

2015

## Population Abundance and Transience of Selected Coastal Plain Crayfishes

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POPULATION ABUNDANCE AND TRANSIENCE OF SELECTED COASTAL  
PLAIN CRAYFISHES

A Thesis

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Master of Science

in

The School of Renewable Natural Resources

by  
Samantha Lott  
B.S., The Rochester Institute of Technology, 2012  
December 2015

## **ACKNOWLEDGEMENTS**

I would like to express my thanks to my fellow graduate students, namely Catherine Reuter and William Budnick, and the undergraduate workers that helped make this project a success. I am particularly grateful for the assistance given by my advisor, Dr. Kaller, who only ever had positive things to say and helped immeasurably with my analytical methods and edits. His willingness to give his time so generously has been much appreciated.

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## ABSTRACT

Crayfish are important for stability, determining ecosystem structure, and ecosystem functions in freshwater habitats. Louisiana has many endemic species of crayfish, but most are poorly described. This study investigated the populations of some of the lesser known crayfishes in the South Central Plains. Specifically, the goals were to examine movement, movement across anthropogenic barriers, and estimate population size of 10 species reported from the area: *Procambarus natchitochae*, *P. vioscai*, *P. clarkii*, *P. acutus*, *P. zonangulus*, *P. tulaneii*, *P. kensleyi*, *Orconectes maletae*, *O. lancifer*, and *O. palmeri*. In combination with a field team, I sampled twelve wadeable streams with DC backpack electrofishers and traps at least twice at 2-3 month intervals during summer, fall, and winter of 2014. Although all sampled crayfish of sufficient size were double marked, recaptures were minimal, thus, generalized N-mixture models were performed on the three most widely captured species to generate population and transience estimates based on sampling unmarked animals over time. All population estimates were very low and were dependent on river basin, specific conductance, and stream width. Although the relationship among species and river basins has been previously described, relationships with stream size and specific conductance were novel. *P. natchitochae* and *P. vioscai* appeared to spatially segregate along a gradient of stream size. Specific conductance, which is an indicator of available calcium, had a positive association with abundance for *P. vioscai*, *P. natchitochae*. *P. natchitochae* and *P. vioscai* showed the possibility of seasonal transience and potential relationships with dissolved oxygen. These results give conservation scientists and managers more information for conservation of Louisiana crayfishes.

## 1. INTRODUCTION

Globally and locally, freshwater habitats provide numerous ecological and economic benefits, but are also at greater risk of more serious decline than terrestrial habitats (Meyer 1990; Sala et al. 2000; Saunders et al. 2002; Dudgeon et al. 2006; Richman et al. 2015). Pollution, habitat degradation, dredging, agricultural and industrial water use, dams, invasive species, and other threats are significant global stream impacts (Meyer 1990; Dudgeon et al. 2006; Freeman et al. 2007, Meyer et al. 2007). In the southeastern United States, these impacts pose a serious threat to regional aquatic biodiversity across multiple species and multiple spatial scales (Lydeard and Mayden 1995; Mulholland et al. 1997; Richter et al. 1997; Warren et al. 2000; Taylor et al. 2007; Haag and Williams 2014).

Crayfishes play an important in the stability, structure, and function and function of lotic systems (Parkyn et al. 1997; Schofield et al. 2001; Wallace & Webster 1996; Richman et al. 2015). Crayfish are omnivores, and although they prefer animal protein, it is not always available (Momot 1995). One of the main food sources in streams for aquatic invertebrates is allochthonous material from the surrounding forest, often in the form of leaf litter (Hollows et al. 2002; Hamilton et al 2004). Crayfish are adept at breaking down and consuming leaf litter, with fragmented particles and waste providing organic food particles for smaller invertebrates (Huryn & Wallace 1987; Usio 2000). Ingested leaf litter assimilates into body tissue, and the energy is made available to predatory organisms higher in the food web (Huner et al. 1978; Rabeni 1992; Foster & Keller 2011).

Feeding and burrowing activities of high density crayfish populations and assemblages can alter aquatic habitat characteristics (Creed & Reed 2004), including alteration of macrophyte abundance, detrital composition, algal density, and fluvial geomorphic processes (Momot 1995; Statzner et al. 2000; Creed & Reed 2004; Shin-Ichiro et al. 2009). Many



crayfishes affect food web structure through removal of aquatic vegetation (Rodríguez et al. 2005) and their complex role as lotic and lentic predators and prey (Dorn & Wojdak 2004). They also significantly affect nutrient dynamics (Covich et al. 1999) and can have great effects in low-nutrient waters by accelerating decomposition, mixing sediments, and affecting microbial communities (Momot et al. 1978; Evans-White & Lamberti 2006).

Despite their importance in ecosystems, crayfishes are second to freshwater mussels as the most jeopardized group of aquatic animals (as a percentage of total species) in the United States (Foster & Keller 2011) due to introduction of non-native species and habitat fragmentation or loss (Fischer & Lindenmayer 2007; Taylor et al. 2007). North America is host to at least 363 native crayfish species, of which only 189 (52.1%) are listed as Currently Stable, the other 47.9% are classified as Endangered, Possibly Extinct and Vulnerable (Taylor et al. 2007). The southeastern United States has the highest crayfish diversity in the world (Hobbs 1974; Taylor et al. 2007; Richman et al. 2015), with 39 species occurring in Louisiana (Walls 2009; Budnick 2015). Consequently, this region offers a unique opportunity to study distribution, habitat requirements, and co-occurrence of multiple species over relatively small spatial scales.

