Stream Fragmentation Thresholds for a Reproductive Guild of Great Plains Fishes

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Available online: 10 Aug 2011

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ABSTRACT: *Impoundments, diversion dams, and stream dewatering have created a mosaic of large river fragments throughout the Great Plains of central North America. Coincident with these habitat changes are massive declines in the distribution and abundance of Great Plains fishes belonging to the "pelagic-spawning" reproductive guild. We analyzed longitudinal fragment lengths (measured in river kilometers, rkm) and literature accounts of population status for eight species from this guild across 60 fragments to derive thresholds in stream length associated with extirpations. Fragment length predicted population status ($F_{2,21} = 30.14$, $P < 0.01$), with lengths averaging 136 ± 21 rkm for extirpated, 226 ± 69 rkm for declining, and 458 ± 137 for stable populations. Fragment length explained 71% of reported extirpations and estimated thresholds in fragment length explained 67% of variation in population persistence. Our findings provide insight into appropriate spatial scales for conducting riverscape conservation approaches that address the hierarchical effects of fragmentation on stream-dwelling fishes.*

Límites de fragmentación fluvial para un gremio reproductivo de peces de las grandes planicies de Norteamérica

RESUMEN: los embalses, presas de derivación y la desviación de caudales han generado un mosaico de fragmentación de los ríos a lo largo de las grandes planicies de la porción central de Norteamérica. De forma paralela a estos cambios, en la región se tienen disminuciones generalizadas en la abundancia y distribución de peces que pertenecen al gremio reproductivo de desovadores pelágicos. Se analizó la dimensión de los fragmentos observados (medida en km de río) y literatura disponible sobre el estado de las poblaciones de ocho especies de dicho gremio, con el fin de determinar medidas límites en la longitud de dichos fragmentos que se encuentran asociados a la extirpación de las poblaciones. La longitud de los fragmentos fue un buen predictor del estado de la población ($F2,21 = 30.14$, $P < 0.01$) con longitudes promedio de 136 ±21 rkm para las extirpadas, 226 ±69 rkm para las que se encuentran en declive y 458 ±137 para las poblaciones estables. La longitud de los fragmentos explicó el 70% de las extirpaciones reportadas y los valores límites de longitud del fragmento explicaron 67% de la variación en la persistencia de las poblaciones. Estos resultados proveen información sobre las escalas espaciales que deben considerar las medidas de conservación de los paisajes fluviales para atender los efectos jerárquicos que la fragmentación tiene sobre los peces demersales de río.

Introduction

Humans have altered biological and ecological processes and influenced the abundance and distribution of organisms on a global scale (Dudgeon et al. 2006; Vorosmarty et al. 2010). In particular, groundwater depletion and impoundment of surface waters have compromised the connectivity of many freshwater ecosystems, constraining the ability of stream organisms to use these habitats (Nilsson et al. 2005). These alterations have imperiled freshwater organisms worldwide, most notably organisms dependent upon streams and rivers for long-term persistence (Lytle and Poff 2004; Nilsson et al. 2005). Although the importance of preserving entire riverscapes has recently been recognized as a viable conservation strategy (Fausch et al. 2002), there is limited information on the spatial scale necessary to preserve biodiversity in lotic systems.

Within the coterminous United States, 85% of large rivers are fragmented by impoundments that divide streams longitudinally, alter flow regimes, and reduce transport of sediments (Hughes et al. 2005). Extensive stream fragmentation, combined with other anthropogenic disturbances (e.g., degradation of water quality, introduction of nonnative species), contributes to the imperiled status of nearly 40% of North American freshwater and diadromous fishes (Jelks et al. 2008). Among these imperiled fishes, small-bodied minnows (family Cyprinidae) that dispense passively drifting eggs and larvae into large flowing streams have declined during the past 60 years. These pelagic-spawning fishes decline in association with human alterations to streams, specifically stream fragmentation (Platania and Altenbach 1998; Luttrell et al. 1999). For example, peppered chub (*Macrhybopsis tetranema*) is now extirpated from 90% of its historical range and persists in only two isolated Arkansas River Basin fragments separated by more than 400 km (Luttrell et al. 1999). Similarly, the federally threatened Arkansas River shiner (*Notropis girardi*) is now extirpated from 80% of its historical range and is currently found in only two isolated fragments of the Arkansas River Basin (Wilde 2002). Documented extirpations of these and other pelagic-spawning cyprinid species coincide with a period of extensive fragmentation of North American rivers from 1950 to 1970 (Cross et al. 1985; Luttrell et al. 1999; Gido et al. 2010).

Reduced stream connectivity is particularly detrimental to pelagic-spawning fishes because of their unique reproductive ecology; for example, pelagic-spawning cyprinids dispense gametes into pelagic zones of flowing streams. Immediately following spawning, water enters cell membranes osmotically and causes eggs to swell and become semibuoyant (in physical terms, slightly negatively buoyant; Bottrell et al. 1964). These semibuoyant eggs remain suspended within the water column at current velocities above 0.01 m/s, drift for 24–28 h before hatching, and then drift for an additional 2–3 days as developing larvae. During the drift period, individuals presumably become displaced great distances downstream (>140 km) from parent localities before complete development of a gas bladder and the onset of exogenous feeding, which allow larval individuals to exit the drift (Moore 1944; Platania and Altenbach 1998). The extent to which larval individuals continue to drift is largely unknown (Durham and Wilde 2008). Consequently, large river fragments (>100 km) are required by drifting eggs and larvae (collectively referred to as "ichthyoplankton"; *sensu* Dudley and Platania 2007) to allow time to develop before being deposited in impounded downstream habitats. Downstream transport is of particular concern because high mortality rates occur among ichthyoplankton deposited within downstream reservoirs, due to suffocation within anoxic sediments or predation from lacustrine species (Platania and Altenbach 1998; Dudley and Platania 2007; Pompeu et al. in press). Spatial dynamics of adult pelagic-spawning cyprinids also are disrupted by stream fragmentation (Luttrell et al. 1999; Bonner 2000). During adult stages, some pelagic-spawning cyprinids are capable of moving upstream on the order of 50 km in less than 72 h (Bestgen et al. 2010) and are presumed to make upstream migrations to recolonize upstream areas (Cross et al. 1985; Bonner 2000). Thus, impoundments also act as barriers to adult dispersal and preclude source–sink dynamics as well as rescue effects (Winston et al. 1991). Stream fragmentation therefore carries the potential to negatively alter the spatial dynamics of pelagic-spawning cyprinids via interruption of dispersal in space (i.e., in downstream and upstream directions) and time (i.e., during ichthyoplankton and adult life stages; Dudley and Platania 2007; Pompeu et al. in press).

