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REGULAR ARTICLE

MUSSEL INVENTORY AND POPULATION DEMOGRAPHICS OF THE FEDERALLY ENDANGERED *POTAMILUS CAPAX* (GREEN 1832) IN THE LOWER WABASH RIVER, ILLINOIS AND INDIANA

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ABSTRACT

The Wabash River is a key component of the freshwater mussel biodiversity of the Ohio River Basin. The basin historically supported approximately 75 mussel species, but currently only 30 are thought to be extant in the mainstem. Though the basin was historically well surveyed, the limited number of recent studies have primarily been small, and the last basin-wide survey effort is already over a decade old. This situation is problematic given that several rare species were historically present and populations of the federally endangered *Potamilus capax* may remain. We surveyed 46 sites within the lower Wabash River (river mile 0.0 to 117.0) to characterize mussel assemblages and distributional patterns. In total, we located 996 live mussels of 23 species. The assemblage was dominated by *Obliquaria reflexa, P. capax, Potamilus fragilis* and *Potamilus ohiensis*, and shell-length frequencies indicated ongoing recruitment of several species, including *P. capax* (multiple size classes). We did not find any evidence of major changes in species distributions or occurrences compared to other recent surveys but we did note a shift from species with equilibrium life-history strategies to species with opportunistic strategies moving downriver. Though the lower Wabash River appears to remain a sanctuary for *P. capax* and other smooth-shelled species, many species that were present historically remain absent.

KEY WORDS: Wabash River, *Potamilus capax*, Indiana, Illinois, mussels, unionid

INTRODUCTION

The Wabash River is a major tributary to the Ohio River, marks the border between Illinois and Indiana, and is an important component of the natural resources of both states due to its diversity of fish, freshwater mussels (Bivalvia: Unionida), and other wildlife and plant species (Fisher 2006; Simon 2006; Stodola et al. 2014). Over 70 native mussel species have been documented in the basin, including several currently listed as either Endangered or Threatened under the US Endangered Species Act, along with several candidates and various Illinois and Indiana state-listed species (Table 1). Unfortunately, mussels in the basin are in decline, and only about 30 species remain extant within the mainstem (Table 1; Fisher 2006; Tiemann et al. 2007; Illinois Endangered Species Protection Board 2020; Indiana Division of Fish and Wildlife 2020). Most of the aforementioned rare/listed species appear to be restricted to tributaries, though occasionally, individuals are found in the mainstem (Fisher 2006; Stodola et al. 2014). One exception is the federally endangered *Potamilus capax*, which can be found throughout the lower Wabash River and is often locally abundant and dominant (Fisher 2006; Stodola et al. 2014).

The mussel fauna of the Wabash River basin has been surveyed regularly over the past 100 years. The first comprehensive basin inventory was completed in 1881 (Stein) and updated by Call, Blatchely, Daniels, Goodrich, van der Schalie, and others (Fisher 2006). Between 1987 and 1991, Cummings et al. (1992) surveyed 100 locations. Fisher (2006) compiled data from various Indiana Department of Natural Resources surveys conducted between 1995 and 2006, along with existing survey information. A more recent survey was conducted by the Illinois Natural History Survey (INHS) and Illinois Department of Natural Resources (ILDNR) in 2011 and 2012, albeit primarily at previously sampled locations (Tieman et al. 2012). Other recent surveys consist of an update on mussel distribution

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Table 1. Freshwater mussel (Bivalvia: Unionida) species previously reported from the Wabash River Basin in Indiana (Fisher 2006) and Illinois (Stodola et al. 2014; ILDNR 2024; INHS 2024), their current state and federal status, and their historical and recent distributions. Abbreviations: C = Candidate species, E = Endangered, EX = extirpated, H = historically reproducing but now absent, L = species still reproducing, R = reintroduced, SSC = State Special Concern, T = Threatened, X = Extinct. Dates indicate the period a species was last found extant. Species names are adjusted to reflect current nomenclature.

				Indiana		Illinois	
Species	Federal Status	IL Status	IN Status	Mainstem	Tributary	Mainstem	Tributary
Actinonaias ligamentina	–	–	–	L	L	1977–1999	2000–2013
Alasmidonta marginata	–	–	–	L	L	–	2000–2013
Alasmidonta viridis	–	–	SSC	–	L	–	2000–2013
Amblema plicata	–	–	–	L	L	2000–2013	2000–2013
Anodontoides ferussacianus	–	–	–	–	L	Pre-1950	2000–2013
Arcidens confragosus	–	–	–	H	L	2000–2013	2000–2013
Cambarunio iris	–	E	SSC	H	L	–	2000–2013
Cumberlandia monodonta	E	E	X	EX	EX	Pre-1950	–
Cyclonaias nodulata	–	–	–	L	L	2000–2013	2000–2013
Cyclonaias pustulosa	–	–	–	L	L	2000–2013	2000–2013
Cyclonaias tuberculata	–	T	–	L	L	1977–1999	2000–2013
Cyprogenia stegaria	E	E	–	H	L	1977–1999	Pre-1950
Ellipsaria lineolata	–	T	–	H	L	1977–1999	Pre-1950
Elliptio crassidens	–	E	SSC	H	L	2000–2013	–
Epioblasma flexuosa	X	–	X	EX	EX	–	–
Epioblasma obliquata	E	–	E	EX	EX	Pre-1950	–
Epioblasma personata	X	–	X	EX	EX	–	–
Epioblasma propinqua	X	–	X	EX	EX	–	–
Epioblasma rangiana	E	E	E	EX	EX	Pre-1950	R
Epioblasma sampsonii	X	–	X	EX	EX	–	–
Epioblasma torulosa	E	–	X	EX	EX	Pre-1950	–
Epioblasma triquetra	E	E	E	H	L	Pre-1950	2000–2013
Eurynia dilatata	–	E	SSC	H	L	Pre-1950	2000–2013
Fusconaia flava	–	–	–	L	L	2000–2013	2000–2013
Fusconaia subrotunda	T	–	X	EX	EX	Pre-1950	–
Hemistena lata	E	–	X	EX	EX	Pre-1950	–
Lampsilis abrupta	E	E	X	EX	EX	Pre-1950	–
Lampsilis cardium	–	–	–	L	L	2000–2013	2000–2013
Lampsilis fasciola	–	E	SSC	L	L	–	2000–2013
Lampsilis hydiana	–	–	–	–	–	Pre-1950	2000–2013
Lampsilis ovata	–	–	SSC	L	L	Pre-1950	–
Lampsilis siliquoidea	–	–	–	L	L	1950–1976	2000–2013
Lampsilis teres	–	–	–	L	L	2014–2018	2000–2013
Lasmigona complanata	–	–	–	L	L	2014–2018	2000–2013
Lasmigona compressa	–	–	–	–	L	–	2000–2013
Lasmigona costata	–	–	–	L	L	Pre-1950	2000–2013
Leaunio lienosus	–	–	SSC	–	L	–	2000–2013
Ligumia recta	–	–	SSC	L	L	Pre-1950	2000–2013
Megalonaias nervosa	–	–	–	H	L	2000–2013	2000–2013

Table 1, continued.