Many of the crayfishes in Louisiana are considered data deficient, i.e., important population parameters, distributional range, and conservation status are poorly described (IUCN 2001; Richman et al. 2015). Some species prefer lotic habitats, some live mostly in still waters, including slack waters of streams and rivers, floodplain ponds, and other lentic habitats, and some are burrowers (Walls 2009). There are three types of burrowing crayfish, categorized as primary, secondary, and tertiary burrowers (Horwitz & Richardson 1986). Primary burrowers almost never move into open water, secondary burrowers spend much of their time hidden underground, and only come out seasonally. Tertiary burrowers only move into burrows for

reproduction (Horwitz & Richardson 1986). This means non-burrowing, lotic and lentic crayfish are more easily observed year-round and are easier to capture and quantify than burrowers.

The Red and Ouachita River basins are understudied regarding resident crayfish assemblages (Budnick 2015). The South Central Plains (US EPA Level III – Daigle et al. 2006) make up much of the Red and Ouachita River Basins, which together support 24 crayfish species (Walls 2009). Because of either primary or secondary burrowing or preference for extremely shallow, muddy seeps or drains, twelve species (*Procambarus jaculus*, *Procambarus geminus*, *Procambarus machardy*, *Faxonella beyeri*, *Faxonella clypeata*, *Faxonella creaseri*, *Cambarus diogenes*, *Cambarus ludovicianus*, *Fallicambarus fodiens*, *Fallicambarus dissitus*, *Cambarellus shufeldtii*, and *Cambarellus puer*) are unlikely to be sampled in flowing waters typical of these drainages. Two species that occur at the extreme northern edges of the South Central Plains within Louisiana (*Procambarus viaeviridis* and *Procambarus elegans*) are also unlikely to be sampled. Thus, routine sampling efforts in these streams should yield *Procambarus natchitochae*, *P. vioscai*, *P. clarkii*, *P. acutus*, *P. zonangulus*, *P. tulane*, *P. kensleyi*, *Orconectes maletae*, *O. lancifer*, and *O. palmeri* (Walls 2009). Aside from the well-studied *P. clarkii* (e.g., Rodríguez et al. 2005), habitat requirements and population status of these species are poorly understood, apart from initial species accounts (summarized in Walls 2009), conservation surveys (e.g., Lester et al. 2005; Kaller et al. 2015), and production aquaculture and commercial harvest research (e.g., Huner et al. 1978).

*P. zonangulus*, like *P. clarkii*, is cultured in Louisiana (Huner & Romaine 1990; Huner 1994) and both are common in ponds and still waters within streams and rivers. *P. zonangulus* and *P. acutus* are very similar species, with indistinguishable life histories, overlapping ranges, and histories of misidentification (Hobbs & Hobbs 1990; Walls 2009). In Louisiana, these

species may exhibit some habitat partitioning with *P. acutus* tending to occur in flowing water and *P. zonangulus*, more frequently found in ponds (Romaine & Lutz 1989; Blank & Figler 1996; Walls 2009).

*Orconectes palmeri* is fairly widespread and locally abundant (Penn 1952; Johnson 2010), with *O. palmeri longimanus* and *O. palmeri palmeri* reported from these two basins. *O. palmeri palmeri* breeds in early spring, the young of the year mature by autumn, and few animals live longer than two years (Payne & Price 1981). Less is known about *O. palmeri longimanus*. *O. maleate*, which is superficially similar to *O. palmeri*, is considered an imperiled species with a limited distribution (Taylor et al 2007; Walls 2009). Like *O. palmeri longimanus*, there is little available information on the specific ecology of *O. maleate*.

Previous work on *P. vioscai* indicated that their biomass was directly and positively related to allochthonous leaf accumulation (Barcza 1994). *P. vioscai* is nocturnal, with a 2-3 year life span. They are tertiary summer burrow spawners that release young in the autumn. Barcza (1994) found that *P. vioscai* exhibited variable non-seasonal movement patterns, with home ranges up to 200m, and seemed to move about the same order of magnitude as other Louisiana crayfish previously studied, like *P. penni* and *P. vittus* (Black 1963). *P. natchitochae* is nearly identical morphologically to *P. vioscai*, and their ecologies and behaviors are likely similar (Walls 1972; Walls 2009). Extensive crayfish surveys by Budnick (2015) in the Calcasieu, Red, Mermentau, and Vermillion-Teche River basins demonstrated that crayfishes were either cosmopolitan (e.g., *P. clarkii*, *P. acutus*, *C. puer*, and *O. lancifer*) or exhibited very restricted distributions (e.g., *P. pentastylus*, *P. natchitochae*, *O. hathawayi blacki*, *O. h. hathawayi*, *O. maleate*). The species with restricted distributions are of significant conservation concern in this region because of challenges in recolonizing in the advent of local extirpation.

Recolonization following local extirpation in this region is complicated by anthropogenic habitat fragmentation and natural biogeographic barriers (Adams et al. 1992). Anthropogenic habitat fragmentation is one of the foremost causes of species loss worldwide, and fragmentation in streams by road crossings is extremely common (Foster & Keller 2011, P  pino et al. 2012). Dams, culverts, and other man-made structures often obstruct or constrict the stream with non-natural substrates like concrete and metal (Anderson et al. 2012, P  pino et al. 2012). This can impede movement by fishes and other aquatic organisms (Warren & Pardew 1998; Anderson et al. 2012). Culverts, in particular, are common and may have a greater overall impact on the movement of crayfishes than dams (Louca et al. 2014) because of low flow velocities and perched downstream openings (Kerby et al. 2005; Louca et al. 2014).

