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Early life history of three pelagic-spawning minnows *Macrhybopsis* spp. in the lower Missouri River

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Life-history characteristics of age-0 sturgeon chub *Macrhybopsis gelida*, shoal chub *Macrhybopsis hyostoma* and sicklefin chub *Macrhybopsis meeki* were compared using several methods. All *Macrhybopsis* species consumed mostly midge pupae, but *M. meeki* had the most general diet (Levins' index, B = 0.22) compared with *M. hyostoma* (B = 0.02) and *M. gelida* (B = 0.09). Morisita's diet overlap index among species pairs ranged from 0.62 to 0.97 and was highest between *M. hyostoma* and *M. gelida*. Daily ages estimated from lapilli otoliths for each species ranged from 15 to 43 days for *M. gelida*, 19 to 44 for *M. hyostoma* and from 16 to 64 days for *M. meeki*. Mean growth rates ranged from 0.79 mm day⁻¹ for *M. meeki* to 1.39 mm day⁻¹ for *M. gelida*. Mortality estimates indicated high daily survivorship rates for *M. meeki* (0.985), but could not be estimated for the other two species. Hatch date histograms were congruent with the belief that *M. hyostoma* and *M. gelida* spawn periodically from June to September. *Macrhybopsis meeki*, however, appeared to respond to a specific spawning cue as hatch dates were unimodal with a peak in July. These results fill a gap in current knowledge of these imperilled species that can be used to guide management decisions.

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Key words: broadcast spawners; daily age; daily growth; diet; hatch date; otolith.

INTRODUCTION

Macrhybopsis species are part of a unique guild of pelagic-broadcast spawning minnows inhabiting the Great Plains of the U.S.A. whose life history requires long (up to 300 km) lengths of riverine habitat for successful reproduction (Dieterman & Galat, 2004; Perkin & Gido, 2011; Hoagstrom & Turner, 2013). Declines of these species have been linked to fragmentation and impoundment that increases egg mortality due to settling, lack of spawning habitat resulting from reduction in discharge and reductions in effective population size (Bonner & Wilde, 2000; Alo & Turner, 2005; Galat *et al.*, 2005*a*; Dudley & Platania, 2007). For example, extant populations of sturgeon chub *Macrhybopsis gelida* (Girard 1856) have been reduced by more than 70% from their native range, whereas shoal chub *Macrhybopsis hyostoma* (Gilbert 1884) has been

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reduced by *c*. 40% (Perkin & Gido, 2011). Although previous studies have properly investigated the adult life stages of these species, there is a paucity of information on early life stages, which may better elucidate factors affecting recruitment (Braaten & Guy, 2002; Everett *et al.*, 2004; Ridenour *et al.*, 2009). Early life stages of fishes are particularly sensitive to anthropogenic alterations of habitat, which can lead to recruitment bottlenecks for fishes (Rice *et al.*, 1987; Scheidegger & Bain, 1995; Humphries *et al.*, 2002; Reeves, 2006).

The Missouri River, one of the largest rivers in the U.S.A., is a native habitat for several Macrhybopsis species, but has been heavily modified and fragmented to fit the needs of human civilization (Petts, 1984; Galat et al., 2005b). The physical effects of these anthropogenic alterations have reduced the total surface area of the Missouri River by over 67%, the total river length by at least 204 km and eliminated over 178 million ha of river channel, erosion zone, floodplain grass and timber and tributary valley lands (Morris et al., 1968; Hesse, 1987). In concert with river alteration, populations of sicklefin chub Macrhybopsis meeki (Jordan & Evermann 1896) and M. gelida have been extirpated from over half of the river's length, and their numbers continue to decline (Galat et al., 2005a). Population densities of Macrhybopsis species in the channelized reach of the Missouri River, Nebraska, were reduced as much as 95% between 1971 and 1992 (Hesse et al., 1993). In Kansas, M. meeki is listed by the state as endangered while *M*. gelida is currently listed as threatened with a proposal to reclassify it as endangered (Haslouer et al., 2005). In addition, these species are important prey items for federally endangered pallid sturgeon Scaphirhynchus albus (Forbes & Richardson 1905) juveniles and adults (Gerrity et al., 2006; Winders et al., 2014). Thus, Macrhybopsis species are not only a component of the resident ichthyofauna that evolved in large, dynamic river systems, but also a critical part of the entire ecosystem upon which other species depend. There is currently a concerted effort to restore S. albus populations and shallow-water habitat in the lower Missouri River (Gemeinhardt et al., 2015; Starks et al., 2015) and understanding the early life history of its major prey base (i.e. *Macrhybopsis* species) can inform this effort. Furthermore, because these species have not been well studied at the early life stage, such information can provide valuable information across their range. As a result, analysis of feeding patterns, growth, survival estimates and hatch dates of YOY Macrhybopsis species found in shallow-water habitat were the objectives of this study.

