

EFFECTS OF RESERVOIR MANAGEMENT ON ABUNDANCE, CONDITION,  
PARASITISM AND REPRODUCTIVE TRAITS OF DOWNSTREAM MUSSELSH. S. GALBRAITH<sup>\*,†</sup> and C. C. VAUGHN*Oklahoma Biological Survey and Department of Zoology, University of Oklahoma, 111 East Chesapeake St., Norman, Oklahoma 73019, USA*

## ABSTRACT

The large-scale impoundment of rivers has led to global declines in freshwater mussel populations. It is important to understand the mechanisms underlying these declines to initiate an effective recovery strategy. We examined population traits of three *Quadrula* species (*Quadrula pustulosa*, *Q. cylindrica* and *Q. quadrula*) at three locations that were exposed to two different reservoir management regimes: releases that mimicked natural flow patterns and releases that were higher and colder in summer months than the natural system. We found lower mussel density, higher hermaphroditism and parasitism rates, and reduced body condition downstream of the dam with unnatural flow regimes. Sex ratios varied on a species and site basis. We found more *Quadrula cylindrica* females than males averaged across all three sampling sites while *Q. pustulosa* was male biased across all sites and at site 1. We observed approximately equal sex ratios in *Quadrula quadrula*. Population disturbances downstream of the more naturally-regulated dam were not as severe. Our data indicate that dam operation can have effects on a variety of mussel life history characteristics that may ultimately reduce population viability. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: unionid; impoundment; dam; temperature; flow; sex ratio; parasitism; hermaphrodite

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## INTRODUCTION

Dams alter physicochemical characteristics of rivers including flow regimes, temperature, light, material cycling and availability and sediment load both upstream and downstream of the dam itself (Benke, 1990; Allan and Flecker, 1993; Poff *et al.*, 2007). These habitat alterations have both direct and indirect effects on aquatic organisms including mortality, disruption of reproductive cues, reduced migration and food web disruption (Poff *et al.*, 1997; Poff and Hart, 2001; Lytle and Poff, 2004). Ecological impacts depend on degree of flow modification relative to pre-impoundment conditions (Poff *et al.*, 1997; Poff and Hart, 2001; Poff *et al.*, 2007). For example, release schedules result in temporarily discordant high and low flows, both on a daily or seasonal basis (Poff *et al.*, 1997; Richter and Richter, 2000).

The large-scale impoundment of rivers has affected organisms on a global scale, including freshwater mussels (Bivalvia: Unionidae), a group of benthic, filter-feeding bivalves that provide important ecosystem services in rivers (Spooner and Vaughn, 2006; Vaughn *et al.*, 2007; Vaughn *et al.*, 2008). Freshwater mussels are one of the most

globally imperiled faunas. As of August 2009, approximately 165 unionid mussels were listed as extinct, critically endangered, endangered, vulnerable or near threatened on the IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org)). Mussels possess a suite of life-history traits that make them highly susceptible to dam-induced habitat alteration (Watters, 2000). Adult mussels are sedentary and therefore have limited ability to seek refuge from certain disturbances (e.g. temperature, drought) (Byrne and McMahon, 1994; Haag and Warren, 2008; Spooner and Vaughn, 2008). Mussels are long-lived, have delayed reproduction and juvenile survivorship is low, which presumably decreases overall recruitment (summarized in McMahon and Bogan, 2001). Mussels also have a complicated life history including a larval stage that is ectoparasitic on fish and host specialists are common (Haag and Warren, 1998; Haag and Warren, 2003; Barnhart *et al.*, 2008). Hermaphroditism can also be common in freshwater mussels, particularly small, isolated populations (Heard, 1975).

Reproduction is one of the most critical periods in a mussel's life and is crucial to conservation efforts. There are often narrow windows during which conditions are optimal for mussel reproduction, and reproductive adults, juveniles or gametes can be extremely sensitive to stressors (Sparks and Strayer, 1998; Heinricher and Layzer, 1999; Galbraith, 2009; Galbraith and Vaughn, 2009). Understanding how human modifications to environmental conditions impact mussel reproduction can be difficult given their long lives,

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delayed reproduction, and complex life cycles. Unfortunately, most conservation research has focused primarily on adult organisms, neglecting the larval, embryonic and gametic stages believed to represent a significant 'bottle-neck' to recruitment.

