950; Platania & Altenbach, 1998; Souchon, Sabaton & Deibel, 2008); however, early life stages of PBS species are particularly sensitive to environmental degradation (Wilde & Durham, 2008) that typically accompanies or is magnified by fragmented connectivity (e.g. dewatering, flow alteration, water pollution, habitat destruction, invasive species; Hoagstrom et al., 2011). Therefore, assessing threats to PBS species from a riverscape perspective, including consideration of the availability and accessibility of habitats, is the most prudent conservation framework (Fausch, Torgersen, Baxter & Li, 2002).

Placing conservation of PBS species within a riverscape perspective requires assessing connectivity across a continuum of directionalities. Longitudinal connectivity is the most commonly assessed directionality in terms of conserving stream fishes (Cote, Kehler, Bourne & Wiersma, 2009; Fullerton, Burnett & Steel, 2010), including PBS species (Dieterman & Galat, 2004; Perkin et al., 2013; Worthington, Brewer, Grabowski, et al., 2014). Fragmented longitudinal connectivity threatens spawning success among PBS species as evidenced by lack of recruits during periods of isolated pool formation, despite evidence that spawning occurs within isolated pools (Durham & Wilde, 2006, 2009a). Furthermore, fragmented longitudinal connectivity threatens ichthyoplankton survival by washing drifting individuals into downstream reservoirs where they eventually settle and suffocate within sediments (Dudley & Platania, 2007; Platania & Altenbach, 1998). Lateral connectivity to floodplains is fragmented when structures such as dikes and levees prevent water and aquatic organisms from accessing the floodplain, resulting in lost floodplain habitat and access to low velocities areas (Barko, Palmer, Herzog & Ickes, 2004; Schlosser, 1991). Compromised floodplain inundation causes lateral habitat fragmentation and loss for PBS species, and threatens juvenile recruitment that might otherwise occur in floodplain nursery habitat (Barko & Herzog, 2003; Costigan & Daniels, 2012; Hoagstrom & Turner, 2015). Further, with increased time since inundation, physicochemical conditions in periodically isolated off-channel habitats can become less suitable for populations of native fishes (Crites, Phelps, McCain, Herzog & Hrabik, 2012). Vertical connectivity between the stream channel, hyporheic zone, and shallow and major aquifers is critical for sustaining base flows in regions such as the Great Plains where groundwater contributions are essential for maintaining natural flow regimes (Dale, Zou, Andrews, Long & Liang, 2015; Poff, Allan & Bain, 1997; Sophocleous, 2002). Severed connectivity to local or regional aquifers caused by groundwater pumping results in population crashes and extirpations of PBS species because sufficient groundwater input is required to ensure juvenile and adult survival during harsh drought or winter conditions (Cross et al., 1985; Falke, Fausch, Magelky, Aldred & Durnford, 2011; Perkin et al., 2017; Pigg, 1991). Disconnection of surface flow

from groundwater sources, together with fragmentation of longitudinal and lateral surface connectivity, is a major driver of the transformation of Great Plains stream-fish assemblages in which PBS species disappear and remaining reproductive guilds persist and dominate (Gido et al., 2010; Perkin, Gido, Cooper, et al., 2015).

The underlying mechanism and major reasoning behind the call for a riverscape-based approach to PBS species conservation is the ratcheting of events invoked by fragmented connectivity (along multiple directional fronts) interacting with natural and anthropogenic disturbances across landscapes (Jackson, Betancourt, Booth & Gray, 2009). Conceptually, ratcheting occurs when a disturbance (natural or anthropogenic) causes change in species distributions or population growth rates and resetting of this change is prohibited by an introduced or derived mechanism(s) (Birkeland, 2004). This has contributed to the demise of PBS species populations in the Great Plains because population recovery following drought or dewatering is precluded by in-stream barriers to dispersal (Kelsch, 1994; Luttrell et al., 1999; Perkin et al., 2013; Perkin, Gido, Costigan, et al., 2015; Winston et al., 1991). Beyond hydrologic disturbances, threats caused by habitat change or non-native species invasions now exist within fragments of previously connected river in which alterations to demographic rates occur in isolation. The ratcheting mechanism is one explanation for why PBS assemblages do not recover when precipitation-mediated surface flows are returned to regions historically supported by groundwater flow (Eberle et al., 1993) or when in-channel flow is maintained but floodplain inundation and habitat maintenance are compromised (Cowley, 2006; Galat, Fredrickson & Humburg, 1998). Thus, because PBS fish populations are regulated and maintained across broad spatial scales (Chase et al., 2015; Perkin & Gido, 2011), isolated stream segments containing appropriate habitat can remain vacant if recolonization from distant source populations is not possible (Luttrell et al., 2002).

