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Habitat use and life history of the vernal crayfish, *Procambarus viaeviridis* (Faxon, 1914), a secondary burrowing crayfish in Mississippi, USA

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ABSTRACT

The Lower Mississippi Alluvial Valley (LMAV) is a species-rich region in North America, but its crayfish community has not been extensively sampled. We investigated the annual life cycle, habitat use, and some morphological characteristics of the vernal crayfish, *Procambarus viaeviridis* (Faxon, 1914), in the Dahomey National Wildlife Refuge, Bolivar County, Mississippi. The refuge was located in the central LMAV near the southern limit of the species. Crayfishes were captured in minnow and habitat traps in three seasonally flooded habitat types: wooded (bottomland hardwood forests), trail, and open habitats. *Procambarus viaeviridis* was the most abundant crayfish in these locations. The species had a two- to three-year lifespan, maturing at the end of the first or the beginning of the second year. Form I males were collected throughout the study, and the smallest had a postorbital carapace length of 15.8 mm. Abundance patterns of form I males and laboratory evidence suggested that breeding peaked in May. Small juveniles became abundant in January and February. No ovigerous females were collected; however, dissection of females held in captivity revealed 106–134 ovarian eggs per female. Pool depth, dissolved oxygen, and pH levels were related to the abundance of *P. viaeviridis*. Collections of *P. viaeviridis* were also common in pools containing the crayfishes *P. acutus* (Girard, 1852) or *Cambarellus puer* Hobbs, 1945.

Key Words: fishes, growth rates, habitat-use models, reproduction timing, seasonal wetlands

INTRODUCTION

Knowledge of the life history of species is central to basic and applied ecology and essential to the effective management and conservation of the species (Krausman & Cain, 2013). Crayfishes serve as ecosystem engineers in aquatic systems due to their ability to change macrophyte biomass, manipulate substrate, and create burrows, along with other ecological services (Chambers *et al.*, 1990; Hanson *et al.*, 1990; Rabeni *et al.*, 1995; Statzner *et al.*, 2003; Stenroth & Nystrom, 2003). Their ecological importance suggests that crayfishes should be incorporated into ecosystem management decisions (Black, 2011), especially in the southeastern United States, where over half (189 of 357 species) of the nation's crayfish species occur (Richman *et al.*, 2015). Despite the importance of crayfishes and their high degree of imperilment (Taylor *et al.*, 2007; Richman *et al.*, 2015), as of 2013, life history studies were published for only 12% of native crayfishes in the U.S. and

Canada, 5% of *Procambarus* species, and 8% of lentic species (Moore *et al.*, 2013). The absence of information on the life history of crayfishes impairs species and population management (Biggins, 2006; Moore *et al.*, 2013).

The vernal crayfish, *Procambarus viaeviridis* (Faxon, 1914), is a secondary burrower that spends part of the year in open water, burrowing as habitats dry. The species occurs in eight states, from southern Illinois south to northern Louisiana and central Alabama (Hobbs, 1989; Walls, 2009). It inhabits sluggish streams, vernal ponds, ditches, lowland lakes, swamps, and sloughs, with a preference for seasonally flooded areas (Bouchard, 1972; Page & Burr, 1973; Payne & Riley, 1974). These essential habitats (Page, 1985; Wehrle *et al.*, 1995) are declining worldwide due to anthropogenic alterations (Danielson, 1988; Tockner & Stanford, 2002). Although *P. viaeviridis* is widespread, its life history is poorly documented. The most extensive life-history study of the species was conducted in

Illinois, near the species' northern range limit, from December 1975 to May 1976 (Page, 1985). Sixteen specimens were collected, including four form I males, but no females carrying pleopodal eggs or young. Nothing has been published pertaining to *P. viaeviridis* life history in the southern part of its range. Intraspecific differences in life histories of crayfishes commonly occur between northern and southern range limits due to differences in climate (Cole, 1954; Leggett & Carscadden, 1978; Momot, 1984).

The Lower Mississippi Alluvial Valley (LMAV), is a species-rich region (Stanturf *et al.*, 2000), although its crayfishes and their communities have not been extensively sampled. The U.S. Fish and Wildlife Service (USFWS) conducted an aquatic survey of the Dahomey National Wildlife Refuge (hereafter, "refuge") in the central LMAV in 2012 (Fig. 1) and collected unusually high numbers of *P. viaeviridis*. The morphologies of the gonopod and annulus ventralis of the specimens differed from those of *P. viaeviridis* collected in some other locations, suggesting that the population may be taxonomically distinct, a question that is currently under investigation. The high abundance and possible taxonomic distinction prompted our study. Our goals were to characterize the life history and habitat use of *P. viaeviridis* in the refuge. Objectives included characterization of the annual life cycle, population age-class structure, growth of individuals of *P. viaeviridis*, and modeling the relationships between catch per unit effort (number of individuals per trap, or CPUE) of the species and the habitat, water quality, and CPUE of other crayfishes and fishes.

MATERIALS AND METHODS

Study area

The study was conducted entirely on the 3,921 ha refuge in Bolivar County, Mississippi (33.707710 °N, -90.930108 °W,

Fig. 1). The refuge, established in 1991, was dominated by mature bottomland hardwood forests and surrounded entirely by row-crop agriculture, including rice, corn, wheat, and soybeans. It was the largest remaining tract of bottomland hardwood forest in northwestern Mississippi outside of the mainline Mississippi River levees (USFWS, 2013). Four tributaries of the Bogue Phalia River traversed the refuge (USFWS, 1993). High rainfall and subsequent stream flooding, normally in winter and spring, partially inundated low areas of the refuge (typically elevations up to 39.6 m above mean sea level; USFWS, 1993), creating numerous flood-plain pools. The pools typically persisted for months, providing habitat for a variety of fauna.

Phase 1 sampling methods

The study was conducted in two phases. In Phase 1, USFWS personnel sampled 20 sites (Fig. 1) from January to May 2012. Sites were chosen by mapping water distribution during the previous winter/spring, directly observing locations where seasonal wetlands occurred to ensure areas were flooded sufficiently for sampling, and subsequently filtering locations to select those representing the range of seasonal wetland habitats available. Sites were then grouped into habitat types based on vegetation types, amount and size of woody debris, and location within the refuge. Three habitat types were sampled: wooded, trail, and open. Wooded sites were within bottomland hardwood forests, had relatively undisturbed soils, and contained some understory vegetation and abundant wood debris. Trail sites were on or along forested dirt roads that were used for hiking. Although these sites had substantial tree canopy, soils were altered and understory vegetation was lacking. Open sites were between forests and gravel roads, contained 5% or less canopy cover, and were mowed at least annually. Sites were

