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REGULAR ARTICLE

CHANGES IN THE MUSSEL FAUNA OF THE JACKS FORK, MISSOURI OVER 35 YEARS AND RELATIONSHIPS WITH SPECIES TRAITS

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ABSTRACT

We conducted a mussel survey of the Jacks Fork, Missouri, an Outstanding National Resource Water, to document mussel diversity and distribution in the watershed, to determine if changes had occurred since a previous survey in 1982, and to relate observed changes to species traits. We surveyed mussels with timed tactile or visual searches at 28 sites during summer from 2017 to 2019 and compared our results with the 1982 survey. Catch per unit effort, number of live individuals, species richness, and diversity were significantly lower in 2017–19 than in 1982. The proportion of extirpation at the 11 resurveyed sites averaged 0.85 (range 0.50–1.00) among species, and the proportion of colonization was 0.0 for all species. There were no differences in the relative abundance of tribes, life-history strategies, or species of conservation concern between the two surveys, suggesting that the decline has occurred evenly across species, tribes, and life-history strategies. Ten species are possibly extirpated from the basin. Causes of the mussel decline in the Jacks Fork basin are unknown.

KEY WORDS: mussels, status, extirpation, colonization, decline, Missouri

INTRODUCTION

The mussel fauna of the Jacks Fork basin of Missouri is part of the Interior Highlands Province of the Mississippian Region (Haag 2010). This province covers two unique uplift areas, the Ozark Plateau and Ouachita Uplands, and it has a mussel fauna of over 70 species (Harris 1999; Haag 2010). Oesch (1995) reported 16 species from the Jacks Fork between 1967 and 1979 but did not report effort or the exact location of some sites (Table 1). Buchanan (1996) surveyed 11 sites in 1982 and observed 15 species, in addition to the invasive bivalve, *Corbicula fluminea*. A 2002 inventory of mussel resources within the Ozark National Scenic Riverways (OZAR) reported eight species from the Jacks Fork, but the survey was limited to only three sites (McClane Environmental Services 2004).

Documenting the distribution and status of mussel species and documenting faunal changes over time is important for conservation and management (MDC 2008; Haag and Williams 2014; FMCS 2016). Species life-history traits and phylogenetic affinity can affect mussel responses to disturbance (Haag 2012; Lopes-Lima et al. 2017). We surveyed 28 sites (historical and new) in the Jacks Fork basin to document the diversity and distribution of the mussel fauna, we compare our results with the 1982 survey to determine if changes have occurred, and we examine those changes in regard to phylogenetic and life-history strategy composition.

METHODS

Study Area

The Jacks Fork is a 79-km-long (1,153 km^2 watershed area) easterly flowing tributary of the Current River (Black River system) in the Ozarks aquatic faunal region of Missouri. The uplifted and unglaciated Ozarks generally lie on Paleozoic sedimentary bedrock and have higher elevations and greater local relief than other regions in Missouri (Steyermark 1968; Pflieger 1989; Panfil and Jacobson 2001; Sowa et al. 2007). Ozark streams typically are high gradient and occupy narrow,

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Table 1. Freshwater mussels reported live or as shells (×) from the Jacks Fork basin, Missouri during 1967–79 (Oesch 1995), 1982 (Buchanan 1996), 2002 (McClane Environmental Services 2004), and 2017–19 (this study). A dash (—) indicates that a species was not observed.

Species	Tribe[1]	Life-history Strategy[2]	Adult Size[3]	1967–79	1982	2002	2017–19
Alasmidonta marginata[4]	Anodontini	P	Medium	×	×	—	—
Alasmidonta viridis[4]	Anodontini	P	Small	×	×	—	×
Lasmigona costata	Anodontini	P	Large	×	×	—	—
Pyganodon grandis	Anodontini	O	Large	×	×	—	×
Strophitus undulatus	Anodontini	P	Medium	×	×	×	×
Utterbackia imbecillis	Anodontini	O	Medium	×	×	—	×
Amblema plicata	Amblemini	E	Large	×	—	—	—
Cambarunio hesperus	Lampsilini	P	Small	×	×	×	×
Lampsilis reeveiana	Lampsilini	P	Small	×	×	×	×
Lampsilis teres	Lampsilini	O	Large	×	—	—	—
Leaunio lienosus[4]	Lampsilini	O	Small	—	—	×	—
Leptodea fragilis	Lampsilini	O	Large	—	×	—	—
Ptychobranchus occidentalis[4]	Lampsilini	E	Medium	×	×	×	×
Sagittunio subrostratus	Lampsilini	O	Medium	×	×	×	×
Toxolasma lividum[4]	Lampsilini	P	Small	×	—	×	—
Toxolasma texasiense[4]	Lampsilini	P	Small	×	—	—	—
Truncilla donaciformis	Lampsilini	O	Small	—	×	—	—
Eurynia dilatata	Pleurobemini	E	Large	×	×	—	×
Fusconaia ozarkensis	Pleurobemini	E	Medium	×	×	×	×
Pleurobema sintoxia	Pleurobemini	E	Medium	—	×	—	—