4.2.2 | Habitat change

Habitat templates function as multiscale filters regulating the occurrences and abundances of species, and appropriate habitat must be maintained to ensure species persistence (Poff & Ward, 1990). However, appropriate or suitable habitat is poorly understood for most PBS species (see Habitat section). Examples of physical aspects of the habitat template associated with PBS species include particular channel-modifying structures in the Missouri River (Ridenour et al., 2009), as well as continuums of depth, velocity and substrate composition in the Arkansas River (Luttrell et al., 2002), Rio Grande (Heard et al., 2012), Brazos River (Wilde & Durham, 2013) and Pecos River (Hoagstrom, Brooks & Davenport, 2008a; Hoagstrom, Archdeacon, Davenport, Propst & Brooks, 2015). In each of these examples, stream flow-governed habitat templates are the "master variable" (sensu Power, Sun, Parker, Dietrich & Wootton, 1995) regulating habitat availability for PBS species (Hoagstrom, Brooks & Davenport, 2008a; Hoagstrom, Brooks & Davenport, 2008b; Worthington, Brewer, Farless, et al., 2014; Worthington, Brewer, Grabowski, et al., 2014). Abundances are lowest in stream reaches characterized by constrained (leveed) channels, homogeneous habitat templates or reduced stream flow.

Regarding the chemical component of habitat templates, many PBS species have broad tolerances to temperature, salinity, dissolved oxygen and suspended solids (Higgins & Wilde, 2005; Matthews, 1987; Ostrand & Wilde, 2001; Taylor, Winston & Matthews, 1993). In many instances, however, anthropogenic alterations to environmental gradients in Great Plains streams have pushed ecosystems beyond the tolerances of PBS species resulting in extirpations or otherwise notable declines in abundance. Examples include amplification of salinity in the lower Pecos River because of flow regulation by reservoirs and reduced springflows from overexploitation of groundwater (Cheek & Taylor, 2016; Hoagstrom, 2009) and a transition to lower flow and higher salinity in portions of the Rio Grande (Miyazono, Patiño & Taylor, 2015).

Intuitively, extreme habitat alterations might be expected to extirpate fish populations or entire communities (e.g. sewage outflows; Cross, 1950), but the effect of shifting habitat templates is confounded somewhat by uncertainty in what constitutes selected versus required habitat (Rosenfeld, 2003). For example, habitat associations of sharpnose shiner appear relatively plastic, varying annually because regional weather patterns and associated stream flows regulate available habitats (Wilde & Durham, 2013). This might help explain the pattern reported by Hoagstrom et al. (2011) in which dewatering and fragmentation posed threats to a greater number of Great Plains PBS species than did habitat or geomorphic changes.

4.2.3 | Non-native species

Management of non-native species might be the largest challenge for conservation biologists to overcome in the future (Allendorf &

Lundquist, 2003). Successful invaders have broad ecological tolerances and thrive in altered river systems (Fausch, 2008; Marchetti, Light, Moyle & Viers, 2004; Poff & Zimmerman, 2010). Transfer of aquatic organisms in anglers' bait buckets is the prevailing source for fish introductions throughout the Great Plains (Hall, 1956; Hoagstrom & Brooks, 2005; Miller, 1953; Moyer et al., 2005; Patrikeev, Bonner & Trujillo, 2005; Robison, 1974a). However, other factors include colonization upstream of reservoirs (Gido & Franssen, 2007; Quist, Hubert & Rahel, 2004), intentional introduction for biological control (Louda, Arnett, Rand & Russell, 2003; Schleier, Sing & Peterson, 2008) and natural migration during high-flow events between proximally close tributaries (Hall, 1956; Miller, 1953). These introductions have the potential to spread foreign parasites and disease (Marcogliese, 2001) and can result in predation of native fishes by exotic piscivores (Gido & Franssen, 2007; Quist et al., 2004), hybridization (Cook, Bestgen, Propst & Yates, 1992; Miller et al., 1989) and competition within the PBS guild (Cross, Gorman & Haslouer, 1983; Felley & Cothran, 1981; Hoagstrom, Zymonas, et al., 2010; Miller, 1953; Moyer et al., 2005) and among reproductive guilds (Schleier et al., 2008).