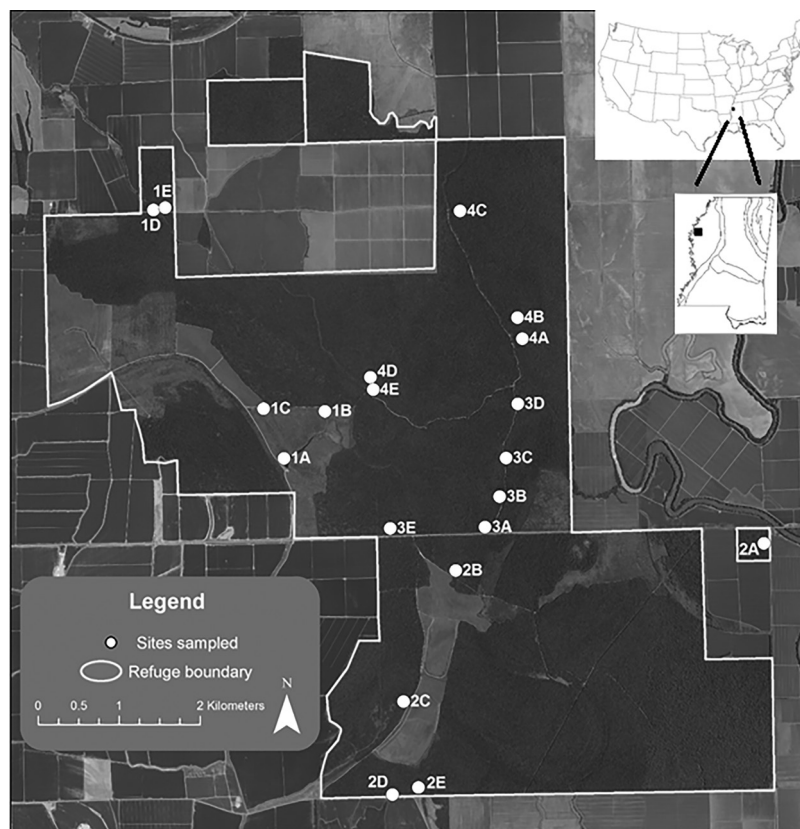


Figure 1. Location of the Dahomey National Wildlife Refuge, Bolivar County, Mississippi, with collection sites shown by labeled circles. Inset shows Mississippi ecoregions and refuge location within Lower Mississippi Alluvial Valley region.

grouped by location into four sampling areas (1–4) with five sites (A–E) each (Fig. 1; Supplementary material Appendix S1).

Sites were sampled on a rotational basis with one area (five sites) sampled each week. The rotation was repeated once data were collected for all four areas. Crayfishes and fishes were collected and habitat was characterized during each sampling round. Specimens were collected using cylindrical minnow traps (419 mm long, 190 mm diameter) with 6.4 mm galvanized steel mesh and two conical entrances, each with a 25.4 mm diameter opening. Traps were baited with Cajun World Crawfish Bait (Purina® Animal Nutrition, Summit, MO). Twenty minnow traps per site were set at the beginning of the week, checked daily, and removed after four nights. Whenever possible, traps were placed near an existing structure, such as against a log, near vegetation, or in a depression, to maximize captures. The number of traps per site was reduced as pools dried, with a minimum of five traps per site. Trapping continued until pool water was too shallow to cover the trap entrances.

Captured fishes were preserved in 5% formalin and identified to species. For both study phases, fish species were classified as predators or non-predators of crayfishes, as defined by the FishTraits database (Frimpong & Angermeier, 2009). All fishes that may eat other juvenile and adult fishes, crayfishes, crabs, frogs, or other amphibians and macroinvertebrate were grouped following Frimpong & Angermeier (2009) and considered potential crayfish predators. Captured crayfishes were preserved in 70% ethanol for laboratory analyses. All preserved crayfishes from both study phases were housed in the USDA Forest Service Center for Bottomland Hardwoods Research (CBHR) laboratory (Oxford, MS), and all preserved fishes were housed in the USFWS Grenada laboratory. Ultimately, all specimens will be deposited in the Mississippi Museum of Natural Science, Jackson.

Habitat characteristics (number of pools, percent canopy cover estimated visually, and presence of leaf litter) and water quality parameters (Table 1; Supplementary material Appendix S2) were measured at each site during each sampling. Water quality was measured at the approximate center of each pool; at sites with multiple pools, it was measured in the same three pools throughout Phase 1. Dissolved oxygen (DO) was measured with a YSI DO 200 portable meter (YSI, Yellow Springs, OH); all other water quality parameters were measured with a Hanna combo pH and EC meter, HI98129 (Hanna Instruments, Leighton Buzzard, UK).

Phase 2 sampling

In Phase 2, 5 of the 20 Phase 1 sampling sites were selected to represent the three habitat types where low to high CPUEs of *P. viaevidis* occurred (low = mean CPUE < 1 crayfish/trap; medium = 1–3; high = > 3). Sites were sampled monthly from November 2013 to June 2014, and in February and March 2015.

We sampled crayfishes with minnow traps (as in Phase 1) and habitat traps in 2013 to 2014, but with only minnow traps in 2015.

Habitat traps consisted of circular, collapsible nets that lay on the substrate topped with shelter bundles (Parkyn *et al.*, 2011); when lifted, the sides of the traps enclosed the shelter bundles, minimizing crayfish escapes. Shelter bundles consisted of branching tops of Asian bamboo (*Phyllostachys* sp.) tied together. The circular nets (Miller Net Company, Memphis, TN) were 46 cm in diameter with 3 mm mesh netting. Three ropes were attached equidistantly on each circular, metal-net frame and joined above the trap for lifting. Organisms were free to come and go until the traps were lifted from the water. All traps were baited with Purina® Cajun World Crawfish Bait.

Up to 20 minnow traps and 12 habitat traps were deployed monthly at each site, with traps placed at least 3 m apart. Whenever possible, traps were placed near an existing structure or in depressions. The number of traps per site depended on the size of the pool, with a minimum of three traps of each type per site. Trapping continued until pool water was too shallow to cover entrances of minnow traps. Minnow traps were set for one night per sample month in 2013 and 2015, and two nights per month (checked daily) in 2014. Habitat traps were deployed continuously during the first seven months of Phase 2 and were checked for crayfishes during each sample (once per month). Traps were added or removed as pool sizes changed, and shelter bundles were replaced as necessary.

Crayfishes and fishes from minnow and habitat traps at each site were kept separately. Most individuals of *P. viaevidis* were preserved in 70% ethanol, with ten specimens kept alive in the laboratory to monitor their growth and reproductive cycles. Other crayfishes were identified to species and sexed in the field, whenever possible, and released; otherwise, they were preserved in 70% ethanol. Fishes were identified in the field and released.

Habitat and water quality parameters measured in Phase 1 (except for total dissolved solids), as well as area and turbidity of pools (see Table 1; Supplementary material Appendix S2) were measured at each site during each sampling. Because water-quality parameters did not differ significantly among pools within sites during Phase 1 (11 sites with >1 pool, ANOVA, all $P > 0.05$), parameters were measured in only the largest pool at each site during Phase 2. Water quality was measured with a Hydrolab Quanta (HACH-Hydrolab, Loveland, CO) that was calibrated before each sampling. From January to May 2014, water temperatures were recorded at 30 min intervals at every site and air temperatures at one site using HOBO Water Temperature Pro v2 data loggers (Onset Corporation, Bourne, MA).

Morphological and reproductive data

In both study phases, crayfish species, sex, and reproductive condition (juvenile female (JF), juvenile male (JM), adult female (F), or adult male form II (MII) or form I (MI)) was recorded. Carapace length (CL), postorbital carapace length (POCL), and width of chela (CW) of *P. viaevidis* were also measured. The right chela

Table 1. Water quality parameters from phases 1 and 2. Water temperature summarizes temperatures recorded during sampling. SD, standard deviation; N, total number of readings.