Numerous studies have documented mussel declines downstream of dams (Suloway *et al.*, 1981; Miller *et al.*, 1984; Williams *et al.*, 1992; Layzer *et al.*, 1993; Vaughn and Taylor, 1999; Garner and McGregor, 2001), but relatively little is known about the mechanisms underlying these declines (Bogan, 1993; Watters, 2000). It is likely that mussel reproduction and condition of both adult and early life stages are affected by dam-induced changes in stream physicochemical parameters. Unionid mussels evolved in rivers that experienced seasonal periods of low and high flow, and recent studies indicate that natural, temporal variability is important for successful recruitment (Vaughn and Taylor, 1999; Gore *et al.*, 2001; Hardison and Layzer, 2001). Freshwater bivalves use water temperature changes as a cue for gamete release (Fong *et al.*, 1995; Galbraith and Vaughn, 2009). Layzer *et al.* (1993) noted that thermal regimes below dams were directly responsible for inhibiting mussel reproduction. Furthermore, Heinricher and Layzer (1999) showed that *Megaloniais nervosa* individuals located downstream of hypolimnetic release dams showed

no indication of reproduction in their gonads or marsupia. Dams also fragment rivers and impede fish host movement potentially limiting dispersal and gene flow (Watters, 1996, 2001; Barnhart *et al.*, 2008).

This study examines population characteristics of downstream unionid mussels in relation to dam management. We compare densities, mussel sex ratio, percent hermaphroditism, body condition and parasite load among three sites in a river influenced by two dams with different management strategies. We then use our results to formulate a conceptual model explaining possible mechanisms underlying mussel decline downstream of dams.

## MATERIALS AND METHODS

### *Study area and species*

The study was conducted in the Little River in southeastern Oklahoma, US (Figure 1), in the Ouachita Mountains region of the Interior Highlands. The Interior Highlands is a centre of speciation for both aquatic and terrestrial organisms, and the Little River historically harboured 37 species of unionid mussels (Mayden, 1985; Moulton and Stewart, 1996; Galbraith *et al.*, 2008). The Little River is influenced by two dams. The mainstem is impounded by