				Indiana		Illinois	
Species	Federal Status	IL Status	IN Status	Mainstem	Tributary	Mainstem	Tributary
Obliquaria reflexa	–	–	–	L	L	2014–2018	2000–2013
Obovaria olivaria	–	–	–	L	L	2000–2013	2000–2013
Obovaria retusa	E	–	X	EX	EX	Pre-1950	–
Obovaria subrotunda	T	–	E	H	L	Pre-1950	1977–1999
Paetulunio fabilis	E	–	E	H	L	–	2000–2013
Plethobasus cicatricosus	E	–	X	EX	EX	Pre-1950	–
Plethobasus cooperianus	E	E	X	EX	EX	–	–
Plethobasus cyphyus	E	E	E	H	L	1977–1999	–
Pleurobema clava	E	E	–	H	L	Pre-1950	2000–2013
Pleurobema cordatum	–	E	SSC	H	L	1977–1999	Pre-1950
Pleurobema plenum	–	–	E	EX	EX	Pre-1950	–
Pleurobema rubrum	–	–	X	EX	EX	Pre-1950	1977–1999
Pleurobema sintoxia	–	–	–	L	L	Pre-1950	2000–2013
Potamilus alatus	–	–	–	L	L	2014–2018	2000–2013
Potamilus capax	E	E	E	L	L	2014–2016	1977–1999
Potamilus fragilis	–	–	–	L	L	2014–2018	2000–2013
Potamilus leptodon	E	E	X	EX	EX	Pre-1950	–
Potamilus ohiensis	–	–	–	L	L	2014–2018	2000–2013
Ptychobranchus fasciolaris	–	E	SSC	H	L	Pre-1950	2000–2013
Pyganodon grandis	–	–	–	L	L	2000–2013	2000–2013
Quadrula fragosa	E	–	–	EX	EX	Pre-1950	–
Quadrula quadrula	–	–	–	L	L	2014–2018	2000–2013
Reginaia ebenus	–	E	SSC	H	L	2000–2013	2000–2013
Sagittunio subrostratus	–	–	–	–	L	Pre-1950	2000–2013
Simpsonaias ambigua	C	E	SSC	H	L	Pre-1950	2000–2013
Strophitus undulatus	–	–	–	L	L	Pre-1950	2000–2013
Theliderma cylindrica	T	E	E	H	L	Pre-1950	2000–2013
Theliderma metanevra	–	T	–	L	L	2000–2013	2000–2013
Toxolasma lividum	–	E	SSC	H	L	Pre-1950	2000–2013
Toxolasma parvum	–	–	–	–	L	2014–2018	2000–2013
Toxolasma texasiense	–	–	SSC	–	L	2000–2012	2000–2013
Tritogonia verrucosa	–	–	–	L	L	2014–2018	2000–2013
Truncilla donaciformis	–	–	–	L	L	2014–2018	2000–2013
Truncilla truncata	–	–	–	L	L	2014–2018	2000–2013
Uniomerus tetralasmus	–	–	–	–	L	Pre-1950	2000–2013
Utterbackia imbecillis	–	–	–	L	L	2000–2013	2000–2013
Utterbackiana suborbiculata	–	–	–	–	L	2014–2015	2000–2013
Venustaconcha ellipsiformis	–	–	–	–	–	Pre-1950	2000–2013
Total Species				66	75	65	58

in the Illinois portion of the basin by INHS based on previously collected data and some limited new data (Stodola et al. 2014), and a few small unpublished surveys conducted by state agencies (ILDNR 2024; INHS 2024).

Despite substantial historical efforts in the Wabash River basin, the most recent comprehensive surveys are more than a decade old. Additionally, previous efforts often have used only shallow-water sampling techniques, limiting surveys to shallow areas and potentially biasing data. As a result, current inferences regarding the health of mussels in the Wabash River basin, including species' conservation status and long-term viability, may be outdated and/or incorrect. Accurately assessing a species' health and status and effectively managing it require reliable, precise, and current abundance and distribution data (Huang et al. 2011). Thus, updated information on the status and health of mussels in the basin is needed to manage and protect them. We used a multimethod sampling approach to evaluate the current diversity, distribution, assemblage structure, health, and viability of the freshwater mussel (hereafter mussel) fauna in the lower Wabash River.

METHODS

Study Area

The Wabash River, located in the midwestern United States, is the third-largest tributary of the Ohio River (Fig. 1). From its headwaters in Fort Recovery, Ohio, the river flows approximately 810 km to its confluence with the Ohio River at the southern end of the Indiana-Illinois border near New Haven, Illinois. The basin drains an area of approximately 85,300 km^2 with a mean annual discharge of 1,000 m^3/s (Pyron et al. 2020). Though several reservoirs are on its tributaries, only one is on the mainstem (near Huntington, Indiana, at river km 662), and the lower portion is the longest undammed river reach east of the Mississippi River (Pyron et al. 2020).

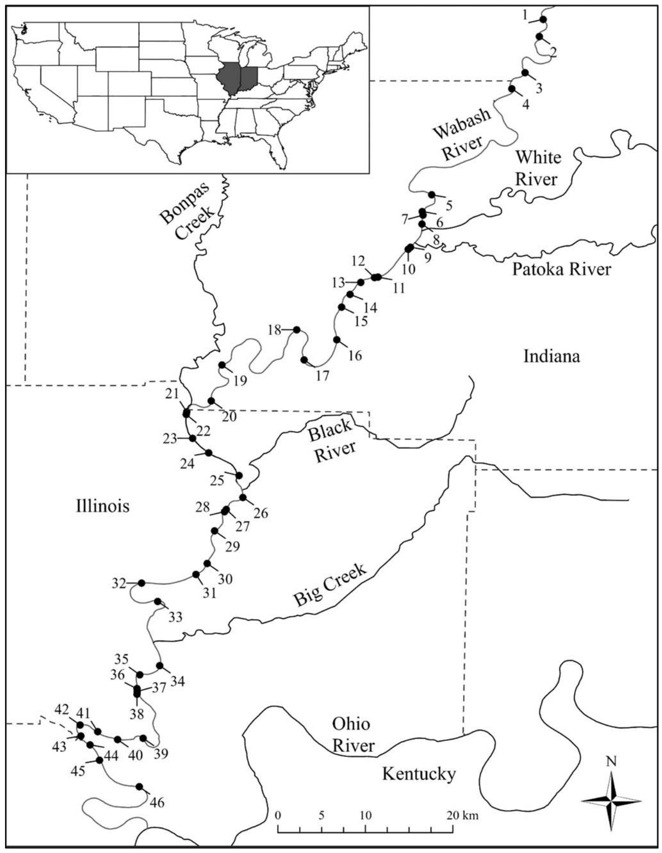

Figure 1. Location of our 46 survey sites within the lower Wabash River.

Survey Methods

Between August 22, 2021, and August 28, 2022, we conducted a multimethod mussel study within the lower Wabash River in conjunction with the ILDNR. We surveyed 46 sites in the lower Wabash River, beginning from just upstream of Mt. Carmel, Illinois (Lawrence County, Illinois), to just upstream of the confluence with the Ohio River (Gallatin County, Illinois; Fig. 1). For this study, we considered the lower Wabash River to be between navigation mile marker 0.0 and 117.0 in Lawrence, Wabash, White, and Gallatin Counties in Illinois and Knox, Gibson, and Posey Counties in Indiana.

The ILDNR selected the survey sites, which consisted of locations where previous survey efforts had occurred or where ILDNR wanted to determine if mussel assemblages and/or federally listed mussel species and other rare species occur. Our goal was to locate mussel assemblages and characterize population demographics (e.g., density, age class structure, etc.), with a particular focus on state and federally listed species. To meet these study goals, and in coordination with ILDNR, we developed a systematic multimethod survey approach, combining three different sampling methods (i.e., timed searches, transects, and quadrats).