	N	Phase 1				N	Phase 2			
		Median	SD	Minimum	Maximum		Median	SD	Minimum	Maximum
Pool depth (cm)	105	15.0	7.4	2.5	41.0	89	18.0	7.3	5.0	42.0
Pool area (m ²)						89	119.5	919.2	1.0	4116.0
Water temperature (°C)	133	14.9	5.3	6.5	28.7	36	14.8	4.92	2.6	23.2
Dissolved Oxygen (% saturation)	119	30.6	20.0	3.5	114.2	36	27.3	19.05	4.1	94.1
Conductivity (µS/cm)	119	150.0	63.5	36.0	480.0	36	88.0	30.0	60.0	200.0
pH	119	7.3	0.3	6.7	8.4	36	6.6	0.21	6.3	7.4
Total dissolved solids (ppm)	119	75.0	31.2	33.0	159.0					
Turbidity (NTUs)						36	32.5	28.5	11.6	137.0

was measured, unless missing or regenerated, in which case the left chela was used. Individuals with both chelae regenerated or missing were excluded from the data set.

A subset (1,287 out of 2,544) of *P. viaeviridis* from Phase 1 were measured, as were all from Phase 2. In Phase 1, we measured all *P. viaeviridis* in one large collection ($N = 237$) and in any collection with fewer than 30 specimens per reproductive condition. For other Phase 1 collections, 25% or at least 30 specimens of each reproductive condition from each sample were measured using a fixed count method (Barbour *et al.*, 1999). Crayfish of one reproductive form were spread evenly across an 18×24 cm pan marked with 12 numbered grid cells. All individuals from three randomly chosen grid cells were measured. If necessary, all individuals from additional, randomly chosen cells were selected until at least 30 were measured. Individuals that looked unique or abnormally large or small were also measured.

Ten individuals of *P. viaeviridis* (7 F and 3 MI) collected in March 2015 from site 3B (wooded habitat) were placed in outdoor tanks at the CBHR laboratory. Tanks were filled months previously, had accumulated leaf litter and detritus, and were colonized by amphibians and invertebrates, such as tadpoles, dragonfly larvae, and mosquito larvae. No additional food was supplied. Pea gravel and bricks were used as substrate and cover in tanks. We measured POCL bimonthly and checked male form and female reproductive condition (glair glands, sperm plugs, or attached eggs). We preserved surviving crayfish and dissected females to count ovarian eggs in October 2015.

Data Analysis

We assessed relative abundances of adult forms and sex ratios using all *P. viaeviridis* from both study phases. We pooled relative abundances of adult forms across sites and summarized by month to characterize adult reproductive timing. Sex ratios were calculated separately for adults and juveniles and tested for deviation from 1:1 using χ^2 tests (stats R package; R Core Team, 2013).

Age-class structure during Phase 2 was examined via the length-frequency method (France *et al.*, 1991). We estimated the number of age groups by month using mixed distribution analysis (flexmix R package) of the length-frequency data (Gruen *et al.*, 2014). Data (POCL) were grouped across sites for each month. Models were run with 1,000 iterations and a four-group maximum assumption (Page, 1985; France *et al.*, 1991). Integrated completed likelihoods (ICL) were used to select the best model (Biernacki *et al.*, 2000).

Growth during Phase 2 was estimated via examination of increases in mean POCL (Muck *et al.*, 2002; Baker *et al.*, 2008). Polynomial length-frequency distribution analysis was used to analyze the relationship between mean POCL of each year class, with the slope of the relationship showing the growth rate between year classes. Monthly growth of the 2013 age-0 *P. viaeviridis* was also estimated through polynomial length-frequency distribution analysis of increases in monthly mean POCL across 15 months, from December 2013 to March 2015. The slope of the relationship was used to estimate monthly growth rates.

Morphological differences among reproductive forms were analyzed to characterize allometry of the *P. viaeviridis* population. All measured individuals were included, with each phase analyzed separately. We used the POCL of the smallest form I male to demarcate juveniles from adults. Welch's ANOVA and post hoc tests were used to analyze differences in ratios of morphometric variables (CW, POCL, and CL) among reproductive forms, while controlling for covariates (habitat and site). Linear relationships between morphometric variables were also estimated for each form.

Relationships of *Procambarus viaeviridis* with habitat and biota

Temperature affects crayfish activity (Mundahl & Benton, 1990; Richards *et al.*, 1995), so we analyzed correlations between

P. viaeviridis CPUE and water temperatures using Pearson's correlation test. We compared CPUE to mean water temperatures at sites on the day of trap setting and to temperatures averaged over two and three days prior (hereafter "three days prior" temperature) to checking traps for both study phases (Westhoff & Paukert, 2014). For Phase 1, we estimated water temperatures from NOAA air temperature data (Westhoff & Paukert, 2014; Greenville, MS, KGLH weather station, NOAA, 2016). Using data from Phase 2, we created a regression equation (three days prior water temperature = $0.7628[\text{NOAA three days prior air temperature}] + 2.1712$, $r^2 = 0.86$) that we then used to estimate the three days prior water temperatures during Phase 1.

We modeled the relationship of *P. viaeviridis* CPUE to habitat and biotic characteristics to examine factors associated with their distribution. We constructed separate models for each study phase using CPUE from minnow trap collections at all sites. We sought to explain variation in *P. viaeviridis* CPUE using habitat type, water quality, and CPUE of fishes and other crayfishes (all parameters except pH were log transformed and are listed in Table 2). Linear mixed-effect repeated measures models were fit with maximum likelihood estimations. In the models, *P. viaeviridis* CPUE was the dependent variable and site was a random effect. The normality assumption for maximum likelihood was met. Interactions of date with all parameters were included in full models. We used the MuMIn R package (Bartón & Anderson, 2002) to analyze all possible models. Model selection was based on corrected Akaike information criterion (AIC_c) because sample sizes were small relative to the number of estimated parameters (Burnham & Anderson, 2002). We compared alternative models by weighting their level of data support (Hurvitch & Tsai, 1989), with the lowest AIC_c value representing the best-supported model. Main effects were removed from the final model if their interactions with date were included as a parameter.

Table 2. Parameters used in model selection for both study phases (unless only one phase indicated). CPUE, catch per unit effort; TDS, total dissolved solids.

Model parameters
Response variable
<i>Procambarus viaeviridis</i> CPUE
Random effect
Site
Fixed effects
Habitat type
Wooded
Trail
Open
<i>Cambarellus puer</i> CPUE
<i>Procambarus acutus</i> CPUE
<i>Procambarus clarkii</i> CPUE (Phase 1 only)
Pool area (m ²) (Phase 2 only)
Depth (cm)
Dissolved oxygen (mg/l)
Conductivity (μS/cm)
pH
Three-day prior temperature (°C)
TDS (ppm) (Phase 1 only)
Turbidity (NTU) (Phase 2 only)
Predatory fish CPUE
Non-predatory fish CPUE
Repeated measure
Collection date

Table 3. Distribution of the crayfish and fish species in vernal pools on the Dahomey National Wildlife Refuge, Bolivar County, MS, during both study phases, with total number of trap nights (TN) indicated. Site numbers correspond with those in Figure 1. Asterisks (*) indicate sites that were sampled in both study phases. All other sites were sampled only during Phase 1. Numbers indicate individuals captured in Phase 1 or in phases 1 and 2. Potential crayfish predators (+) are indicated for fish species. Fish species with < 10 captured individuals are not included.