Some of the most marked effects of non-native fish on PBS species have stemmed from introductions of other members of the PBS guild. Non-native introductions have been suggested for five of the 17 species reviewed here (Table 5; Witmer & Fuller, 2011). Introductions of plains minnow and Arkansas River shiner in the Pecos River, NM and the Red River shiner in the Arkansas River basin have received the greatest attention, probably because they led to rapid colonization of large lengths of river by non-natives. A review of rapid species replacements in Great Plain rivers highlighted three commonalities: (i) the introduced competitor was larger in body size; (ii) establishment

TABLE 5 Known or suspected pelagic-broadcast spawning cyprinids that have been introduced outside of their native range (species list from Witmer & Fuller, 2011)

Species	Basin—River introduced into	Method of introduction	References ^a
Plains minnow	Rio Grande—Pecos River Colorado—San Juan River	Bait bucket release	1–4
Red River shiner	Arkansas River—Cimarron River	Bait bucket release	5–9
Smalleye shiner	Colorado River—Colorado River	Bait bucket release	10–12
Arkansas River shiner	Rio Grande—Pecos River Red River—Washita River, Red River	Bait bucket release	13–16
Sharpnose shiner	Red River—Red River	Bait bucket release/possible natural spread via floodplain connectivity following high flows	12, 17, 18
	Colorado River—Colorado River	Bait bucket release	

^aReferences: 1 Cook et al. (1992); 2 Moyer et al. (2005); 3 Hoagstrom, Zymonas, et al. (2010); 4 Fuller and Neilson (2015); 5 Felley and Cothran (1981); 6 Cross et al. (1983); 7 Gotelli and Kelley (1993); 8 Luttrell et al. (1995); 9 Pigg, Coleman and Gibbs (1997); 10 Hubbs et al. (1991); 11 Wilde and Urbanczyk (2013); 12 U.S. Fish and Wildlife Service (2014); 13 Cross (1970); 14 Bestgen et al. (1989); 15 Pigg (1991); 16 Hoagstrom and Brooks (2005); 17 Hall (1956); 18 Miller (1953).

occurred in modified habitats; and (iii) replacements were between closely related species (Hoagstrom, Zymonas, et al., 2010).

The plains minnow was first introduced into the Pecos River, NM, in the early 1960s in the vicinity of Sumner Reservoir (Bestgen & Platania, 1991) and has subsequently colonized over 300 rkm (Hoagstrom, Zymonas, et al., 2010). Genetic data (mtDNA and microsatellites) indicate that the Pecos River population of plains minnow originated from two different sources, which, based on proximity, likely were the Red River and the Canadian River of the Arkansas River system (Moyer et al., 2005). Except for one outlier, all Pecos River haplotypes fell into two clades, one from the Red River and one from the Canadian River. Genetic simulations indicated that the introduced population originated with 32–115 founders, probably as a result of bait bucket transport.

The Pecos River introduction of plains minnow led to the rapid (<10 years) exclusion of Rio Grande silvery minnow from the river, although other PBS species remain (Figure 6b–d; Hoagstrom, Zymonas, et al., 2010). Allozyme and morphological analyses conducted after the replacement found potential hybrids to be rare, but this did not rule out past hybridization and genetic introgression (Bestgen & Propst, 1996; Cook et al., 1992). Subsequent morphological analyses found no notable evidence of introgression, leaving competitive replacement by plains minnow as the most likely cause of the extirpation of Pecos River Rio Grande silvery minnow (Hoagstrom, Zymonas, et al., 2010; Moyer et al., 2005).

The Arkansas River shiner population in the Pecos River is thought to have originated from a bait bucket introduction in the late 1970s in the area of Sumner Reservoir, from where it colonized >350 rkm in <10 years (Bestgen et al., 1989). The Canadian River apparently was the source for the introduced population based on microsatellite loci and mtDNA analyses (Osborne, Diver, et al., 2013). Multiple introductions have been inferred from the presence of multiple reservoirs within the colonized reach (Bestgen et al., 1989). The retention of high diversity in the Pecos River population likely reflects the introduction of relatively large numbers of individuals and rapid population expansion (Osborne, Diver, et al., 2013). More recent surveys suggest Arkansas River shiner has been extirpated from the lower Pecos and is now less abundant than previously recorded in the upper Pecos (Hoagstrom & Brooks, 2005).

Ironically, the introduced Pecos River population of Arkansas River shiner rapidly colonized a large area, while the native range underwent a severe contraction. This decline has been partly attributed to the non-native presence of another PBS species, the Red River shiner, which was first recorded in the Cimarron River of the Arkansas River basin in 1976 (Marshall, 1978). The Red River shiner is now widely distributed in the Cimarron River (Cross et al., 1983; Felley & Cothran, 1981).