Timed searches.—For each site, we delineated a 300-m linear length of the river as the survey area. Initially, surveyors sampled for mussels for a combined one person-hour. Sampling was spatially distributed across the entire river, with one-third of search effort spent equally along each bank (extending 10 to 15 m riverward), and midchannel. Following this, we examined abundances and species richness from each section, and spent five additional person-hours surveying the section with the greatest abundance and richness (resulting in a total of six person-hours per site). If it was not apparent which section had the highest abundance and species richness (i.e., if one section had high abundance of a single species while another had lower abundances but higher species richness), then search effort was evenly split between each section. If no live or fresh dead mussels were located, no additional survey effort beyond the initial person-hour occurred. After the six person-hours of sampling, all mussels were returned to the approximate collection location after processing and before additional transect and quadrat surveys.

Transects.—Based on the results of timed searches, sites 9, 15, 16, 18, 20, 23, 25, 26, 31, 32, 33, 37, 45, and 46 were selected for additional transect surveys. Site selection was based on several factors, including mussel abundance and species richness from timed searches, *P. capax* abundance, and spatial placement of the site within the study area. At each site, we placed nine 100-m transects perpendicular to river flow. Sites 18, 20, 26, 32, 37, and 46 contained the highest abundances of *P. capax* and/or other species in timed searches and were assigned an additional nine transects. Transects began at the upstream end of the 300-m site along the bank with the greatest mussel abundance and species richness. Transects (n = 180) were placed every 10 m moving downstream and were subdivided into 10-m intervals. Mussels and data were collected for each 10-m interval (n = 1,800 × 10-m intervals). All mussels were returned to the approximate collection location after processing and prior to quadrat surveys.

*Quadrats.—*We conducted quadrat surveys at all sites where transect sampling occurred. We used a systematic sampling design with one random start and 0.25 m^2 quadrats (Strayer and Smith 2003). We excavated by hand the substrate from each quadrat to a depth of approximately 15 cm and sieved it through a 6.4 mm mesh to collect any mussels (Vaughn et al. 1997; Obermeyer 1998). We sampled 12 quadrats at each site, but as with transect samples, sites 18, 20, 26, 32, 37, and 46 were assigned 12 additional quadrats (n = 146 × 0.25 m^2 quadrats; overall area surveyed = 60 m^2).

*Mussel sampling.—*We searched sites visually and tactilely, which provides the most accurate results for mussel species richness, evenness, and abundance (Hornbach and Deneka 1996; Vaughn et al. 1997). We surveyed using wading or snorkeling techniques in shallow water (depths ≤ 1 m) and SCUBA techniques in deeper habitat. Generally, we first conducted a visual search, followed by a tactile search, where we disturbed the substrate to a depth of about 5 cm to dislodge buried mussels and to move obstructions, such as woody debris or large rocks. After tactile searches, we conducted an additional visual search to collect exposed mussels. We kept mussels submerged in water until survey efforts and processing were complete. All mussels were returned to their approximate collection location after processing.

We identified and measured shell length (nearest 0.1 mm) of all live mussels and took photographic vouchers. We collected, identified, and enumerated fresh dead shells. Species located as weathered and relic dead shell were recorded but not enumerated. Shells were considered fresh dead if both valves were present, the nacre lustrous, the hinge flexible, and the periostracum intact. Fresh dead shells were recorded as a positive species occurrence. We measured shell length of all fresh dead shells of federally listed species. We visually assessed the general substrate composition at each site but did not quantify substrate particle size.

Data Analysis

*Individual survey method analyses.—*We used timed search data (combined for each site) to calculate CPUE (mussels/person-hour) estimates. To determine if horizontal mussel distribution (i.e., from bank to midchannel) was even, we ran two regression analyses using log transformed total mussel abundance and species richness from each 10-m transect interval (n=1,800) as response variables and distance from the bank as the predictor variable. We used data from quadrat samples to calculate density (mussels/m^2).

*Comparison between sampling methods.—*We ran three ANOVAs to test for significant differences in (1) average shell lengths within species, (2) total mussel abundance, and (3) species richness among the three different survey methods. We ran a Tukey's post hoc test to determine the pairwise differences between survey methods. We used data only from the 14 sites where all sampling methods were employed.

*All survey methods.—*We combined data from all samples of each survey method type to provide a total species list, total species abundance and relative abundance (species abundance/total abundance), and we assigned mussels life-history strategies (opportunistic, periodic, or equilibrium) following Haag (2012) and Moore et al. (2021). For species without a published life-history strategy, we assigned strategies based on those of similar species (e.g., species from the same genus) and our knowledge of the respective species' behaviors (Table 2). We used our total abundances and species richness to calculate Shannon-Wiener species diversity (H') and Pielou's evenness (J') indices for each site. To examine changes in the mussel community along the river, we ran eight regression analyses using abundance, species richness, CPUE, H' index, J' index, and relative abundance of each of the three life-history strategies at each site as response variables and site location as the predictor variable. We defined site location as the distance moving upstream from the confluence with the Ohio River and calculated distance using the U.S. National Hydrography dataset to trace the entire length of the Wabash River. We then plotted site locations in ArcGIS and used the "Locate Feature" geoprocessing tool to generate distance by locating where the site intersected the river polyline.

The proportion of fresh dead shell in an assemblage was used as an index of recent mortality, which can indicate recent stress events (Dunn et al. 2020). We calculated the percentage of recent mortality (number fresh dead/[number fresh dead + number live]) for all species using data from all survey methods. Pooling data from all sampling sites and methods, we tested for differences in average shell length between live and fresh dead *P. capax* using an ANOVA.

We used shell length as a proxy for age to assess recent recruitment for each species. Mussels ≤ 40 mm in length were considered recent recruits (Obermeyer 1998; Smith and Crabtree 2010; Ford et al. 2023) for all species except *P. capax, Toxolasma parvum*, *Truncilla donaciformis*, and *T. truncata*. Due to its large maximum size (approximately 150 mm; Peck et al. 2014), *P. capax* recruits were considered those ≤50 mm in length (Wentz et al. 2009), and due to their small maximum size and age of maturity, recruits of *T. parvum, T. donaciformis*, and *T. truncata* were considered those ≤30 mm in length (Haag 2012). Shell length-frequency histograms were created for the six most-abundant species. These histograms were used to identify individual recruitment cohorts and to assess the viability of these species.

Table 2. Summary of freshwater mussel (Bivalvia: Unionida) data from the lower Wabash River using timed search, transect, and quadrat sampling methods. Abbreviations: n = total number of mussels, RA = relative abundance (percent representation of a species in the assemblage), CPUE = catch-per-unit-effort (mussels/person-hour), Rec. = proportion of recruits, Density = mussels/m^2, Occ. = percent occurrence (percentage of sites occupied by a species), and Mort. = proportion of recent mortality. No recruits were located in the quadrat samples. A dash (–) indicates a species was not detected.