		Sites																				
Taxon	Species	1A	1B	1C	1D	1E	2A	2B*	2C	2D	2E	3A*	3B*	3C*	3D	3E	4A*	4B	4C	4D	4E	Total
Crayfishes	TN	150	150	135	135	120	150	150/153	165	135	150	90/168	135/331	120/288	105	150	90/242	90	90	90	90	2,400/1,182
	<i>Procambarus viaeivridis</i>	0	93	0	95	23	1	225/32	0	109	149	215/67	1,118/707	68/102	36	21	67/203	87	18	102	73	2,478/1,111
	<i>P. clarkii</i>	12	0	0	0	0	34	2/0	117	2	11	0/0	0/0	0/0	0	0	0/0	0	0	0	0	178/0
	<i>P. acutus</i>	0	11	4	0	1	4	33/1	2	141	181	176/0	125/290	439/816	187	65	32/32	0	1	2	0	1,404/1,139
	<i>Cambarellus puer</i>	0	1	0	0	0	0	2/0	0	0	0	1/1	33/381	168/29	2	8	0/1	0	0	0	0	215/411
	<i>Creaserinus fodiens</i>	0	0	0	0	0	0	0/0	0	0	0	0/0	0/0	0/0	0	1	0/0	0	0	0	0	1/0
Fishes	(Cottle, 1863)																					
	<i>Amia calva</i> Linnaeus, 1766+	0	0	0	0	0	0	0/0	281	0	0	0/0	0/0	0/0	0	0	0/0	0	0	0	0	281/0
	<i>Lepomis cyanellus</i>	259	30	4	0	0	0	1/2	1	0	4	0/0	3/8	5/13	3	0	4/28	0	0	0	0	311/51
	Rafinesque, 1819+																					
	<i>L. gulosus</i>	41	7	0	0	0	0	0/0	0	0	0	0/0	1/3	0/7	0	0	0/0	0	0	0	0	49/10
	(Cuvier, 1829)+																					
	<i>L. symmetricus</i>	23	4	0	0	0	0	0/0	1	0	0	0/0	0/0	0/0	0	0	0/0	0	0	0	0	28/0
	Forbes, 1883																					
	<i>Gambusia affinis</i>	112	1	2	0	0	0	2/0	160	31	23	0/0	218/2	0/0	0	0	0/0	4	0	0	0	553/2
	Baird & Girard, 1853																					
<i>Aphredoderus sayanus</i>	0	0	0	0	0	0	0	0/1	0	0	0	0/0	1/22	0/10	0	0	0/1	0	0	0	0	1/34
Gilliams, 1824+																						

RESULTS

The persistence of pools varied by study phase and site. During Phase 1, pools persisted in all 20 sites from January to March 2012. Three sites were dry by April, 15 by May, and all dry by June 2012. Pools persisted in all five sites from November 2013 to May 2014 during Phase 2. Three sites were dry in June, and all dried by July 2014.

Five crayfish species and 12 fish species were collected. During Phase 1, four crayfish species co-occurred with *P. viaeviridis* (Table 3, Supplementary material Appendix S3). *Procambarus viaeviridis* and *P. acutus* (Girard, 1852) were the most common crayfishes, constituting 58% and 33%, respectively, of the total catch and occurring at 16 of the 20 sites (Table 3, Supplementary material Appendix S3). During Phase 2, three crayfish species were collected, and *P. acutus* was the most abundant (43% of total catch; Table 3, Supplementary material Appendix S3). We collected *P. viaeviridis* with 12 fish species, including eight crayfish predators, over the entire study period. Fish species represented by more than 10 individuals are listed in Table 3. Additional predatory fishes captured included *Lepomis macrochirus* Rafinesque, 1819 ($N = 6$), *Ameiurus melas* (Rafinesque, 1820) ($N = 7$), *A. natalis* (Lesueur, 1819) ($N = 3$), and *Esox americanus* Gmelin, 1789 ($N = 1$); non-predatory fishes included *Notemigonus crysoleucas* (Mitchill, 1814) ($N = 6$) and *Opsopoeodus emiliae* Hay, 1881 ($N = 1$) (Supplementary material Appendix S4).

Life history

Sex ratios of *P. viaeviridis* were biased for adults but not juveniles in both phases of the study. Males constituted 64% of adults collected in Phase 1 (M:F = 1.8, $\chi^2_{1,919} = 69.7$, $P < 0.001$) and 58% in Phase 2 (M:F = 1.4, $\chi^2_{1,678} = 17.2$, $P < 0.01$). Adult females were collected in all sample months, whereas adult males were not collected in January 2012 or February 2015 (Fig. 2). Males constituted 75% of adult collections from February to April 2012 and 77% of collections from May to June 2014. Sex ratios of juveniles were unbiased (Phase 1: JM:JF = 1.2, $\chi^2_{1,363} = 3.37$, $P = 0.07$; Phase 2: JM:JF = 0.9, $\chi^2_{1,337} = 0.50$, $P = 0.48$).

One to two age classes were indicated for *P. viaeviridis* in each month, except in January 2014, when three age classes were present (Fig. 3). Mean POCL of age 0 and age 1 increased from December 2013 to March 2014 (3.1 to 11.0 mm and 19.5 to 21.8 mm, respectively). From April to June 2014, the mean POCL of the lone age class, which overlapped the March 2014 age 0 and 1 classes, increased from 17.0 mm to 20.4 mm. The mean POCL of age 2 in January 2014 was 24.6 mm. Mean POCL of age classes were similar when sexes were analyzed separately.

Younger *P. viaeviridis* grew faster than older individuals based on our observed cohorts. Age 0 individuals grew twice as fast as age 1 individuals from December 2013 to June 2014 (POCLa = $9.47 + 11.49a - 1.89a^2$, $a = \text{age}$, $r^2 = 0.67$). On average, age 0 *P. viaeviridis* grew 20 mm (from 3 to 23 mm POCL), during their first 14 months (December 2013 to February 2015; Fig. 4), with similar growth rates for male and females ($t_8 = 0.16$, $P = 0.88$).

Form I males were collected throughout the study, but their relative abundance varied widely. The smallest form I male was 15.8 mm POCL. Form I males were present in all but two samples and outnumbered form II males in 9 of 12 months when males were collected (Fig. 2). Females constituted over 50% of adult *P. viaeviridis* collected early in each sampling season (January 2012, November 2013 to January 2014, and February 2015), but less than 25% collected late in each season (February to April 2012, and May to June 2014; Fig. 2). Juveniles were collected in every sample. Individuals of a cohort first appeared in December, becoming abundant in January and February (Fig. 3).

No females with glair or pleopodal eggs or young were collected, but by May 2015 all 7 females held in laboratory tanks exhibited glair and all 3 males were form I. All females dissected in October contained ovarian eggs (range = 106–134) ($N = 3$, mean POCL = 26.5 ± 0.76), but did not exhibit glair.