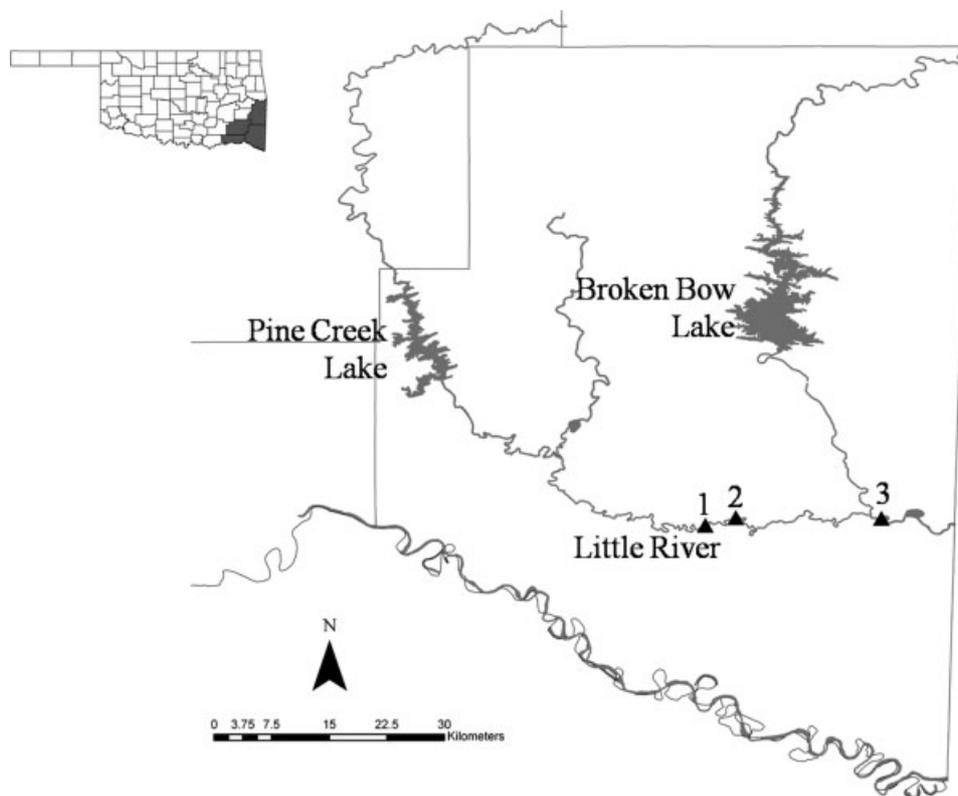


Figure 1. Location of sampling sites in the Little River in southeastern Oklahoma, USA

Pine Creek Reservoir (PCR), which is used for flood control, municipal water supply and recreation (OWRB, 2007). The Mountain Fork River is a major tributary of the Little River and is impounded by Broken Bow Reservoir (BBR). BBR is a hypolimnetic release dam primarily used to generate hydroelectric power and to provide large pulses of coldwater during summer months for a non-native, stocked trout fishery (ODWC, 2008).

We chose three sites with abundant, diverse mussel assemblages (Vaughn and Taylor, 1999; Galbraith *et al.*, 2008) and different flow and temperature regimes. Site 1 was located ~60 km downstream of PCR, site 2 was located ~5 km downstream from site 1 (65 km downstream of PCR). Both sites 1 and 2 were located upstream from the confluence of the Mountain Fork River (Figure 1). Site 3 was located ~85 km downstream of PCR and 40 km downstream from BBR (Figure 1). All sites were on the relatively pristine USFWS-operated Little River National Wildlife Refuge and experienced similar watershed land use (OWRB, 2007).

We studied three species in the genus *Quadrula*: the pimpleback (*Q. pustulosa*), the rabbitsfoot (*Q. cylindrica*) and the mapleleaf mussel (*Q. quadrula*). These species co-occur in many rivers in the Mississippi Basin (Parmalee and Bogan, 1998). Several members of this genus are either federally endangered (e.g. *Q. fragosa*) or listed as species of special concern (*Q. cylindrica*). Therefore, we were particularly interested in the reproductive biology of this genus. Because of their widespread distribution, however, data collected on these species will also pertain to other mussel species.

#### Environmental parameters

We collected water temperature data every 30 min for an entire year using HOBO (Onset, Pocasset, MA, USA) data loggers (Galbraith and Vaughn, 2009). We also gathered online reservoir intake and release data from the US Army Corps of Engineers for both PCR (<http://www.swt-wc.usace.army.mil/PINE.lakepage.html>) and BBR (<http://www.swt-wc.usace.army.mil/BROK.lakepage.html>) and analysed these data for patterns in inflow and outflow. The reservoir data that we examined were collected between January 1995 and December 2006.

#### Mussel sampling

In August 2005 we quantitatively sampled mussels at the three sites to estimate population densities. At each site we excavated 30, randomly-placed 0.25 m<sup>2</sup> quadrats to a depth of ~15 cm, and identified and measured mussels, and returned mussels to their original location (Vaughn *et al.*, 1997; Strayer and Smith, 2003). On a monthly basis from September 2005 through August 2006 (except during

December, January and March due to inclement weather and high water), we used timed searches to collect as many members of each species as possible. Timed searches consisted of at least 2 h of searching for mussels by hand, snorkel, or SCUBA. We collected, marked, weighed and measured as many individuals of each species as we could find. We also collected a small (~50 µl) gonad sample from the visceral mass with a syringe and preserved the samples in 10% buffered formalin. This non-lethal technique for determining sex in non-sexually dimorphic mussels allows large sample sizes without killing individuals (Shiver, 2002; Saha and Layzer, 2008). We examined gonad samples under a microscope to determine sex (including hermaphroditism) and to determine presence or absence of sterilizing trematodes (Jokela *et al.*, 1993).