	Timed Search				Transect			Quadrat			All Methods		
Species	*n*	RA	CPUE	Rec.	*n*	RA	Rec.	*n*	RA	Density	Occ.	Rec.	Mort.
Equilibrium Species													
Amblema plicata	24	2.7	0.1	–	–	–	–	–	–	–	6.5	–	4.0
Cyclonaias nodulata	8	0.9	<0.1	–	–	–	–	–	–	–	15.2	12.5	–
Cyclonaias pustulosa	31	3.4	0.2	–	–	–	–	–	–	–	15.2	12.9	–
Megalonaias nervosa	4	0.4	<0.1	–	–	–	–	–	–	–	8.7	–	20.0
Quadrula quadrula	79	8.8	0.4	10.1	6	6.6	16.7	–	–	–	43.5	10.7	4.5
Reginaia ebenus	7	0.8	<0.1	–	–	–	–	–	–	–	6.5	–	22.2
Theliderma metanevra	4	0.4	<0.1	–	–	–	–	–	–	–	8.7	–	–
Tritogonia verrucosa	53	5.9	0.3	–	1	1.1	–	–	–	–	34.8	–	5.3
Total	210	23.3	1.0		7	7.7	–	–	–	–			
Opportunistic Species													
Lampsilis teres	2	0.2	<0.1	–	–	–	–	–	–	–	4.3	–	50.0
Lasmigona complanata	2	0.2	<0.1	–	–	–	–	–	–	–	4.3	–	–
Potamilus alatus	12	1.3	0.1	–	3	3.3	–	–	–	–	21.7	–	16.7
Potamilus capax	139	15.4	0.7	–	24	26.4	–	3	60.0	0.05	47.8	1.8	60.2
Potamilus fragilis	86	9.6	0.4	20.7	24	26.4	–	1	20.0	0.02	52.2	20.7	32.3
Potamilus ohiensis	125	13.9	0.6	15.2	18	19.8	–	–	–	–	60.9	13.3	23.1
Pyganodon grandis	2	0.2	<0.1	–	1	1.1	–	–	–	–	4.3	–	25.0
Toxolasma parvum	1	0.1	<0.1	–	–	–	–	–	–	–	2.2	–	–
Truncilla donaciformis	7	0.8	<0.1	100.0	2	2.2	50.0	–	–	–	8.7	88.9	18.2
Truncilla truncata	13	1.4	0.1	100.0	1	1.1	–	–	–	–	15.2	21.4	17.6
Utterbackia imbecillis	1	0.1	<0.1	–	–	–	–	–	–	–	2.2	–	50.0
Utterbackiana suborbiculata	DS	–	–	–	–	–	–	–	–	–	2.2	–	100.0
Total	390	43.3	1.9		73	80.2		4	80.0	0.07			
Periodic Species													
Lampsilis cardium	3	0.3	<0.1	–	–	–	–	–	–	–	2.2	–	–
Lampsilis ovata	1	0.1	<0.1	–	–	–	–	–	–	–	2.2	–	–
Obliquaria reflexa	255	28.3	1.2	20.4	9	9.9	44.4	1	20.0	0.02	47.8	21.1	2.6
Obovaria olivaria	41	4.6	0.2	7.3	2	2.2	50.0	–	–	–	23.9	9.3	4.4
Total	300	33.3	1.2		11	12.1		1	20.0	0.02			
Total	900	90.4	4.3		91	9.1		5	0.5	0.08			

RESULTS

Overall Results

We surveyed approximately 13.8 linear km of the Wabash River. Across all sites, substrate consisted primarily of stable silt (16.9%) and sand (74.8%), with some small amounts of gravel (7.6%), cobble (0.3%), boulder (0.1%), and clay (0.3%) along the banks. Gravel and cobble were more prevalent at upstream sites (Sites 1–8), and substrate became primarily sand downstream of the confluence with the White River (downstream of site 8; Fig.1). Substrate in the center of the channel consisted entirely of loose gravel and/or sand.

We detected 996 live mussels of 23 species (Table 2), approximately 30.7% of the historical mussel assemblage known from the basin. Live mussels were found at 33 sites (71.7%), and the total number of live mussels ranged from 0 to 118 per site (mean ± SE: 21.7 ± 4.2). *Obliquaria reflexa* was the most abundant species, comprising 26.6% of all mussels collected. The federally endangered *P. capax* and the nonlisted *Potamilus ohiensis* and *Potamilus fragilis* were the second-, third-, and fourth-most abundant species comprising 16.7%, 14.4%, and 11.1% of total mussels, respectively (Table 2).

Species richness ranged from 0 to 13 (mean ± SE: 4.4 ± 0.6) species per site. Patterns of ubiquity varied by species, and only five species were widely distributed across the lower basin, occurring at ≥ 20 sites: *P. ohiensis* ($n = 28$), *P. fragilis* ($n = 24$), *P. capax* ($n = 22$), *O. reflexa* ($n = 21$), and *Quadrula quadrula* ($n = 20$). Most species ($n = 17$) occurred at ≤ 10 sites each. Three species were represented by a single live individual: the Indiana species of special concern *Lampsilis ovata* (Site 10), the nonlisted *T. parvum* (Site 20), and *Utterbackia imbecillis* (Site 6). Species with an opportunistic life-history strategy represented the greatest relative abundance (46.9%) and species richness (11 live species) within the assemblage, followed by periodic species (31.3%, 4 live species). Opportunistic species were the dominant life-history strategy at > 50% of sites and were found at all sites with live mussels. Both equilibrium and periodic life histories were primarily represented by a single species at a site.

Total mussel abundance and CPUE significantly decreased moving downstream toward the confluence with the Ohio River. Species richness, species diversity (H'), and species evenness (J') also declined but not statistically significantly (Figs. 2a–e). In addition, the relative abundance of species with equilibrium and periodic life histories, respectively, significantly declined moving downstream (Figs. 2f and h). Conversely, opportunistic life histories significantly increased moving downstream (Fig. 2g). Our findings indicate a shift from species with periodic and equilibrium life histories to primarily opportunistic species in a downstream direction.

Fresh dead shell material was found for 17 species but primarily consisted of *P. capax*, *P. fragilis*, and *P. ohiensis* (93.0% of fresh dead). One species, *Utterbackiana suborbiculata* (Site 37), was represented as fresh dead shell material only (Table 2). Mortality of *P. capax* was 58.8%, and average fresh dead shells were significantly longer (ANOVA: $F_{1,401} = 13.339$, $P < 0.05$) than live individuals (Fig. 3).

We observed numerous size classes for several species, and 13.1% of collected mussels were recruits, primarily *O. reflexa* ($n = 56$), *P. fragilis* ($n = 23$), and *P. ohiensis* ($n = 19$). Three *P. capax* recruits as well as several individuals from the subsequent size class were located, and small (<70 mm) *P. capax* were located at nine sites. Shell length-frequency-plots of the six most abundant species exhibited a general bell-shaped curve, indicating annual recruitment (Figs. 4a–f). All six exhibited unimodal shell length-frequency distributions except *P. ohiensis* (Fig. 4c) and *P. fragilis* (Fig. 4d), which exhibited two distinct modal peaks indicating two cohorts.

Timed Searches (46 Sites)

We spent a total of 211 person-hours conducting timed searches (Tables 2 and 3) at the 46 sites. The majority of mussels ($n = 900$; 90.4%) and all 23 species were detected in timed searches (Table 2). *Obliquaria reflexa*, *P. capax*, *P. ohiensis*, and *P. fragilis* were the most abundant species, and several species were found only in timed searches. Overall CPUE was 4.3 mussels/person-hour and ranged from 0 to 19.7 mussels/person-hour (mean ± SE: 3.3 ± 0.7 mussels/person-hour) per site. CPUE was highest for sites 6, 8, 13, and 32, respectively (Table 3).

Transects (14 Sites)

We located 91 live mussels of 11 species in transect samples. These consisted primarily of *P. capax*, *P. fragilis,* and *P. ohiensis*, all opportunistic species. Across the 1,800 10-m transect intervals, mussels were located significantly more often (Regression: $R^2 = 0.623$, $P = 0.007$; Fig. 5a) and with greater species richness (Regression: $R^2 = 0.652$, $P = 0.005$; Fig. 5b) within the first 10 m from the bank. The majority of mussels (> 80%) and all 11 species were found in the first 10 m from the bank. More than 90% of *P. capax* were found in the first two intervals (Fig. 5a).