Form I male *P. viaeviridis* had proportionally larger chelae, on average, than did all other reproductive forms, but POCL:CL ratios did not differ among forms. Form I male CW:POCL ratios averaged 41% and 48% larger in phases 1 and 2, respectively, than those of all other forms (Phase 1: $F_{4,636} = 1165.82$, $P < 0.001$, post-hoc tests: $P < 0.001$; Phase 2: $F_{4,799} = 817.99$, $P < 0.001$, post-hoc tests: $P < 0.001$). CW:POCL ratios in both phases were also smaller for adult females than males (post-hoc tests: $P < 0.001$) and for juveniles than adults (post-hoc tests: $P < 0.001$; Fig. 5). Ratios of CW:POCL did not differ among habitat types (Phase 1: $F_{2,15} = 1.56$, $P = 0.24$; Phase 2: $F_{2,2} = 2.95$, $P = 0.25$). Mean POCL:CL ratios in both phases were larger across all adult forms (0.83) than across juvenile forms (0.82) (Phase 1: $F_{4,219} = 2.95$, $P = 0.02$, post-hoc test: $P = 0.008$; Phase 2: $F_{4,859} = 8.71$, $P < 0.001$, post-hoc test: $P < 0.001$). These differences were statistically significant, but probably not biologically significant (CL = $1.2566(\text{POCL}) - 1.1152$, $r^2 = 0.88$, pooled across all forms). One female had hooks on its third and fourth pereopods, similar to the hooks on a form I male.

Relationships of *Procambarus viaeviridis* with habitat and biota

Phase 1 models assessed sites with and without *P. viaeviridis*. Pool depth, pH, collection date, and CPUE of *P. acutus* and *Cambarellus*

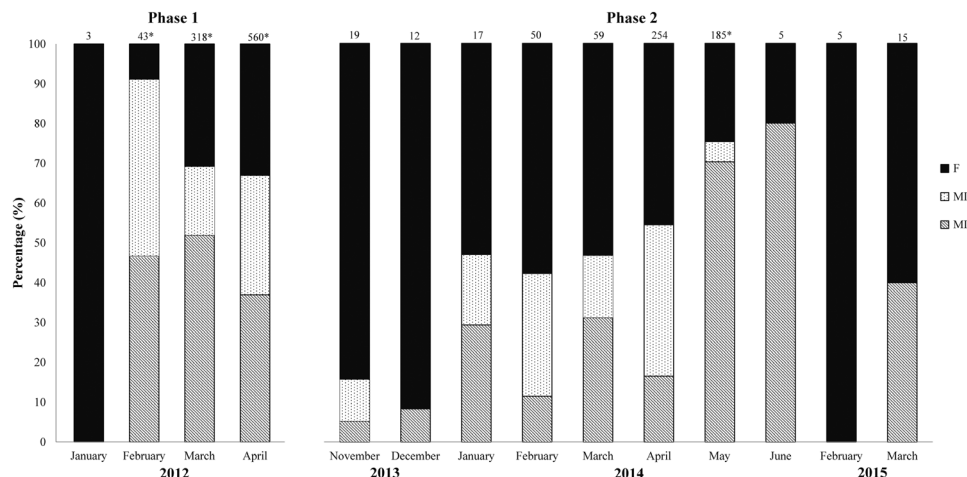


Figure 2. Percentage of collected adults of *Procambarus viaeviridis* that were females (F), form I males (MI), or form II males (MII) in each sampling month during Phase 1 (2012) and Phase 2 (2013 to 2015) of the study. Sample sizes indicated above bars. Asterisks (*) indicate sex bias in sample (χ^2 , $P < 0.001$).

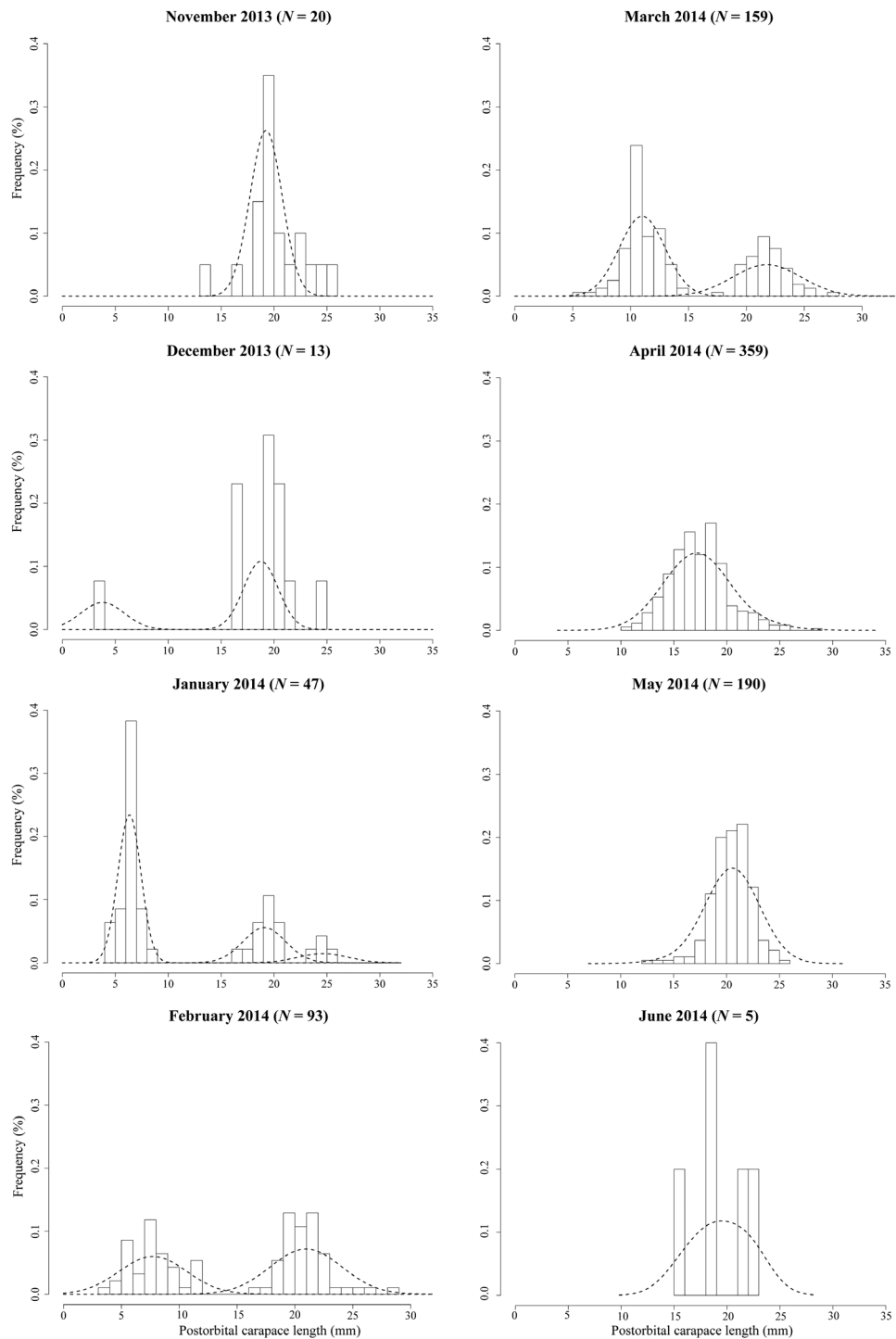


Figure 3. Frequency of postorbital carapace length for samples of *Procambarus viaeviridis* from 2013 to 2014. Dashed lines represent age classes estimated using mixed distribution analyses, with peaks at age class median lengths.

puer Hobbs, 1945 were all associated with variation in *P. viaeviridis* CPUE in Phase 1 (Table 4). Depth and *P. acutus* CPUE were included as main effects in the best model, whereas collection date influenced the relationship between *P. viaeviridis* CPUE and both *C. puer* CPUE and pH.

