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Biotic and Abiotic Influences on Population Characteristics of *Procambarus clarkii* in the Atchafalaya River Basin, Louisiana

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Abstract.— Crayfish harvested from the Atchafalaya River Basin (ARB) comprise the majority of Louisiana wild crayfish landings. However, other than annual flooding influences, it is difficult to elucidate inter-annual harvest differences and intra-annual population variability among habitats. This research investigated biotic and abiotic effects on populations of red swamp crawfish, *Procambarus clarkii,* at 16 locations in the southeastern ARB that were sampled semi-monthly during the 2008 and 2009 crayfish seasons. *Procambarus clarkii* catch per unit effort (CPUE) increased nearly 600% between years despite similar hydrologic regimes, physicochemical conditions, and littoral macrophyte densities. Increased allochthonous inputs, near anoxic conditions, and reduced fish predation associated with the passage of Hurricane Gustav over the ARB on 1 September 2008 likely contributed to the increased *P. clarkii* CPUE observed during 2009, and decreased crayfish size. Reduced size in 2009 indicated density-dependent growth, which was evident in a significant negative correlation between CPUE and carapace length. *Procambarus clarkii* exhibited trends of lower CPUE and reduced carapace length in habitats subject to chronic sub-optimal water quality. [*Keywords*.— density-dependence; growth; macrophytes; red swamp crawfish; water quality].

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INTRODUCTION

The crayfish industry in Louisiana is the largest in the United States (McClain et al. 2007) with a value of more than $209 million (LSUAC 2012). The red swamp crawfish, *Procambarus clarkii* (Girard), and the southern white river crawfish, *Procambarus zonangulus* Hobbs and Hobbs, are harvested from managed ponds (farmed) and natural habitats (wild-caught) throughout Louisiana, with *P. clarkii* comprising the majority of landings. Farmed production of crayfish has increased over the past several decades and extensive research has examined *P. clarkii* responses to environmental parameters in these controlled aquaculture environments. In contrast, there has been limited research into the ecological influences on Louisiana *P. clarkii* populations from natural environments, which often exhibit episodic water level fluctuations and extensive variability in biotic and abiotic factors that can affect crayfish harvest and population structure.

Over 90% of the wild crayfish harvest in Louisiana comes from the Atchafalaya River Basin (ARB) located in south-central Louisiana (Isaacs and Lavergne 2010; Figure 1), and landings have averaged 6.9 million kg annually over the last three decades. The crayfish harvest in the ARB coincides with the annual Atchafalaya River flood pulse, which varies substantially from year to year (Bonvillain et al. 2008) and significantly influences the magnitude of annual crayfish landings (Bryan et al. 1976; Pollard et al. 1983; Alford and Walker 2013). During the historic 1993 flood in the Mississippi River, the crayfish yield was a record 22.5 million kg, whereas drought conditions during 2000 limited production to only 178,000 kg. This dependence on water level results in unpredictable annual harvests and fluctuations in market demands and prices (Dellenbarger and Luzar 1988). Although there is no regulated crayfishing season, the harvesting period primarily occurs when rising river levels inundate the ARB floodplain, causing crayfish to emerge from burrows, grow rapidly, and mate. When flood waters recede, most crayfish will retreat to burrows where they persist during the dewatered floodplain period.

As ARB floodplain water levels stabilize and temperatures increase during late spring and summer, increasing rates of organic matter decomposition on the floodplain reduce water column dissolved oxygen (DO) concentrations. The temporal and spatial extent of hypoxia (DO ≤ 2.0 mg L^{-1}) has been exacerbated in recent decades by anthropogenic modifications (e.g., levee and canal construction, distributary closures, and flood control structures) of the ARB for oil and gas exploration and floodway maintenance. These changes to historic river-floodplain connectivity and ARB