Stream fragmentation might provide a mechanistic pathway useful in predicting population declines among imperiled Great Plains pelagic-spawning cyprinids. Within the Great Plains region of North America, pelagic-spawning cyprinids historically dominated vertebrate assemblages within prairie rivers (Cross and Moss 1987; Gido et al. 2010). Documentation of reproductive strategies and egg types places four broadly distributed imperiled Great Plains cyprinids in this guild: Arkansas River shiner (Moore 1944), peppered chub (Bottrell et al. 1964), plains minnow (*Hybognathus placitus*; Platania and Altenbach 1998), and sturgeon chub (*Macrhybopsis gelida*; Hoagstrom et al. 2006). Similarities in morphology, larval drift catches, and available (although limited) information on re-

productive strategy suggest potential for an additional four cyprinids that either broadcast drifting eggs or have an obligatory drifting larval stage: the shoal chub (*Macrhybopsis hyostoma*; Eisenhour 2004), silver chub (*Macrhybopsis storeriana*; Simon 1999), flathead chub (*Platygobio gracilis*; Cross et al. 1985; Durham and Wilde 2008), and prairie chub (*Macrhybopsis australis*; Eisenhour 2004). Numerous proposed drivers exist for the declines of these species, including alterations in streamflow timing and magnitude (Taylor and Miller 1990); poor recruitment associated with reduced streamflows (Wilde and Durham 2008); changes to instream habitat, including substrate compaction and channel homogenization (Cross and Moss 1987); introduction of nonnative taxa; and changes in water quality (Gido et al. 2010). However, reported declines transcend a spatial scale ranging over 20° of latitude and have occurred within 13 regionally distinct North American ecoregions (as defined by Jelks et al. 2008), where all of the above drivers may not be operating. A unifying theme among reported declines is that stream fragmentation is capable of disrupting pelagic-spawning cyprinid life history (as described above) and might represent a primary regulator of species decline. Effects of fragmentation are seemingly not equal among all pelagic-spawning cyprinids, as evidenced by differential levels of extirpation and persistence of guild members within similarly sized fragments (Platania and Altenbach 1998). Consequently, the need exists to identify species-specific threshold levels of fragmentation that might explain declines among numerous fishes across large spatial and temporal scales.

We examined the relationship between stream fragmentation and reported declines among eight species of imperiled Great Plains pelagic-spawning cyprinids. Specifically, we sought to (1) compile literature accounts for the occurrence and status of pelagic-spawning cyprinids within fragmented streams; (2) determine the relationship between population status and stream fragment length; and (3) estimate minimum fragment lengths associated with population persistence. Our test of the extent to which stream fragmentation has imperiled these fishes provides a framework that can be used by managers to select habitats needed to conserve populations of these highly threatened fishes.

Methods
Study Area
The North American Plains comprise a semi-arid region that was historically dominated by grassland, prairie, and steppe biomes that span from Alberta, Canada, to the Rio Grande Basin, Mexico. The plains are bordered to the west by the Rocky Mountains and to the east by the Mississippi River. Consequently, most large-order plains rivers flow west to east within three major basins: the Missouri River, Arkansas River, and Red River basins (Matthews and Zimmerman 1990). These river basins occur in two major plains regions—the Great Plains and Osage Plains (collectively referred to as the Great

Plains hereafter) and span the majority of 10 states: Montana, North Dakota, South Dakota, Wyoming, Nebraska, Colorado, Kansas, Oklahoma, New Mexico, and Texas. Additionally, southern portions of the Great Plains are drained by river basins that empty directly into the Gulf of Mexico, including the Brazos, Colorado, San Antonio Bay, Nueces, and Rio Grande basins. Throughout this region, portions of large prairie rivers characterized by low gradients, sandy bottoms, relatively high turbidity and lying within the coterminous United States were chosen based on inhabitance by pelagic-spawning cyprinids and availability of historical ichthyofauna data.

Evaluating Extent of Stream Fragmentation

Stream fragments were included based on occurrence of instream barriers, historical inhabitance by targeted species, and availability of historical fish assemblage data. Upstream and downstream limits of fragments were defined by one of four instream barriers to fish movement: (1) dams associated with impoundments, hydroelectric energy generation, or water diversions; (2) lentic environments created at upstream extents of reservoirs; (3) stream desiccations occurring as a consequence of anthropogenic water withdrawals; and (4) the upstream natural distribution of targeted species. Distribution of dams was evaluated using the National Inventory of Dams compiled by the United States Army Corp of Engineers and through inspection of aerial photography. Areas of stream desiccation were identified during reviews of literature pertaining to distributions of Great Plains fishes (e.g., Cross et al. 1985; Luttrell et al. 1999), and the period of time for which dewatered streams occurred was quantified using United States Geological Survey (USGS) streamflow data. Streamflow data were downloaded from USGS gauges for the period following most major alterations to flow regime associated with groundwater withdrawals (1969–2009; Milly et al. 2005; Gido et al. 2010), and discharge values (mean annual and monthly median) were quantified and compared to available historical data (pre-1968) using indicators of hydrologic alteration (Richter et al. 1996). Though stream desiccations are likely semipermeable barriers, they were included because of the substantial period of the year in which movement was precluded (Luttrell et al. 1999) and because pelagic-spawning cyprinids typically do not occupy ephemeral streams (Cross et al. 1985). When barriers isolated populations in upstream segments, the extent of target species natural distributions within upstream reaches was based on accounts in Lee et al. (1980) following the methods of Dudley and Platania (2007).

Stream lengths between barriers were quantified in river kilometers (rkm) using the stream layer associated with the National Hydrography Dataset (NHD) from the USGS. Stream lengths were measured along the main channel, excluding oxbows or parallel secondary channels. When data were available, all adjoining main-stem fragments within a basin were targeted. We excluded main-stem sections of the Missouri and Mississippi rivers because of large differences in stream size and relatively sparse historical data. Stream fragment length was then used as a continuous variable to test for species-specific changes in population status and fragment length thresholds in population persistence.

Historical Changes in Fish Assemblages

We reviewed literature accounts regarding the contemporary (1969–2009) and historical (pre-1968) occurrence of eight target species within each fragment. Species were included if found in at least four stream fragments and occurrences were not limited to main-stem Mississippi or Missouri rivers. Confirmed and suspected pelagic-spawning cyprinids targeted throughout the Great Plains were the plains minnow, Arkansas River shiner, sturgeon chub, peppered chub, flathead chub, shoal chub, silver chub, and prairie chub. In general, these species inhabit perennial Great Plains prairie streams where their distributions are limited to main-stem habitats including shallow, braided, and sandy shoals and backwaters where historical (pre-1968) seining data were commonly collected.