MATERIALS AND METHODS

Macrhybopsis spp. were collected by U.S. Army Corps of Engineers biologists as part of a larger project investigating responses of juvenile fishes to restoration activities in the lower Missouri River. Fishes were collected from May to August 2012 at six sites (Fig. 1) using bow-mounted push trawls (2·4 m wide with $2 \text{ m} \times 0.76 \text{ m} \times 0.38 \text{ m}$ otter doors) and bow-mounted benthic otter trawls (4·9 m wide with $2 \text{ m} \times 0.91 \text{ m} \times 0.38 \text{ m}$ otter doors). Both trawls had 4 mm mesh nets and were deployed according to the Missouri River Standard Operating Procedures for Fish Sampling and Data Collection (Welker & Drobish, 2010). Habitats sampled were primarily classified as shallow water (<1·5 m deep, <0·6 m s⁻¹ water velocity), which has been found to be conducive to age-0 year fishes (Lister & Finnigan, 1997; Schiemer *et al.*, 2001, 2003).

Macrhybopsis spp. were identified to species based on a recently developed suite of characteristics that have shown 90% accuracy at this life stage as verified through genetic analysis (J. Dattilo, unpubl. data), measured for total length (L_T , mm), and dissected to remove gut



FIG. 1. Missouri River extending across the state of Missouri along with sites sampled for age-0 year *Macrhy*bopsis spp. in 2012.

and lapilli otoliths. Gut contents were removed, counted and identified to the lowest practical taxonomic level. Feeding patterns were assessed using a graphical method to characterize feeding strategy (specialization *v*. generalization), relative prey importance (rare or dominant) and niche variation (high within or high among individual variation) (Costello, 1990; Amundsen *et al.*, 1996). This method plots prey-specific abundance against frequency of occurrence. Prey-specific abundance was calculated using the equation: $P_i = \left\{ \left[\left(\sum S_i \right) \left(S_{ii}^{-1} \right) \right] 100 \right\}$, where P_i represents prey-specific abundance of prey *i*, S_i equals the abundance of prey *i* in stomachs and S_{ii} equals the total abundance of prey in predators that contain prey *i*. Frequency of occurrence was calculated by dividing the number of fish containing a specific prey item by the total number of fish (within a species) with food in their stomachs (Chipps & Garvey, 2007).

Furthermore, diversity of prey items consumed by each species was quantified with the Levins' index (Levins, 1968; Marshall & Elliott, 1997). Values of Levins' index range from 0 (specialized diet) to 1 (generalized diet) (Spiegel *et al.*, 2011).

Morisita's index was used to quantify niche overlap between the species pairs (Morisita, 1959; Chipps & Garvey, 2007). When prey numbers are available, Morisita's index is recommended as the most robust and accurate measure of niche overlap (Smith & Zaret, 1982).

Each lapillus was fixed to slides using thermoplastic quartz cement (Hugh Courtright and Co. Ltd; www.right-tape.com) with the macular hump facing down. Daily ages of all specimens were estimated by counting presumptive daily rings with a Motic BA400 stereomicroscope (Motic, Xiamen Electric Group; www.motic-electric.com). All otoliths were immersed in oil and read whole. Slides were randomized and ages were estimated twice by one person. The greatest age was assigned if the two estimates differed by <10%. If estimates differed by >10%, a third estimate was obtained. Estimates that did not fall within 10% after three examinations were removed from further analysis (specimens removed included four *M. gelida*, 10 *M. hyostoma* and six *M. meeki*). Otoliths from individuals >50 mm were opaque and age estimation was increasingly difficult for these specimens. Larger fishes have larger otoliths, including a more bulbous macular hump in the lapillus which could hinder ring visibility and affect ring counts (Assis, 2005;