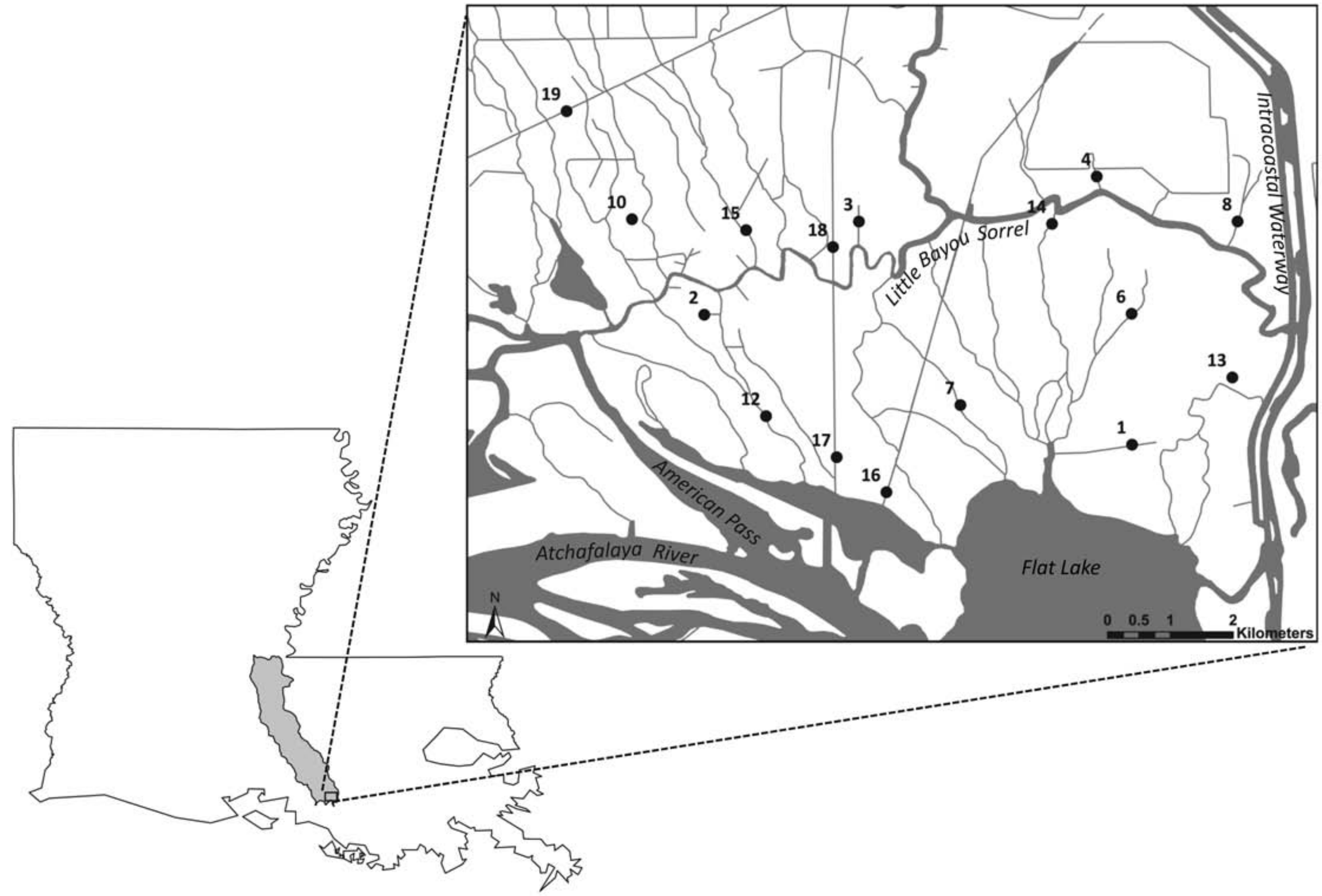

Figure 1. The Atchafalaya River Basin (shaded area) in south-central Louisiana and *Procambarus clarkii* sampling locations (n = 16) during the 2008 and 2009 crayfish seasons.

geomorphology have increased sedimentation (Hupp et al. 2008, 2009) and altered water circulation, flow patterns, and water quality (Sabo et al. 1999a), resulting in hypoxic conditions that can persist for several weeks to months across much of the floodplain (Sabo et al. 1999b).

Procambarus clarkii are more tolerant of low oxygen concentrations than other crayfish (Nyström 2002) and have developed several behavioral and physiological adaptations to cope with periods of sub-optimal DO conditions (see McMahon 1986; Reiber 1995; McMahon 2002). Although compensatory mechanisms afford *P. clarkii* the ability to tolerate poor water quality, chronic exposure could impact population vigor through reduced survival (Avault et al. 1975; Melancon and Avault 1977; McClain 1999; Sladkova and Kholodkevich 2011), growth (Jussila and Evans 1997; McClain 1999; McClain et al. 2007), and size at maturity (Huner and Romaire 1978; McClain 1999). Aquatic macrophytes, which are abundant throughout the lower ARB, may also play a significant role in enhancing or reducing the effects of seasonal water quality fluctuations on *P. clarkii* ecology. Dense beds of hydrilla, *Hydrilla verticillata* (L. f.) Royle, have been shown to promote sub-surface hypoxia in the ARB (Colon-Gaud et al. 2004), presumably by reducing water circulation and increasing benthic decomposition rates. However, plant beds can also provide forage, shelter (Jordan et al. 1996b; Harper et al. 2002; Garvey et al. 2003; Foster and Harper 2006), and diurnal DO refugia (Miranda et al. 2000; Troutman et al. 2007; Bunch et al. 2010) to littoral crayfish, resulting in positive relationships between crayfish and macrophyte densities (Jordan et al. 1996a).

The lack of an active management program has resulted in little research on the ecology of *P. clarkii* in the ARB and the environmental factors that structure crayfish populations and harvests in this system. Other than the obvious influences of annual water level fluctuations on *P. clarkii* activity levels, it has been difficult to elucidate inter-annual harvest differences and intra-annual population variability among habitats. Further, without adequate empirical knowledge of environmental influences on ARB crayfish ecology, it is difficult to assess the potential effects of federal and state water management projects on crayfish populations and harvests. Consequently, the objectives of this research were to examine the effects of water quality, habitat, and crayfish density on population characteristics of this economically and ecologically important crayfish in the southeastern ARB.

Study Area

The 5,000 km^2 ARB is the largest bottomland hardwood river-floodplain system in North America (Lambou 1990) and is comprised of shallow headwater and backwater lakes, numerous natural bayous and excavated canals, and seasonally flooded swamps. The Atchafalaya River, the dominant feature of the ARB and the major distributary of the Mississippi River, receives 30% of the combined volumes of the Mississippi and Red Rivers, and is regulated by the US Army Corps of Engineers through two water control structures and a hydropower channel. Water also enters the southeastern margin of the ARB through the Intracoastal Waterway. Although the timing, magnitude, and duration of the flood pulse varies annually, the ARB floodplain is typically inundated in the spring, with dewatering occurring throughout the summer to early fall (Lambou 1990; Fontenot et al. 2001; Bonvillain et al. 2008). Development of spatially extensive and temporally persistent hypoxia (Sabo et al. 1999b; Rutherford et al. 2001) is associated with floodplain inundation and rising water temperatures (Kaller et al. 2011). Additionally, invasive aquatic macrophytes such as hydrilla, water hyacinth *Eichhornia crassipes* (Mart.) Solms, alligator weed *Alternanthera philoxeroides* (Mart.) Griseb., and salvinia (*Salvinia* spp.) dominate the ARB aquatic macrophyte community and contribute to water quality impairment (Walley 2007). Sedimentation in the ARB contributes to increased elevations, reduced hydroperiods (Hupp et al. 2008), and conversion of open waters and bald-cypress swamps to bottomland hardwood forests (Ford and Nyman 2011). Although much of the upper ARB has filled, which has reduced crayfish production in these areas, the majority of the lower ARB still consists of bald-cypress swamps and continues to produce large crayfish harvests.

MATERIALS AND METHODS

Field Collections

Sixteen locations within a 40 km^2 area of the southeastern ARB were selected for semi-monthly crayfish sampling (Figure 1). Sample locations included the range of habitats typically found throughout the lower ARB (i.e., they were characterized by variable morphology, hydrologic connectivity, physicochemistry, and macrophyte density and composition). Crayfish were collected during the 2008 and 2009 crayfish "seasons" (6 March to 12 August 2008 and 2 March to 13 July 2009), which occurred when the Atchafalaya River stage at Butte La Rose, Louisiana (US Army Corps of Engineers gauge 03120) was greater than 2.5 m and floodplain habitats in the study area began to experience overbank flooding (Hupp et al. 2008).

Five pillow design traps per site were baited with 150 g (Beecher and Romaire 2010) of Purina Cajun World™ manufactured bait and allowed to soak overnight and catch per unit effort (CPUE) was determined as the number of crayfish per trap. Traps were constructed from 0.772 cm galvanized square wire mesh and were 122 cm in height with two 5 cm funnel openings on the bottom. Commercial crayfish traps (1.905 cm mesh) generally retain market size individuals that have carapace lengths (CL) $\geq$ 37 mm, but we used a smaller mesh size in order to sample juvenile crayfish as well. Traps were deployed at least 20 m apart on the floodplain and were secured to the surrounding trees or suitable vegetation. We identified all captured crayfish to species and recorded sex, reproductive form (males only) and standard CL (mm) for all individuals.