Because of differences in sampling methodologies and purposes among published studies, data were used to define four coarse levels of population status: stable, declining, extirpated, and rare. Stable status indicated populations with no reduction in abundance (e.g., density, relative abundance, rank abundance) or distribution (e.g., area inhabited, presence/absence among sampling sites) through time, despite monitoring over a 20-year period. Declining (or depleted) status indicated populations with reductions in either abundance or distribution among sampling periods spread over a period of at least 20 years. Extirpated (or undetectable) status indicated populations not detected within a given fragment in at least 20 years despite continued monitoring. Rare status indicated species that were historically reported within fragments with low frequency or in low abundance; rare occurrences were not included in statistical analyses. Thirty-three published and unpublished accounts were used in describing population statuses of target species. These accounts were partitioned among species-specific descriptions ($n = 6$; e.g., Luttrell et al. 1999), regional reviews of numerous species-specific accounts ($n = 5$; e.g., Eisenhour 2004), unpublished assemblage data specific to one or more fragments ($n = 4$; e.g., G. Wilde, Texas Tech University, unpublished data), and published accounts specific to one or more fragments included in this study ($n = 18$; e.g., Hoagstrom et al. 2011).

Data Analysis

We used stream fragment length as a continuous independent variable to test the hypothesis that the status of populations occurring within larger fragments is more likely to be stable. A single-factor analysis of variance (ANOVA) was used to test for differences in mean stream lengths for fragments with stable, declining, or extirpated populations of each species. We

used a Bonferroni adjustment to control for experiment-wise error associated with conducting ANOVAs for eight species (α = 0.05/8 = 0.006). Post hoc multiple comparisons among the three population types were conducted within species using Fisher's least significant differences (LSD; α= 0.006). Additionally, we tested for differences in population status among grand means of fragment lengths for all species combined (i.e., mean fragment lengths for each population status were combined among species) using an ANOVA and Fisher's LSD.

Initial observations indicated that many species did not persist in shorter fragment lengths, supporting published accounts of pelagic-spawning cyprinid extirpations in shorter fragments of the Rio Grande Basin of New Mexico (Dudley and Platania 2007). Accordingly, we tested for minimum thresholds in fragment length associated with population status of each species using classification tree analysis (CTA; De'ath and Fabricius 2000). We asked whether thresholds existed for species persistence (i.e., extant populations) and local extinction, which might lend insight into the minimum possible fragment length needed to maintain pelagic-spawning cyprinid populations. For extinction threshold analysis, declining and stable populations of species were combined to represent fragments capable of supporting persistence of pelagic-spawning species, although we acknowledge that declining populations may in fact be related to fragment length (Dudley and Platania 2007; this study).

Finally, we used polynomial logistic regression to model fragment length (predictor variable) against extirpations within pelagic-spawning assemblages (i.e., all pelagic-spawning species within a fragment) for each fragment (response variable) to assess the relationship between fragmentation and extirpation at the guild level. The coefficient of determination was calculated using the Nagelkerke R^2 value (Nagelkerke 1991). We then regressed our estimated thresholds in fragment length (predictor variable) against the percentage of extant populations (response variable) for each species to quantify the relationship between fragment thresholds and population persistence.
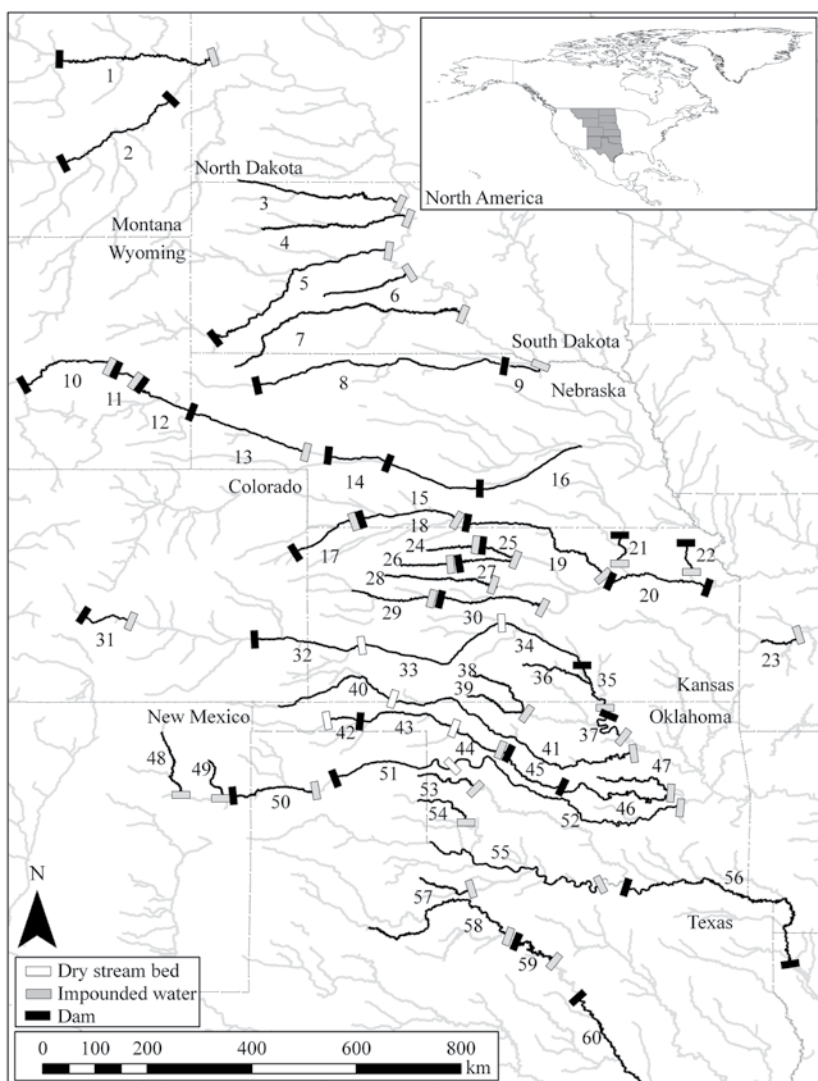
Results

Within the Great Plains region of North America, 60 stream fragments met the requirements for inclusion in our study (Figure 1). The length of these fragments ranged from 38 to 705 rkm (Table 1). Barriers to fish dispersal included 36 dams associated with water diversions, hydroelectric generation, and reservoir storage; 39 lower bounds defined by impounded water; 21 upper bounds defined by upstream extent of pelagic-spawning cyprinid natural distributions; and 6 localized regions where water withdrawals resulted in reduced discharges and stream desiccation. Streamflows were reduced by 48–83% among fragments associated with stream dewatering, which generally resulted in discharge values of 0 m³/s throughout pe-

lagic-spawning cyprinid reproductive seasons (May–August) as well as most of the year (up to 310 days; Table 2).