Quadrats (14 Sites)

Across the 60 m^2 surveyed via quadrat sampling, we located only five live mussels of three species. Overall, density (0.08 mussels/m^2) was low and ranged from 0.00 to 0.33 mussels/m^2 (mean ± SE: 0.12 ± 0.04 mussels/m^2; Table 3) per site. Density was highest for *P. capax* (Table 2), which was the only species with more than a single individual located in quadrats.

Comparison Between Sampling Methods

Mussel abundance (ANOVA: $F_{2,135} = 20.03$, $P < 0.001$) was significantly affected by survey methods, with abundance greater in timed searches than transect (Tukey: $P < 0.001$) or quadrat samples (Tukey: $P < 0.001$). Species richness (ANOVA: $F_{2,135} = 43.85$, $P < 0.001$) was also significantly affected by survey methods, with greater richness in timed searches than transect (Tukey: $P < 0.001$) or quadrat samples (Tukey: $P < 0.001$). Average *P. ohiensis* shell lengths were significantly different among survey methods (ANOVA: $F_{1,79} = 13.697$, $P < 0.001$), and were significantly longer in transect samples than in timed searches (Tukey post hoc tests significant at $P < 0.001$). Shell length was not significantly affected by survey method in any other species (Table 4).

DISCUSSION

Building on previous research (Fisher 2006; Stodola et al. 2014), this study presents the results of a large-scale survey of the diversity, distribution, and population structure of mussels in the lower Wabash River. Recent surveys recorded approximately 30 mussel species in the mainstem Wabash River, and the lower Wabash River appears to support about

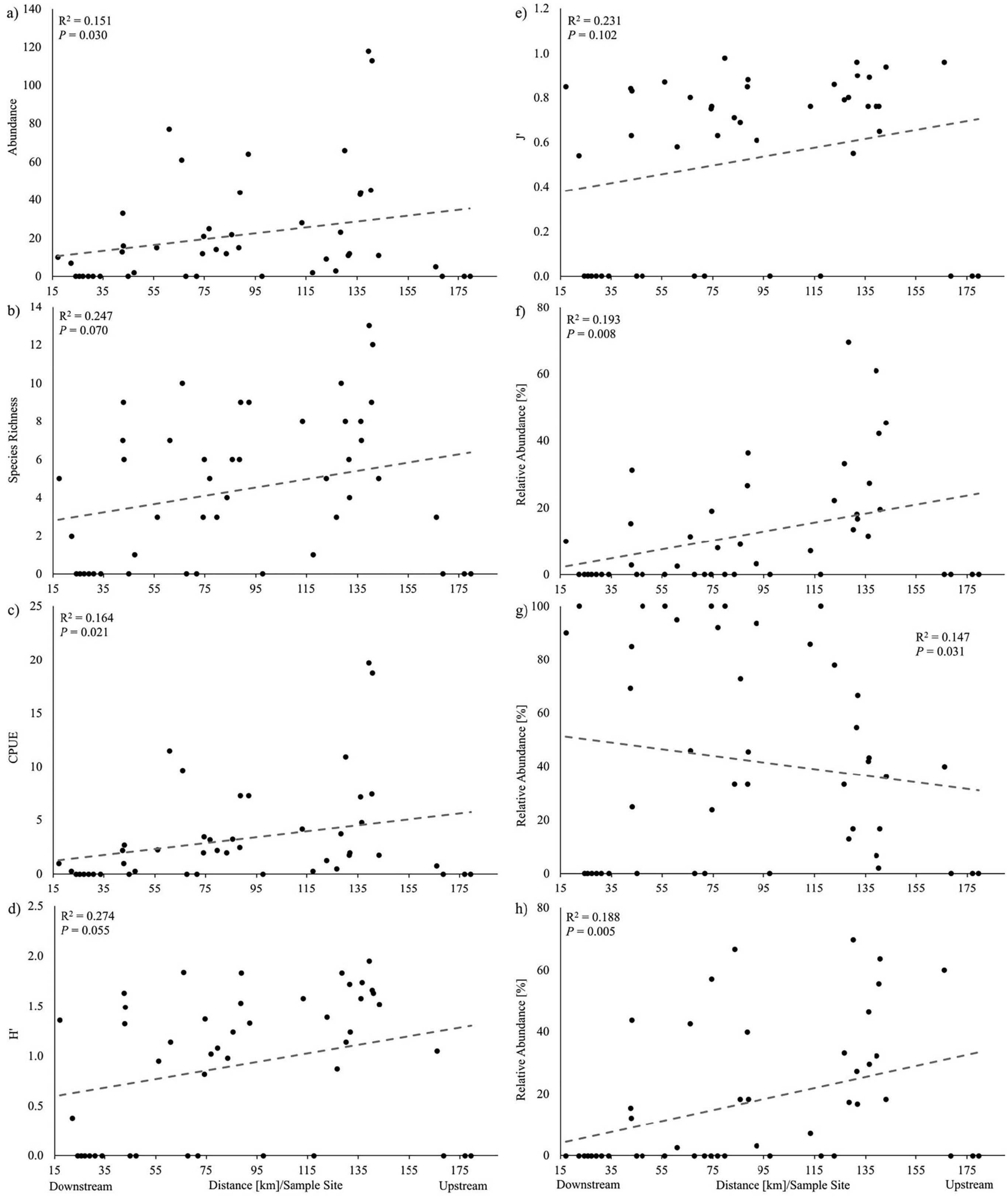

Figure 2. Scatterplots and corresponding regression lines and statistics for (a) total mussel abundance, (b) catch-per-unit-effort (CPUE = mussels/person-hour), (c) species richness, (d) species diversity (H'), (e) species evenness (J'), and relative abundance of mussel species with (f) equilibrium, (g) opportunistic, and (h) periodic life-history strategies per site with increasing distance (km) from the confluence with the Ohio River. Site 46 is the closest to the confluence with Ohio River, and Site 1 is the farthest.

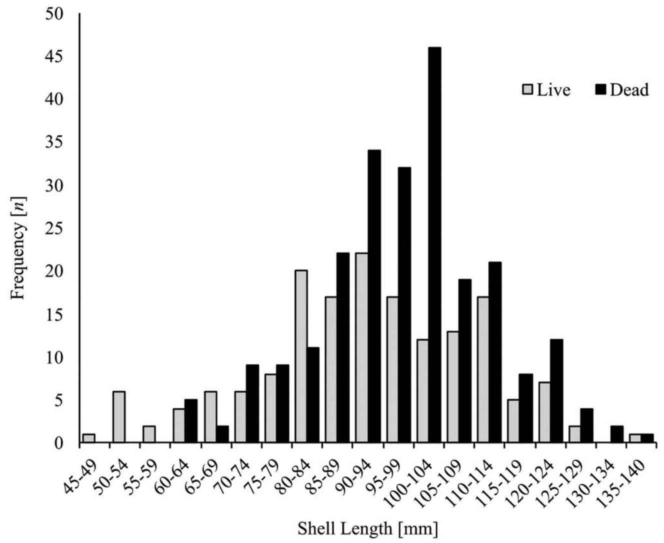

Figure 3. Shell length-frequency plots of live and dead *Potamilus capax* found at our 46 survey sites in the lower Wabash River.