TABLE I. Summary of the analysed age-0 year *Macrhybopsis* species caught in the lower Missouri River, Missouri. Descriptions include number of specimens (n), mean \pm s.D. total length (L_{T}) , Levins' index of specialization (B) and Morisita's overlap index (M)

Species	п	$L_{\rm T}$ (mm)	В	М
Macrhybopsis gelida	40*	31.0 ± 14.5	0.09	0.97 (M. gelida–M. hyostoma)
Macrhybopsis hyostoma	44†	32.1 ± 9.9	0.02	0.62 (M. hyostoma–M. meeki)
Macrhybopsis meeki	67‡	30.1 ± 10.3	0.22	0.65 (M. meeki–M. gelida)

* L_T and s.D. included two other individuals, one with an empty gut and one that was not preserved correctly. $\dagger L_T$ and s.D. included two individuals with empty stomachs.

 $\sharp L_{\rm T}$ and s.D. included one individual with an empty stomach.

Murie et al., 2006; Durham & Wilde, 2008). Therefore, otoliths from individuals >50 mm were placed on slides with the macular hump facing up and polished with 2000 grit polishing paper and 0.3 micron alpha alumina powder (Electron Microscopy Sciences; www.emsdiasum.com) to increase ring visibility. Estimated ages were then subtracted from capture date to estimate hatch date. Although age estimates have not been validated for these species, daily increment formation has been validated for other species of Cyprinidae (Smith & Walker, 2003; Durham & Wilde, 2008) with the first ring forming at hatch (Smith & Walker, 2003; Durham & Wilde, 2005). Catch curve analysis was used to estimate daily survival rate (S) of each species with the equation $S = e^{-Z}$, where Z (instantaneous mortality rate) is the slope of the relationship between the natural logarithm number of individuals captured $(\ln N)$ and daily age as determined through linear regression (Essig & Cole, 1986; Durham & Wilde, 2008). Survival estimates with corresponding 95% C.I. were only reported for linear regressions meeting the statistical significance level of $P \le 0.05$ (*i.e.* slope Z significantly different from 0). Linear regression analyses were also performed between estimated age and $L_{\rm T}$ to estimate daily growth and size at hatch. All regression analyses were conducted with SigmaPlot v. 13 (Systat Software Inc.; www.sigmaplot.com) software. Age-at-capture frequencies were also plotted by date and site.

RESULTS

FEEDING PATTERNS

Juvenile *Macrhybopsis* fed on a variety of prey types and feeding patterns varied among species (Table I and Fig. 2). Feeding patterns of *M. meeki* were the most varied of the three species, indicating a more general (Levins' index, B = 0.22) and different feeding strategy from *M. hyostoma* (Morisita's overlap index, M = 0.62, Levins' index, B = 0.02) and *M. gelida* (M = 0.65, B = 0.09). The three dominant prey items consumed were midge pupae (mostly Chironomidae), Cladocera and midge larvae (mostly Chironomidae). Less common prey items included Hydropsychidae and Hydroptilidae larvae (order Trichoptera), Ephemeroptera larvae (mostly Heptageniidae), Ostracoda, Copepoda nauplii, Cyclopoidea Copepoda and Odonata larvae.

Macrhybopsis hyostoma and *M. gelida* diets were very similar (Morisita's overlap index = 0.97). Both diets were dominated by midge larvae, which occurred in over 73% of individuals. This represented a more specialized feeding strategy [Levins' index, B = 0.02 (*M. hyostoma*), B = 0.09 (*M. gelida*)] than observed for *M. meeki* (B = 0.22). The main diet difference between *M. hyostoma* and *M. gelida* was midge pupae, which *M. gelida* consumed in greater quantity when present in the diet. Although terrestrial invertebrates appeared to be consumed differently, these were represented by only three

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FIG. 2. (a) Amundsen index graph indicating, feeding strategy, prey importance and niche width contribution of prey categories and specifically for age-0 year (b) *Macrhybopsis gelida*, (c) *Macrhybopsis hyostoma* and (d) *Macrhybopsis meeki* sampled from the lower Missouri River, Missouri, in 2012. Prey items: Cladocera (□), nauplii (■), Cyclopoidea (○), midge larvae (●), midge pupae (▽), Ephemeroptera larvae (▼), Hydropsychidae larvae (△), Hydroptilidae larvae (▲), Odonata larvae (◇), Ostracoda (◆) and terrestrial invertebrates (×).

items: an Annelida worm consumed by *M. hyostoma* and an Arachnida spider and a Tipulidae (order Diptera) larvae-adult instar consumed by *M. gelida*.