#### Data analyses

Individual mussels were only represented once in all of our data analyses (i.e. recaptured mussels were not included). We analysed log of mean mussel density (from quadrat data collected in August 2005) on a species-by-site basis using a two-way ANOVA with a Tukey *post hoc* comparison. We used  $\chi^2$  analysis to determine differences in parasite presence or absence among sites. To do this, we pooled all parasitized individuals collected during the year-long field study within each site. It is a general assumption in models of parasite infection that parasite transmission is a function of host density (May and Anderson, 1979; Toft *et al.*, 1991; Loot *et al.*, 2005). Therefore, we assumed that rates of parasitism should be a function of mussel density and weighted our expected proportions in our  $\chi^2$  by species density at each site. To do this, we multiplied the expected number of parasitized individuals (i.e. equal numbers among sites) by the relative differences in mussel density among sites to come up with a weighted expected number of parasitized individuals.

We estimated mussel body condition for each individual collected over the course of the year using the Fulton's *K* metric in which body condition ( $K$ ) =  $l^3/w(10^6)$ , where  $l$  is mussel shell length and  $w$  is mussel wet weight (including the shell). This measure of condition has been traditionally used in the aquaculture literature (Mgaya and Mercer, 1995), but has been successfully applied to freshwater mussels (Spooner and Vaughn, 2008). Low body condition individuals had lower wet weights relative to shell length whereas high body condition individuals were heavier than predicted by length. We used ANOVA and a Tukey *post hoc* comparison to test for differences in body condition among sites. Because the three species differed in their body size and shape (and potentially growth constraints) we did not compare differences in body condition among species using this metric.

We used  $\chi^2$  to determine if sex ratios were equal both between and within individual sites. We also used  $\chi^2$  to test for differences among sites in incidence of hermaphroditism (both female and male gametes present in the same gonad), again using the mussels collected during the year-long field study. We tested the null hypothesis that hermaphrodites are equally distributed among all three sites (i.e. expected numbers of hermaphrodites should be equal at all sites).

## RESULTS

There were differences in reservoir release patterns between PCR and BBR (Figure 2). PCR releases almost identically mimicked reservoir inflows during the entire year, with

slight deviations during February and March. On the other hand, BBR releases varied considerably from inflow with reservoir release substantially higher than inflow during summer months when natural stream flow is generally low. These differences in reservoir release patterns translated into differences in water temperature at the mussel beds (Table I). In particular, Site 3 has significantly colder summer temperatures and warmer winter temperatures than the other two sites because of its location downstream of BBR (Table I; Galbraith and Vaughn, 2009).

We found significant differences in mussel density (Table II) among sites ( $F_{(2,261)} = 29.25$ ,  $p < 0.001$ ) and species ( $F_{(2,261)} = 165.79$ ,  $p < 0.001$ ) and a significant site-by-species interaction ( $F_{(4,261)} = 19.92$ ,  $p < 0.001$ ). Densities of all three species were significantly different