Crayfishes often exhibit a stationary phase that may last up to a year, followed by a nomadic phase in which they move to a new area (Gherardi et al. 2000), and these changes in behavior may complicate conservation efforts by obfuscating research on movement patterns and timing, as well as, cause crayfish to move from managed habitat as part of natural nomadic movements. The upper limit of crayfish movements in North America has been estimated at 3000 m<sup>2</sup> (Guan 1997; Gherardi et al. 2000). However, most studies of crayfish movement have been done in the warmer months when crayfish movement is at its peak (Bubb et al. 2004; Johnson et al. 2014), with few studies examining movement behavior during colder months. Net distances moved range from 2.65 m/d (winter) to 4.1 m/d (summer) (Bubb et al. 2002; Bubb et al. 2004). Most field studies have used radio transmitters or passive integrated transponder (PIT) tags glued to the carapace of the crayfish. Although this allows for very precise location of crayfish over short times, the tags fall off when the crayfish molts, often after only a few weeks (Frisch & Hobbs 2006).

Laboratory studies have demonstrated the Visual implant elastomer (VIE; Northwest Marine Technologies, Inc.) and coded wire tags (CWT) to be effective crayfish tags (Isely & Eversole 1998; Jerry et al. 2001; Clark & Kershner 2006). Individually numbered CWTs are injected into the musculature just under the exoskeleton on the abdomen. VIE is a two-part compound that is mixed prior to injection under the exoskeleton. It solidifies into a flexible bio-compatible solid after a few hours and is visible on the ventral part of the abdomen. The benefit of these tags over other marking procedures includes the relative cost and duration of the tags. These tags are inexpensive, and very likely to stay within the crayfish throughout their lifetime. Mortality is low, and retention rates are high, though retention is higher for CWT than VIE (Isely & Eversole 1998; Clark & Kershner 2006). Another benefit is being able to tag small or juvenile individuals. Coded wire tags can be used on individuals as small as 20 mm total length, and VIE can be used on individuals as small as 13 mm carapace length (Isely & Eversole 1998; Jerry et al. 2001; Clark & Kershner 2006).

My goal in this project was to inform conservation strategies for stream crayfishes by addressing movement, anthropogenic barriers to movement, and population estimates. Specifically, I planned to use mark-recapture to examine crayfish movement through culverts. I hypothesized that the barrier effect would vary by type of culvert. Additionally, I hypothesized that population estimates from this study would support the general consensus (e.g., Taylor et al. 2007) regarding the relative commonness or rarity of these stream crayfish species.

## 2. METHODS

### 2.1 Site Selection

Twelve road crossings in the Red and Ouachita River basins, within the Level III South Central Plains ecoregion, were selected as study sites (Figures 1 and 2). This ecoregion is understudied and keeping the sites within two river basins allowed for comparison between different species in different basins, while keeping sample sizes for each basin high. Previous biogeographic studies of aquatic invertebrates have reported high taxonomic similarity among basins with a given ecoregion and greater dissimilarity among ecoregions (Hughes et al. 1994; Rabeni & Doisy 2000; Kaller et al. 2013) suggesting that sampling be restricted to only this ecoregion to increase the potential to sample these species. Based on Walls (2009), Kaller et al. (2015), and Budnick (2015), sites expected to have high density of crayfishes were chosen to maximize the number of crayfish captured and tagged. We confirmed expectations during the first trap set. If the first trap set collected at least ten crayfish, we concluded there was sufficient density of crayfish to proceed.

In total, 31 potential streams were evaluated, and 19 were rejected because no crayfish were sampled during evaluation (6), too few crayfish were sampled (11), or extremely low dissolved oxygen levels resulted in mortality in traps (2). Of the five streams where *P. acutus* were sampled (Cow Bayou, Flat Branch, Iatt Creek tributary, Flat Branch, Little Six Mile Creek, and Sibley Creek tributary), three streams where *P. kenslyi* were sampled (Little Six Mile Creek tributary, Matsu Bayou tributary, and Sibley Lake tributary), three streams where *P. natchitochae* were sampled (Iatt Creek tributary, Dartigo Creek, and Hurricane Creek tributary), three streams where *P. vioscai* were sampled (two Trout Creek tributaries and Kitterlin Creek tributary), and one stream with *O. malatae* (Hurricane Creek tributary), too few crayfish were

sampled for the selection criteria. Low dissolved oxygen resulted in complete (Bad Gully) or near total mortality (Flat Branch), resulting in site exclusion.

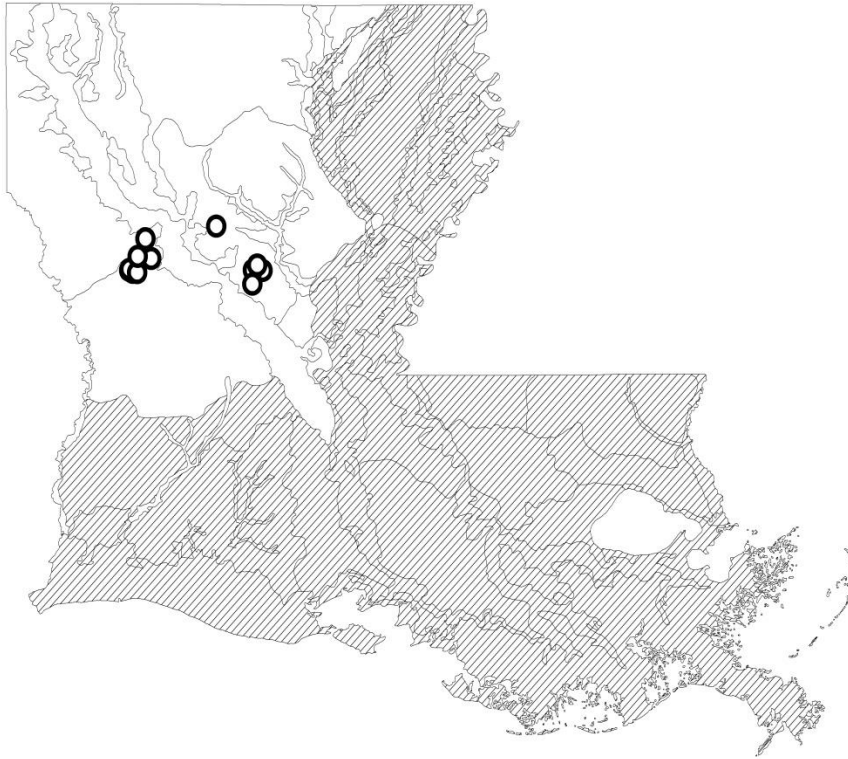


Figure 1. Sites are shown as open circles on the Level III Ecoregion map. All sites are within the South Central Plains (white). Lines delineate the Level IV Ecoregions.