Population status of confirmed or suspected pelagic-spawning cyprinids consisted of 57% extirpated, 21% declining, and 22% stable populations (n = 157 observations among species). Among 90 extirpations, 8 occurred in the northern region of the Great Plains (Montana, North Dakota, South Dakota, Wyoming), 45 in the central region (Nebraska, Colorado, Kansas), and 37 in the southern region (New Mexico, Texas, Oklahoma). Among species, the plains minnow occurred in the greatest number of fragments (n = 48) and the narrowly distributed prairie chub occurred in the fewest (n = 4). Three stream fragments exhibited extensive dewatering and various levels of fragmentation because of temporal variation in stream desiccations between barriers; these included the Arkansas River and upper reaches of the Cimarron River in southwestern Kansas (i.e., fragment ID numbers 33, 40, 41; Cross et al. 1985; Luttrell et al. 1999). We initially retained these fragments in our study because they represented historical occurrences of species, but in each case fragmentation was confounded by loss of a definable fragment length. Among the remaining fragments (n = 57), stream lengths differed according to population status for plains minnow ($F_{2,42}$ = 24.92, P < 0.01, Bonferroni adjusted), Arkansas River shiner ($F_{2,13}$ = 24.97, P < 0.01), sturgeon chub ($F_{2,9}$ = 11.45, P = 0.03), flathead chub ($F_{2,23}$ = 14.40, P < 0.01), shoal chub ($F_{2,13}$ = 15.23, P < 0.01), and silver chub ($F_{2,11}$ = 98.71, P < 0.01). ANOVA could not be conducted for peppered chub or prairie chub because of rare occurrences of persistent populations, but the association between population status and fragment length was consistent with other species (Figure 2). Grand mean river kilometer lengths differed ($F_{2,21}$ = 30.14, P < 0.01) among all species combined and averaged (plus or minus standard deviation) 136 (±21) for extirpated, 226 (±69) for declining, and 458 (±137) for stable populations.

Fragment length thresholds associated with localized extirpations varied by species. Classification tree analysis produced models that significantly differed from random (α = 0.05), successfully classified populations as extant or extirpated (as measured by Cohen's kappa, k), and produced estimated minimum thresholds in fragment length (rkm) associated with population persistence for plains minnow (115 rkm, P < 0.01, k = 0.81), Arkansas River shiner (217 rkm, P = 0.01, k = 0.77), sturgeon chub (297 rkm, P = 0.01, k = 0.79), flathead chub (183 rkm, P < 0.01, k = 0.85), shoal chub (103 rkm, P < 0.01, k = 0.75), and silver chub (203 rkm, P < 0.01, k = 0.8). Model calculation of minimum threshold lengths was not possible for peppered chub or prairie chub because each of these species included only one declining and one stable population. For both species, the median fragment length between declining and extirpated population statuses was used to estimate the minimum threshold necessary for population persistence, resulting in threshold estimates of 205 rkm for peppered chub and 128

Figure 1. Distribution of North American Great Plains stream fragments included in analyses. Fragment numbers correspond with descriptions in Table 1.

cluding fragment ID numbers 33, 40, and 41). Similarly, estimated minimum thresholds in fragment length for the eight species included in our analysis explained 67% ($R^2 = 0.67$, $P < 0.01$) of the variation in the number of extant populations (Figure 3b).

Discussion
Fragmentation Drives Imperilment

Pelagic-spawning cyprinid assemblages inhabiting fragmented streams throughout the Great Plains represent a disappearing guild of fishes, as evidenced by high imperilment rates and conservation listings at state, regional, and national levels (Jelks et al. 2008). Reported reductions in abundance and distribution include extirpation from 45% of its historical range for the sturgeon chub (Rahel and Thel 2004), 55% for shoal chub (Luttrell et al. 1999), 80% for Arkansas River shiner (Wilde 2002), and 90% for peppered chub (Luttrell et al. 1999). Our findings supported extirpation from a majority (i.e., >50%) of fragments included in this study for the flathead chub (61%), silver chub (64%), and sturgeon chub (75%) and values that closely match previously reported extirpations for the Arkansas River shiner (79%) and peppered chub (88%). Similar extirpations have occurred among six species of pelagic-spawning cyprinids in the Rio Grande and Pecos River basins of New Mexico and Texas, where the Rio Grande shiner *Notropis orca* and Rio Grande bluntnose shiner *Notropis simus simus* are now extinct and remaining species are restricted to river fragments more than 100 kilometers in length (Dudley and Platania 2007). Two species of pelagic-spawning cyprinids endemic to the Brazos River of Texas, the sharpnose shiner *Notropis oxyrhynchus* and small-eye shiner *Notropis buccula*, are now restricted to approximately one third of their historical range because of stream fragmentation and associated effects of reservoirs (Durham and Wilde 2009b). These reported patterns of decline are evident across a large spatial extent (i.e., the entire Great Plains), include multiple taxonomic levels (i.e., 4 genera, 16 species, 2 subspecies; Platania and Altenbach 1998; Durham and Wilde 2009b; this study), span 13 North American ecoregions, and collectively include 8% of the imperiled freshwater cyprinids in North America (Jelks et al. 2008). Consequently, pelagic-spawning cyprinids represent a substantial challenge for conservation of biodiversity in North America.

Though previous studies have formulated a number of reasons for observed declines, our synthesis of declines suggests that imperilment of pelagic-spawning cyprinids is a direct con-

rkm for prairie chub. These estimates combined with CTA results produced minimum length thresholds ranging from 103 to 297 rkm, below which species-specific extirpations occurred.

When pelagic-spawning cyprinid assemblages were considered and the proportion of species extirpated from assemblages regressed against stream fragment length, differential thresholds in persistence contributed to a logistic relationship (Figure 3a). This pattern was characterized by 100% extirpation of pelagic-spawning assemblage members within fragments less than 103 rkm, variable percentages in extirpation among fragments ranging from 103 to 297 rkm, and no reported extirpations among fragments greater than 297 rkm in length. Stream fragmentation explained 71% (Nagelkerke $R^2 = 0.71$, $P < 0.01$) of pelagic-spawning assemblage member extirpations within the 57 stream fragments included in our analysis (ex-

TABLE 1. Description, length (rkm), and population status (S, stable; D, declining; E, extirpated; R, rare) of eight Great Plains fishes (1, plains minnow; 2, flathead chub; 3, sturgeon chub; 4, silver chub; 5, shoal chub; 6, peppered chub; 7, Arkansas River shiner; 8, prairie chub) within 60 stream fragments. Full citations for works referenced within the table are available upon request or see Perkin et al. (2010).