[1]Tribe designations from Lopes-Lima et al. (2017).
[2]Life-history strategy: P = periodic, O = opportunistic, E = equilibrium (Haag 2012, Moore et al. 2021).
[3]Small (≤7.6 cm), medium (7.7–15.1 cm), and large (≥15.2 cm) on the basis of maximum sizes reported in Oesch (1995).
[4]Missouri species of conservation concern (MDC 2022).

steep-sided valleys bordered by high bluffs, and base flows are often maintained by springs (Pflieger 1989; Panfil and Jacobson 2001). The Jacks Fork has an average gradient of 1.3 m/km, and the upper section (above the confluence with Leatherwood Creek, Fig. 1) flows through a narrow valley. The channel of the lower section is less confined, resulting in more extensive gravel bar areas than the upper river; however, stream reaches in the lower section can be less stable and provide less suitable mussel habitat. As a gravel-dominated river, the Jacks Fork is naturally active, with high flows mobilizing bed material, creating gravel bars and driving channel migration (Erwin et al. 2021).

Presettlement land cover in the basin consisted of oak (*Quercus* spp.) and oak/pine (*Pinus* spp.) woodlands, with occasional prairie and savannah openings and fens (Nigh and Schroeder 2002). Presently, land cover is dominated by forest with approximately one-third in grassland or cropland; there are only two urban centers with >500 people. Nearly 19% of the basin is in public ownership. Springs contribute a considerable portion of the base flow of the Jacks Fork, and Alley Spring, with a discharge of approximately 3.5 m^3/s, is the largest of 48 known springs in the basin (Wilkerson 2001; Erwin et al. 2021). The Jacks Fork is designated an Outstanding National Resource Water, and since 1964 nearly its entire length has been managed by the National Park Service as part of OZAR (Wilkerson 2001).

Compared with rivers in other regions of Missouri, Ozark streams such as the Jacks Fork overall are less affected by physical alterations such as agriculture and channelization (Sowa et al. 2007). Threats to water quality in the basin include gravel mining, livestock access to riparian zones, runoff from cleared land, and seven National Pollution Discharge Elimination System discharges in the basin (Wilkerson 2001). Water quality is also affected by periodically high fecal coliform levels, and an 11.3-km segment of the lower Jacks Fork is under a total maximum daily load for fecal coliform, assumed to originate from failing on-site septic systems (Wilkerson 2001; MDNR 2004).

Field Sampling

We surveyed mussels during summer low-flow conditions from 2017 to 2019 at 11 sites previously surveyed by Buchanan (1996; hereafter, "resurveyed" sites) and 17 previously unsurveyed sites encompassing 74.5 km of the Jacks Fork, 18.5 km of the North Prong Jacks Fork, and 15.5 km of the South Prong Jacks Fork (Fig. 1). We did not survey additional tributaries because they are too small to support substantial mussel faunas. New sites were selected on the basis of the presence of suitable mussel habitat (e.g., stable gravel or gravel/sand substrate, bluff pools) and to provide even spatial coverage throughout the watershed. We followed the survey methods used by Buchanan (1996) in his 1982 survey. At least two surveyors conducted timed tactile and visual searches in