Depth was negatively correlated with *P. viaeviridis* CPUE. Increases in CPUE in late February and March (Fig. 6A) occurred during a decline in pool depths (Fig. 6B, Table 4). *Procambarus viaeviridis* CPUE was positively correlated with *P. acutus* CPUE (Table 4); 60% of collections that contained *P. viaeviridis* also

contained *P. acutus*. In the beginning of Phase 1, CPUEs of *P. viaeviridis* and *C. puer* were slightly negatively correlated, but this correlation became increasingly more positive with time. The relationship between *P. viaeviridis* CPUE and pH changed inconsistently over time and was not subject to simple interpretation.

Phase 2 models evaluated the differences among five sites all containing *P. viaeviridis*. Dissolved oxygen, pH, predatory fishes, and the relationship of time of the year and CPUE of non-predatory fishes were all associated with variation in *P. viaeviridis* CPUE in Phase 2 (Table 4). *Procambarus viaeviridis* CPUE increased with

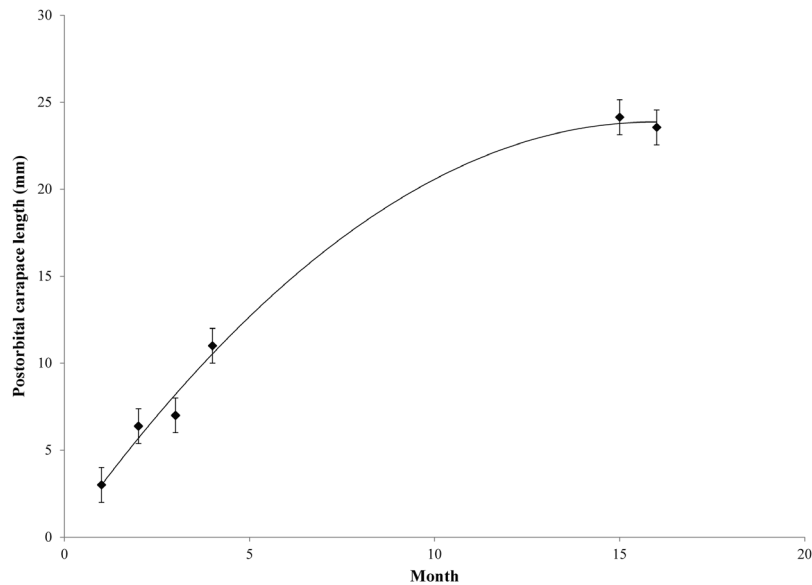


Figure 4. Polynomial model describing growth rate of age class 0 cohort of *Procamburus viaeviridis* over 16 months beginning in December 2013 ($POCL_t = 0.1267 + 3.1197t - 0.107t^2$, $r^2 = 0.88$); POCL = postorbital carapace length, t = month, month 1 = December 2013. Points indicate mean (± 1 SE) age-0 POCL during each sampling period.

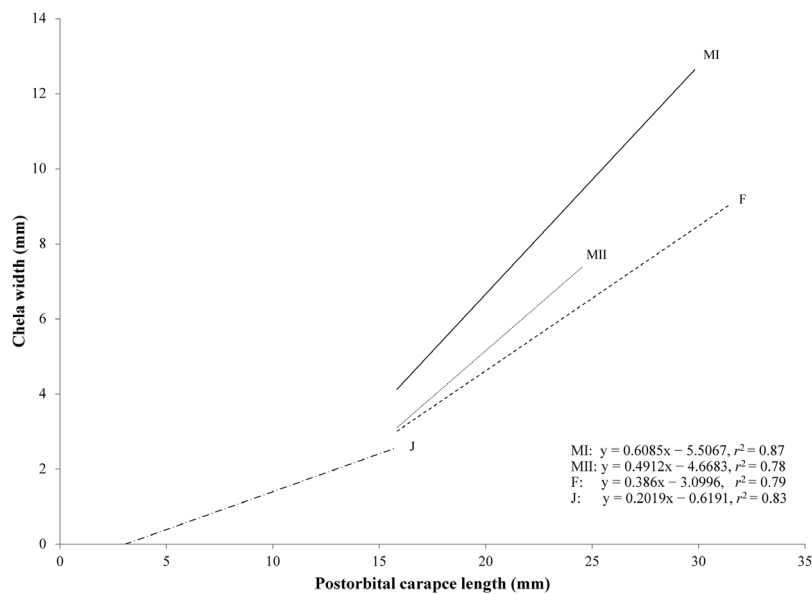


Figure 5. Relationship of width of chela (mm) of *Procamburus viaeviridis* to postorbital carapace length (mm) for each form; juvenile males and females were combined; MI = form I males, MII = form II males, F = females, J = juveniles.

time, peaking in May (Fig. 7A), as pH decreased (Fig. 7B, Table 4). *Procamburus viaeviridis* CPUE increased with DO and predatory fishes CPUE (Table 4). Non-predatory fishes were collected in only three months during Phase 2 and were inconsistently related to *P. viaeviridis* CPUE.

Captures of *P. viaeviridis* exhibited a threshold response to water temperature, with CPUE increasing with temperatures above 10.5 °C (Fig. 8). Although temperature affected crayfish CPUE, it was also positively correlated with collection date, causing temperature to be left out of all models.

DISCUSSION

Procamburus viaeviridis was the most abundant crayfish in the seasonal wetland habitats of the refuge and was collected during

every sample month. Form I males were collected throughout the study, albeit sometimes in low numbers. The smallest form I male (POCL = 15.8 mm) was observed in June 2014, suggesting that males can reach maturity as early as 7 months of age.

Monthly changes in relative abundances of adults and juveniles provided clues to the timing of copulation and reproduction. Newly hatched juveniles became abundant in January and February and form I males in May, consistent with a population in Illinois (Page, 1985). No females with pleopodal eggs or young were collected in either study phase, but females constituted most of the adult *P. viaeviridis* collected from November to March 2014 and less than 20% of adults collected in May 2014. This abrupt change in female abundance in traps suggests that copulation and subsequent burrowing of females probably occurred in April or May, consistent with inferences made in Illinois (Page, 1985) and Missouri (Pflieger, 1996). Changes also occurred in the abundance

Table 4. Best linear mixed-effect repeated measures models of the relationship of *Procambarus viaevidis* CPUE to habitat and water-quality parameters, catch per unit effort (CPUE) of sympatric crayfishes and fishes, and their interactions with collection date. AIC_c, corrected Akaike information criterion; asterisks (*) indicate interactions between parameters.