	Fragment description	Length	1	2	3	4	5	6	7	8	References
1	Yellowstone River between Fort Peck Dam and upper reaches of Lake Sakakawea	327	S	D	D						18, 19, 33
2	Yellowstone River between Cartersville Dam and Intake Dam	266	S	S	E						18, 19, 33
3	Mainstem Grand River of South Dakota upstream of Lake Oahe	256	S	S	E						29, 30, 33
4	Mainstem Monroe River of South Dakota upstream of Lake Oahe	387	S	S							30, 33
5	Cheyenne River between Angostura Dam and upper reaches of Lake Oahe	395	S	S	S						30, 31, 33
6	Mainstem Bad River of South Dakota upstream of Lake Sharpe	184	S	S							29, 30, 33
7	Mainstem White River of South Dakota upstream of Lake Francis Case	705	S	S	S						30, 33
8	Niobrara River between Box Butte Dam and Spencer Dam	445		S							26, 29
9	Niobrara River between Spencer Dam and upper reaches of Lewis and Clark Lake	65	E	E	E	E					11, 26, 33
10	North Platte River between Alcova Dam and upper reaches of Glendo Reservoir	228	S	D							12, 33
11	North Platte River between Glendo Dam and upper reaches of Guernsey Reservoir	46	E	E	E						11, 26, 33
12	North Platte River between Guernsey Dam to Wyoming/Nebraska diversion dam	96	E	E	E						11, 26, 33
13	North Platte River between Wyoming/Nebraska diversion dam and upper reaches of McConaughy Reservoir	198	S		E						11, 12,33
14	North Platte River between Kingsley Dam and Diversion dam at North Platte, Nebraska	96	E	E							12, 33
15	Platte River North Platte diversion dam to weir dam near Elm Creek, Nebraska	133	D	E	E		D				11, 14, 26, 33
16	Platte River between weir dam near Elm Creek, Nebraska, and Columbus, Nebraska	217	S	D	E	D	D				11, 14, 26, 33
17	Republican River between dam at Bonny, Colorado, and upper reaches of Swanson Reservoir	136		E							4, 26
18	Republican River between Trenton Dam and upper reaches of Harlan County Reservoir	181		E		E	D				4, 11, 33
19	Republican River between Harlan County Dam and upper reaches of Milford Reservoir	332	S	D		D	S				4, 26, 33
20	Kansas River between Milford Dam and Bowersock Dam	177	E	E	E	E	E				4, 6, 11, 33
21	Big Blue River between Marysville Dam and upper reaches of Tuttle Creek Reservoir	66					E				23
22	Delaware River between Mission Lake Dam and upper reaches of Perry Lake	61		E		E	E				4
23	Osage River upstream of upper reaches of Truman Reservoir	85				E	E				16, 20
24	North Fork Solomon River upstream of upper reaches of Kirwin Reservoir	109	E								4, 22, 33
25	North Fork Solomon River between Kirwin Dam and upper reaches of Waconda Reservoir	93	E								4, 22, 33
26	South Fork Solomon River between Hoxie, Kansas, and upper reaches of Webster Reservoir	90	E								4, 22, 33
27	South Fork Solomon River between Webster Dam and upper reaches of Waconda Reservoir	134	E								4, 22, 33
28	Saline River upstream of upper reaches of Wilson Reservoir	189	E			E					4, 15, 33
29	Smokey Hill River between Wallace County, Kansas and upper reaches of Cedar Bluff Reservoir	173	D								15, 33
30	Smokey Hill River between Cedar Bluff Dam and upper reaches of Kanopolis Reservoir	222	D								15, 33
31	Arkansas River between Salida, Colorado, and dam at Florence, Colorado	119		E							26
32	Arkansas River between John Martin Dam and Lakin, Kansas	179		E				E			5, 20, 33
33	Arkansas River between Lakin, Kansas, and Great Bend, Kansas	290	E	E				E	E		5, 20, 27, 28, 33

TABLE 1. (continued)

	Fragment description	Length	1	2	3	4	5	6	7	8	References
34	Arkansas River between Great Bend, Kansas, and weir dam at Wichita, Kansas	178	E	E		E		E	E		5, 20, 27, 28, 33
35	Arkansas River between weir dam at Wichita, Kansas, and upper reaches of Kaw Reservoir	153	D			E	E		E		5, 20, 27, 28, 33
36	Ninnescah/Arkansas rivers between Cairo, Kansas, and upper reaches of Kaw Reservoir	251	D			D		S	D		4, 28, 33
37	Arkansas River between Kaw Dam and upper reaches of Keystone Lake	120	D			E	S	E	E		20, 25, 27, 33
38	Mainstem Medicine Lodge River upstream of upper reaches of Great Salt Plains Lake	165	D					E	E		5, 33
39	Mainstem Salt Fork Arkansas River upstream of upper reaches of Great Salt Plains Lake	163	E					E	E		5, 33
40	Cimarron River between Castaneda, Oklahoma, and just east of Liberal, Kansas	277	E	E				E	E		5, 33
41	Cimarron River between just east of Liberal, Kansas, and Keystone Lake	434	D					E	D		5, 20, 33
42	North Canadian River between Pony Creek confluence and Optima Dam	38	E					E	E		7, 9, 20, 33
43	North Canadian River between Optima Dam and Fort Supply (Wolf Creek Confluence)	191	D					E	E		7, 9, 20, 33
44	North Canadian River between Fort Supply and upper reaches of Canton Lake	139	D					E	E		7, 9, 20, 33
45	North Canadian River between Canton Dam and Overholser Dam, Oklahoma City	161	D					E	E		7, 9, 20, 33
46	North Canadian River between Overholser Dam and upper reaches of Urika Reservoir	339							R		9, 33
47	Deep Fork River upstream of upper reaches of Lake Eufaula	183					E		E		9, 20, 33
48	South Canadian River upstream of upper reaches of Conchas Lake	180	E	E					E		8, 33
49	Ute Creek between Gladstone, New Mexico, to upper reaches of Ute Reservoir	189	D	E				E	E		17, 33
50	South Canadian River between Ute Dam and upper reaches of Lake Meredith	220	D	E				D	D		21. 33
51	South Canadian River between Sanford Dam and Roger Mills County, Oklahoma	214	D	R				E	E		1, 21, 33
52	South Canadian River between Roger Mills County, Oklahoma and Urika Reservoir	462	S				S	R	S		1, 9, 20, 25, 33
53	Washita River upstream of upper reaches of Foss Reservoir	93								E	24, 33
54	North Fork of the Red River upstream of upper reaches of Altus Reservoir	108	E							E	10, 33
55	Upper Red River between Prairie Dog Town Fork and upper reaches of Lake Texoma	455	S							S	13, 33
56	Red River between Denison Dam and Dam at Shreveport, Louisiana	689	S			S	S				25, 33
57	North Fork Wichita River between Truscott, Texas, and upper reaches of Lake Kemp	149	D							D	2, 33
58	Brazos River between McMillan Dam and upper reaches of Possum Kingdom Reservoir	616	S				S				2, 33
59	Brazos River between Morris Sheppard Dam to upper reaches of Lake Waco	171	E				D				3
60	Brazos River downstream of Waco Dam to Gulf of Mexico	645				S	S				32