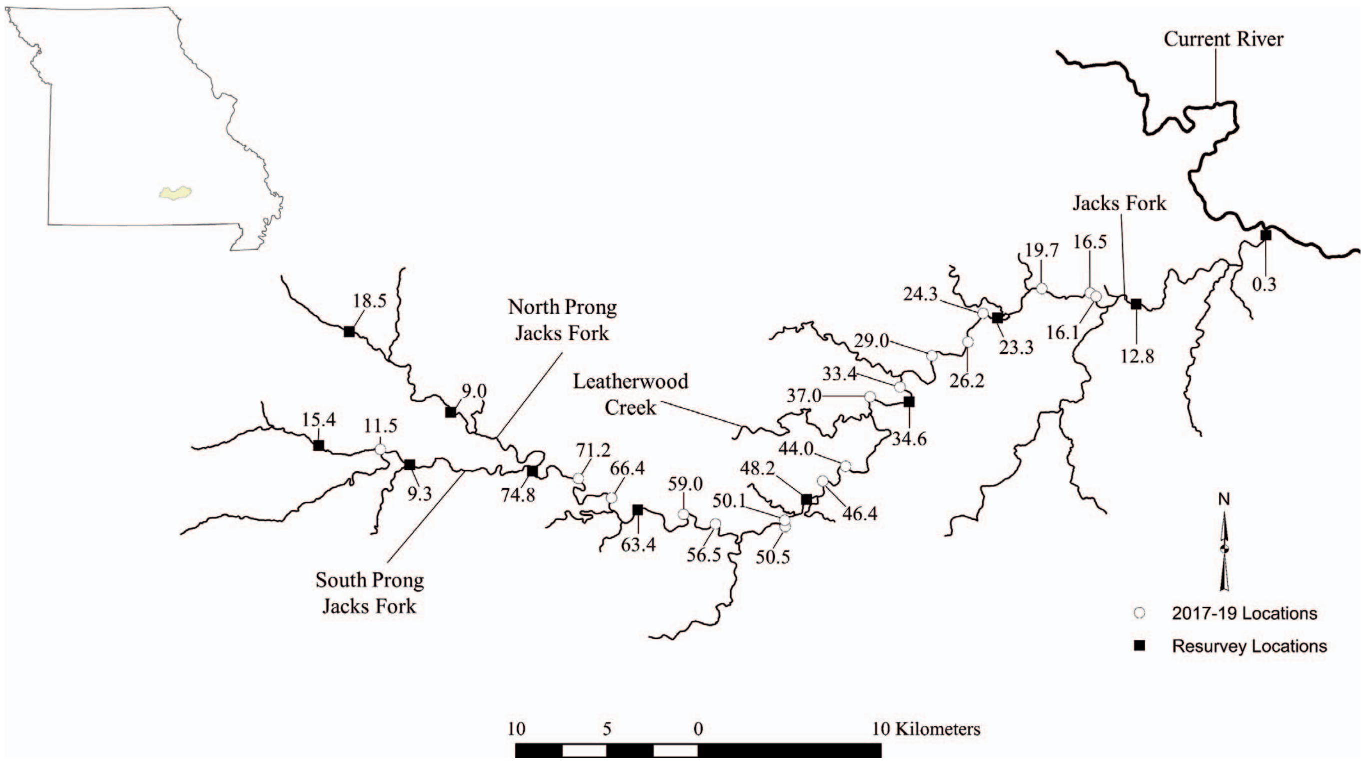

Figure 1. Sites surveyed for freshwater mussels in the Jacks Fork basin in 2017–19. Site numbers refer to river kilometer, measured from the stream mouth. Inset map shows the location of the Jacks Fork basin in Missouri, USA.

all available habitats at a site while wading or snorkeling. Search time at each site depended on the amount of available habitat.

Search time in our study averaged 2.4 person-hours/site across all sites (range 1.0–5.5; Table 2). At resurveyed sites, we attempted to survey the same area surveyed in 1982, on the basis of Buchanan's field notes (archived at Missouri Department of Conservation, Columbia). If field notes were not specific, or if the habitat at a site had changed to the extent that features could not be discerned, we surveyed represen-

Table 2. Sample effort and mussel community metrics in the Jacks Fork basin, Missouri at all 28 sites surveyed in 2017–19 and at 11 sites surveyed in 1982 (Buchanan 1996) and 2017–19 (resurveyed sites). All values are mean (SD). CPUE = catch per unit effort. Species richness is reported for live individuals or shells of any condition (live + shell), and live individuals or fresh dead shells (live + FD). H_B = Brillouin's index of diversity, E = evenness, RA = relative abundance, and SOCC = Missouri species of conservation concern.

	2017–19			Resurveyed Sites	
Parameter	All Locations	Upper Jacks Fork	Lower Jacks Fork	1982	2017–19
Sample effort (person-hours)	2.4 (1.2)	2.6 (1.1)	2.6 (1.5)	1.8 (0.8)	3.1 (1.6)
CPUE (number of live mussels/person-hour)	14.6 (27.2)	30.0 (36.0)	6.0 (14.0)	28.2 (31.7)	5.5 (14.4)
Richness (live + shell)	2.5 (2.0)	4.2 (0.9)	2.0 (1.8)	4.4 (2.7)	2.1 (2.1)
Richness (live + FD)	2.1 (1.8)	3.8 (1.1)	1.3 (1.3)	3.9 (2.5)	1.4 (1.6)
Number of individuals	37.8 (73.2)	73.0 (92.0)	21.0 (58.0)	54.3 (59.4)	22.6 (60.3)
H_B	0.5 (0.3)	0.7 (0.3)	0.3 (0.3)	1.0 (0.5)	0.5 (0.4)
E	0.6 (0.2)	0.6 (0.2)	0.6 (0.3)	0.7 (0.2)	0.6 (0.2)
Anodontini RA	0.5 (1.6)	1.4 (2.4)	0.0 (0.0)	5.6 (13.0)	0.5 (1.6)
Lampsilini RA	48.6 (44.3)	69.0 (30.0)	50.0 (50.0)	58.2 (39.3)	34.2 (46.0)
Pleurobemini RA	15.1 (26.6)	29.0 (29.0)	8.0 (25.0)	18.0 (29.4)	10.8 (27.0)
Opportunistic RA	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	6.3 (18.3)	0.0 (0.0)
Periodic RA	22.9 (35.2)	21.0 (27.0)	34.0 (45.0)	41.8 (31.0)	20.4 (34.9)
Equilibrium RA	41.3 (43.9)	79.0 (27.0)	24.0 (40.0)	33.7 (31.4)	25.1 (38.8)
SOCC RA	26.4 (34.6)	50.0 (32.0)	16.0 (32.0)	16.8 (19.9)	14.3 (27.4)