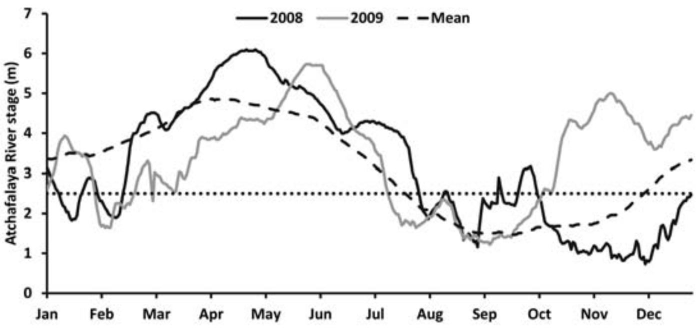

Figure 2. Daily Atchafalaya River stage at Butte La Rose, Louisiana (US Army Corps of Engineers gauge 03120) during the 2008 and 2009 sample years and the 54-year mean daily stage from 1959 – 2010. The horizontal dotted line represents floodplain inundation level (2.5 m) in the study area.

On each sampling date, surface DO (mg L^{-1}), temperature (°C), pH, specific conductance (mS cm^{-1}), and turbidity (NTU) were measured at each sample site with a handheld multiparameter water quality sonde (YSI model 6820, Yellow Springs, Ohio), and daily stage of the Atchafalaya River was obtained from the Butte La Rose gauge. Surface and bottom water column physicochemical measurements were taken when water depth exceeded 1 m. Percent coverage by species of aquatic macrophytes within a one-meter radius of every trap was recorded on each sample date. Relative densities recorded at all traps within a site were then averaged to obtain a mean macrophyte density per site.

Data Analysis

All statistical analyses were performed with SAS version 9.3 (SAS Institute Inc., Cary, North Carolina) and significance for all tests was determined using a 0.05 Type I error rate. For all analyses, DO was square root transformed, turbidity was $\log_{(e)}$(turbidity + 1) transformed, and CPUE was $\log_{(e)}$(CPUE + 1) transformed to stabilize error variances and meet distributional assumptions of parametric statistics. Homogeneity of variance was examined with Levene's test and Welch's analysis of variance (ANOVA) was used for unequal variance models.

We used ANOVA (PROC MIXED) to evaluate differences in historic monthly mean Atchafalaya River stages from 1959 to 2010 and monthly stages during the 2008 and 2009 crayfish seasons. To evaluate potential stratification of water column physicochemistry, we compared surface and bottom DO and temperature ($\log_{(e)}$ transformed) measurements in separate mixed model ANOVAs. An inter-annual difference in physicochemical parameters was assessed with multivariate analysis of variance (MANOVA).

To examine variability in water quality among sampling locations, a principal component analysis (PCA) of DO, temperature, pH, specific conductance, and turbidity was conducted for each sample year. We retained principal components (PC) with eigenvalues greater than one and physicochemical variables with eigenvectors greater than 0.4 (Hardle and Simar 2007). Site scores on PC1 and PC2 were plotted for each year to illustrate clustering of sites with similar physicochemical characteristics.

Procambarus clarkii CL for the total catch, market size individuals, and Form I males, as well as CPUE for total catch

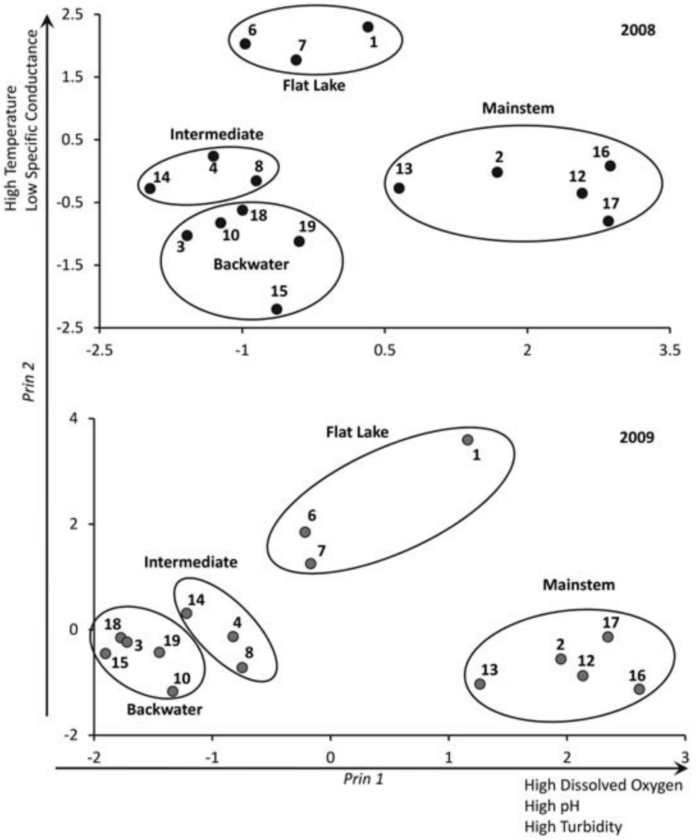

Figure 3. Biplots of principal components analysis of physicochemical parameters collected at crayfish sampling locations ($n = 16$) in the lower Atchafalaya River Basin during the 2008 and 2009 crayfish seasons. Sample dates in 2008 range from 6 March to 12 August ($n = 10$) and 2009 samples dates range from 2 March to 13 July ($n = 10$).