1: Gene Wilde, Texas Tech University, unpublished data; 2: Fran Gelwick, Texas A&M University, unpublished data; 3: Jack Davis, Brazos River Authority, unpublished data; 4: Keith Gido, Kansas State University, unpublished data; 5: Cross et al. (1985); 6: Cross and Moss (1987); 7: Pigg (1987); 8: Sublette et al. (1990); 9: Pigg (1991); 10: Winston et al. (1991); 11: Hesse et al. (1993); 12: Lynch and Roh (1996); 13: Taylor et al. (1996); 14: Chadwick et al. (1997); 15: Eberle et al. (1997); 16: Pflieger (1997); 17: Pittenger and Schiffmiller (1997); 18: Patton et al. (1998); 19: Helfrich et al. (1999); 20: Luttrell et al. (1999); 21: Bonner and Wilde (2000); 22: Eberle et al. (2002); 23: Gido et al. (2002); 24: Eisenhour (2004); 25: Miller and Robison (2004); 26: Rahel and Thel (2004a); 27: Rahel and Thel (2004b); 28: Haslouer et al. (2005); 29: Hoagstrom et al. (2006); 30: Hoagstrom et al. (2007a); 31: Hoagstrom et al. (2007b); 32: Runyan (2007); 33: Hoagstrom et al. (2010).

TABLE 2. Fragment number, United States Geological Survey (USGS) gauge number, flow period, and historical (pre-1968) and contemporary (1969–2009) values for mean annual flow (MAF; m³/s), median number of zero flow days, and median monthly flow values (m³/s) for cyprinid reproductive seasons (May–August) for stream fragments associated with dewatering and desiccation.

Fragment number	USGS gauge	Flow Period	Historical						Contemporary					
			MAF	Zero days	May	June	July	August	MAF	Zero days	May	June	July	August
33[a]	7139000	1938–2009	5.68	0	0.40	0.76	0.40	0.31	2.97	211	0.00	0.00	0.00	0.00
34[a]	7141220	1999–2009	NA	NA	NA	NA	NA	NA	3.76	119	0.01	0.02	015	0.00
41[a]	7155590	1971–2009	NA	NA	NA	NA	NA	NA	0.23	310	0.00	0.00	0.00	0.00
42[b]	7232500	1932–1993	0.84	2	0.14	0.07	0.09	0.05	0.15	186	0.04	0.00	0.00	0.00
44[b]	7234000	1938–2009	2.79	72	0.86	0.80	0.46	0.03	0.5	60	0.32	0.13	0.00	0.00
52[b]	7228000	1938–2009	11.65	0	0.35	2.34	0.60	0.37	1.94	0	1.46	1.20	0.32	0.27

[a]Desiccations associated with reduced species distributions (Cross et al. 1985).
[b]Desiccations and dewatering associated with reduced species distributions (Pigg 1991).
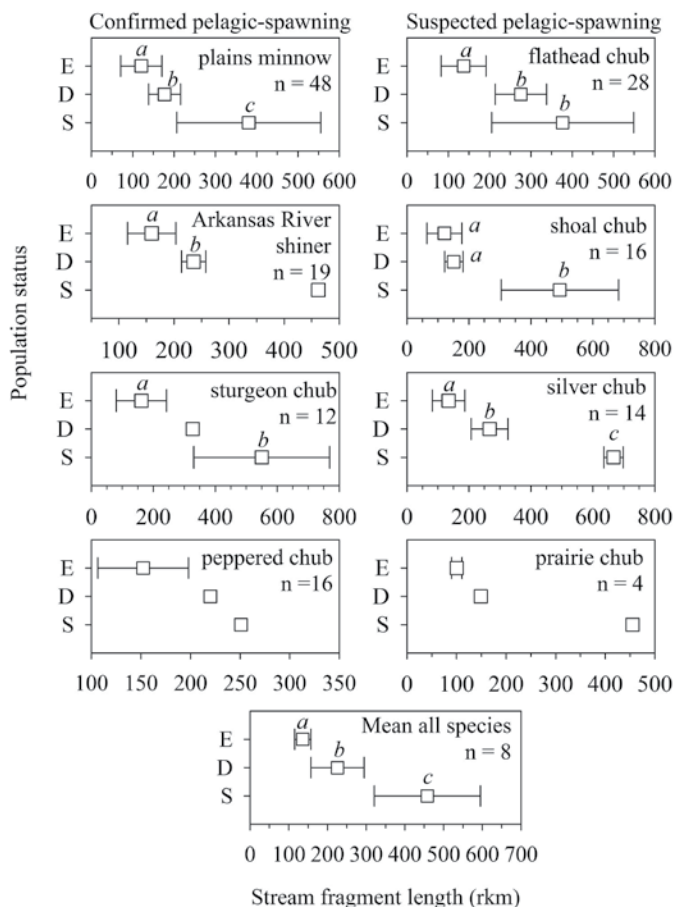
Figure 2. Mean (plus or minus standard deviation) stream fragment lengths (rkm) for confirmed (left column), suspected (right column), and combined (bottom, center) Great Plains pelagic-spawning cyprinid populations according to population status: extirpated (E), declining (D), and stable (S). Lowercase letters represent statistical differences among statuses (see text for statistical procedures).
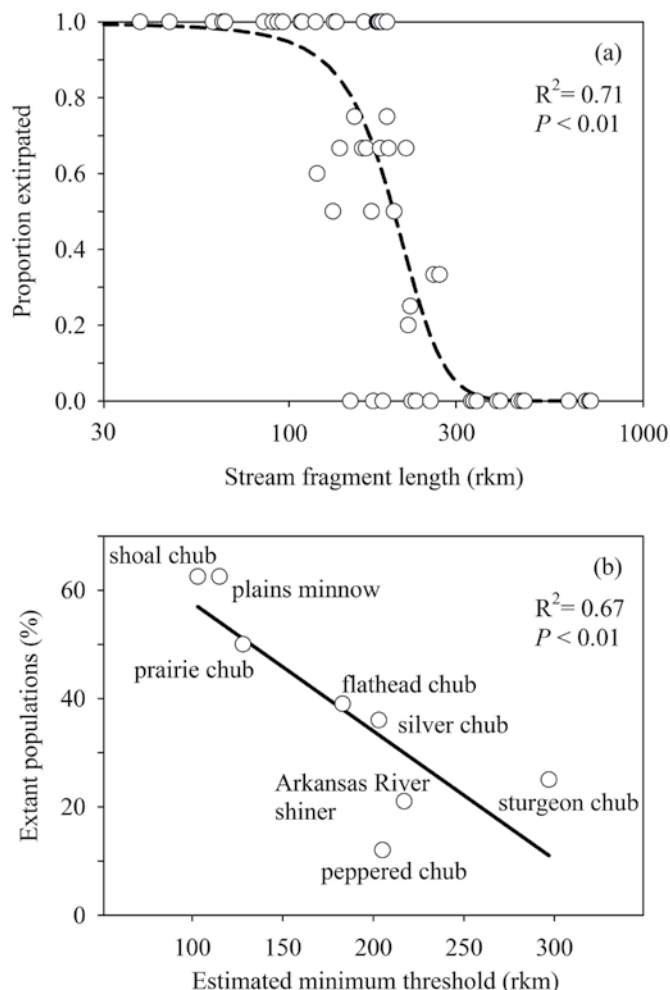
Figure 3. Proportion of species extirpated from Great Plains pelagic-spawning cyprinid assemblages as a function of stream fragment length measured in river kilometers (x-axis log-scaled). (b) Percentage of extant populations for eight Great Plains pelagic-spawning species as a function of the estimated minimum threshold (rkm) necessary for persistence.