tative mussel habitats at the site. Search time in 1982 averaged 1.8 person-hours/site (range 0.8–3.8; Table 2; Buchanan 1996). During both surveys, shells were collected during and outside of timed searches but were not included in estimates of abundance (see subsequent). We classified shells as fresh dead (FD; intact periostracum and lustrous nacre), weathered dead (WD; intact periostracum but weathered, chalky nacre), or subfossil (SF; shell chalky with no periostracum) following Southwick and Loftus (2003).

Data Analysis

We characterized species richness, diversity, abundance, and composition of the mussel communities at each site for both the 1982 and 2017–19 surveys. We calculated species richness in two ways: (1) the total number of species collected live and as FD shells (live + FD) and (2) the total number of species collected live and as shell material in any condition (live + shell). Because sites in both surveys were selected nonrandomly, and because visual and tactile techniques are often biased toward large or sculptured species, we calculated Brillouin's index of diversity (H_B) and Brillouin's evenness (E) with the R package tabula (version 4.1.3; Magurran 1996; Vaughn et al. 1997; Frerebeau 2019; R Core Team 2022). Brillouin's index of diversity describes only the known collection and is preferred when catchability of the study organism is not random; values for the index rarely exceed 4.5 (Magurran 1996). These are calculated as:

$$H_B = \frac{1}{N}\log\left(\frac{N!}{n_1!n_2!n_3!\cdots}\right)$$

and

$$E = \frac{H_B}{H_B\max},$$

where N = total individuals collected, n_1, n_2, n_3 = number of individuals belonging to each species, and

$$H_B\max = \frac{1}{N}\times\ln\times\frac{N!}{\{[N/S]\}!^{s-r}\times\{([N/S]+1)!\}^r}$$

where S = species richness and

$$r = N - S[N/S].$$

We computed catch per unit effort (CPUE; number of live individuals/person-hour) as a measure of abundance. To describe the composition of the mussel community at each location, we calculated the relative abundances of individual species, life-history strategies (opportunistic, periodic, equilibrium), tribes (Anodontini, Lampsilini, Pleurobemini), and Missouri species of conservation concern (SOCC) that were detected live (Table 1). Opportunistic species exhibit a short life span with early sexual maturity, moderate-to-high fecundity, and moderate-to-large adult body size. Equilibrium species exhibit a longer life span, later sexual maturity, variable fecundity, and moderate-to-large adult size. Periodic species exhibit an intermediate life span, early-to-moderate sexual maturity, low-to-moderate fecundity, and small-to-moderate-sized adults (Haag 2012; Moore et al. 2021). Within the Unionidae, tribes represent differing suites of morphological, life-history, and behavioral traits and their relative abundances within a community are hypothesized to reflect habitat or water-quality factors (Lopes-Lima et al. 2017; Dunn et al. 2020). Missouri SOCC are considered critically imperiled, imperiled, or vulnerable in the state and include state or federally endangered or threatened species (MDC 2022).

To examine colonization and extirpation since 1982, we calculated the colonization proportion (p_c) and extirpation proportion (p_e) for all 14 species, three tribes, and three life-history strategies that were detected live in either period from at least one of the resurveyed sites (Gotelli 2001). These proportions are calculated as:

$$p_c = \frac{\text{Number of times a location unoccupied in 1982 was occupied in 2017-19}}{\text{Total number of previously unoccupied locations}}$$

and

$$p_e = \frac{\text{Number of times a location occupied in 1982 was unoccupied in 2017-19}}{\text{Total number of occupied locations censused}}$$

We tested for significant differences in the relative abundances of tribes and life-history strategies among all sites surveyed in 2017–19 with a Kruskal–Wallis test (H) and Dunn's post hoc test (z) with Bonferroni adjustment using the R package dunn.test ($P \leq 0.05$; Dinno 2017; R Core Team 2022). To examine spatial differences between the upper (above Leatherwood Creek; sites 44.0–74.8; Fig. 1) and lower sections of Jacks Fork (sites 0.3–37.0), we tested for differences in community metrics between those sections with a Kruskal–Wallis test (R Core Team 2022). To determine if community changes had occurred since 1982, we tested for significant differences in community metrics between time periods for the 11 resurveyed sites and the calculated p_c and p_e values for all species with a Kruskal–Wallis test (R Core Team 2022). We also calculated species rank abundances for both time periods at the resurveyed sites with the R package BiodiversityR (Kindt and Coe 2005; Foster and Dunstan 2010; R Core Team 2022).