Model (parameters)	AIC _c	Beta	Standard error	t value	P value
Phase 1 (2012)	51.26				
Date * <i>Cambarellus</i>		0.28	0.03	8.75	< 0.001
puer CPUE					
Date * pH		0.18	0.05	3.67	0.002
<i>Procambarus acutus</i>		0.34	0.10	3.32	0.006
CPUE					
Depth		- 0.95	0.13	3.75	0.001
Phase 2 (2013–2014)	31.52				
Dissolved oxygen (mg/l)		0.17	0.09	2.01	0.05
Predatory fishes CPUE		1.46	0.74	1.98	0.05
pH		- 7.07	1.70	- 4.17	0.004
Date * non-predatory		0.14	0.05	2.68	0.01
fishes CPUE					

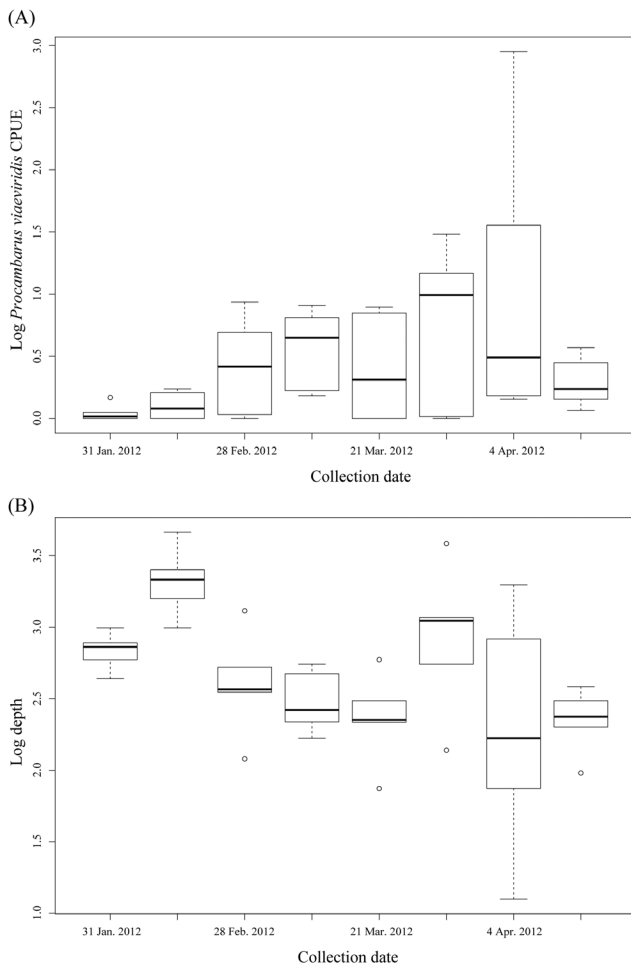


Figure 6. Box plots of log transformed *Procambarus viaevidis* catch per unit effort (CPUE, number per trap) and depth during Phase 1 of study. Boxes indicate 25th, 50th, and 75th percentiles, whiskers represent minimum and maximum values (excluding outliers), and dots represent outliers.

of form I and II males. Form II males were common from January to April, whereas form I males constituted 70% of the adult population in May, further indicating that breeding may peak in May.

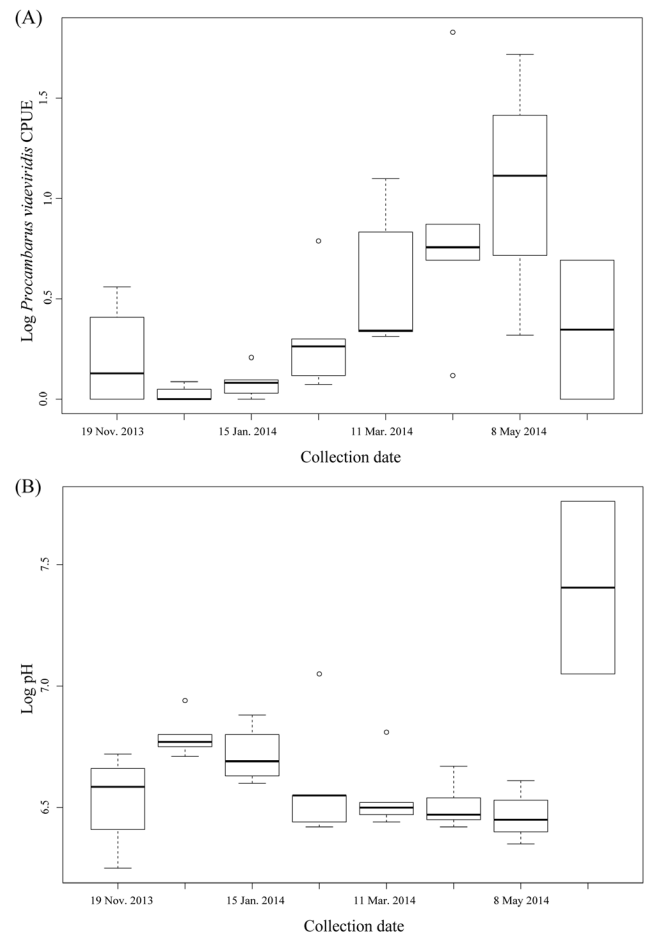


Figure 7. Box plots of log transformed *Procambarus viaevidis* catch per unit effort (CPUE, number per trap) and pH during Phase 2 of study. Boxes as in Fig. 6.

A protracted reproductive season is possible, with females storing sperm to use for later fertilization (Berrill & Arsenaault, 1982, 1984; Snedden, 1990). Biases in relative abundances may also be associated with our trapping methods, which sometimes favor males (Stuecheli, 1991; Dorn et al. 2005).

Laboratory observations further corroborated our inference about reproductive timing. Captive male *P. viaevidis* belonged to form I and females had glair in May 2015, and by October, each female had > 100 ovarian eggs. Losses of eggs from ovaries to stage III young for *P. hayi* (Faxon, 1884) and *P. clarkii* (Girard, 1852), were 38.3% and 41.3%, respectively (Penn, 1943; Payne, 1971). At a 41.3% loss rate, the specimens of *P. viaevidis* we dissected would have produced 41–55 stage III young. This is the first reported estimate of *P. viaevidis* fecundity, although it is based on a small sample size of crayfish held in captivity for six months.

No quantitative sampling took place during dry months (generally July to October), but as pools dried, sites were searched for burrows. Several burrows were observed as pools became fragmented in late spring, and a few individuals (< 10) were found crossing land. *Procambarus viaevidis* were excavated from burrows 15–30 cm deep in Illinois (Page 1985) and from burrows < ~40 cm deep without chimneys in vernal pools and roadside ditches in Alabama (M.R. Kendrick, South Carolina Department of Natural Resources, personal communication, 2017).