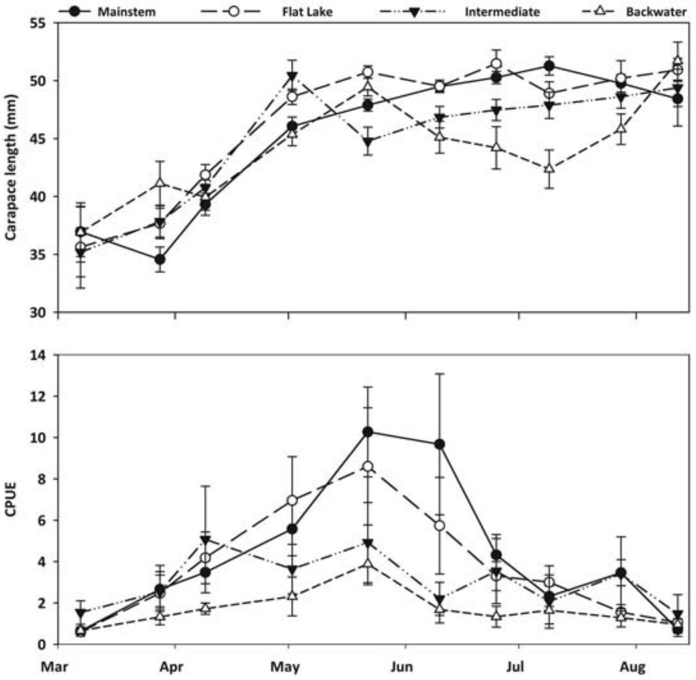

Figure 4. Mean (±SE) carapace length and catch per unit effort (CPUE) of *Procambarus clarkii* from sample location classifications of physicochemistry during the 2008 crayfish season.

and market size individuals, at sampling locations were compared among four apparent physicochemical site groupings for each sample year. Additionally, to investigate the effect of macrophyte density, sites were separated into three groups based on total macrophyte density (coverage of all species combined) for each sample year: low (0 – 33%), medium (34 – 66%), and high (67 – 100%). Physicochemical and macrophyte density groupings for 2008 and 2009 were analyzed with separate nested general linear mixed models that included sample location as a random effect. A first order heterogeneous autoregressive covariance structure was used to account for temporal correlation between sample events for all 2009 CPUE analyses and a variance components covariance structure was applied to CL and 2008 CPUE analyses (Bissonette and Storch 2007). Comparisons among groups were examined with Tukey-Kramer *post hoc* adjustments.

In order to investigate possible intraspecific density-dependent growth in sampled *P. clarkii* populations, we first grouped individuals into either early or late season samples for both years based on mean water temperatures. Favorable water temperature for *P. clarkii* growth is approximately 24°C (McClain 2010). Therefore, early season groups consisted of individuals from the first five sample dates (i.e., 6 March to 22 May 2008 and 2 March to 28 April 2009) with mean water temperatures < 24°C. Late season groups comprised the final five sample dates (i.e., 10 June to 12 August 2008 and 14 May to 13 July 2009) when mean water temperatures exceeded 24°C. Late season samples occurred after peak CPUE, which occurred on the fifth sample date during both sample years. Separate ANOVAs were used to examine differences in water temperature between sample years for early and late season groups. Differences in mean CL for each sample location between early and late season groups were compared to mean sample location CPUE values for each sample year with a Pearson correlation. Site 16 was omitted from 2009 correlation analysis because of a missing sample event in the late season group.

RESULTS

Water Level and Physicochemistry

The 2008 Atchafalaya River flood pulse inundated floodplain habitats for over six months, reaching its peak in late April and slowly declining to August (Figure 2). The 2009 flood pulse exhibited a lower magnitude and duration compared to 2008, however, water levels were sufficiently high to inundate floodplain areas for approximately five months. Peak water levels occurred in early June with a rapid decline through July (Figure 2). Comparisons of the hydrograph during the 2008 (March – August) and 2009 (March – July) crayfish seasons and the 52-year mean monthly Atchafalaya River stage indicated significantly higher monthly stages in April ($P = 0.009$) and July ($P = 0.004$) 2008 and June 2009 ($P = 0.034$). Atchafalaya River stage at Butte La Rose remained at or above 2.5 m during the 2008 and 2009 crayfish seasons for 154 and 133 days, respectively.

Analyses of surface and bottom water temperature ($F_{1,202} = 0.07$, $P = 0.786$) and DO ($F_{1,202} = 0.12$, $P = 0.730$) concentrations indicated homogeneous floodplain water column physicochemistry,

Table 1. Least-squares means (±SE) carapace length (CL [mm]; total number captured, market size [CL ≥ 37 mm], and Form I male) and catch per unit effort (CPUE; total number captured and market size) of *Procambarus clarkii* from sample location classifications of physicochemical parameters during the 2008 and 2009 crayfish seasons. CPUE values were $\log_{(e)}(\text{CPUE} + 1)$ transformed for analysis. Location classifications with different letters indicate a significant difference ($P < 0.05$) within a population metric (row) for each year. Table abbreviations include: MS (mainstem), FL (Flat Lake), IN (intermediate), and BW (backwater).

		Location classifications			
Year	**Population metric**	**MS**	**FL**	**IN**	**BW**
2008	CL	44.5 ± 1.6^{a}	46.6 ± 1.9^{a}	47.1 ± 1.7^{a}	45.2 ± 1.5^{a}
	CPUE	1.4 ± 0.2^{a}	1.4 ± 0.2^{ab}	1.2 ± 0.2^{ab}	0.9 ± 0.2^{b}
	Market CL	48.4 ± 1.0^{a}	48.9 ± 1.2^{a}	48.2 ± 1.2^{a}	48.2 ± 1.0^{a}
	Market CPUE	1.5 ± 0.1^{a}	1.5 ± 0.2^{ab}	1.3 ± 0.2^{ab}	1.1 ± 0.1^{b}
	Form I male CL	50.4 ± 1.2^{a}	50.1 ± 1.4^{a}	49.2 ± 1.5^{a}	50.0 ± 1.2^{a}
2009	CL	44.3 ± 1.1^{a}	39.9 ± 1.0^{b}	41.9 ± 0.9^{ab}	41.5 ± 0.8^{ab}
	CPUE	2.1 ± 0.2^{bc}	3.4 ± 0.3^{a}	3.2 ± 0.3^{ab}	2.0 ± 0.2^{c}
	Market CL	48.0 ± 0.5^{a}	42.9 ± 0.6^{c}	44.5 ± 0.5^{bc}	46.4 ± 0.5^{ab}
	Market CPUE	1.9 ± 0.2^{b}	3.5 ± 0.2^{a}	3.2 ± 0.2^{a}	2.0 ± 0.2^{b}
	Form I male CL	51.7 ± 0.8^{a}	45.6 ± 0.8^{b}	47.7 ± 0.6^{b}	50.5 ± 0.7^{a}

thus only surface water quality observations were used for all subsequent analyses. Comparison of physicochemistry at sampling locations did not reveal a significant difference between 2008 and 2009 (Wilks' Lambda = 0.97, $F_{5,309} = 1.82$, $P = 0.108$).