75% of these (Fisher 2006; Stodola et al. 2014; ILDNR 2024; INHS 2024), though they account for only about a third of the mussel species historically known from the basin. Our results are similar to those of Fisher (2006) and Stodola et al. (2014) in terms of the species detected and their distribution across the lower Wabash River. For example, *O. reflexa, P. alatus, P. ohiensis,* and *Q. quadrula* were previously highly ubiquitous and remain so, while historically rare species, such as *Megalonaias nervosa* and *Reginaia ebenus*, remain rare (Fisher 2006; Tieman et al. 2012; Table 2). That said, differences in sampling methods, survey effort, and reporting limit comparability with our study. Our length-frequency plots indicated multiple size classes for several species, and the presence of small (< 70 mm) *P. capax* and other species is encouraging and indicates ongoing recruitment (Fig. 4a–f). Unfortunately, no recruits of *M. nervosa* and *R. ebenus* were located, and both species are thought to be functionally extirpated from the mainstem (Fisher 2006; Tieman et al. 2012).

In general, abundance, CPUE, and species richness declined moving downstream (Fig. 2), and mussels were widely spatially distributed with limited chance of detection beyond the bank (Figs. 5a, b). More than 90% of mussels were found in the timed searches when surveyors could search large areas of a site and focus on areas where mussels were located (i.e., the banks). Usually, mussel abundances and species richness increase with increasing river size, as larger waterbodies typically have more and varied available habitat and can support dense and diverse mussel aggregations (Haag 2012; Ford et al. 2016). Conversely, small streams have limited habitat and support few and scattered aggregations with fewer species (Atkinson et al. 2012; Haag 2012; Ford et al. 2016). The limited and decreasing species richness and abundances of mussels in the lower Wabash River more closely resembled aggregations in smaller stream habitats rather than those in medium/large streams, likely due in part to the habitat homogeneity found throughout much of our study area. This pattern is especially prominent following Site 8, after which population demographic variables shifted and declined, and the assemblage makeup changed (Table 3; Fig. 2a–h).

Following the confluence with the White River, a distinct substrate shift occurred. The White River inputs large amounts of fine sediment into the basin (Pyron et al. 2020), and the substrate shifted from a gravel, sand, and silt mixture to almost exclusively sand/silt, a habitat typically more often utilized by smooth-shelled opportunistic species (Haag 2012). Species with opportunistic life histories tend to have traits that facilitate colonization and survival in more oligotrophic, degraded, or unsuitable habitats (i.e., shifting silt/sand, unconsolidated gravel). Conversely, equilibrium species tend to have traits that favor stable and suitable habitats, while periodic species are intermediate in their traits (Haag 2012). As expected with this habitat change to a silt/sand substrate, the mussel community in our study area shifted from mostly sculptured species with equilibrium and periodic life-history strategies to primarily smooth-shelled, opportunistic species (Table 3). Of species with opportunistic life-history strategies found in our study, 100% of *P. capax*, 100% of *P. alatus*, 93.7% of *P. fragilis*, and 88.1% of *P. ohiensis* were located downstream of Site 8. These are silt/sand preferring species, with smooth and globose shell morphologies that enhance movement in fine substrates (Watters 1994; Haag 2012). Many opportunistic species also utilize multiple common fish species as hosts, enabling them to spread quickly and easily (Haag 2012). Seven of the opportunistic species detected in this study (*Pyganodon grandis* and all *Potamilus* and *Truncilla* species) are known to use *Aplodinotus grunniens* as a host, an abundant and widespread fish species in the Wabash River (Jacquemin et al., 2015). Interestingly, *O. reflexa* and *Amblema plicata* have also been found to use *A. grunniens*, and this may explain their relatively high abundance despite non-opportunistic life-history strategies (Freshwater Mussel Host Database, 2017).

Primarily, mussels were located on gently sloping banks along the edges of sand bars (Fig. 5a, b) and were rarely found in the loose sand/gravel substrates midchannel, likely due to the substrates' instability, which precludes mussels from anchoring (Haag 2012). When mussels were present in the midchannel, abundance and CPUE were low, aggregations were absent, and individuals were widely dispersed (Fig 5a, b). The most practical survey method was to walk along banks looking for movement trails, which could be followed. Mussels would often be buried at the end of trails, some of which terminated out of water. Mussels out of water would often be buried to the water table, possibly enabling them to remain moist until water levels rose (Gough et al. 2012; Galbraith et al. 2015; Mitchell et al. 2018). We found several fresh dead shells with scratches