RESULTS

During 2017–19, we collected 1,058 live individuals of six species and shells only of four additional species, and we observed live individuals or shells at 18 of the 28 sites (Table 3). *Corbicula fluminea* was observed live or as shells at 16 sites. Catch per unit effort ranged from 0 to 132.4 live individuals/person-hour (mean = 14.6), and the mean number of live individuals/site was 37.8 (range 0–331; Table 2). Species richness ranged from 0 to 5/site for both live + shell (mean = 2.5) and live + FD (mean = 2.1). Diversity (H_B) ranged from 0.0 to 1.0 (mean = 0.5) and E from 0.3 to 1.0

Table 3. Results of mussel surveys in the Jacks Fork basin, Missouri, 2017–19. Site numbers refer to river kilometer, measured from the mouth. Numbers for each species represent the number of live individuals at a site; the presence of shells is indicated as FD = fresh dead, WD = weathered dead, SF = subfossil; CPUE= catch per unit effort. *Corbicula fluminea* presence is noted as live (L) or shells (FD or WD). SOCC = Missouri species of conservation concern. RA = relative abundance. An asterisk (*) indicates sites that were sampled in 1982. The division between the upper and lower Jacks Fork is between sites 37.0 and 44.0. A dash (—) indicates that a species was not observed live or as shells.

	North Prong		South Prong			Jacks Fork								
Genus/Species	18.5*	9.0*	15.4*	11.5	9.3*	74.8*	71.2	66.4	63.4*	59.0	56.5	50.5	50.1	48.2*
Alasmidonta viridis	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Pyganodon grandis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Strophitus undulatus	—	—	—	—	—	—	1	—	1	—	—	—	—	—
Utterbackia imbecillis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cambarunio hesperus	—	—	—	—	—	1	2	2	—	4	3	3	1	—
Lampsilis reeveiana	—	—	—	—	—	1	SF	7	5	FD	8	3	4	2
Ptychobranchus occidentalis	—	—	—	—	—	WD	2	63	10	21	61	31	45	WD
Sagittunio subrostratus	—	—	—	—	—	WD	—	—	—	—	—	—	—	—
Eurynia dilatata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fusconaia ozarkensis	—	—	—	—	—	19	17	39	3	11	22	12	13	—
Corbicula fluminea	—	—	—	—	—	L	L	WD	L	L	L	L	L	—
Species richness (live + shell)	0	0	0	0	0	5	5	4	4	5	4	4	4	2
Live species richness (live + FD)	0	0	0	0	0	3	4	4	4	5	4	4	4	1
Total live individuals	0	0	0	0	0	21	22	111	19	38	94	49	63	2
Sample effort (person-hours)	1.3	2.1	1.3	1.2	1.6	3.3	1.8	2.7	5.5	2.2	3.0	1.6	2.0	1.5
CPUE (mussels/person-hour)	0.0	0.0	0.0	0.0	0.0	6.4	12.2	41.1	3.5	17.3	31.3	30.6	31.5	1.3
Brillouin's index (H_B)	—	—	—	—	—	0.3	0.6	0.9	0.9	1.0	0.9	0.9	0.7	0.0
Evenness (E)	—	—	—	—	—	0.3	0.5	0.7	0.8	0.8	0.7	0.7	0.6	—
Anodontini RA	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.0	5.3	5.3	0.0	0.0	0.0	0.0
Lampsilini RA	0.0	0.0	0.0	0.0	0.0	9.5	18.2	64.9	78.9	65.8	76.6	75.5	79.4	100.0
Pleurobemini RA	0.0	0.0	0.0	0.0	0.0	90.5	77.3	35.1	15.8	28.9	23.4	24.5	20.6	0.0
Opportunistic RA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Periodic RA	0.0	0.0	0.0	0.0	0.0	9.5	13.6	8.1	31.6	15.8	11.7	12.2	7.9	100.0
Equilibrium RA	0.0	0.0	0.0	0.0	0.0	90.5	86.4	91.9	68.4	84.2	88.3	87.8	92.1	0.0
SOCC RA	0.0	0.0	0.0	0.0	0.0	0.0	9.1	56.8	52.6	60.5	64.9	63.3	71.4	0.0