Population Characteristics

We collected 2221 and 15,324 *P. clarkii* during the 2008 and 2009 crayfish seasons, respectively. Comparisons of inter-annual mean CPUE (±SE) at sampling locations revealed a significantly higher CPUE in 2009 (21.1 ± 1.9) than in 2008 (3.1 ± 0.3; Welch's $F_{1,246.1} = 148.17$, $P < 0.001$). *P. clarkii* collected in 2008 had a significantly larger mean CL (46.5 ± 0.2 mm) than individuals from the 2009 season (42.0 ± 0.1 mm; Welch's $F_{1,2646.7} = 578.03$, $P < 0.001$).

The PCA of water quality parameters at sampling sites in 2008 had two components with eigenvalues greater than 1.0 that explained 71% of the physicochemical variation among sample locations. Turbidity, DO, and pH were positively correlated with PC1, whereas temperature was positively and specific conductance was negatively correlated with PC2. Plots of site scores on PC1 and PC2 demonstrated that physicochemical characteristics tracked spatial groupings closely (Figure 3). Mainstem sites (2, 12, 13, 16, and17) located in the southwest and southeast portions of the study area received influxes of well-oxygenated mainstem water from the Atchafalaya River and Intracoastal Waterway, resulting in higher DO, pH, and turbidity levels. Flat Lake sites (1, 6, and 7) displayed higher temperatures and lower specific conductance measurements than other locations and slightly lower pH and DO levels than mainstem locations, although chronic hypoxia (persisting for several weeks to months) was not associated with these sites. Backwater sites (3, 10, 15, 18, and 19) were characterized by high specific conductance and low turbidity, pH and DO concentrations. Low DO water from the surrounding floodplain caused chronic hypoxia at these sites for the majority of the crayfish season. Intermediate sites (4, 8, and 14) functioned as a transition zone between backwater areas and Flat Lake locations. These sites tended to have lower turbidity, pH, and DO concentrations than mainstem and Flat Lake sites but not as chronically low as backwater locations. In addition, DO concentrations at intermediate sites decreased from east to west with distance from the Intracoastal Waterway. Mainstem and Flat Lake locations produced slightly larger individuals during

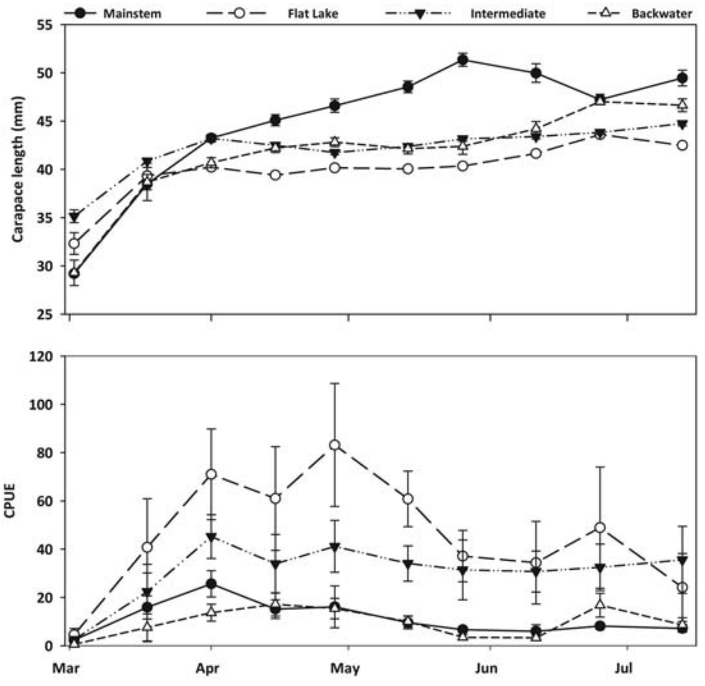

Figure 5. Mean (±SE) carapace length and catch per unit effort (CPUE) of *Procambarus clarkii* from sample location classifications of physicochemistry during the 2009 crayfish season.