sequence of stream fragmentation. This pattern is seemingly driven by instream barriers precluding upstream migration of adults (Luttrell et al. 1999) as well as reduced downstream dispersion and recruitment of drifting ichthyoplankton (Dudley and Platania 2007). Throughout the Great Plains, we found that estimated minimum thresholds in fragment length varied among eight species but were consistently more than 100 rkm in length. Suspected pelagic-spawning shoal chub exhibited the shortest threshold in longitudinal length (103 rkm), which was consistent with Platania and Altenbach's (1998) conclusion that the speckled chub (*Macrhybopsis aestivalis*; once synonymous with shoal chub; Eisenhour 2004) require relatively shorter stream lengths for completion of life history. Our estimated minimum thresholds for Arkansas River shiner and peppered chub (217 and 205 rkm, respectively) were consistent with Bonner and Wilde's (2000) conclusion that the Canadian River between Ute and Meredith reservoirs (220 rkm) represents the near minimum length required for completion of their reproductive cycles. Furthermore, our estimated minimum threshold of 297 rkm for sturgeon chub resembled the apparent minimum stream length necessary for persistence of the closely related sicklefin chub (*Macrhybopsis meeki*; i.e., 301 rkm; Dieterman and Galat 2004).

Throughout the Great Plains, we found that extirpation of pelagic-spawning cyprinids occurred to the highest extent in the central and southern Great Plains regions, where notable reductions in discharge have occurred since at least the 1970s

Our results contradict the findings of Medley et al. (2007) and Widmer et al. (2011), who suggested that given the appropriate habitat complexity, reproduction and recruitment of pelagic-spawning fishes is possible in stream fragments less than 100 rkm. However, the above studies were based only on modeling the retention of artificially manufactured eggs and did not consider the many factors that long stream fragments can play in the success of these species (Zymonas and Propst 2009). A notable oversight of these studies is the potential for an obligate drifting larval stage, which might contribute to the need for increased longitudinal distances within fragmented streams given that drifting might not cease at the end of the egg developmental phase. The extent to which larval individuals continue to drift is unknown for many of the species included in this study, but high abundances during drift sampling suggest that drift frequently occurs among larval pelagic-spawning fishes (Simon 1999; Durham and Wilde 2008). The paucity of data related to reproductive mechanisms for suspected pelagic-spawning fishes and for patterns in larval drift among all species in this study suggests that future research into declining Great Plains cyprinids is necessary. However, conservation approaches aimed at mitigating massive declines of poorly stud-

ied species necessitate management actions based on the best available biological data (Richter et al. 2003). Imperilment associated with stream fragmentation provides a parsimonious mechanism that links widely dispersed literature accounts of decline among eight highly imperiled Great Plains fishes and likely provides a framework for future investigations related to potential conservation approaches.

The Hierarchal Effects of Fragmentation

Stream fragmentation produces a hierarchy of environmental changes that imperil stream-dwelling fishes through direct and indirect pathways. Notable environmental changes associated with construction of large instream barriers include alteration of downstream flow regimes, water temperatures, and channel morphologies (Poff et al. 1997). Direct consequences of altered flow regimes include removal of high flow pulses that cue synchronization of spawning, increase spawning intensity, and maintain eggs in suspension long enough for hatching (Moore 1944; Bottrell et al. 1964). Reductions in mean annual discharge negatively affect some pelagic-spawning species because recruitment of age-0 individuals is directly dependent upon discharge (Wilde and Durham 2008; Durham and Wilde 2009a). Throughout the Great Plains, we found that extirpation of pelagic-spawning cyprinids occurred to the highest extent in the central and southern Great Plains regions, where notable reductions in discharge have occurred since at least the 1970s (Cross et al. 1985; Gido et al. 2010). In these cases, reductions in discharge likely contributed to declines and extirpations by inducing both fragmentation and negative effects on reproductive success. For example, groundwater withdrawals in western Kansas have contributed to dry streams during 70–99% of pelagic-spawning cyprinid reproductive seasons (May–August), providing limited opportunity for spawning and successful recruitment (Aguilar 2009). Projected changes in climate suggest that this region of the Great Plains will undergo further reductions in stream discharge associated with variation in precipitation and evapotranspiration cycles (Milly et al. 2005). Consequently, the possibility exists for reductions in discharge, related to both anthropogenic withdrawal and climate change, to contribute to an increase in declines and extirpations among Great Plains pelagic-spawning cyprinids in this region (Taylor 2010). This conclusion is consistent with the findings of a recent large-scale literature review that found that alteration to magnitude of discharge was detrimental to many fluvial organisms, notably fishes (Poff and Zimmerman 2010).