(mean = 0.6). The relative abundances of SOCC ranged from 0.0% to 90.6% (mean = 26.4%). The relative abundance of Lampsilini ranged from 0.0% to 100.0% (mean = 48.6%) and Pleurobemini ranged from 0.0% to 90.5% (mean = 15.1%). Relative abundance differed among life-history strategies ($H = 20$, df = 2, $P < 0.0001$), and there were significantly fewer Anodontini (mean relative abundance = 0.5%) than Lampsilini ($z = -4.73$, $P < 0.0001$) or Pleurobemini ($z = -2.44$, $P = 0.02$), and significantly fewer Pleurobemini than Lampsilini ($z = 2.3$, $P = 0.03$). No Amblemini or Quadrulini were observed. The relative abundance of equilibrium strategists ranged from 0.0% to 93.1% (mean = 41.3%) and periodic strategists ranged from 0.0% to 100.0% (mean = 22.9%). Relative abundance differed among life-history strategies ($H = 20$, df = 2, $P < 0.0001$), and there were significantly fewer opportunistic strategists (mean relative abundance < 0.1%) than equilibrium ($z = -4.11$, $P = 0.0001$) or periodic strategists ($z = 4.32$, $P < 0.0001$). There was no difference in the relative abundance of equilibrium and periodic strategists ($z = 0.21$, $P = 1.00$).

Compared with the lower river, the upper Jacks Fork had significantly higher CPUE ($H = 8$, df = 1, $P = 0.004$), species richness as both live + shell ($H = 8$, df = 1, $P = 0.005$) and live + FD ($H = 12$, df = 1, $P = 0.0006$), number of live individuals ($H = 9$, df = 1, $P = 0.003$), and H_B ($H = 4$, df = 1, $P = 0.03$) (Table 2). In addition, the upper Jacks Fork had significantly higher relative abundance of Pleurobemini ($H = 9$, df = 1, $P = 0.003$), equilibrium strategists ($H = 6$, df = 1, $P = 0.01$), and Missouri SOCC ($H = 5$, df = 1, $P = 0.03$) than did the lower Jacks Fork.

The SOCC *Ptychobranchus occidentalis* was the most abundant species, with 762 individuals observed (relative abundance = 72.0%), and it was observed live or as shells at 15 sites (Table 3). *Lampsilis reeveiana* was the most widely distributed species, with live individuals or shells occurring at 16 sites. We found 178 live individuals of *Fusconaia ozarkensis* (relative abundance = 16.8%), 45 *Cambarunio hesperus* (relative abundance = 4.3%), and two live individuals each of *Alasmidonta viridis* and *Strophitus undulatus*. *Pyganodon grandis*, *Sagittunio subrostratus*, and *Eurynia dilatata* were represented only by WD or SF shells, and *Utterbackia imbecillis* was represented only by FD shells. We found no live individuals or shells of 10 species previously

Table 3, extended.

Jacks Fork															Totals		
46.4	44.0	37.0	34.6*	33.4	29.0	26.2	24.3	23.3*	19.7	16.5	16.1	12.8*	0.3*	No. live	L + FD	L + shell	RA
—	FD	—	WD	—	—	—	—	—	—	—	—	—	—	2	2	3	0.2
—	—	—	—	—	—	—	—	—	—	—	—	—	SF	0	0	1	0.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	2	0.2
—	—	—	—	—	—	—	—	FD	—	—	—	—	—	0	1	1	0.0
4	7	3	7	WD	—	2	3	—	—	—	—	—	3	42	13	14	4.3
19	2	WD	9	1	—	—	3	—	5	—	—	—	—	69	14	16	6.5
300	43	23	162	WD	—	—	—	—	—	—	—	—	1	762	12	15	72.0
—	—	—	—	—	—	—	—	—	—	—	—	WD	—	0	0	2	0.0
—	—	—	—	—	—	—	—	—	—	—	—	—	WD	0	0	1	0.0
8	2	1	25	6	—	—	—	—	—	—	—	—	—	178	13	13	16.8
L	L	L	—	FD	L	WD	—	WD	L	—	—	WD	—	—	13	17	—
4	5	4	5	4	0	1	2	2	1	0	0	1	4				
4	5	3	4	2	0	1	2	1	1	0	0	0	2				
331	54	27	203	7	0	2	6	0	5	0	0	0	4				
2.5	2.0	2.0	4.2	3.0	1.2	1.0	1.5	5.3	2.5	1.5	1.0	3.3	4.5				
132.4	27.0	13.5	48.3	2.3	0.0	2.0	4.0	0.0	2.0	0.0	0.0	0.0	0.9				
0.4	0.6	0.4	0.7	0.3	—	0.0	0.5	—	0.0	—	—	—	0.4				
0.3	0.5	0.4	0.5	0.5	—	—	1.0	—	—	—	—	—	0.8				
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
97.6	96.3	96.3	87.7	14.3	0.0	100.0	100.0	0.0	100.0	0.0	0.0	0.0	100.0				
2.4	3.7	3.7	12.3	85.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0				
6.9	16.7	11.1	7.9	14.3	0.0	100.0	100.0	0.0	100.0	0.0	0.0	0.0	75.0				
93.1	83.3	88.9	92.1	85.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0				
90.6	79.6	85.2	79.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0				