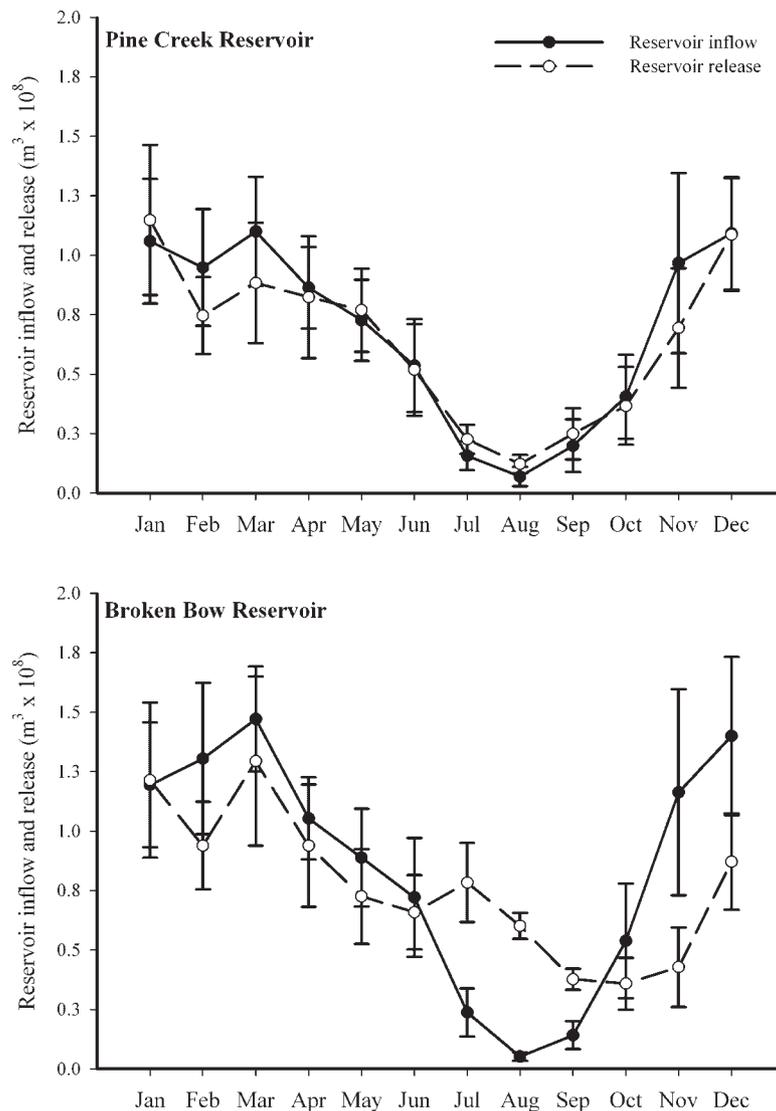


Figure 2. Mean monthly ( $\pm$  SE) reservoir inflow and release for Pine Creek Reservoir (PCR) and Broken Bow Reservoir (BBR). Data were collected between January 1995 and December 2006 by the US Army Corps of Engineers

Table I. Mean seasonal temperature ( $\pm$  SE) for each of our three sampling sites. Temperature was recorded every 30 min with HOBO™ loggers. Data from Galbraith and Vaughn (2009)

Site	Season	Mean temperature ( $^{\circ}$ C)
Site 1	Fall	17.26 (0.57)
	Winter	8.44 (0.16)
	Spring	19.08 (0.47)
	Summer	30.13 (0.18)
Site 2	Fall	17.80 (0.54)
	Winter	8.89 (0.14)
	Spring	18.52 (0.44)
	Summer	30.60 (0.14)
Site 3	Fall	17.25 (0.47)
	Winter	9.22 (0.14)
	Spring	18.89 (0.43)
	Summer	25.91 (0.14)

from each other with *Q. pustulosa* having the highest density followed by *Q. cylindrica* and *Q. quadrula*, respectively. Mussel densities overall were lowest at site 3.

Sterilizing trematodes were generally rare, and found only in *Q. pustulosa* (present in 17 of 460 individuals). We found a significant difference in parasite load among sites ( $\chi^2_{(2)} = 12.85$ ,  $p = 0.002$ ), with higher rates of parasitism than expected at site 3 (Table II).

There were significant differences in mussel body condition across sites (*Q. cylindrica*:  $F_{(2,111)} = 18.51$ ,  $p < 0.001$ ; *Q. pustulosa*:  $F_{(2,272)} = 16.49$ ,  $p < 0.001$ ; *Q. quadrula*:  $F_{(2,34)} = 5.89$ ,  $p = 0.006$ ). Body condition in all three species was consistently lowest at site 3. Female *Q. pustulosa* at site 3 had significantly lower body condition than males (Table II; Figure 3).

There were also differences in sex ratio of each species (Table II). Combining data from all three sites, *Q. cylindrica* had significantly more females ( $\chi^2_{(1)} = 4.03$ ,  $p = 0.045$ ); however, we did not observe differences at individual sites.

Table II. Demographic parameters for *Quadrula* species at three sites in the Little River, Oklahoma. *N* is the total number of individuals sampled over the course of our year-long field study. Mean ( $\pm$  SE) mussel density was estimated from quadrat sampling in August 2005. Number of observed (and expected) parasitized individuals, mean ( $\pm$  SE) body condition of each species, proportion of males in the population and the number of observed (and expected) hermaphroditic individuals were quantified based on data from our year-long field study. See Results section for statistical significance