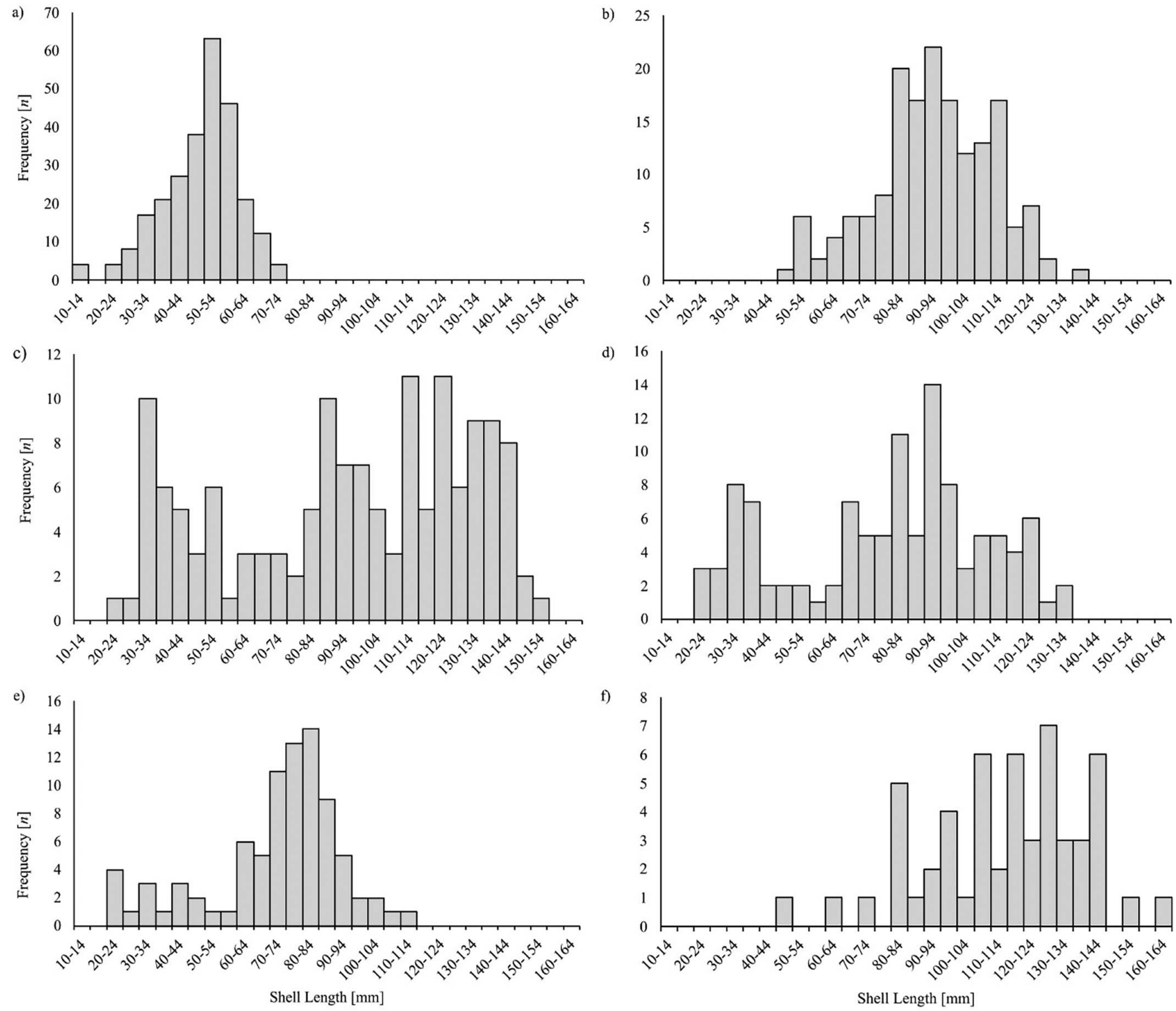

Figure 4. Shell length-frequency plots of the six most abundant species found at our 46 survey sites in the lower Wabash River. (a) *Obliquaria reflexa* ($n =$ 265), (b) *Potamilus capax* ($n = 166$), (c) *Potamilus ohiensis* ($n = 143$), (d) *Potamilus fragilis* ($n = 111$), (e) *Quadrula quadrula* ($n = 85$), and (f) *Tritogonia verrucosa* ($n = 54$).

and teeth marks next to freshly dug holes, suggesting that terrestrial, opportunistic molluscivores may capitalize on these trails.

Our results generally support the greater efficiency of timed searches and transect surveys for estimating species richness but did not support the greater efficiency of quadrat surveys for detecting smaller individuals. Typically, timed searches and transects provide better estimates of species richness because a larger area can be searched, while excavated quadrat sampling provides better estimates of recruits or small species (Vaughn et al. 1997; Obermeyer 1998; Smith et al. 1999). However, in our study, average lengths in quadrat samples were longer than in timed searches or transect samples (Table 4) for two of three species. These differences may be explained by the sand/silt substrate and the wide spatial distribution of mussels. The absence of hard substrate facilitated locating mussels of all sizes (smallest individual = 12 mm). Additionally, mussels were so widely distributed that the probability of an individual being in a quadrat was low (Table 4), and quadrat sampling does not appear productive in this system. Nevertheless, our results show that the use of multiple sampling methods in conjunction can provide more robust assessments of abundance, species richness, and size distributions.

Potamilus capax

Our results indicate that the lower Wabash River continues to support *P. capax*, though it was widely spatially

Table 3. Summary of sampling data from the lower Wabash River, including survey method(s), mussel abundance, species richness and density estimates, survey effort in person-hours, diversity and evenness indices, and the relative abundances of mussel life-history strategies. Abbreviations: TS = timed search, TR = transect, QT = quadrat, *n* = total number of mussels, CPUE = catch-per-unit-effort (mussels/person-hour; data from timed searches), density = mussels/m^2 (data from quadrat samples), E = equilibrium, O = opportunistic, P = periodic, H' = Shannon Wiener species diversity index, and J' = Pielou's evenness index. A dash (–) indicates mussels were not detected.

Site	Survey Method	*n*	Species Richness	Survey Effort	CPUE	Density	Life-History Strategy % E	% O	% P	H'	J'
1	TS	0	0	1	0.0	–	–	–	–	–	–
2	TS	0	0	1	0.0	–	–	–	–	–	–
3	TS	0	0	1	0.0	–	–	–	–	–	–
4	TS	5	3	6	0.8	–	–	40.0	60.0	1.05	0.96
5	TS	11	5	6	1.8	–	45.5	36.3	18.2	1.52	0.94
6	TS	113	12	6	18.8	–	19.5	16.8	63.7	1.63	0.65
7	TS	45	9	6	7.5	–	42.2	2.2	55.6	1.66	0.76
8	TS	118	13	6	19.7	–	61.0	6.8	32.2	1.95	0.76
9	TS, TR, QT	44	7	6	4.8	0.33	27.3	43.2	29.5	1.74	0.89
10	TS	43	8	6	7.2	–	11.6	41.9	46.5	1.58	0.76
11	TS	12	4	6	2.0	–	16.7	66.6	16.7	1.24	0.9
12	TS	11	6	6	1.8	–	18.2	54.5	27.3	1.72	0.96
13	TS	66	8	6	11.0	–	13.6	16.7	69.7	1.14	0.55
14	TS	23	10	6	3.8	–	69.6	13.0	17.4	1.83	0.8
15	TS, TR, QT	3	3	6	0.5	0.00	33.3	33.3	33.3	0.87	0.79
16	TS, TR, QT	9	5	6	1.3	0.00	22.2	77.8	–	1.39	0.86
17	TS	2	1	6	0.3	–	–	100.0	–	0.00	0.00
18	TS, TR, QT	28	8	6	4.2	0.00	7.1	85.8	7.1	1.58	0.76
19	TS	0	0	1	0.0	–	–	–	–	–	–
20	TS, TR, QT	64	9	6	7.3	0.00	3.2	93.6	3.2	1.33	0.61
21	TS	44	9	6	7.3	–	36.4	45.4	18.2	1.83	0.88
22	TS	15	6	6	2.5	–	26.7	33.3	40.0	1.53	0.85
23	TS, TR, QT	22	6	6	3.3	0.00	9.1	72.7	18.2	1.24	0.69
24	TS	12	4	6	2.0	–	–	33.3	66.7	0.98	0.71
25	TS, TR, QT	14	3	6	2.2	0.00	–	100.0	–	1.08	0.98
26	TS, TR, QT	25	5	6	3.2	0.33	8.0	92.0	–	1.02	0.63
27	TS	21	6	6	3.5	–	19.0	23.9	57.1	1.37	0.76
28	TS	12	3	6	2.0	–	–	100.0	–	0.82	0.75
29	TS	0	0	1	0.0	–	–	–	–	–	–
30	TS	0	0	1	0.0	–	–	–	–	–	–
31	TS, TR, QT	61	10	6	9.7	0.33	11.5	45.9	42.6	1.84	0.8
32	TS, TR, QT	77	7	6	11.5	0.00	2.6	94.8	2.6	1.14	0.58
33	TS, TR, QT	15	3	6	2.3	0.00	–	100.0	–	0.95	0.87
34	TS	2	1	6	0.3	–	–	100.0	–	0.00	0.00
35	TS	0	0	1	0.0	–	–	–	–	–	–
36	TS	16	6	6	2.7	–	31.3	25	43.7	1.49	0.83
37	TS, TR, QT	33	9	6	1.0	0.33	3.0	84.9	12.1	1.32	0.63
38	TS	13	7	6	2.2	–	15.4	69.2	15.4	1.63	0.84
39	TS	0	0	1	0.0	–	–	–	–	–	–
40	TS	0	0	1	0.0	–	–	–	–	–	–

Table 3, continued.

Site	Survey Method	*n*	Species Richness	Survey Effort	CPUE	Density	Life-History Strategy % E	% O	% P	H'	J'
41	TS	0	0	1	0.0	–	–	–	–	–	–
42	TS	0	0	1	0.0	–	–	–	–	–	–
43	ST	0	0	1	0.0	–	–	–	–	–	–
44	ST	0	0	1	0.0	–	–	–	–	–	–
45	TS, TR, QT	7	2	6	0.3	0.00	–	100.0	–	0.38	0.54
46	TS, TR, QT	10	5	6	1.0	0.33	10.0	90.0	–	1.36	0.85
Total		996	23	211	4.3	0.08	21.8	46.9	31.3		

distributed. It was located at 22 sites but was found only downstream of site 8 (Fig. 1). Abundances were low per site and only four sites had > 10 individuals. The species was usually found in water ≤ 1 m in depth within the first 10-m from the bank (> 70% of total *P. capax*), in sand and silt substrates, congruent with habitat observations made in other studies (Miller and Payne 2005; Peck et al. 2014). Interestingly, a single individual was located on the substrate surface in the midchannel of the river and may have been washed into the area (Fig. 5a).