Figure 2. Sites are shown as green markers on the River Basin map. All sites are within the Red and Ouachita River Basins.

## 2.2 Field Sampling

Sites consisted of a 100-m sampling reach centered on a road crossing and were sampled with four minnow traps upstream and four minnow traps downstream of the road crossing, with tilapia filets used as bait. Traps were set overnight and pulled the next day, given that most crayfishes prefer to move at night (Johnson et al. 2014). Traps were set in the first four appropriate crayfish habitats observed moving in either direction from the road access point (i.e., the first pool, undercut bank, and debris pile detected each had a trap, with the fourth in another of the previous habitats). Trap set and pull times were recorded. Sampling occurred during summer (July-September 2014), fall (October-November 2014), and winter (February-March 2015) periods.



Electrofishing has been an effective method for crayfish sampling in previous studies (Alonso 2001; Rabeni et al. 1997; Budnick 2015) and was used to supplement trap collections. We electrofished 50-m reaches twice upstream and downstream of the road crossing beyond the pools formed by the road crossing with one or two DC backpack electrofishers (HT-2000 Halltech Aquatic Research, Inc.), depending on stream width. We anticipated minimal crayfish mortality from these sampling methods, apart from potential predation within traps.

Collected crayfishes were identified, measured, sexed, and marked with sequential CWT and VIE tags. Although *P. acutus* and *P. zonangulus* females are indistinguishable on site and have co-occurring ranges, *P. acutus* is more lotic in its habitat preferences, so we treated all of them as *P. acutus* (Walls 2009). Only Crayfish larger than 40 mm total length were tagged to avoid possible growth or survival problems with smaller individuals (Isely & Eversole 1998; Clark & Kershner 2006). This still allowed tagging of most crayfishes caught that could be readily identified in the field. Different colors of elastomer were used upstream and downstream to differentiate where the crayfish were caught and released. Different colors were also used if there were multiple streams sampled within a few kilometers up or downstream. After marking, all crayfishes were released back into their respective capture locations.

Sites were re-sampled 2-3 months later, and we assumed most crayfishes would have survived this interval, given life expectancies between one and six years depending on the species (Momot 1967; St. John 1976). All crayfish caught after the first round of sampling were passed over a CWT detector, with a positive signal allowing us to check for the VIE tag for estimation of tag loss (Frisch & Hobbs 2006). Individual CWTs were collected from recaptured euthanized crayfish at the end of the study to identify individuals to the date they were tagged.

At each site, we measured pH, specific conductance, temperature, turbidity, and dissolved oxygen before sampling at single points above and below the crossing with a handheld multiprobe (YSI® Sonde 9130). We also measured current velocity just under or inside the road crossing at the upstream and downstream ends, as well as just in front of and just below the crossing with a portable flow meter (SONTEK Flowtracker® Doppler). . Current velocity was measured no more than 5 cm above the bottom of the stream in order to measure the flows experienced by crayfish (Foster & Keller 2011). We also measured depth inside the road crossings and the main channel. We obtained an average stream width by taking ten measurements three meters apart, both upstream and downstream from the road-impacted segment of the stream.

### **2.3 Analysis**

Recaptures were too few for estimating abundance and transience through mark-recapture analyses. Instead, we modeled the abundance of the three most frequently sampled crayfish species (*P. vioscai*, *P. natchitochae*, and *O. palmeri*) against habitat variables for substrate, river basin, specific conductance, and average stream width with species-specific open population n-mixture models (Royle 2004; Dail & Madsen 2011; Fiske & Chandler 2011; Table 1. N-mixture models exploit the hierarchical nature of generalized linear models (Faraway 2006; Royle & Dorazio 2008) by fitting a logistic model to determine the probability of detecting crayfish, given habitat characteristics, and fitting a Poisson model to estimate abundance, given detection probability from the logistic model. Additionally, parameters for recruitment and apparent survival, or exodus from the site, between visits may be determined (Dail & Madsen 2011). Each parameter (detection, abundance, immigration/survival, and emigration/exodus) may have covariates (e.g., habitat components). Habitat components considered for detection modeling

were turbidity, depth, and a combination of turbidity and depth. Abundance estimates included stream width, river basin (Red or Ouachita), specific conductance (as a measure of calcium in the water), and substrate type. Transience estimation, as described by recruitment to a site and departure from the site, included measurements of current velocity and dissolved oxygen, which were expected to change among visits.

After constructing three sets of species-specific candidate models, including a global model with all habitat components, a null model, and combinations of habitat components from complex to simple, models were selected for interpretation and abundance estimation based on the following criteria. The model satisfied the principle assumption of linearity (i.e., the expected value of the link transformed parameter estimate was linearly related to the linear combination of explanatory variables and covariates; Faraway 2006; Agresti 2015). The model(s) exhibited the lowest AIC (Akaike's Information Criterion) among candidates. Finally, the model's bootstrapped goodness-of-fit  $\hat{c}(\frac{x^2}{d.f})$  estimates did not indicate over- or underdispersion following guidelines in Zuur et al. (2009). If a single top model for a species was not selected, model averaging following Burnham and Anderson (2002) was used for interpretation and abundance estimation. All analyses were performed in Program R (vers. 3.3.1, R Core Team 2015).