Site	Species	<i>N</i>	Mussel density (# individuals/m <sup>2</sup> )	# parasitized individuals	Mean body condition	Proportion of males	# hermaphrodites
Site 1	<i>Q. cylindrica</i>	81	2.4 (0.62)	0	133.89 (1.81)	0.37	1 (1.33)
	<i>Q. pustulosa</i>	99	10.27 (2.04)	3 (5.3)	443.36 (7.90)	0.61	0 (1)
	<i>Q. quadrula</i>	14	0.13 (0.13)	0	284.74 (9.13)	0.57	1 (1.67)
Site 2	<i>Q. cylindrica</i>	33	1.07 (0.50)	0	150.25 (3.22)	0.45	2 (1.33)
	<i>Q. pustulosa</i>	115	20.67 (2.16)	6 (9)	441.08 (7.70)	0.54	0 (1)
	<i>Q. quadrula</i>	16	0.53 (0.25)	0	317.39 (13.16)	0.38	0 (1.67)
Site 3	<i>Q. cylindrica</i>	6	0.27 (0.19)	0	113.10 (1.56)	0.67	1 (1.33)
	<i>Q. pustulosa</i>	88	3.73 (0.83)	8 (2.6)	386.58 (6.75)	0.51	3 (1)
	<i>Q. quadrula</i>	8	0 (0)	0	256.46 (11.69)	0.50	4 (1.67)

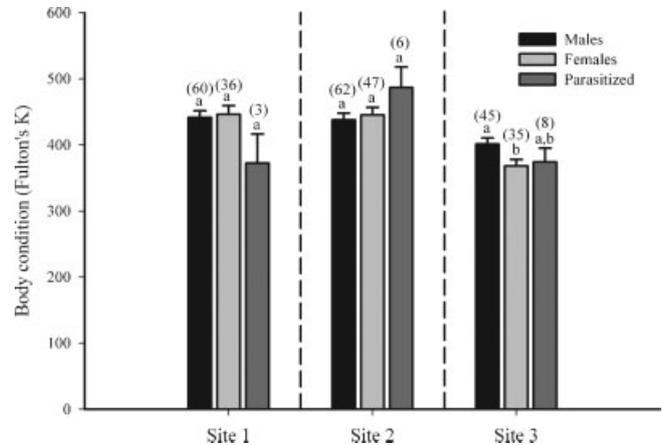


Figure 3. Mean ( $\pm$  SE) body condition of unparasitized males and females and parasitized *Q. pustulosa* at each site (sex cannot be determined in parasitized individuals). Bars with different letters are significantly different from one another within a site based on ANOVA and Tukey *post hoc* comparisons. Significant differences between sites are reported in the results section. Numbers in parentheses represent the total number of individuals of each sex collected over the year-long field study

There were significantly more *Q. pustulosa* males than females ( $\chi^2_{(1)} = 8.4$ ,  $p = 0.004$ ) at all sites combined and at site 1 ( $\chi^2_{(1)} = 6$ ,  $p = 0.01$ ) but no differences between the sexes at sites 2 and 3. *Quadrula quadrula* had equal sex ratios at the three sites combined and within each individual site.

We found a significant difference in the proportion of hermaphroditic individuals among sites ( $\chi^2_{(2)} = 6$ ,  $p = 0.05$ ; Table II). There was no difference among sites in the frequency of *Q. cylindrica* hermaphrodites ( $\chi^2_{(2)} = 0.5$ ,  $p = 0.78$ ). However, site 3 had significantly more hermaphroditic *Q. pustulosa* ( $\chi^2_{(2)} = 6$ ,  $p = 0.05$ ) and marginally more *Q. quadrula* hermaphrodites ( $\chi^2_{(2)} = 5.2$ ,  $p = 0.07$ ) than expected. Incidence of hermaphroditism ranged

between 0 and 7% for sites 1 and 2, but for site 3 was as high as 17% in *Q. cylindrica* and 50% in *Q. quadrula*.

## DISCUSSION

River reaches downstream from dams often experience unseasonal temperature and flow regimes, anoxic conditions, altered patterns of sediment deposition, erosion and particulate organic matter concentrations (Allan, 1995). However, dam management can further influence downstream populations. PCR releases mimic natural variability in rainfall and tributary inflow received by the reservoir. BBR summer releases are cold due to their point of origin (the hypolimnion) and high release volumes to maintain cold water for the downstream trout hatchery (ODWC, 2008). This water exceeds the amount of water naturally entering the reservoir from tributary inflow and rainfall. As a consequence, the mussel populations downstream of BBR experience colder than normal summer temperatures (Table I), higher flow and potentially limited food availability in the form of phytoplankton (Galbraith and Vaughn, 2009) compared to mussel beds downstream of PCR (sites 1 and 2). These factors appear to translate into reduced reproductive success downstream from BBR (Galbraith and Vaughn, 2009).