Although the above examples highlight successful establishment of PBS species outside their native ranges, other introductions of group members have failed to result in self-sustaining populations. Examples include a record of plains minnow from the San Juan River, Utah (Fuller & Neilson, 2015), far west of the native range. Non-native occurrences of Arkansas River shiner are reported from multiple locations in the Red River basin, although these appear not to have not

led to established populations (Cross, 1970; Pigg, 1991). Similarly, and except for the Cimarron River, Red River shiner apparently is not established in the Arkansas River basin despite sporadic records from across the basin (Luttrell, Underwood, Fisher & Pigg, 1995; Pigg, 1987). Factors explaining establishment versus non-establishment are not well understood and represent an area where further research might aid conservation of PBS cyprinids.

4.2.4 | Overall threats to PBS species

Results from our review show that the threats to PBS species are multifaceted and inherently interlinked (Figure 10). To conceptualize threats across the life history of PBS species, we broadly follow the five categories of anthropogenic drivers highlighted by Dudgeon, Arthington and Gessner (2006): overexploitation, water pollution, flow modification, habitat degradation and species invasion. However, we consider fragmentation as a subcategory to habitat degradation because it is a key driver of PBS decline, especially given its role in promoting flow alteration and changing geomorphological complexity. The threat combinations and their interactions vary at the different key life-history stages (Figure 10). Beginning with adults, habitat degradation (often in the form of longitudinal fragmentation) and flow alteration interact to truncate upstream adult migration through physical barriers or reducing flow connectivity. The linkage between habitat and flow is unidirectional for reproduction, with habitat degradation (often driven by longitudinal fragmentation due to dam construction) eliciting changes to the natural flow regime which disrupts spawning cues (Archdeacon, Henderson, Austrung & Cook, 2015; Durham & Wilde, 2008, 2009a, 2014). Ichthyoplankton downstream drift is disrupted by the interaction among flow, habitat and water quality. Longitudinal fragmentation is again a key driver, creating physical barriers, and in combination with flow modification, reducing habitat complexity (Worthington, Brewer, Farless, et al., 2014) and lateral connectivity (Medley & Shirey, 2013) that would otherwise promote ichthyoplankton retention (Chase et al., 2015). Furthermore, modified flow regimes and habitat disconnection both longitudinally and laterally alter the physicochemical condition of rivers, with potential consequences for ichthyoplankton drift dynamics (Cowley et al., 2009; Medley & Shirey, 2013). Growth and survival of juveniles and adults are also affected by the interaction of flow, habitat and water quality. For growth, changing flow patterns and a disconnection of the channel from floodplain habitat has the potential to reduce important allochthonous organic material and terrestrial invertebrate sources (Cowley et al., 2006; Davenport et al., 2013; Wilde et al., 2001). In addition, reservoir construction is thought to provide a competitive advantage to sight-feeding species by reducing turbidity (Dieterman & Galat, 2004; Everett et al., 2004; Griffith, 2003; Haslouer et al., 2005). Survival of adults and juveniles may be compromised when low flows linked to habitat alteration result in fish being confined to isolated pools that may be accompanied by high salinity (Ostrand & Wilde, 2004) and extreme temperatures and anoxic conditions. Survival may also be negatively affected by the interactions with non-native species (e.g. Hoagstrom, Zymonas, et al., 2010) that may be introduced by anglers as bait fish, a potential source of overexploitation.

Challenges	Opportunities	Approaches and applications
1. Understanding life history	1. Study autecology, movement, drift, variation in life history-focused monitoring	Population modelling, tagging, microchemistry Experimental population reintroductions Survival and propagation
2. Geomorphic and channel changes	2. Improve or focus existing monitoring	Egg drift and retention studies
3. Flow regulation	3. Improved understanding of implications of flow variation	Experimental flow releases Mine existing historical data
4. Habitat associations unknown	4. Pair routine surveys with ongoing habitat restorations	Detection probability models applied to monitoring data
5. Habitat fragmentation	5. Reestablishment of (meta)populations	Fishways and small barrier removal Experimental population reintroductions Augmentation from source stock
6. Baseline genetic data missing	6. Periodic or routine genetic monitoring	Tissue collections during routine surveys
7. Non-native invasions (fish, vegetation)	7. Control non-native invasions	Beetle introduction, burning, herbicides
8. Landscape/riverscape scale analyses limited	8. Coordinated research	Federal, state and non-governmental agencies