Table 1. Mean habitat characteristics (standard error) of each site

Site	River Basin	Dominant Substrate	Average Stream Width (m)	Stream Width Standard Error (m)	Conductivity (µs/cm)	Conductivity Standard Error (µs/cm)
Bayou Blue	Red	Sand	3.00	0.35	0.060	0.00
Big Creek	Ouachita	Leaf litter	6.63	0.29	0.043	0.00
Big Creek Tributary	Ouachita	Sand	5.81	0.49	0.050	0.00
Bayou Chiori	Red	Silt	3.98	0.17	0.080	0.01
Chiori Tributary	Red	Silt	5.31	0.23	0.088	0.20
Beaver Creek	Red	Silt	2.71	0.11	0.110	0.00
Dry Prong	Ouachita	Leaf litter	2.93	0.27	0.048	0.00
Gray Creek	Red	Sand	3.20	0.15	0.170	0.00
Redland Creek	Red	Sand	4.11	0.26	0.105	0.04
Clear Branch	Ouachita	Gravel & hardpan	2.43	0.14	0.078	0.01
Sibley Lost Bayou	Red	Silt	4.45	0.22	0.165	0.01
Trout Creek	Ouachita	Sand	5.58	0.26	0.070	0.00

(Table 1. Continued)

Site	Summer DO (mg/L)	Summer DO Standard Error (mg/L)	Summer Flow (m/s)	Summer Flow Standard Error (m/s)	Fall Dissolved Oxygen (mg/L)	Fall Dissolved Oxygen Standard Error (m/s)	Fall Flow (m/s)	Fall Flow Std Error (m/s)
Bayou Blue	8.74	0.00	0.11	0.00	9.59	0.51	0.16	0.00
Big Creek	7.75	0.01	0.01	0.05	9.33	0.01	0.00	0.04
Big Creek Tributary	8.08	0.02	0.17	0.05	10.38	0.66	0.15	0.02
Bayou Chiori	5.09	0.15	0.02	0.01	7.08	0.07	0.12	0.05
Chiori Tributary	5.54	0.05	0.01	0.00	6.76	0.08	0.00	0.00
Beaver Creek	5.09	0.00	0.01	0.00	6.83	0.08	0.07	0.06
Dry Prong	7.28	0.46	0.01	0.00	6.17	0.01	0.00	0.00
Gray Creek	4.26	0.00	0.01	0.04	1.15	0.01	0.00	0.09
Redland Creek	7.79	0.40	0.13	0.02	11.02	0.03	0.08	0.00
Clear Branch	7.59	0.00	0.01	0.00	5.65	0.23	0.00	0.00
Sibley Lost Bayou	5.10	0.40	0.02	0.01	6.16	0.00	0.00	0.00
Trout Creek	7.08	0.08	0.11	0.03	7.99	0.16	0.10	0.03

### 3. RESULTS

We tagged and released 631 individual crayfishes, and only recaptured six *P. vioscai* and one *P. acutus*. Recaptured crayfishes were not analyzed, because use of the known recaptures would violate model assumptions. Over the course of the study, at the twelve selected sites, I collected 332 *P. vioscai* (46% frequency of occurrence), 29 *O. palmeri* (39% frequency of occurrence), 269 *P. natchitochae* (53% frequency of occurrence), 13 *O. maleate* (11% frequency of occurrence), 13 *P. acutus* (18% frequency of occurrence), 14 *P. tulane*i (7% frequency of occurrence), 2 *P. clarkii* (7% frequency of occurrence), and 1 *P. kensleyi* (3.5% frequency of occurrence; Table 2). I did not collect any *P. lancifer*. Among the five species not included in the n-mixture models, *P. acutus* was the most common, occurring at 3 of 12 sites and during all sampling periods (Clear Branch) followed by *P. clarkii* (2 of 12 sites, summer only) and *O. malatae* (2 of 12 sites, summer and fall). *P. tulane*i and *P. kensleyi* were only sampled at one site apiece. Interestingly, where sampled, *P. tulane*i was relatively abundant.

Top models for detection probabilities ordered by AIC for each species included the null model and varied by depth and/or turbidity (Table 3). *O. palmeri* detection depended on turbidity, and *P. vioscai* and *P. natchitochae* on neither (null).

Basin was the most commonly included variable in the abundance and transience models (4 of 5 possible models), followed by specific conductance (2 of 5 possible models) and stream width (2 of 5 possible models; Tables 3 and 4). For *P. vioscai*, competing models required averaging among models for: 1) basin alone; 2) conductivity, and basin covariables; and 3) width, basin, flow, and dissolved oxygen abundance and detection covariables. The top model for *P. natchitochae* had stream width, specific conductance, basin, and dissolved oxygen in the model. Many of these parameters had errors greater than the parameter itself with estimates

overlapping 0 suggesting weak relationships (Table 4). The top abundance and transience model for *O. palmeri* was the null model.

Transience, or immigration and emigration to or from a site, was related to flow and/or dissolved oxygen. Only *P. natchitochae* and *P. vioscai* exhibited patterns in site transience (Table 5). *P. vioscai* was decreasingly likely to colonize from summer through winter, however, when the species did colonize, colonization was augmented by higher dissolved oxygen and higher current velocity. *P. vioscai* was likely to leave sites as summer progressed to winter and even more likely to leave when dissolved oxygen was lower and when current velocity was higher. However, all of these estimates overlapped 0, and thus were statistically weak, although potentially biologically meaningful. *P. natchitochae* was likely to colonize and likely to avoid sites with low dissolved oxygen. These estimates did not overlap 0 and were statistically and likely biologically meaningful. *P. natchitochae* was unlikely to leave sites, but more likely to leave sites when there was high dissolved oxygen, which again overlapped 0 and is not robust.