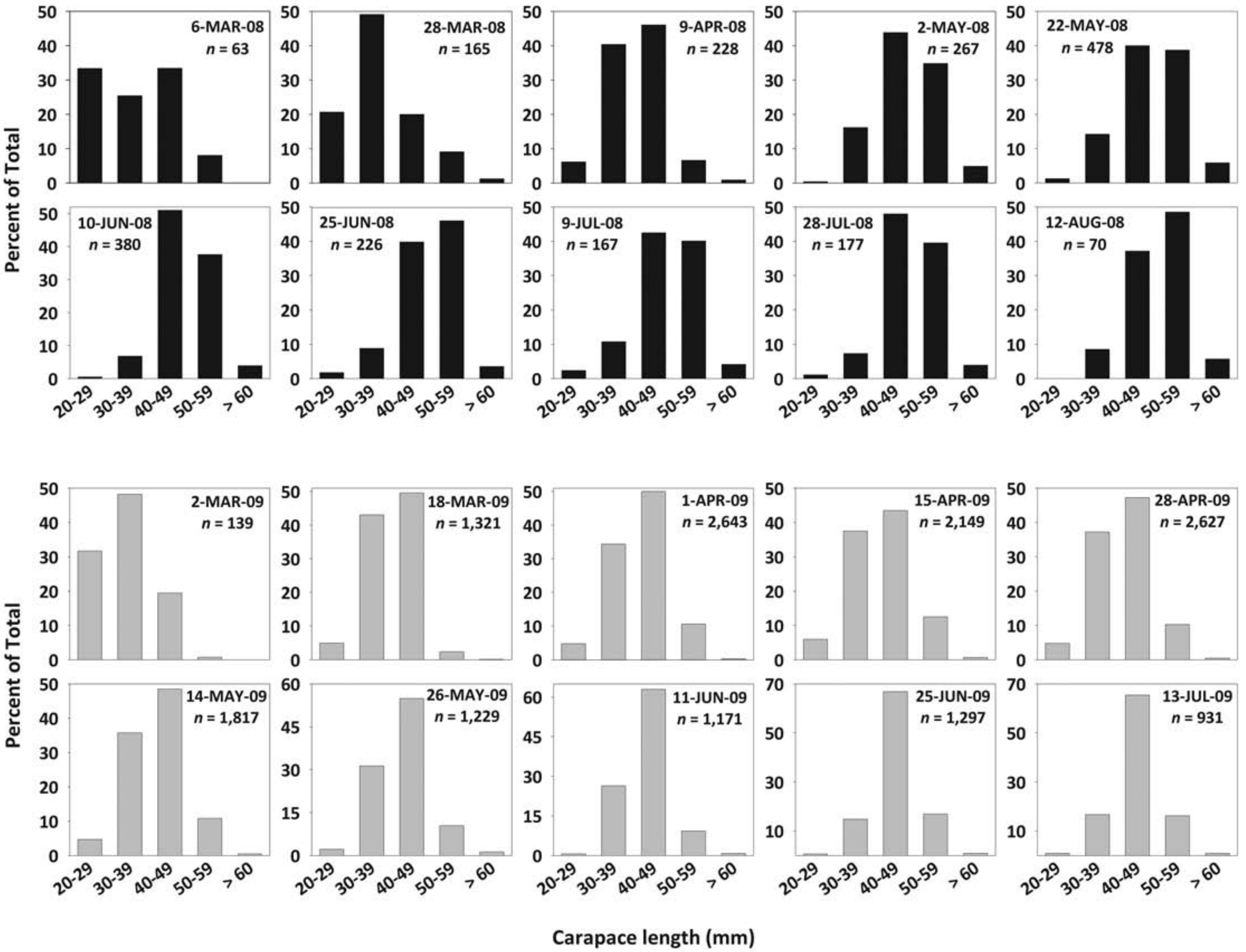

Figure 6. Length frequencies for *Procambarus clarkii* collected at 16 sample locations in the lower Atchafalaya River Basin during the 2008 (black bars) and 2009 (grey bars) crayfish seasons.

the latter portion of the crayfish season, whereas backwater sites displayed slight CL declines (Figure 4). However, comparisons of *P. clarkii* CL among the four physicochemical groups did not detect significant differences for total catch, market individuals, or Form I males (Table 1). Mainstem and Flat Lake locations also consistently had higher CPUE during much of the crayfish season and, excluding the last sample event, backwater sites produced the lowest CPUE values on every sample date (Figure 4). Additionally, CPUE was significantly higher at mainstem locations compared to backwater locations for total population and market size individuals (Table 1).

The 2009 PCA yielded PCs with the same variable correlations as 2008, which explained 85% of the physicochemical variation among sample locations (Figure 3). During the 2009 crayfish season, mainstem locations produced the largest mean *P. clarkii* from 1 April to the season's conclusion, whereas Flat Lake sites yielded the smallest individuals during the same period (Figure 5) and a significantly smaller mean CL compared to mainstem sites (Table 1). Further, market size individuals at mainstem and backwater locations were larger than individuals from Flat Lake sites, with intermediate sites yielding smaller individuals than mainstem locations (Table 1). Flat Lake and intermediate locations yielded the highest CPUE values throughout the 2009 crayfish season (Figure 5). Flat Lake locations had significantly higher CPUE than mainstem and backwater sites, and CPUE at intermediate locations were higher than backwater sites (Table 1). CPUE of market size individuals was significantly greater at Flat Lake and intermediate locations, although Form I males were smaller than those at mainstem and backwater sites (Table 1).

In 2008, sites with low relative densities of aquatic macrophyte (sites 1, 2, 3, 4, and 17) had significantly smaller *P. clarkii* compared to medium (sites 6, 7, 12, 14, and 16) and high density (sites 8, 10, 13, 15, 18, and 19) locations (Table 2). Conversely, 2008 CPUE was significantly lower at high macrophyte density locations (Table 2). Comparisons of 2009 macrophyte density groups did not detect any differences in CPUE or CL among low (sites 1, 2, 4, 8, 13, and 17) medium (sites 3, 6, 7, 12, and 16), and high density (sites 10, 14, 15, 18, and 19) locations (Table 2).

Table 2. Least-squares means (±SE) carapace length (CL [mm]) and catch per unit effort (CPUE) of *Procambarus clarkii* from aquatic macrophyte relative density classifications at sampling locations during the 2008 and 2009 crayfish seasons. CPUE values were $\log_{(e)}$(CPUE+1) transformed for analysis. Relative densities with different letters indicate a significant difference ($P < 0.05$) within a population metric (row) for each year.

		Relative macrophyte density		
Year	**Population metric**	**Low (0–33%)**	**Medium (34–66%)**	**High (67–100%)**
2008	CL	43.5 ± 1.2^{b}	46.4 ± 1.2^{a}	47.2 ± 1.2^{a}
	CPUE	1.4 ± 0.1^{a}	1.5 ± 0.1^{a}	0.7 ± 0.1^{b}
2009	CL	42.3 ± 1.1^{a}	42.2 ± 1.2^{a}	42.2 ± 1.2^{a}
	CPUE	2.5 ± 0.3^{a}	2.6 ± 0.4^{a}	2.4 ± 0.4^{a}

During the 2008 crayfish season, mean *P. clarkii* CL at the 16 sampling locations ranged from 40.2 to 52.7 mm while CPUE values ranged from 0.6 to 7.2. Site 8 had the lowest CPUE (0.6 ± 0.2) but the largest mean CL (52.7 ± 1.1 mm) among the 16 sample locations. The largest mean CPUE value (7.2 ± 2.2) was recorded at site 12 which produced 12.9% of the total *P. clarkii* captured during the 2008 season. In the 2009 crayfish season, mean *P. clarkii* CL at the 16 sampling locations ranged from 38.7 to 47.6 mm and CPUE values ranged from 4.4 to 76.6. Site 6 produced 22.7% of the total *P. clarkii* captured and the highest CPUE (76.6 ± 10.8), however, mean CL (39.9 ± 0.1 mm) was the second lowest among sampling locations. Additionally, the five locations with the largest mean CLs (sites 2, 12, 10, 16, and 17) were in the bottom half of sampling location CPUE values. Mean CPUE values at all sampling locations increased from 2008 to 2009 and mean CL decreased at all sites between the two sample years except at sites 2 and 4. Sites 6, 8, and 13 exhibited the largest decreases in mean CL between 2008 and 2009 (-9.1, -9.1, and -11.4 mm respectively) and three of the five largest increases in mean CPUE (72.1, 33.8, and 23.9 respectively). Length frequencies of *P. clarkii* during the 2008 and 2009 crayfish seasons revealed a larger percentage of individuals in the 50 to 59 and > 60 mm CL size classes in the total catch during 2008, with 40 to 49 mm individuals dominating the latter portion of the 2009 season (Figure 6). Furthermore, early to late season differences in mean *P. clarkii* CL at each sampling location displayed a significant negative correlation with mean site CPUE in 2009 ($r = -0.7036$, $P = 0.004$; Figure 7), with no correlation detected in 2008. No difference in water temperature was observed between 2008 and 2009 for both early and late season groups.