AGE, GROWTH AND MORTALITY

Ages could be estimated for 31 *M*. gelida, 30 *M*. hyostoma and 53 *M*. meeki (Table II). Ages ranged from 15 to 43 days for *M*. gelida, from 19 to 44 days for *M*. hyostoma and from 16 to 64 days for *M*. meeki. Slopes of regressions for catch curve analyses were not significantly different from 0 for *M*. gelida (first-order polynomial regression, $F_{1,18} = 3.44$, P > 0.05) and *M*. hyostoma (first-order polynomial regression, $F_{1,14} = 2.89$, P > 0.05), so no estimate of daily *S* was produced for these two species. The catch curve analysis for *M*. meeki was statistically significant (first-order polynomial regression, $F_{1,24} = 5.14$, P < 0.05), with a slope Z = -0.015 (95% c.I.:

Species	Number of specimens aged	Mean±s.D. age (days)	Per cent daily survival	Size at hatch (mm; y-intercept estimate from regression)	Growth rate (mm day ⁻¹ ; slope estimate from regression)	77
Macrhybopsis gelida	31	26.5 ± 7.6	NA*	-7.45	1.39	0.77
Macrhybopsis hyostoma	30	26.7 ± 5.6	NA*	(-15.36 to 0.47) -2.88	(1.11 to 1.68) 1.24	0.56
	ر بر م	0 11 - 1 00	0.005	(-14.35 to 8.60)	(0.82 to 1.67)	
Macrnybopsis meeki	cc	9.11 ± 1.20	0.971 to 0.999)	5.21 (1.70 to 8.72)	0.79 (0.69 to 0.89)	79.0

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-0.029 to -0.001), which translated to an estimate of S = 0.985 (95% c.i.: 0.971 to 0.999). Regressions of $L_{\rm T}$ on age were significant for each species, explaining from 56 to 82% of the variation (*M. gelida*, first-order polynomial regression, $F_{1,29} = 98.3$, P < 0.01; *M. hyostoma*, first-order polynomial regression, $F_{1,28} = 36.4$, P < 0.01; *M. meeki*, first-order polynomial regression, $F_{1,51} = 236$, P < 0.01; Table II and Fig. 3). Mean daily growth rates, as estimated from the slope of linear regressions, ranged from 0.79 mm day⁻¹ for *M. meeki* to 1.39 mm day⁻¹ for *M. gelida*. *y*-Intercept values from regressions indicated variation in size at hatch: -7.45 mm for *M. gelida*, -2.88 mm for *M. hyostoma* and 5.21 mm for *M. meeki*, although the estimated values for *M. gelida* and *M. hyostoma* included 0 within their respective 95% c.i.

AGE AT CAPTURE AND HATCH DATE

Patterns of hatch dates varied among species (Fig. 4). *Macrhybopsis gelida* spawned throughout the summer, ranging from early May to late August. *Macrhybopsis hyos-toma* were represented by three distinct spawning events in late May, mid-July and mid-August. *Macrhybopsis meeki* hatch dates showed a distinct, bell-shaped curve that started in early June, peaked in mid-July and subsided in mid-August.

Distribution of ages for all species matched the hatch date patterns observed in Fig. 4 (Fig. 5). *Macrhybopsis gelida* and *M. hyostoma* age frequencies were variable throughout the summer while *M. meeki* individuals were progressively older as time passed. Over 92% of individuals from all the three species collectively were caught in the sites grouped in the middle of the sampling extent (Lisbon, Jameson and Overton; Table III).

DISCUSSION

The present results suggest differential feeding patterns as well as potential differences in reproductive output and growth among species. Notably, *M. meeki* were the most different, having the least specialized diet, but a potentially specific spawning cue, whereas the other two species had more specialized diets but more general spawning patterns.

Diet studies offer an opportunity to understand some basic, yet important, aspects of biology that can be used for management purposes. Results of this study fill a gap in a sparsely populated field of data on prey use by these species. Few studies exist on *M. hyostoma* diets and these report varying results. For example, adult populations in Wisconsin were shown to rely on Coleoptera, Hemiptera, Odonata and Trichoptera (Becker, 1983) compared with populations farther south that consumed midges exclusively (Starrett, 1950). In Texas, diets of adult *M. hyostoma* had a high occurrence of midge and Trichoptera larvae (Williams, 2011). Data from this study of juvenile diets are comparable only with juveniles in the lower Brazos River, Texas, where mostly detritus and sand were consumed (Williams, 2011). It is difficult to determine if these differences could be attributed to habitat or diet plasticity, but additional studies in more areas would help determine the adaptability of this species to prey availability.