Population estimates were low for all species sampled, with highest being 4.76 ( $\pm 1.564$ ) individuals per 100-m reach, which was consistent with generally low observed estimates (Table 6, Figure 3). However, across models, abundance estimates were generally lower than the number of animals collected. Additionally, population estimate errors were generally quite high, with one species in particular having standard errors over 750 individuals (*P. natchitochae*).

Table 2. The observed number of each species by sampling site. Trib. = tributary

Site	<i>Procambarus acutus</i>			<i>Procambarus natchitochae</i>			<i>Procambarus vioscai</i>			<i>Orconectes palmeri</i>		
	Summer	Fall	Winter	Summer	Fall	Winter	Summer	Fall	Winter	Summer	Fall	Winter
Bayou Blue	0	0	NA	24	62	NA	0	0	NA	0	0	NA
Big Creek	0	0	NA	0	0	NA	23	14	NA	7	1	NA
Big Creek Trib	0	0	0	0	0	0	16	15	18	2	3	1
Bayou Chiori	0	0	NA	14	23	NA	0	0	NA	0	0	NA
Chiori Trib	0	0	NA	8	20	NA	0	0	NA	0	0	NA
Beaver Creek	2	0	NA	13	28	NA	0	0	NA	0	0	NA
Dry Prong	0	0	NA	0	0	NA	25	12	NA	1	1	NA
Gray Creek	0	0	0	36	58	25	0	0	0	2	2	0
Redland Creek	5	0	NA	31	10	NA	0	0	NA	0	0	NA
Clear Branch	2	2	2	0	0	0	5	9	4	0	0	0
Sibley Lost Bayou	0	0	NA	8	28	NA	0	0	NA	0	0	NA
Trout Creek	0	0	0	0	0	0	18	18	36	7	2	0

Site	<i>Orconectes malatae</i>			<i>Procambarus tulaneii</i>			<i>Procambarus clarkii</i>			<i>Procambarus kensleyi</i>		
	Summer	Fall	Winter	Summer	Fall	Winter	Summer	Fall	Winter	Summer	Fall	Winter
Bayou Blue	0	0	NA	0	0	NA	1	0	NA	0	1	NA
Big Creek	0	0	NA	0	0	NA	0	0	NA	0	0	NA
Big Creek Trib	0	0	0	0	0	0	0	0	0	0	0	0
Bayou Chiori	1	0	NA	0	0	NA	0	0	NA	0	0	NA
Chiori Trib	10	2	NA	0	0	NA	0	0	NA	0	0	NA
Beaver Creek	0	0	NA	0	0	NA	0	0	NA	0	0	NA
Dry Prong	0	0	NA	0	0	NA	0	0	NA	0	0	NA
Gray Creek	0	0	0	0	0	0	0	0	0	0	0	0
Redland Creek	0	0	NA	0	0	NA	1	0	NA	0	0	NA
Clear Branch	0	0	0	10	0	4	0	0	0	0	0	0
Sibley Lost Bayou	0	0	NA	0	0	NA	0	0	NA	0	0	NA
Trout Creek	0	0	0	0	0	0	0	0	0	0	0	0



Table 3. The top models for each species (relative difference between lowest AIC with each model) after disregarding the models that did not meet linearity criteria ordered by AIC (Aikaike's Information Criterion). AICwt is the relative importance of each model compared to the others in the table. Models highlighted also passed the goodness of fit test. Width = stream width. Cond = Specific conductance. Basin = river basin. Sub=substrate. Flow = stream velocity. DO = dissolved oxygen.

<i>a) Orconectes palmeri</i>				<i>b) Procambarus natchitochae</i>			
Models	AIC	dAIC	AICwt	Model	AIC	dAIC	AICwt
WidthCondBasinflow	52.16	0.00	0.16	WidthCondBasinDO	165.16	0.00	1.00
WidthBasin	52.35	0.19	0.15	DO	175.81	10.65	0.00
Cond	52.89	0.73	0.11				
Null	53.02	0.86	0.11				
WidthCond	54.74	2.58	0.04	<i>c) Procambarus vioscai</i>			
WidthCondSubBasin	54.80	2.64	0.04	Model	AIC	dAIC	AICwt
Width	54.89	2.73	0.04	WidthBasinflowDO	88.40	0.00	0.34
Sub	55.06	2.90	0.04	WidthCondSubBasin	89.35	0.96	0.21
WidthBasinflow	55.08	2.92	0.04	SubBasin	89.62	1.23	0.18
WidthCondBasinflowDO	55.11	2.95	0.04	WidthBasin	90.24	1.84	0.14
Condflow	55.39	3.23	0.03	Basin	90.40	2.01	0.13
Basin	55.46	3.30	0.03	WidthCondBasin	90.41	2.02	0.12
SubBasin	55.83	3.67	0.03	CondSubBasin	90.60	2.20	0.11
WidthSubBasinflow	56.13	3.97	0.02	CondBasin	92.36	3.96	0.05
CondDO	56.30	4.14	0.02	WidthSubBasinDO	94.39	6.00	0.02
DO	56.40	4.24	0.02	WidthSub	99.80	11.40	0.00
CondSub	56.57	4.41	0.02				
CondBasinflow	56.60	4.43	0.02				
WidthSubflow	56.79	4.63	0.02				
WidthSubBasin	57.66	5.50	0.01				
WidthSub	58.79	6.63	0.01				
WidthCondSub	60.76	8.60	0.00				
WidthSubBasinDO	61.57	9.41	0.00				
WidthCondSubBasinDO	63.30	11.14	0.00				

Table 4. Parameter estimates of variables selected by abundance modeling.