Densities of all three *Quadrula* species were lower at site 3 than at sites 1 and 2. In addition, we found that mussels at site 3 exhibited greater evidence of stress than mussels at sites 1 and 2, with higher rates of parasitism in *Q. pustulosa* (Table II) and lower body condition for all three mussel species (Table II and Figure 3). Further, we found a higher frequency of hermaphroditism in both *Q. pustulosa* and *Q. quadrula* at site 3 (Table II). We do not know the mechanisms by which altered temperature and flow regimes are impacting mussel reproduction downstream of BBR, but they likely include multiple pathways, all of which ultimately may result in the long-term demise of mussel populations (Figure 4). Disruptions to reproductive cues

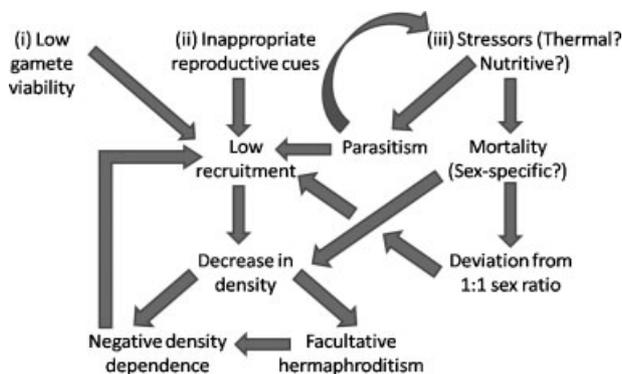


Figure 4. Conceptual model demonstrating the potential effects of dams on reproductive and population traits in mussels

downstream of dams have resulted in reproductive failure of some mussel species (Layzer *et al.*, 1993; Heinricher and Layzer, 1999), and there is evidence that low water temperatures may be disrupting 'typical' seasonal patterns in gametogenesis in the Little River (Galbraith and Vaughn, 2009).

Hermaphrodites often are common in small, genetically isolated populations or in stressful environments and are believed to counteract Allee effects (Ghiselin, 1969; Heard, 1975). Hermaphrodites generally constitute a small proportion (usually less than 10%) of freshwater mussel populations (Haggerty *et al.*, 1995; Garner *et al.*, 1999; Haag and Staton, 2003). However, we found 17% of *Q. cylindrica* and 50% of *Q. quadrula* were hermaphroditic at site 3. Little is known about the factors (temperature, genetics) that govern sex determination in freshwater mussels. Further investigation is needed to determine whether altered thermal regimes downstream of dams could directly cause hermaphroditism by interfering with 'normal' sex-determination.

Lower body condition (such as that observed downstream of BBR) also may increase susceptibility to parasite infection (Gangloff *et al.*, 2008). Sterilizing trematode loads vary among freshwater mussels, but some populations have been found to have infection rates of 100% (Henley *et al.*, 2007). We found parasitism rates < 10%. Trematodes were found only in *Q. pustulosa* and were highest at site 3. Although there was no significant difference in body condition between parasitized mussels and non-parasitized males and females, we examined a relatively small number of parasitized individuals ( $N=17$ ). Further analysis is needed to confirm if low body condition makes particular individuals more susceptible to infection or if the parasites themselves lower body condition of mussels post-infection (Gangloff *et al.*, 2008). We did not find mature gametes in parasitized individuals, suggesting that these trematodes completely sterilize their hosts. This has severe consequences for *Q. pustulosa* reproduction; a substantial portion of individuals are not reproducing, thus lowering the effective population size. Because the syringe biopsy technique only collects gonad samples from a small portion of the viscera, it is plausible that we could have missed localized infestations of parasites or hermaphroditic tissue. Therefore, our estimates of these factors should be considered minimum levels for our sites.