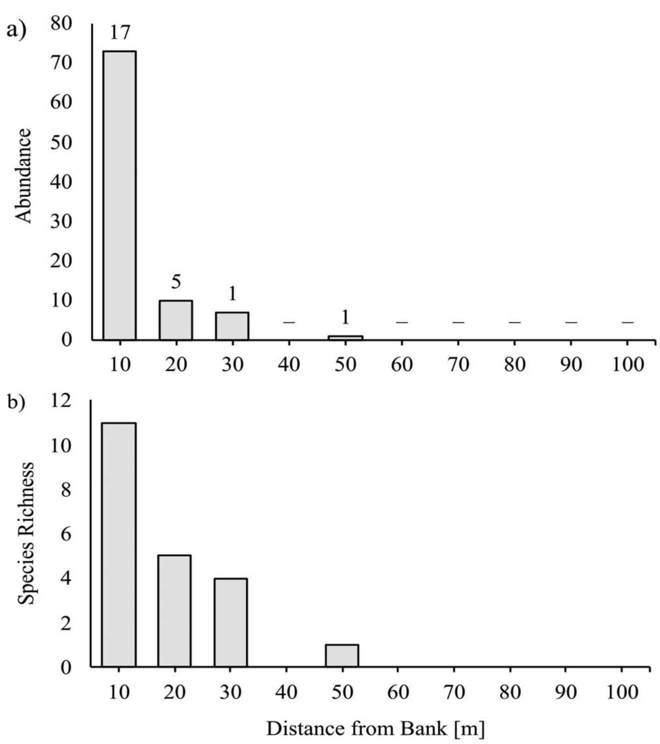

Figure 5. Mussel abundance (a) and species richness (b) per 10-m interval from transect samples. Data are combined from all transects (n = 180) by 10-m interval, and for all species. Values above the columns are *Potamilus capax* abundances found in each interval. A dash (–) indicates no *P. capax* were detected in the interval.

Potamilus capax mortality observed in our study was similar to that reported by Tiemann et al. (2012; 75.9%), though higher than those of other studies (Miller and Payne 2005; Peck et al. 2014). Fresh dead shells were abundant, and at some sites, they were so prevalent the entire search effort could have been spent recovering them. We found many adult live *P. capax* stranded, gaping and in distress, in shallow pools with elevated water temperatures. Though we also located fresh dead *P. ohiensis* and *P. fragilis*, neither were found in comparable numbers, despite similar behaviors, habitat preferences, and fish hosts (Haag 2012; Table 2). The high adult mortality may be a natural occurrence or an artifact of an environmental event. Future studies could explore if it was caused by a unique event, a natural generational process, or some other factor.

Despite high mortality, multiple size classes of *P. capax* were present, including several small individuals (Figs. 3 and 4b), and recruitment appears to be occurring at nearly half of sites. The rapidly declining abundance of individuals ≥ 120 mm probably indicates the size at which age-related mortality occurs. Although considered a low-density species (Miller and Payne 2005), *P. capax* appears stable and healthy in the lower Wabash River, especially compared to other federally listed mussels. For example, *Lampsilis higginsii* is thought to have historically comprised approximately 0.50% of an assemblage in the upper Mississippi River (Havlik and Marking 1981), and *Plethobasus cyphyus* made up 0.03% of the fauna in a survey of the Ohio River (Ford, unpublished data). In contrast, *P. capax* made up 16.70% of our assemblage. Unfortunately, we could not compare our data with historical assemblages, as those data are lacking. Regardless, the overall demography of the *P. capax* population mirrors other studies (Harris 2001; Miller and Payne 2005) and suggests moderate but relatively steady annual recruitment, high longevity, and moderately low annual mortality during the earliest and middle parts of the lifespan.

CONCLUSIONS

This study describes the current status and distribution of mussels in the lower Wabash River and builds on previous

Table 4. Total abundance (n), shell lengths (mean ± SE [range]), and proportion of recruits (Rec.) per species found using each sampling method at the 14 sites in the lower Wabash River where all sampling methods were used. Also presented are the results (F values [degrees freedom] and P values) of the ANOVA model comparing shell length among methods. A dash (–) indicates a species was not detected.

	Timed Searches			Transect Samples			Quadrat Samples			ANOVA (Shell Lengths)	
Species	*n*	Length (mm)	Rec.	*n*	Length (mm)	Rec.	*n*	Length (mm)	Rec.	*F* (df)	*P*
Equilibrium Species											
Quadrula quadrula	13	55.7 ± 6.4 (23–86)	38.5	6	73.3 ± 10.2 (26–93)	16.7	–	–	–	2.282 (1, 17)	0.149
Tritogonia verrucosa	5	125.0 ± 10.8 (96–154)	–	1	70.0 ± 0.0 (70)	–	–	–	–	4.302 (1, 4)	0.107
Opportunistic Species											
Potamilus alatus	2	123.5 ± 14.5 (109–138)	–	3	100.0 ± 20.1 (77–140)	–	–	–	–	0.700 (1, 3)	0.464
Potamilus capax	120	91.3 ± 1.6 (49–126)	0.8	24	91.0 ± 3.5 (60–126)	–	3	104.3 ± 1.9 (102–108)	–	0.871 (2, 144)	0.421
Potamilus fragilis	51	70.9 ± 3.2 (25–118)	19.6	24	70.9 ± 6.7 (24–121)	37.5	1	47.0 ± 0.0 (47)	–	0.408 (2, 73)	0.666
Potamilus ohiensis	63	82.1 ± 3.9 (30–142)	14.3	18	112.7 ± 7.0 (52–141)	–	–	–	–	13.697 (1, 79)	<0.001
Pyganodon grandis	–	–	–	1	156.0 ± 0.0 (156)	–	–	–	–	–	–
Truncilla donaciformis	2	25.0 ± 5.0 (20–30)	100.0	2	25.0 ± 8.0 (17–33)	50.0	–	–	–	0.000 (1, 2)	1.000
Truncilla truncata	4	38.0 ± 4.8 (25–48)	25.0	1	54.0 ± 0.0 (54)	–	–	–	–	2.210 (1,3)	0.234
Periodic Species											
Obliquaria reflexa	20	43.0 ± 2.4 (22–60)	45.0	9	43.8 ± 3.7 (30–57)	44.4	1	52.0 ± 0.0 (52)	–	0.324 (2, 27)	0.726
Obovaria olivaria	23	58.3 ± 3.2 (23–78)	8.7	2	56.0 ± 23.0 (33–79)	50.0	–	–	–	0.036 (1, 23)	0.851
Total	303			91			5				

research (Fisher 2006; Stodola et al. 2014). Additionally, we provide evidence that the use of multiple sampling methods in conjunction can provide more robust assessments of mussel abundance, species richness, diversity, and population demographics. Though much depleted from historical norms, the lower Wabash River continues to support about a third of its original mussel community and does not appear altered since the most recent surveys more than a decade ago. Unfortunately, suitable habitat for many species was largely lacking and will likely remain so. Regardless, the lower Wabash River will likely continue to retain reproducing populations of *P. capax* and other smooth-shelled species unless large-scale alterations of the river occur.

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