<b>Species (<i>Procambarus</i> or <i>Orconectes</i>)</b>	<b>Intercept</b>	<b>Intercept error</b>	<b>Basin</b>	<b>Basin error</b>	<b>Sp. Cond. (<math>\mu\text{s}/\text{cm}</math>)</b>	<b>Sp. Cond. error (<math>\mu\text{s}/\text{cm}</math>)</b>	<b>Average width (m)</b>	<b>Average width error (m)</b>	<b>Leaf litter</b>	<b>Leaf litter error</b>	<b>Sand</b>	<b>Sand error</b>	<b>Silt</b>	<b>Silt error</b>
<i>P. vioscai</i>	3.02	0.62	-5.26	0.97	1.33	6.32	0.26	0.10	N/A	N/A	N/A	N/A	N/A	N/A
<i>P. natchitochae</i>	-11.81	397.44	15.92	397.44	5.72	8.99	-0.37	-1.10	N/A	N/A	N/A	N/A	N/A	N/A
<i>O. palmeri</i>	1.19	0.25	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table 5. Parameter estimates of variables selected by transience modeling.

Species ( <i>Procambarus</i> )	Intercept	Intercept error	Dissolved oxygen (mg/L)	Dissolved oxygen (mg/L) error	Flow (m/s)	Flow error (m/s)
<i>P. vioscai</i> immigration	-72.14	892.00	8.19	92.20	13.45	927.40
<i>P. vioscai</i> emigration	211.60	426.00	-27.40	55.00	60.00	113.00
<i>P. natchitochae</i> immigration	7.67	0.90	-0.97	0.18	N/A	N/A
<i>P. natchitochae</i> emigration	-96.10	166.00	20.60	36.00	N/A	N/A

Table 6. Population estimates of each species by each site, using the single top model or averaged model parameters.

*a) Orconectes palmeri*

Site	Population Estimate	Error
Clear Branch	1.19	0.25
Dry Prong	1.19	0.25
Big Creek	1.19	0.25
Big Creek Tributary	1.19	0.25
Trout Creek Tributary	1.19	0.25
Bayou Blue	1.19	0.25
Gray Creek	1.19	0.25
Redland Creek	1.19	0.25
Sibley Lost Bayou	1.19	0.25
Bayou Chiori	1.19	0.25
Chiori Tributary	1.19	0.25
Beaver Creek	1.19	0.25

Table 6. Continued.

***b) Procambarus natchitochae***

<b>Site</b>	<b>Population Estimate</b>	<b>Error</b>
Clear Branch	0.00	395.45
Dry Prong	0.00	392.42
Big Creek	0.00	390.50
Big Creek Tributary	0.00	391.47
Trout Creek Tributary	0.00	391.90
Bayou Blue	3.36	792.10
Gray Creek	3.92	792.87
Redland Creek	3.21	791.28
Sibley Lost Bayou	3.43	791.44
Bayou Chiori	3.12	791.20
Chiori Tributary	2.67	789.80
Beaver Creek	3.75	792.87

***c) Procambarus vioscai***

<b>Site</b>	<b>Population Estimate</b>	<b>Error</b>
Clear Branch	3.74	1.36
Dry Prong	4.09	1.32
Big Creek	4.77	1.56
Big Creek Tributary	4.57	1.53
Trout Creek Tributary	4.54	1.63
Bayou Blue	0.00	2.27
Gray Creek	0.00	2.99
Redland Creek	0.00	2.67
Sibley Lost Bayou	0.00	3.08
Bayou Chiori	0.00	2.50
Chiori Tributary	0.00	2.68
Beaver Creek	0.00	2.56