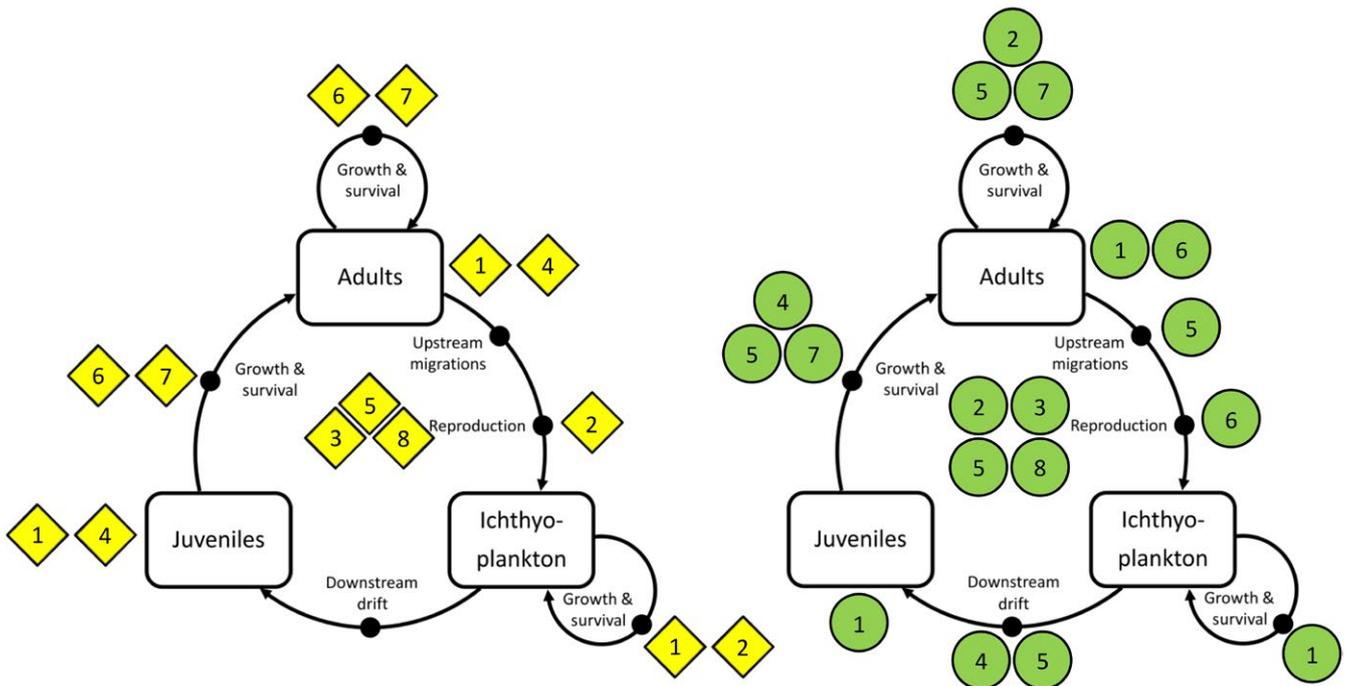


FIGURE 10 Challenges, opportunities, and approaches and applications for conserving pelagic-broadcast spawning (PBS) cyprinids of the Great Plains. Lower panels illustrate life-cycle diagrams for PBS cyprinids illustrating life stages (boxes) and life-history processes (points on arrows). Eight challenges facing conservation of PBS cyprinids at specific life stages or affecting specific life-history processes are shown on the left (yellow diamonds), and research and conservation opportunities associated with each challenge are given on the right (green circles). Challenges and opportunities shown in the centre are those identified as overarching issues that affect all life stages and therefore are highest priority

4.3 | Conservation challenges and opportunities

Although multiple factors are associated with the decline of PBS species (Figure 10), we suggest that it is possible to prioritize efforts to counteract continued declines. First, it is prudent to maintain or increase current levels of riverine connectivity. Evidence indicates that many PBS populations rely on extensive stream distances to persist over time. However, the interaction of fragmentation with other major threats such as flow alteration and drought may be substantial. Removal of small barriers to flow may be an option for increasing free-flowing distances, with the caveat that dam removal requires consideration of unforeseen consequences (e.g. Beatty, Allen & Lymbery, 2017). Second, greater effort to coordinate research across universities, non-governmental organizations, and state and federal agencies would focus resources on addressing the key challenges facing PBS species. Our bibliographic analysis suggested that research on PBS species is driven less by conservation need than by size of the species distribution. Similar mismatches between research effort and conservation priority have been highlighted for other taxa (Amori & Gippoliti, 2000; Brito, 2008; Brito & Oprea, 2009). The mismatch for PBS fishes might reflect geographical proximity of widely distributed species to greater numbers of researchers or, alternatively, overlapping research priorities at the state level. A coordinated, conservation-targeted management and research agenda across the PBS guild would be a more efficient use of resources. In particular, a coordinated effort to conduct riverscape analyses of the species where existing monitoring efforts may be elevated to fill knowledge gaps may be particularly useful (Figure 10).