Our sex ratio data also point to a decrease in effective population size throughout the Little River, regardless of distance downstream of a dam. We found significant female-biased sex ratios in *Q. cylindrica* but found a male-biased sex ratio in *Q. pustulosa*. Deviations from a 1:1 sex ratio appear to be common in freshwater mussels (Bauer, 1987; Downing *et al.*, 1989; Byrne, 1998; Garner *et al.*, 1999; Haag and Staton, 2003; McIvor and Aldridge, 2007). In our

system, sex ratios could be equal at conception, with later sex-specific mortality skewing the adult sex ratio. Other possibilities are that one sex (females in *Q. pustulosa* and males in *Q. cylindrica*) has higher rates of parasite infections or that the skewed sex ratio is simply a phase in the development of hermaphroditism within the population (McIvor and Aldridge, 2007; Yusa, 2007). We were unable to confirm or refute the parasitism hypothesis since there were no mature gametes found in any of our parasitized individuals. Nonetheless, the male-biased sex ratio in *Q. pustulosa* indicates that there are fewer female individuals available for reproduction, and thus *Q. pustulosa* abundance is likely on the decline. Galbraith *et al.* (2005) found that *Q. pustulosa* densities in the nearby Kiamichi River, Oklahoma dropped an average of 85% across 10 monitoring sites in a period of less than 15 years. A final explanation for unequal sex ratios could be that our sampling methods under sampled one sex or the other; however, given our rigorous sampling over the course of an entire year we have no reason to believe that this is the case.

Our data indicate that there are complex, indirect effects of dams on mussel reproductive traits. We realize that our data are limited to three sites and two dams within a narrow geographic range. However, other studies have also found that unnatural temperature regimes can have profound, chronic influences on reproduction and population dynamics of species downstream of dams, including not only mussels, but other invertebrates and fish (Munn and Brusven, 1991; Layzer *et al.*, 1993; Voelz *et al.*, 1994; Heinricher and Layzer, 1999; Clarkson and Childs, 2000; Haxton and Findlay, 2008). Our study, in combination with these others, suggests that improper water management and disruption of thermal cues is a serious issue that warrants further investigation, particularly on a larger, continental scale. Therefore, we used our results and the literature to formulate a conceptual model exploring the potential mechanisms underlying unionid declines below dams (Figure 4). The model is not intended to be exhaustive, but to generate testable hypotheses to guide future work in this area. We realize the reproductive trends we observed may not be the result of dams alone. The Little River, and most other rivers across North America, has been altered by other human disturbances (clearing of riparian vegetation, agricultural run-off, channelization, etc.), which could further feed into the model.

Strayer *et al.* (2004) noted that one of the major challenges facing our understanding of unionid decline is that long-lived species like mussels can often persist for decades under conditions of negative population growth. One route of unionid decline leading to negative population growth could be via decreased gamete viability under altered thermal conditions (Figure 4i). Freshwater mussel sperm are only motile within a narrow thermal range (Galbraith, 2009) and

non-motile sperm cannot be used for reproduction (Cierieszko *et al.*, 2001). This could lead to poor recruitment downstream of dams, thus lowering overall mussel densities over time (Figure 4i). A second route of decline could be through direct disruption of reproductive cues (Figure 4ii). We have evidence this is occurring in the Little River (Galbraith and Vaughn, 2009), which could also be contributing to a negative density-dependent feedback loop. It is also plausible that unusual flow, temperature or food availability could cause stress to downstream mussel beds (Figure 4iii; Elser and Kimmel, 1985). Marine mussels exposed to extreme temperatures and low food availability experience sub-lethal, physiological stress effects as well as direct mortality (Incze *et al.*, 1980; Dahlhoff *et al.*, 2002). Therefore, it is not unreasonable that these factors would also influence freshwater mussel body condition thereby decreasing survivorship and eventually overall mussel density. High prevalence of hermaphroditism, parasitism and skewed sex ratios are likely to fit into this model and play a role in the slow demise of mussel beds (Figure 4). Strayer *et al.* (2004) mention the need to identify demographic and physiological indicators of mussel population stress as a means of early detection of population decline. These factors may be easily-quantified, candidate characteristics that allow us to assess trends in mussel populations and predict mussel loss.

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