reported from the basin (*Alasmidonta marginata*, *Lasmigona costata*, *Amblema plicata*, *Lampsilis teres*, *Leptodea fragilis*, *Toxolasma lividum*, *Toxolasma texasiense*, *Truncilla donaciformis*, *Leaunio lienosus*, *Pleurobema sintoxia*).

Values for most community metrics were lower in 2017–19 than 1982 (Table 2). There was a significant decline in CPUE ($H = 5$, df = 1, $P = 0.02$), number of live individuals ($H = 4$, df = 1, $P = 0.04$), live + shell richness ($H = 4$, df = 1, $P = 0.04$), live + FD richness ($H = 6$, df = 1, $P = 0.01$), and H_B ($H = 4$, df = 1, $P = 0.05$). Evenness was the only community metric that did not differ between time periods ($H = 1.4$, df = 1, $P = 0.23$). Faunal composition also differed between time periods. In 1982, 14 species were represented by live individuals, but only five species were represented by live individuals in 2017–19 (Fig. 2, Table 4). *Lampsilis reeveiana* was the most abundant species in 1982, representing 34.5% of live individuals, but it represented only 6.8% of individuals at the resurveyed sites in 2017–19. *Ptychobranchus occidentalis* was the most abundant species in 2017–19 (72.0% of individuals), but it represented only 30.8% of live individuals in 1982. There were no differences in proportional representation of tribes, life-history strategies, or SOCC between time periods ($H = 0.7$–3.3, df = 1, $P = 0.07$–0.4).

Mean extirpation proportion (p_e) across the 14 species detected live in 1982 was 0.85 (range 0.50–1.00, Table 5). Colonization proportion (p_c) was 0.00 for all species, and p_e was significantly higher than p_c ($H = 20$, df = 1, $P < 0.0001$). Anodontini had the highest extirpation proportion ($p_e = 0.80$) of the three tribes, and opportunistic life-history strategists had the highest extirpation proportion ($p_e = 1.00$).

DISCUSSION

Our results suggest that mussel abundance, diversity, and richness have declined substantially in the Jacks Fork since 1982. Ten species present in 1982 may be extirpated in the basin. We cannot account for species nondetection but given that effort in 2017–19 was greater than in 1982, and no shells of these species were found in 2017–19, these species are, at best, extremely rare in the basin. In addition, three species reported in 1967–79 have not been seen since that time (*Amblema plicata*, *Lampsilis teres*, *Toxolasma texasiense*).

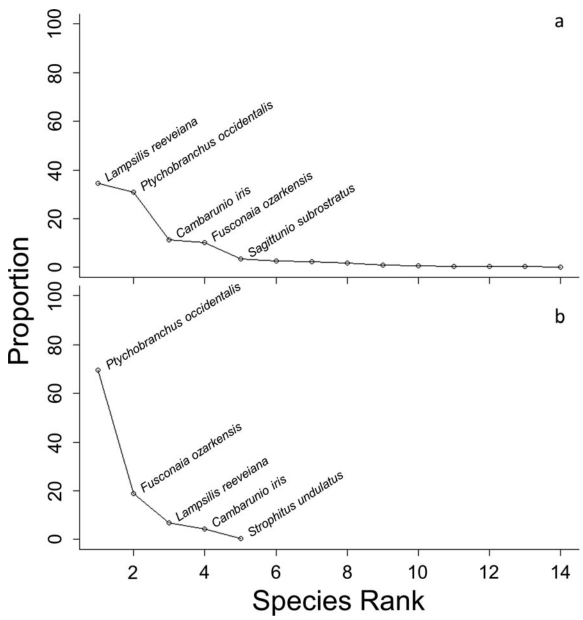

Figure 2. Species rank abundance plots for 11 sites surveyed in the Jacks Fork basin in (a) 1982 and (b) 2017–19.

Table 5. Colonization proportion (p_c) and extirpation proportion (p_e) for species, tribes, and life-history strategies detected live at 11 sites in the Jacks Fork, Missouri, during 1982 (Buchanan 1996) and 2017–19.