We identified eight key challenges and research-management opportunities related to the conservation of PBS species (Figure 10). There are three central challenges where timely efforts to fill knowledge gaps would be the most beneficial to species persistence, and five other areas where greater information would be beneficial to help establish an adaptive management programme for PBS recovery. Each challenge has associated learning opportunities to improve our conservation strategies. Lastly, we suggest approaches that would be useful for addressing each challenge (Figure 10). This synthesis alongside other PBS species comparisons (Hoagstrom & Turner, 2015; Hoagstrom et al., 2011) will benefit future research and conservation strategies.

4.3.1 | Understanding life history

A general lack of a basic understanding of life-history requirements is impeding the conservation and management of threatened species (Cooke, Paukert & Hogan, 2012). This is manifested for most PBS species by the paucity of available information on water-quality tolerances and life-history characteristics (see below for specific examples of knowledge gaps). The information available is highly variable among PBS species. For some, this reflects relatively recent recognition as a distinct species (Eisenhour, 1999, 2004). Conversely, Arkansas River shiner and Rio Grande silvery minnow are two of the better-studied species, likely due to their listed status. The implied

need for greater impetus and funding for autecological studies are set against the background of declining natural history education and publication (McCallum & McCallum, 2006; Tewksbury, Anderson & Bakker, 2014).

This review was framed around a specific reproductive guild, but we acknowledge that our understanding of the reproductive strategy of the species covered is far from complete (see Table 1). For example, Hoagstrom and Turner (2015) suggest research into the recruitment ecology of PBS fishes is in its infancy and that geographical adaptations are apparent. Meaningful conservation strategies for imperilled PBS species depend on a sound understanding of the reproductive biology of individual species. For instance, Medley and Shirey (2013) suggest that under more natural river morphologies, Rio Grande silvery minnow might spawn in inundated floodplain environments promoting egg entrainment rather than in the main channel where eggs are subject to long-distance downstream dispersal. Clarification of such issues is central to producing efficient strategies for the conservation of PBS species. For example, existing knowledge suggests a large portion of the species migrate long distances, so preventing further fragmentation is beneficial. However, some proportion of these populations also reproduce within shorter fragments, but it is unclear how this occurs and under what environmental conditions (e.g. channel complexity). Additional movement studies (e.g. Chase et al., 2015; Wilde, 2016) are needed to clarify the migration and spawning needs of PBS species. Such information might explain why certain species have been more successful under altered flow regimes than others (e.g. Red River shiner versus Arkansas River shiner in the Cimarron River). Understanding the critical fragment length needed for upstream and downstream movements (Perkin & Gido, 2011; Wilde & Urbanczyk, 2013) might highlight areas where restoring connectivity could aid population persistence or re-establishment.

Despite the perceived importance of age-0 survival to the ecology of PBS species, research examining growth rates of early life stages is particularly lacking. Declining wild populations will only hinder future research opportunities. Age and growth studies of laboratory-reared fish are an option, but they offer only limited application to conservation and management. Increased efforts to measure growth rates at early life stages, identify environmentally sensitive age classes and detect variation in age and growth trends among species may be important to preventing future declines. For example, there is evidence that some portion of these populations are recruiting in a limited extent of river (e.g. Chase et al., 2015), but the responsible factors are poorly understood. Further, nutrient loads have been noted as one factor related to the decline of pelagic fishes and food web changes of the San Francisco Estuary (Glibert, 2010), but we are unaware of food web examination within Great Plains rivers.

4.3.2 | Flow regulation

In the face of climate change and future water demand, identifying relationships between manageable flow metrics (e.g. magnitude of flow during the spawning season) and persistence of PBS populations would benefit conservation efforts. For example, understanding

survival related to spawning conditions is important for modelling population responses to flow alteration. Currently, the most pressing flow need seems to be stream connectivity during low-flow conditions over a stream length allowing successful egg and larvae development (Durham & Wilde, 2006, 2008, 2009a; Mills & Mann, 1985; Nunn, Cowx, Frear & Harvey, 2003; Perkin & Gido, 2011). However, this might change with a better understanding of the role higher flows play in population persistence (e.g. Worthington, Zhang, Logue, Mittelstet & Brewer, 2016). It would also be advantageous to better understand the primary (e.g. photoperiod) versus secondary spawning cues (e.g. increased discharge) of these species. Furthermore, understanding interactions between flow dynamics and life-history events is critical for ensuring conditions for persistence of PBS species are maintained. Linking egg retention and survival of different life stages of PBS species to different habitats might provide insightful management options. For example, would providing access to the floodplain promote egg retention, and offset losses due to fragmented drift distances? Most research has focused on stream drying, fragmentation, and egg drift and retention. However, effort to ensure the success of remaining population strongholds (e.g. South Canadian River for Arkansas River shiner) would benefit from knowing what level of flow alteration and types of flows are important to population persistence.