Indirect effects of instream barriers such as deep storage reservoirs alter downstream thermal regimes and channel morphologies. Reservoirs that release water from the hypolimnion contribute to cooler tailwater temperatures, and effects extend many kilometers downstream (Edwards 1978). Development rates of drifting eggs and larvae are prolonged during cooler water temperatures, contributing to the need for further downstream transport before free-swimming larval stages are
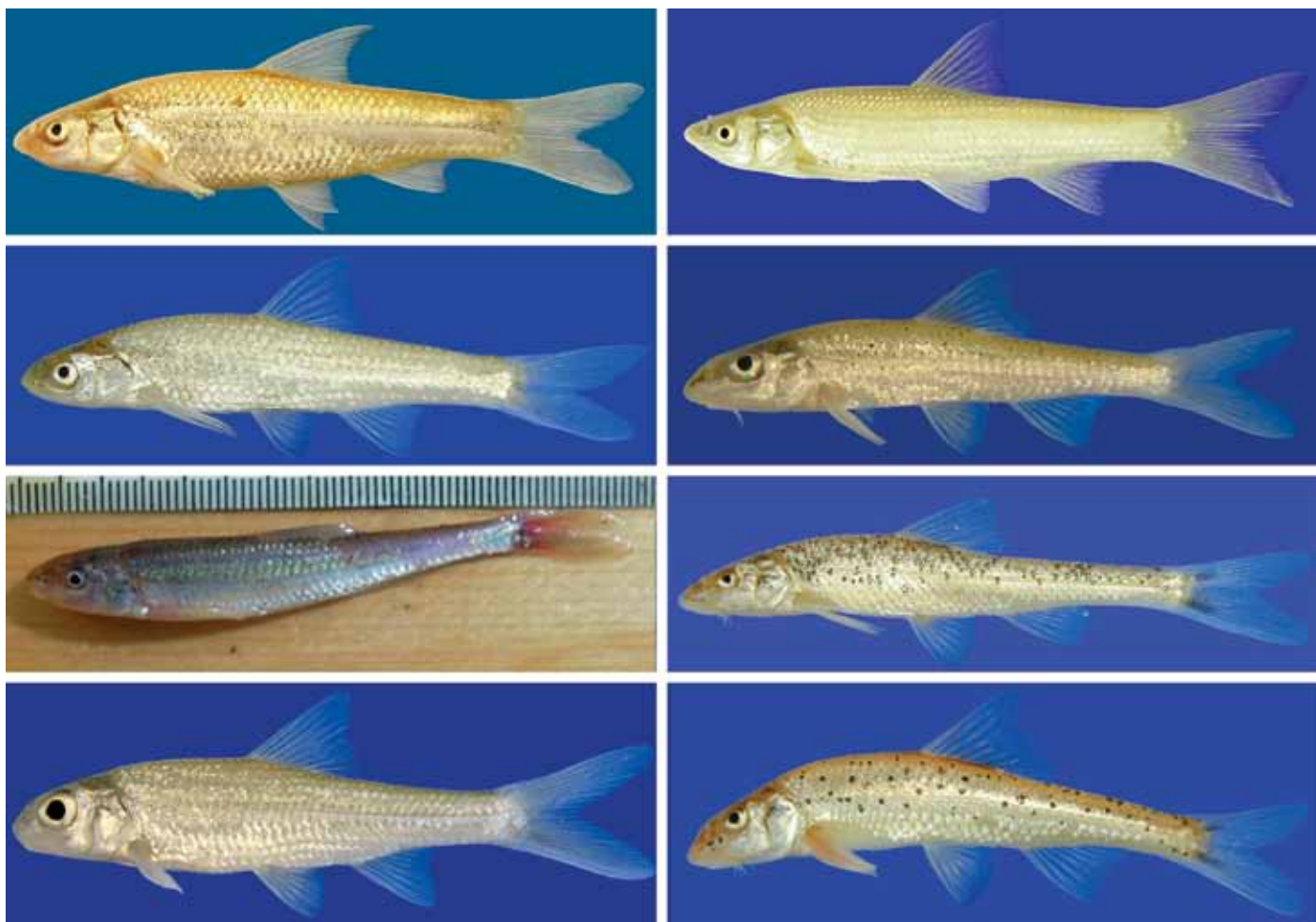
Great Plains cyprinids suspected or confirmed as members of the pelagic-spawning reproductive guild. Species are (left column, top to bottom) plains minnow (*Hybognathus placitus*), Arkansas River shiner (*Notropis girardi*), sturgeon chub (*Macrhybopsis gelida*), silver chub (*Macrhybopsis storeriana*); (*right column, top to bottom*) flathead chub (*Platygobio gracilis*), shoal chub (*Macrhybopsis hyostoma*), peppered chub (*Macrhybopsis tetranema*), and prairie chub (*Macrhybopsis australis*). Photos courtesy of Chad Thomas (Texas State University; all except sturgeon chub) and Ann Marie Reinhold (Montana State University; sturgeon chub).

reached. Similarly, sustained high flows associated with reservoir releases contribute to increased downstream transport through homogenization of habitat (e.g., deep, incised channels) and increased rate of flow (Dudley and Platania 2007). Our analysis did not include measurements of water temperature or channel morphology, two factors that might be manipulated more easily than removal of large impoundments or diversion dams to facilitate prelarval development within stream fragments (Widmer et al. 2011). However, our findings across a diversity of streams with regional variation in temperature and channel morphology suggest that fragment lengths less than 100 rkm were correlated with extirpation of pelagic-spawning cyprinids in areas upstream of impoundments, where habitat complexity is not altered by reservoir management. This patterned occurred for seven fragments in which 100% of pelagic-spawning cyprinids were extirpated, suggesting that mitigation of extirpation through restoration of habitat complexity should not discount overall fragment length. Additional support for the importance of long river fragments for all eight species in-

cluded in this study is the occurrence of declining populations within intermediate-length fragments. These declines might be related to time-lag effects associated with reduced reproductive success ultimately arising from changes in flow regime (Perkin and Bonner 2011) or possibly because fragment lengths (i.e., patch sizes) are no longer large enough to support historical population sizes (Aló and Turner 2005).

Mitigation Potential and Broader Implications

Future approaches targeting enhanced conservation of Great Plains pelagic-spawning cyprinids, as well as a diversity of stream-dwelling organisms, will likely require restoration or preservation of connectivity within stream systems. In particular, the use of fishways that allow passage in an upstream direction for a wide range of fishes (Prchalová et al. 2006) are likely of great conservation value. However, a paucity of empirical data exists pertaining to the passage of small-bodied cyprinids through fishways, though existing evidence suggests that passage is possible (Prchalová et al. 2006; Bestgen et al. 2010).

The greater challenge will ultimately involve the downstream passage of drifting ichthyoplankton, especially through large reservoirs (Agostinho et al. 2007; Pompeu et al. in press). We are unaware of initiatives aimed specifically at allowing the downstream transport of ichthyoplankton through reservoirs in fragmented river systems, which is perhaps the greatest challenge associated with conservation of pelagic-spawning cyprinids. Additional conservation options for mitigating the effects of fragmentation include management of flow regimes that target recruitment of native fishes (Propst and Gido 2004), release of epilimnetic water to minimize thermal alterations (Dudley and Platania 2007), and management of instream habitat complexity to facilitate increased heterogeneity (Widmer et al. 2011). Ecological benefits of these mitigation approaches hold potential for improving the conservation status of many diadromous and freshwater fishes not included in this study (Jelks et al. 2008) as well as riparian vegetation forms, unionid mussels, and aquatic invertebrates (Lytle and Poff 2004). Unregulated, interconnected river systems have driven the adaptation and evolution of fluvial organisms, and preservation of stream communities will ultimately require trade-offs between ecological needs of streams and human needs associated with freshwater resources (Richter et al. 2003; Lytle and Poff 2004; Limburg et al. 2011). Restoration approaches targeting improvement at riverscapes scales hold potential for successful species and ecosystem preservation; however, such approaches are limited by the ability to identify appropriate spatial scales at which to implement management actions (Fausch et al. 2002). Our findings suggest that providing connectivity at spatial scales on the order of hundreds of river kilometers is likely necessary for the preservation of at least one diverse functional group of stream-dwelling organisms in the Great Plains, which is consistent with recent calls for improving or maintaining connectivity within steams across the globe (e.g., Nilsson et al. 2005; Agostinho et al. 2007; Dudley and Platania 2007).

Acknowledgments

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