Species	p_e	p_c
Alasmidonta viridis	1.00	0.00
Lasmigona costata	1.00	0.00
Pyganodon grandis	1.00	0.00
Strophitus undulatus	0.67	0.00
Utterbackia imbecillis	1.00	0.00
Cambarunio hesperus	0.57	0.00
Lampsilis reeveiana	0.50	0.00
Leptodea fragilis	1.00	0.00
Ptychobranchus occidentalis	0.50	0.00
Sagittunio subrostratus	1.00	0.00
Truncilla donaciformis	1.00	0.00
Eurynia dilatata	1.00	0.00
Fusconaia ozarkensis	0.63	0.00
Pleurobema sintoxia	1.00	0.00
Mean	0.85	0.00
Anodontini	0.80	0.00
Lampsilini	0.38	0.00
Pleurobemini	0.63	0.00
Opportunistic	1.00	0.00
Periodic	0.38	0.00
Equilibrium	0.50	0.00

There was no evidence of colonization for any species in the Jacks Fork, and the extinction probability was $\geq$0.50 for all species, suggesting that local populations are not viable and hold an extinction debt from which additional extirpations should be expected in the future (Gotelli 2001; Vaughn 2012).

We found no differences in the composition of the Jacks Fork mussel assemblage between 1982 and 2017–19 with respect to tribe or life-history strategy, suggesting that the decline has occurred evenly across the fauna. However, most apparently extirpated species are short lived, and surviving species that declined in relative abundance also are short lived (*Strophitus undulatus*, *Cambarunio hesperus*, *L. reeveiana*). The only species that increased in relative abundance are relatively long lived (*Ptychobranchus occidentalis*, *Fusconaia ozarkensis*). Rapid disappearance of short-lived species and longer persistence of long-lived species is a common characteristic of enigmatic mussel declines or other changes in mussel assemblages (Haag 2012, 2019; Hornbach et al.

Table 4. Rank, catch per unit effort (CPUE), abundance, and proportion of species detected live at 11 sites in the Jacks Fork, Missouri during 1982 (Buchanan 1996) and 2017–19.

	1982				2017–19			
Species	Rank	CPUE	Abundance	Proportion	Rank	CPUE	Abundance	Proportion
Alasmidonta viridis	11	0.2	3	0.5	—	—	—	—
Lasmigona costata	14	0.1	1	0.2	—	—	—	—
Pyganodon grandis	8	0.5	10	1.7	—	—	—	—
Strophitus undulatus	7	0.7	13	2.2	5	0.03	1	0.4
Utterbackia imbecillis	9	0.3	6	1.0	—	—	—	—
Cambarunio hesperus	3	3.4	68	11.4	4	0.3	11	4.4
Lampsilis reeveiana	1	10.3	206	34.5	3	0.5	17	16.8
Leptodea fragilis	10	0.2	4	0.7	—	—	—	—
Ptychobranchus occidentalis	2	9.2	184	30.8	1	5.1	173	69.5
Sagittunio subrostratus	5	1.0	20	3.4	—	—	—	—
Truncilla donaciformis	13	0.1	2	0.3	—	—	—	—
Eurynia dilatata	6	0.8	16	2.7	—	—	—	—
Fusconaia ozarkensis	4	3.1	61	10.2	2	1.4	47	18.9
Pleurobema sintoxia	12	0.2	3	0.5	—	—	—	—

2017; Khan et al. 2020). The Jacks Fork does support a substantial population of the Missouri SOCC *P. occidentalis*. However, we have no information about size or age structure of mussel populations in the Jacks Fork or whether recruitment is occurring. Unless recruitment is occurring for *P. occidentalis* and *F. ozarkensis*, these species can be expected to decline in the future as remaining adults die.

We have no information about the causes of the mussel decline in the Jacks Fork. The stream experienced a 500-yr flood event during April–May 2017 that caused pronounced geomorphic changes in its channel (Heimann et al. 2018), but we do not know if this event is related to the mussel decline. If this flood event was the cause of the mussel decline, it means that the decline happened abruptly, immediately before our survey, rather than gradually since 1982. However, we did not observe large numbers of recently dead shells during our survey, and mussels are thought to be adapted to frequent bed disturbance from high-flow events (Sansom et al. 2018). The lower 11.3 km of the Jacks Fork is affected by high fecal coliform bacteria, presumably from failing on-site wastewater systems (MDNR 2004). Properly functioning on-site wastewater systems can have no measurable impacts on mussels, but failing systems can be a source of ammonia, which is harmful to mussels (Goudreau et al. 1993; Mummert et al. 2003; Grabarkiewicz and Davis 2008). However, we have no data on ammonia concentrations in the Jacks Fork and its potential linkage with mussel declines (Wilkerson 2001). As is the case for many streams in the USA, the mussel decline in the Jacks Fork is enigmatic and its causes are unknown (Haag and Williams 2014).

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