4.3.3 | Habitat fragmentation

Habitat fragmentation is a coarse-scale regulator of PBS species persistence, interacts with multiple other threats, and must be addressed to ensure persistence of the reproductive guild. Conservation actions addressing the effects of habitat fragmentation include re-establishment of metapopulation dynamics via improved connectivity where possible. This would involve restoring connectivity among now fragmented, historically continuous stream habitats. The most direct approach is removal of dams and stream-flow diversion barriers. Removal of dams is frequently mentioned in the stream restoration literature (Palmer, Bernhardt & Allan, 2005), but generally is precluded by societal demands (Blanchet, Rey, Etienne, Lek & Loot, 2010). Providing passage for PBS species around large mainstem barriers might be infeasible, but encouraging re-establishment upstream of smaller low-head structures affords an opportunity for conservation gains (Pennock, Bender, Hofmeier, Mounts & Waters, 2017). An impediment to progress in this area is the absence of behavioural and fish passage studies for many PBS species. However, small numbers of tagged Rio Grande silvery minnow were recorded ascending a rock channel fishway, allowing passage around a water diversion structure on the middle Rio Grande, New Mexico (Archdeacon & Remshardt, 2012). Further, Pennock, Bender, et al., 2017 show three species of small-bodied minnows, including Plains Minnow, were able to use a fishway to move upstream of a low-head dam in the Arkansas River, Kansas. Therefore, suitably designed fish passes have the potential to allow upstream movement of PBS species to re-establish previously inaccessible areas. However, knowledge of swimming performance and behaviours associated with potential fishways would benefit bypass design.

4.3.4 | Landscape-scale analyses

The geographical extent (particularly historically) of many PBS species, requires modelling potential drivers of decline at the landscape scale, which in turn requires collating data sets across agencies, state and national boundaries, and time periods (Perkin, Gido, Cooper, et al., 2015; Worthington, Brewer, Grabowski, et al., 2014). Furthermore, the broad scales over which PBS life-history cycles are completed mean that critical life-history events (e.g. upstream migration, downstream drift, growth and survival of ichthyoplankton, juveniles and adults) should be monitored across political boundaries, as suggested for other taxa (Pracheil, Pegg, Powell & Mestl, 2012). However, our ability to detect trends is hindered by differences in survey methods, different geographical and taxonomic biases, and recording errors in the data (Troia & McManamay, 2016, personal observation). In addition, many such data sets are stored in disparate locations requiring time-consuming organization and validation. This is partially addressed by meta-databases (e.g. Multistate Aquatic Resources Information System, www.marisdata.org and the Fishes of Texas, www.fishesoftexas.org), but rapid identification and communication of population changes require greater coordination between monitoring organizations, additional assessment and cleaning of existing data.

4.3.5 | Habitat associations

Additional research on habitat requirements of PBS species is needed to enhance conservation efforts (Cooke et al., 2012). Habitat associations are documented for certain PBS species, but little is known for many others (see Table 2). Further, management of PBS species could be improved by investigating seasonal habitat shifts (e.g. Matthews & Hill, 1980) and requirements at different life stages such as larval fish and eggs (Magana, 2012; Medley & Shirey, 2013). These efforts could be completed in conjunction with ongoing monitoring efforts if a more coordinated effort was implemented across political boundaries. Furthermore, pairing habitat-association studies with ongoing habitat restoration actions is one way of leveraging existing funds and efforts to discover habitat requirements of PBS species. This would involve a variety of activities described in the Rio Grande silvery minnow recovery plan (U.S. Fish & Wildlife Service, 2010), many of which apply to other PBS species. These include, among others activities, developing a thorough understanding of stream flows and other habitat features necessary for the life stages of the species, managing water releases from dams in ways that heighten reproduction and recruitment, and physical modification of the stream channel and floodplain to maximize local recruitment. In combination with these activities, agencies could integrate monitoring efforts to improve our understanding of habitat use by these species (see next section).