Variation in chela width is common in crayfishes and is often related to sex and reproductive form (Bovbjerg, 1956; Weagle & Ozburn, 1970). Chelae of *P. viaevidis* were sexually dimorphic, with CW:POCL ratios increasing from females to form II males to

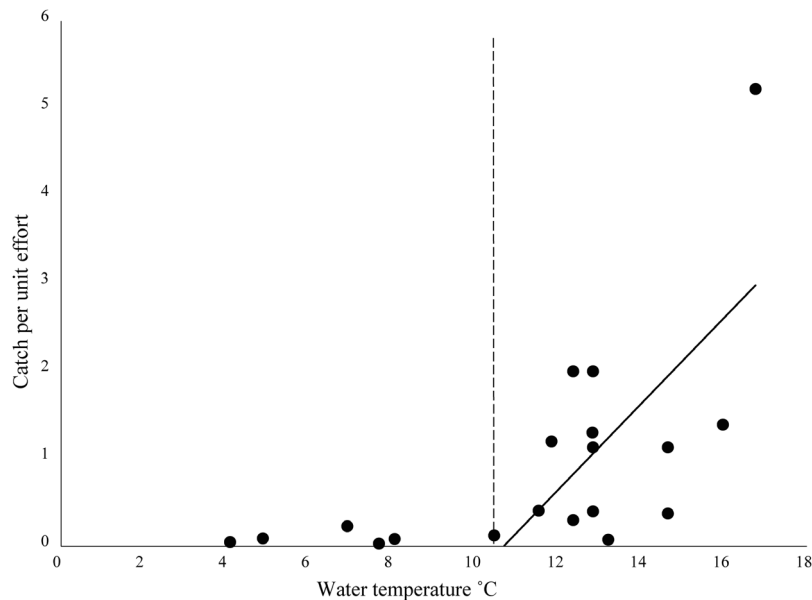


Figure 8. Relationship of catch per unit effort (CPUE, number per trap) of *Procambarus viaeviridis* to water temperatures averaged over three days prior to collections during Phase 2 of study. Linear regression line (solid line) shown for CPUE at temperatures (temp.) above the threshold (dashed line) of 10.5 °C (CPUE = 0.4904temp. - 5.2377, $r^2 = 0.41$; $F_{1,12} = 9.38$, $P = 0.01$).

form I males. Chelae are important in foraging and defense from predators; however, sexual dimorphic chela indicate the importance of large chelae in male intrasexual competition (Stein, 1976; Snedden, 1990).

Length-frequency distributions of *P. viaeviridis* near its northern range limit suggested a two-year life span (Page, 1985). We estimated a two- to three-year life span for *P. viaeviridis* near its southern range limit. Three age classes were estimated during only one month, but low numbers of individuals in the age-2 size range (POCL = 24–30 mm, Fig. 3) were collected throughout the study. Small sample sizes in the largest size category impeded recognition of an age-2 class by our length frequency analysis during other months. Regardless, the majority of the population lived two years, with some individuals surviving to their third year. The largest *P. viaeviridis* collected by Page (1985) was 32.3 mm CL, which coincides with age-2 (28–34 mm CL) crayfish in our study. The small sample size ($N = 16$) in that study may have similarly limited the ability to detect more than two age classes.

Temperature regulates activity level in crayfishes (Capelli & Magnuson, 1974; Somers & Stechey, 1986). Although we observed *P. viaeviridis* active in water under ice, as did Page (1985), *P. viaeviridis* seldom entered traps when three-day prior water temperatures were below the 10.5 °C threshold. Above the threshold, three-day prior water temperatures were positively correlated with *P. viaeviridis* CPUE (Fig. 8). *Cambarus bartonii* (Fabricius, 1798) also reduced activity in cold temperatures, with significantly fewer females collected at temperatures below 11 °C (Somers & Stechey, 1986).

Biological assemblages in seasonal wetlands depend on habitat type and water quantity and quality (Simon *et al.*, 2000). Changes in these parameters can cause cascading effects on the biota and ecosystem function of seasonal wetlands (Simon *et al.*, 2000). Pool depth had the strongest association with *P. viaeviridis* CPUE across sites with and without *P. viaeviridis* (Phase 1). Dissolved oxygen and pH were associated with CPUE among sites containing *P. viaeviridis* (Phase 2).

The relationship between pH and *P. viaeviridis* CPUE was context-dependent, differing during both phases of the study. The relationship of pH and *P. viaeviridis* CPUE during Phase 1 differed in magnitude and direction over time, whereas pH was negatively correlated with *P. viaeviridis* CPUE throughout Phase 2. The pH

range (6.26–8.45) throughout the study was within the optimal range for species of *Procambarus* (Holdich, 2002). Decomposition and release of CO₂ may have contributed to lower pH values at sites with high leaf litter and detritus, providing more refuge and probably more food for *P. viaeviridis*. Fishes may be less tolerant than crayfishes at a low pH, so living in lower pH environments may benefit crayfishes by relieving predation pressure from fishes (Seiler & Turner, 2004).

Depth was negatively correlated with *P. viaeviridis* CPUE in Phase 1. Depth decreased over time, with pools in January and February 33% deeper than in March and April. Decreasing depth was associated with increasing temperature and a probable increase in crayfish activity (Mundahl & Benton, 1990; Richards *et al.*, 1995). Crayfish were also concentrated as pool size decreased, which may have increased trapping efficiency. Numerous amphibians, including newts, sirens, and leopard and bull frogs, all crayfish predators, inhabit seasonal wetlands in the refuge (unpublished data, USFWS). Amphibians tend to prefer deep pools with longer hydropereids for breeding (Brooks & Hayashi, 2002; Karraker & Gibbs, 2010), possibly increasing predation of crayfishes. Conversely, deeper pools may protect crayfishes from terrestrial predators such as raccoons, ducks, herons, and ibis (Fleury & Sherry, 1995; Englund & Krupa, 2000; Wolff *et al.*, 2016), all crayfish predators that were present on the refuge. Furthermore, although depth may affect site selection, its exclusion from Phase 2 models indicated that pool depth did not influence crayfish abundance at occupied sites.

Predatory fishes were positively correlated with *P. viaeviridis* CPUE in Phase 2. Predatory fishes can reduce crayfish abundance (Garvey *et al.*, 2003; Wootton & Power, 1993); however, because crayfish shelter (leaves, wood, and vegetation) was abundant, bottom-up effects (i.e., refuge availability and substratum) rather than top-down effects (i.e., predator-prey relationships) may have a greater influence on crayfish population size. (Nyström *et al.*, 2006). Of the predatory fishes we collected, all were small juveniles that were not likely to consume large juvenile or adult *P. viaeviridis*.

Future sampling efficiency for catching large numbers of *P. viaeviridis* can be improved by considering habitat, water quality, and temperature. The best habitats for collecting *P. viaeviridis* were in seasonal wetlands with pools present for three or more months.

Conditions became most favorable in these wetlands as pool-water levels declined and three-day-averaged water temperatures rose above 10.5 °C, where we also found *P. acutus* or *C. puer*. A more complete description of the life history of *P. viaeviridis*, however, will require sampling during periods when pools are greatly reduced or dry. Sampling during these months will require burrow excavation and will probably yield low numbers, but could provide important information about ovigerous females, reproductive timing, and habitat use. Better information on the distribution of the species is necessary to assess its conservation and management needs.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Appendix. Location, habitat classification, and total trap nights for sampling sites in Dahomey National Wildlife Refuge, Bolivar County, MS, USA.

S2 Appendix. Habitat and water quality measurements.

S3 Appendix. Total number of crayfishes collected.

S4 Appendix. Total number of fishes collected by species.

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