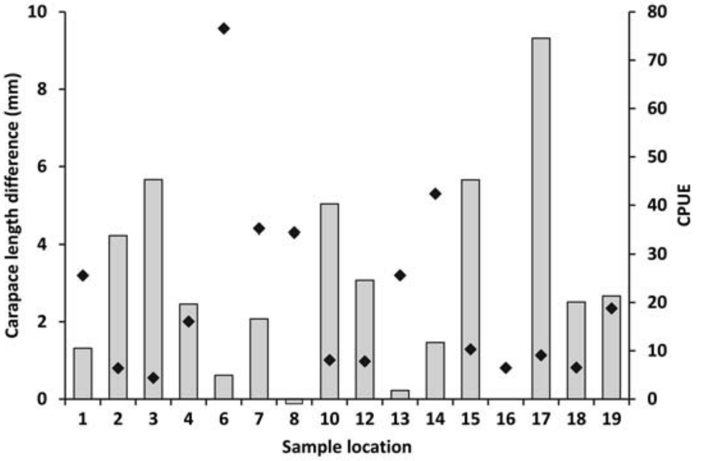

Figure 7. Differences in mean *Procambarus clarkii* carapace length between early and late season groups (bars) and mean catch per unit effort (CPUE) for each location (diamonds) during the 2009 crayfish season. Site 16 was omitted from analysis because of missing sample event in the late season group.

DISCUSSION

Although environmental variables may structure local *P. clarkii* populations on a site specific scale, the hydrologic cycle of the Atchafalaya River has a basin-wide effect on the ARB crayfish assemblage and is the ultimate determinate of the magnitude of the annual crayfish harvest. The timing, magnitude, and duration of the flood pulse are all important hydrologic components in structuring the annual ARB crayfish harvest (Alford and Walker 2013), with reduced floodplain inundation resulting in below average crayfish harvests (e.g., 2000 and 2006). Both 2008 and 2009 experienced flood pulses conducive to above average crayfish yields. From March to August, 2008 there were 144 days of Atchafalaya River stages at Butte La Rose at or above 3.7 m, whereas 2009 experienced 100 days above this benchmark, defined by Hupp et al. (2008) as the stage at which the majority of ARB floodplain habitats are inundated. The 2008 flood was characterized by high water levels and prolonged floodplain inundation, which protracted the crayfish season until mid to late August. Although the 2009 flood pulse was a lower magnitude and duration event than 2008, floodplain inundation was more than sufficient to provide a favorable crayfish season that lasted until mid to late July.

Despite similar crayfish seasons in terms of timing and hydrologic conditions favorable to crayfish harvests, *P. clarkii* population characteristics at our sampling locations differed substantially between sample years. Although the annual commercial crayfish yield in the ARB increased 22% from 2008 to 2009 (LSUAC 2012), total abundance and CPUE at sampling locations both increased almost 600% between years. During the 2009 crayfish season, CPUE at our sampling locations mirrored CPUE data collected from multiple sample locations throughout the southeastern ARB (C. P. Bonvillain, unpublished data). However, CPUE at sampling locations during the 2008 crayfish season was much lower than other southeastern ARB locations

(C. P. Bonvillain, unpublished data), suggesting that population densities at our sample locations may have been experiencing a localized population reduction. Anecdotal evidence from personal communications with local crayfish harvesters suggests that crayfish yields in the area of our sample locations were low in 2008 and the preceding few years. This was also apparent in a reduced commercial crayfish harvest in the area, as evidenced by few observed crayfish traps compared to 2009 (C. P. Bonvillain, personal observation). Causes of localized crayfish reductions and the duration of these phenomena remain unclear. One possible explanation is high commercial crayfishing pressure over several years may temporarily reduce the abundance of crayfish in these areas. Bryan et al. (1976) observed lower *P. clarkii* abundance in areas of the ARB with high commercial crayfishing pressure than areas that experienced lower fishing pressure.

The passage of Hurricane Gustav over the ARB on 1 September 2008 appears to have indirectly influenced crayfish populations and contributed to increased abundance at the local and basin scale. Hurricane Gustav, a strong category 2 hurricane on the Saffir-Simpson scale with measured wind speeds in excess of 166 km/h at landfall (Beven and Kimberlain 2009), produced extensive defoliation throughout the ARB. DO concentrations began to decline two days post-landfall throughout the lower ARB and reached near anoxic levels (Bonvillain et al. 2011), resulting in an extensive fish kill estimated at 128 million individuals (LDWF 2008). *Procambarus clarkii* and other aquatic detritivores may benefit from hurricane associated defoliation and low DO levels that reduce densities of invertivorous fishes. Because of Gustav-related increases in allochthonous debris inputs and widespread fish kills, 2009 crayfish populations experienced decreased predatory pressure and an abundant food supply, which may have contributed to increased *P. clarkii* abundance (e.g., Seiler and Turner 2004; Birnbaum et al. 2007; Dorn 2008). Similar increases in shrimp landings have been observed after hurricane passage in estuarine systems (Burkholder et al. 2004; Stevens et al. 2006). Although the passage of Hurricane Andrew over the ARB in 1992 resulted in extensive fish kills similar to Hurricane Gustav, because river stages in the ARB were extremely high in 1993, it is difficult to gauge the storm-related indirect effects on ARB crayfish populations for this storm event.