The few studies of *M. gelida* food habits vaguely describe them as carnivorous minnows feeding mostly on small invertebrates living on the bottom substrata (Reigh & Elsen, 1979). Results of this study indicate that juvenile *M. gelida* rely heavily on midge larvae, but without knowledge of prey availability, it is not known if this pattern



FIG. 3. Total length (L_T) and estimated age from backcalculation of otolith daily rings for age-0 year (a) *Macrhybopsis gelida*, (b) *Macrhybopsis hyostoma* and (c) *Macrhybopsis meeki* sampled from the lower Missouri River, Missouri, in 2012. The curves were fitted as (a) y = -7.45 + 1.39x, (b) y = -20.88 + 1.24x and (c) y = 5.21 + 0.79x.



FIG. 4. Hatch date histograms estimated from backcalculation of otolith daily rings for age-0 year (a) *Macrhybopsis gelida*, (b) *Macrhybopsis hyostoma* and (c) *Macrhybopsis meeki* sampled from the lower Missouri River, Missouri, in 2012.

occurs due to the species specializing on midge larvae, or because only midge larvae are available for consumption.

Only one other diet study of *M. meeki* is available for comparison, which reported Simuliidae larvae and other insect exoskeletons in the guts (Reigh & Elsen, 1979). *Macrhybopsis meeki* have a reduced number of cutaneous taste buds, but an increased number of internal taste buds and buccal folds, when compared with *M. gelida* (Davis & Miller, 1967; Dieterman & Galat, 2005). This suggests that *M. gelida* may be able to find prey more effectively in turbid systems, whereas *M. meeki* may be more efficient sorting and concentrating food after it has been ingested (Davis & Miller, 1967). These alternative feeding strategies could be selective given reported differences in



FIG. 5. Estimated age in relation to collection date for age-0 year (a) *Macrhybopsis gelida*, (b) *Macrhybopsis hyostoma* and (c) *Macrhybopsis meeki* sampled from the lower Missouri River, Missouri, in 2012. Capture locations as indicated in Fig. 1: Rush (●), Worthwine (O), Lisbon (▲), Jameson (△), Overton (■) and Littles (□).

habitat use. *Macrhybopsis gelida* were associated with areas that have higher water velocity and increased substratum size where a food-finding strategy would be beneficial compared with *M. meeki* that inhabit areas with decreased velocity and smaller substratum types where prey sorting after ingestion may be more important (Everett *et al.*, 2004).

Size at age for age-0 *M. meeki* and *M. hyostoma* was consistent with other studies that assigned age from length-frequency histograms (Dieterman *et al.*, 2006; Williams, 2011), although no study that has directly estimated daily age for these species was found in a literature search. Durham & Wilde (2008) verified daily increment deposition in other Great Plains minnows, sharpnose shiner *Notropis oxyrhynchus* Hubbs & Bonham 1951, smalleye shiner *Notropis buccula* Cross 1953 and plains minnow *Hybognathus placitus* Girard 1956, 30 days post-marking. Age estimates were obtained

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Species	Rush	Worthwine	Lisbon	Jameson	Overton	Littles
Macrhybopsis gelida	8.6	2.9	45.7	24.7	11.4	5.7
Macrhybopsis hyostoma	2.5	0.0	50.0	27.5	17.5	2.5
Macrhybopsis meeki	0.0	0.0	88.1	6.8	1.7	3.4

 TABLE III. Proportion (%) of Macrhybopsis spp. caught by site in the lower Missouri River, May to August 2012. Sites are ordered from upstream to downstream (see Fig. 1)

up to 75 days, demonstrating the utility for estimating daily age of this group of fishes and similar to the results observed in this study.