4.3.6 | Geomorphic and other channel changes

Stream channels are naturally dynamic and experience dramatic geomorphic change when flows are regulated or non-native riparian

vegetation invades. Understanding how shifting channel morphologies influence spawning habitat, ichthyoplankton drift and retention, and juvenile survival and recruitment will be critical for conserving PBS species. This challenge might be matched by opportunities presented by existing monitoring. Monitoring is often hindered by uncertainties associated with sampling, even if standardized, across the spatially and temporally dynamic plains stream environment. Monitoring of PBS species is generally based on seining, mostly due to the relatively shallow stream environment and regions of high conductivity where electrofishing is not effective. Monitoring programmes that include multiple gear types targeting unique life stages (e.g. drift nets for ichthyoplankton, seining for juveniles and adults) and corrections for gear-environment biases are essential. This would include techniques accounting for detection probability of rare species (e.g. occupancy modelling, MacKenzie, Nichols, Royle, Pollock & Bailey, 2006) or assemblage members (e.g. capture efficiency models, Price & Peterson, 2010), or statistical techniques accounting for changes in more abundant species across environmental gradients (Royle, 2004; Royle & Dorazio, 2006). Similarly, multigear approaches allow for detection of multiple year-classes of large-river fishes such as sturgeon (R.A. Hrabik, unpublished data). At a minimum, such techniques would help clarify uncertainties around PBS species abundance estimates made under varying conditions (i.e. either over time or at the "same" site). Further, these techniques, combined with sufficient sampling effort, would improve our understanding of the importance of certain habitat features to persistence. These efforts could be done through refinement of existing sampling protocols by multiple agencies. The effort may be as simple as collecting covariates suspected to affect detection at each site or a more focused effort to collect repeat surveys at each site may be needed.

4.3.7 | Genetics

Except for Rio Grande silvery minnow and bluntnose shiner, existing levels and geographical patterns of genetic diversity are poorly known for PBS species. Baseline data on genetic structure of these populations will provide perspective for future genetic monitoring and management. For example, Arkansas River plains minnow might be a genetic resource for management of the genetically depauperate Platte River population (Osborne, Perkin, Gido & Turner, 2014). Similarly, the relatively high genetic diversities of the non-native Pecos River populations of plains minnow and Arkansas River shiner make them potentially important genetic resources for future conservation activities; both species are declining in their native ranges, suggesting that genetics management might intensify in the future. However, the advisability of such interbasin transfers is complicated and requires careful consideration. George, Kuhajda, Williams, Cantrell and Rakes (2009) provide thorough guidelines for translocation programmes.

Once baseline genetic structure is established, subsequent monitoring can provide a relatively sensitive estimate of population trends and the status of a population (Osborne et al., 2014). Local

changes in allele frequency suggest small variance effective population sizes and this, particularly if there are losses of allele diversity, would signal a need for further investigation into the status of the population and potential management intervention. For example, an augmentation programme apparently has slowed the loss of genetic diversity in the severely depleted Rio Grande silvery minnow (Osborne et al., 2012). However, depending on the immediate history of the wild population, supplementation can have either a positive or a negative effect on the genetically effective population size (N_e). Loss of genetic diversity between parents and offspring occurred in all of three captive breeding strategies for Rio Grande silvery minnow, and the strategies differed in egg viability (Osborne, Perez, Altenbach & Turner, 2013). For captive production, Osborne, Perez, et al., 2013 recommended communal spawning with equal sex ratios. A pedigree-based mating programme aimed at maximizing N_e would be advisable if the situation reaches the point where most wild reproduction is by fish reared from captive broodstock (Osborne, Perez, et al., 2013). Finally, genetic monitoring can also inform our understanding of the effects of habitat fragmentation on population structure (Aló & Turner, 2005).

4.3.8 | Non-native invasions

Aquatic research is impeded by the lack of species-specific methods for non-native fish control (Witmer & Fuller, 2011) and uncertainty for removal of non-native vegetation along channel margins. Piscicides have been the most effective removal tool (Finlayson, Schnick & Cailteux, 2000), but are not specific to non-native fishes. Aquatic barriers, predator stocking and sterilants are also options for species control (Dawson & Kolar, 2003); however, these may have negative effects on the native inhabitants as well (Quist et al., 2004; Schleier et al., 2008). Management of non-natives is confounded for PBS species because the most severe effects so far documented involve non-natives that are highly similar to, and closely related to, the affected native. It may be more prudent to restore some natural system function via hydrology (Sax & Brown, 2000). For example, large spring flooding, in combination with mechanical removal of salt cedar *Tamarix* spp, led to more diverse habitat for native fishes via promotion of channel complexity (Keller, Laub, Birdsey & Dean, 2014). Channel modification via salt cedar invasions is common in the south-west USA where flow modifications have occurred. It is unclear how the changes in channel morphology relate to persistence of different life stages of PBS and a potential conservation opportunity includes pairing fish and channel cross-sectional surveys with ongoing non-native riparian vegetation removal programmes.

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SUPPORTING INFORMATION

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