Procambarus clarkii size (CL) also demonstrated marked differences between sample years, with increased CPUE resulting in smaller crayfish sizes throughout the 2009 crayfish season, whereas 2008 had a much higher percentage of large size class individuals (50 – 59 and > 60 mm size classes; Figure 6). The increase in crayfish abundance and decrease in *P. clarkii* size during the 2009 crayfish season indicates density-dependent growth at both the basin and local scales. Density-dependent growth in *P. clarkii* has been demonstrated in numerous environments (Jarboe and Romaire 1995; McClain 1995a, b; Ramalho et al. 2008; McClain 2010) and is of particular interest to commercial crayfish operations because of the higher market price for larger individuals (McClain and Romaire 1995; McClain et al. 2007). Depressed growth at high densities can be the result of increased social agonistic interactions and/or decreased food and habitat availability (Flint and Goldman 1977; Jones and Ruscoe 2000; Karplus and Barki 2004), although density-dependent growth reductions can occur in the absence of nutritional limitations (McClain and Romaire 1995; Romaire and Villágran 2010). Density-dependent effects on crayfish size were also evident among the 2009 physicochemical site groupings, with Flat Lake and intermediate locations producing considerably higher CPUE values but smaller individuals than mainstem and backwater locations. Form I male *P. clarkii* at these locations exhibited smaller mean CLs, which mirrored total population responses. These results agree with other studies that describe smaller Form I males from high density areas (Jarboe and Romaire 1995; Alcorlo et al. 2008). Site 6 best illustrates density-dependent growth during the 2009 crayfish season. Site 6 had a considerably higher mean CPUE (76.6) than other sample locations, however, mean CL of *P. clarkii* was only 39.9 ± 0.1 mm, not much larger than the minimum market size of 37 mm. Although areas such as site 6 produce extremely large yields, they are less desirable to commercial harvesters because of the associated smaller crayfish size. Differences in *P. clarkii* mean CL from early to late season also demonstrated a significant negative correlation with CPUE in 2009. Although not a direct measure of somatic growth, differences in mean CL between early and late seasons can serve as an indicator of *P. clarkii* growth rates, particularly during the latter half of the crayfish season when temperature and density effects on growth are more pronounced (McClain 1995a, b). *P. clarkii* from the six highest CPUE locations (1, 6, 7, 8, 13, and 14), all with mean CPUE values greater than 20, exhibited the smallest size increases during 2009 (Figure 7), suggesting density-dependent growth at these high yield locations. Conversely, a correlation between early to late season CL differences and mean CPUE was not observed during the relatively low-density 2008 season (the largest mean CPUE value at sampling locations was only 7.2 ± 2.2).

The observed increase in the number of crayfish harvesters and traps at sample locations in 2009 by the senior author suggests an increase in harvest pressure in the area compared to 2008. Although the possibility existed that harvesters may have biased *P. clarkii* carapace length values by removing larger individuals from the population, we do not believe that harvesting influenced crayfish size for two reasons. First, crayfish in high density areas were likely to have remained stunted even when individuals were removed from the population (Jarboe and Romaire 1995). Secondly, mean *P. clarkii* CL at our sampling locations was similar to mean CL of individuals sampled throughout the southeastern ARB in 2009 (C. P. Bonvillain, unpublished data), suggesting that the increased harvest pressure at our sampling locations did not influence the observed CL measurements.

Although abiotic variables undoubtedly influence crayfish population characteristics (Nyström 2002), relative crayfish density appears to exert a greater influence on ARB crayfish population structure than any of the measured physicochemical factors, which may be more influential during periods of low crayfish density (e.g., 2008 sampling season). Responses of *P. clarkii* density and size to physicochemical variables in backwater locations suggest possible sub-optimal water quality effects. Backwater locations, which typically experienced chronic hypoxia as well as the lowest DO, pH, and turbidity levels, produced the lowest CPUE values during both sample years. Although differences among 2008 physicochemical site groupings were not significant, smaller *P. clarkii* were captured from backwater locations during the latter half of the season (Figure 4). Carapace length differences attributable to reduced water quality during 2009 may be somewhat distorted due to density-dependent effects (i.e., smaller mean CLs observed at Flat Lake and intermediate locations were likely a consequence of density-dependent growth rather than the presence of larger individuals at mainstem and backwater locations). However, backwater and sufficiently-oxygenated mainstem locations, neither of which exhibited density-dependent crayfish growth, exhibited similar mean CPUE values in 2009, but backwater locations produced smaller individuals (Figure 5). Crayfish exposed to higher DO concentrations, as observed at mainstem locations, generally have shorter intermolt periods and faster growth (Jussila and Evans 1997), whereas chronic hypoxic exposure, especially during juvenile stages, has been shown to suppress growth (McClain 1999) and increase mortality rates (Avault et al. 1975; Melancon and Avault 1977; McClain 1999; Sladkova and Kholodkevich 2011). Availability of high-quality invertebrate food sources (Olsson et al. 2008) may have also been limited in sub-optimal water quality habitats. Reduced macroinvertebrate abundance (Davidson et al. 1998; Battle and Mihuc 2000) and decreased *P. clarkii* hemolymph protein concentrations (Bonvillain et al. 2012) have been observed in hypoxic areas of the ARB. Active foraging and food consumption may be diminished in hypoxic waters (Das and Stickle 1993; Paschke et al. 2010), resulting in reduced protein concentrations and subsequent growth in starved individuals (Wen et al. 2007).

Macrophyte densities in backwater areas may have also influenced observed CPUE and CL measurements. Backwater locations were generally associated with high macrophyte densities, which contribute to lower sub-canopy DO, pH, and turbidity levels by reducing water circulation and increasing benthic decomposition rates (Mwabvu and Sasa 2009). High macrophyte densities may also inhibit crayfish movements towards traps and result in reduced CPUE and/or increased capture of juvenile *P. clarkii* associated with macrophyte beds (Harper et al. 2002), resulting in reduced CL measurements. However, overall, aquatic macrophyte density did not appear to negatively influence *P. clarkii* abundance and size, at least relative to density and physicochemical effects. In fact, dense aquatic macrophyte stands in hypoxic areas may have provided crayfish with diurnal DO refugia (Miranda et al. 2000; Fontenot et al. 2001; Troutman et al. 2007; Bunch et al. 2010), structure to support air-water interface access (Avault et al. 1975; McClain et al. 2007), and cover from littoral predators (Jordan et al. 1996a, b; Garvey et al. 2003; Foster and Harper 2006). Interestingly, medium macrophyte densities produced a non-significant trend of higher CPUE during both sample years and significantly larger individuals than the low macrophyte density group in 2008. Perhaps medium macrophyte densities provide optimal structure for *P. clarkii* while avoiding problems associated reduced water circulation, high benthic decomposition rates, and chronic water column hypoxia.

In addition to their economic value, *P. clarkii* are key components in the ARB trophic web and a major diet constituent of many ARB fishes (Lambou 1961; Dugas et al. 1976; Snedden et al. 1999; Miller 2013). Despite their economic and ecological significance, few studies have examined wild *P. clarkii* populations in Louisiana, and ecological influences on population dynamics are poorly understood. Results from this study suggest reduced CPUE and CL in individuals sampled from chronically sub-optimal water quality areas, and reduced individual size at locations supporting high population densities. However, *P. clarkii* are well adapted to swamp habitats (Walls 2009), are tolerant of relatively poor water quality environments (Nyström 2002; Bonvillain et al. 2012), and continue to thrive in the ARB despite intense harvest pressure and tremendous annual variability in flooding characteristics, water quality, and macrophyte abundance.

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