Fishes in Great Plains streams commonly exhibit a bet-hedging strategy of prolonged reproductive output throughout their spawning period (Durham & Wilde, 2005), but these strategies are apparently species-specific. Macrhybopsis hyostoma and *M. gelida* appear to follow a punctuated strategy of reproduction with spates of spawning throughout the year (Dieterman et al., 2006). In contrast, M. meeki exhibited a bell-shaped pattern, with a peak in July. Interestingly, the patterns of hatch dates between M. meeki and M. gelida were very different even though these species are closely related with similar minimum river lengths required for population persistence (c. 300 km; Perkin & Gido, 2011). Species-specific differences in reproduction modes for pelagic-spawning minnows have not been addressed much previously, but this study suggests that they exist. For example, M. gelida in the Brazos River, Texas, had a trimodal distribution of oocyte sizes and reproduced from early spring to late autumn (Williams, 2011) in concert with the hatch dates from this study. Because fishes in this study were caught in similar habitats at the same times of year, the differences observed probably reflect real differences in reproduction and not artefacts of sampling. Thus, while M. gelida and M. meeki both require long reaches of unfragmented river, M. meeki may be tied to a more specific spawning cue, as suggested by their unimodal peak in hatch dates. Oocyte development in mature M. meeki indicated the capacity for multiple spawning during a season (Dieterman et al., 2006), although most females exhibited unimodal distributions of egg diameter. While a unimodal oocyte diameter distribution mirrors findings of unimodal hatch date frequency in this study, M. meeki have been observed spawning multiple times within the same season in laboratory settings (J. Albers, unpubl. data). It appears likely then that this species exhibits batch-spawning with the majority of individuals spawning at the same time in response to some unknown cue with the potential for additional, opportunistic spawning at other times.

Interestingly, older individuals (>45 days) of both *M. hyostoma* and *M. gelida* were not collected in this study, potentially explained by either mortality or capture efficiency. Mortality could not be estimated for these species because of a lack of a statistically significant negative slope. Mortality, however, is unlikely to explain the lack of older individuals because it would imply differential mortality for older fishes, which has not been shown in similar species (Wilde & Durham, 2008). More likely is that sampling was inefficient at capturing older, larger individuals because they could avoid the sampling gear or they moved out of the sampling area and were unavailable to be captured. Either explanation could affect estimates of spawning distribution, but to what degree is unknown. Few attempts have been made to study these small-bodied fishes in large rivers, which remain challenging to researchers. Estimates of growth based on otolith examination lend credence to capture efficiency decline of *M. hyostoma* and *M. gelida*. Growth rates of these two species were markedly greater $(1.24 \text{ mm day}^{-1} \text{ for } M. hyostoma$ and 1.38 mm day^{-1} for *M. gelida*) than the estimate of 0.79 mm day⁻¹ for *M. meeki*, suggesting larger individuals of the former two species recruited past the gears or moved to non-sampled areas sooner than *M. meeki*, differentially affecting the distribution of sizes in the catch. The estimated survival estimate for *M. meeki* was slightly higher than for other small-bodied fishes inhabiting large rivers (0.920–0.964; Wilde & Durham, 2008), but the estimate obtained in this study was based on a relatively small sample size and would improve with increased numbers of fish examined. But, extrapolated through an entire year, this daily survival estimate translates to an annual survival estimate of *c*. 0.0041, which is very similar to that reported for peppered chub *Macrhybopsis tetranema* (Gilbert 1886) (0.00479) and Arkansas River shiner *Notropis girardi* Hubbs & Ortenburger 1929 (0.00480), lending credibility to the estimate obtained (Wilde & Durham, 2008).

Regardless, the results of this study have implications for managing aquatic ecosystems by suggesting that co-occurring *Macrhybopsis* species cannot be managed collectively as one suite of pelagic-spawning minnows. For example, *M. tetranema* and *M. hyostoma* co-occurred in the Cimarron River, Oklahoma, and both became extirpated in *c*. 1966, but *M. hyostoma* was able to re-colonize from other sources across a large reservoir and expand in the Cimarron River after 1991 (Luttrell *et al.*, 1999). *Macrhybopsis hyostoma* then appears to occupy a more general niche, requiring shorter fragments of river to successfully reproduce, and is more able to expand its population meaning management actions directed at this species will probably not protect its more niche-specialist congeners.

This study contributes significantly to understanding the ecology of these pelagic-spawning minnows. While some data for comparison exist, most are solely focused on adult life stages. Examination of early life stages is a notable gap of knowledge in the biology of these species. The autecological information provided by this study could be used in part with other findings to form a holistic management strategy to conserve these imperilled species.

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