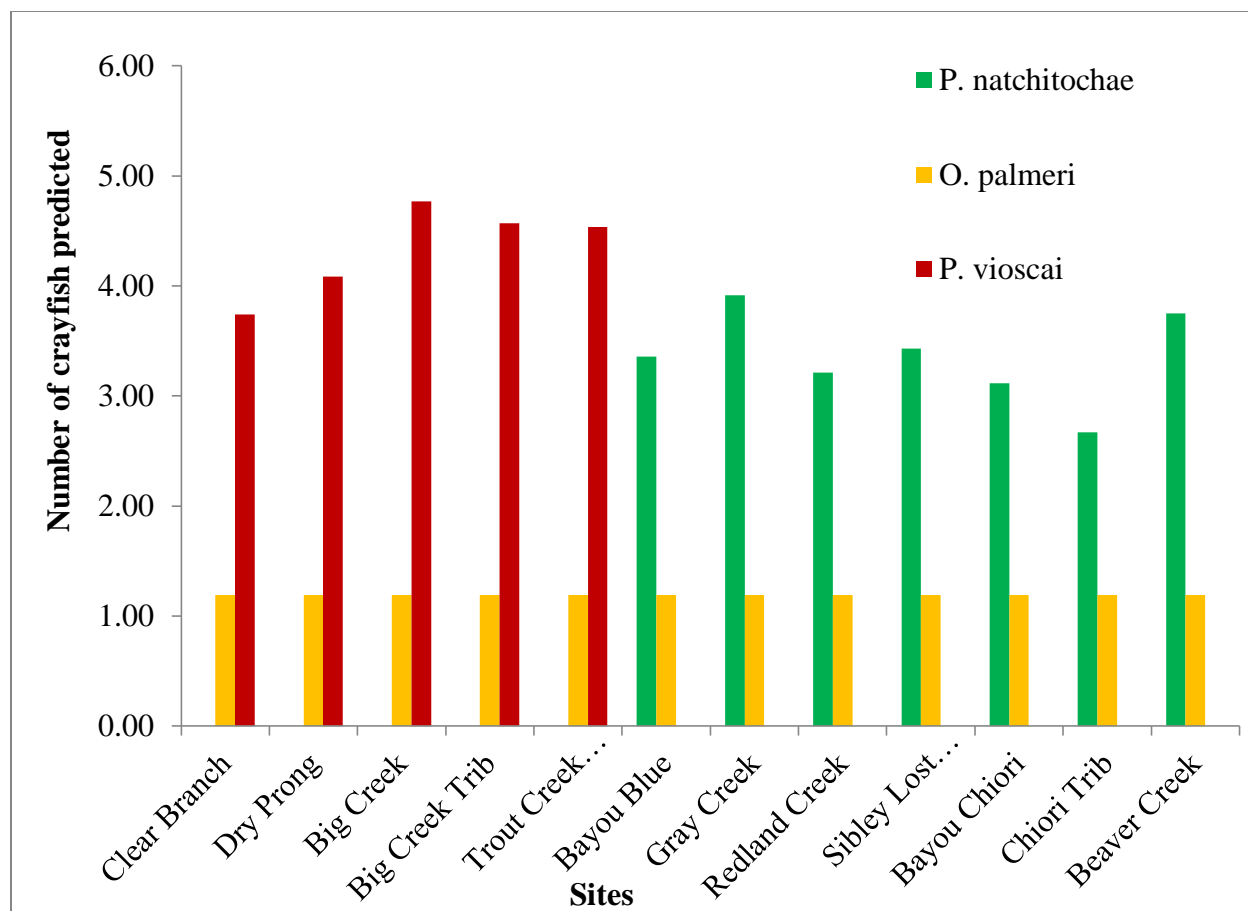


Figure 3a. Model population estimates of crayfish species (either *Procambarus* or *Orconectes*) at each site. Standard error bars removed for clarity.

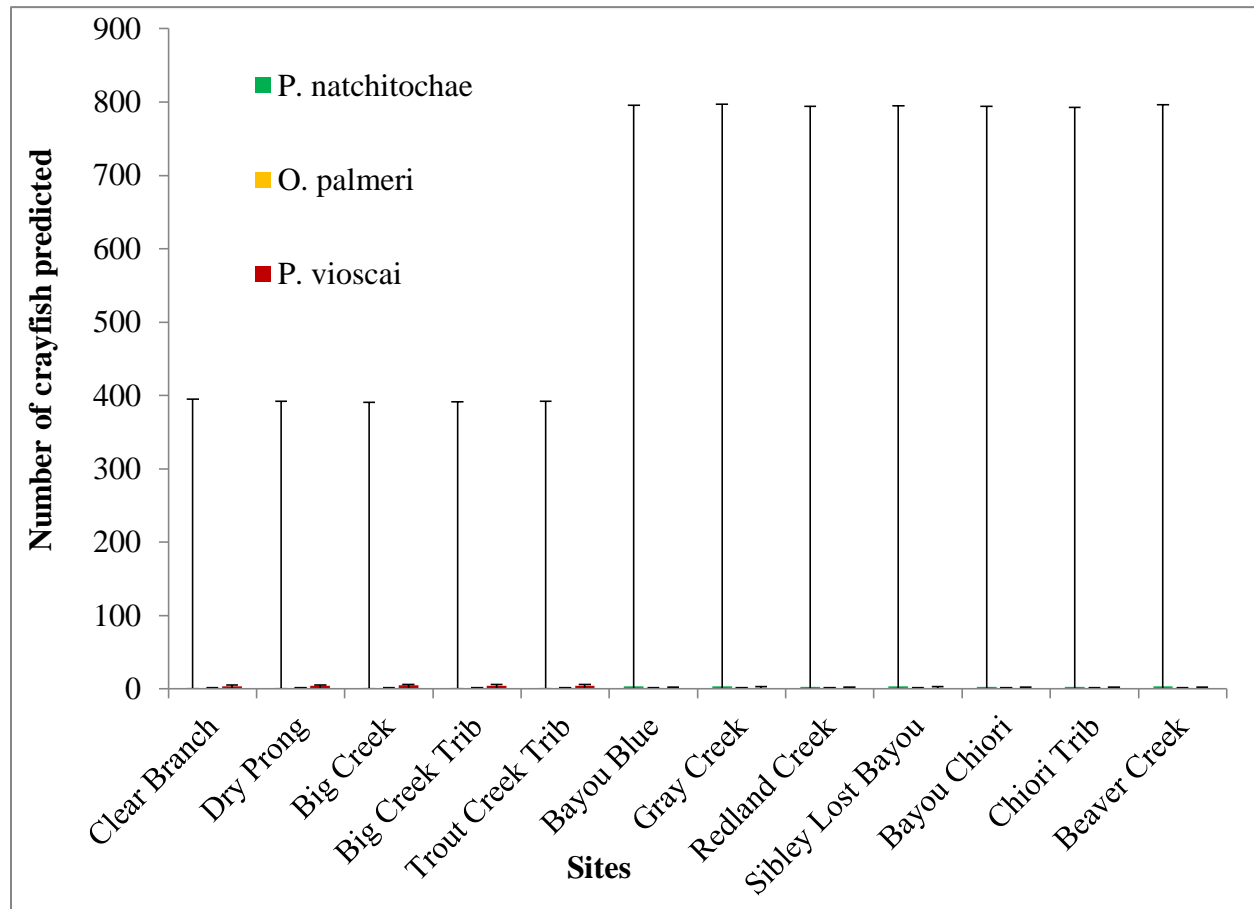


Figure 3b. Population estimates with standard error bars of crayfish species at each site.

#### 4. DISCUSSION

Despite low recaptures that prevented assessment of the role of culverts as barriers, our results indicated that I was able to generate valuable data on larger scale movement and population metrics for multiple species of crayfish. Crayfish abundance differed by river basin, and stream width and specific conductance contributed significantly to crayfish abundance variability among streams. Transience of some species was affected by dissolved oxygen concentration and current velocity, though the relationships were quite different between two supposedly similar species. Overall, crayfish abundances were low across all study sites and lower than previous studies.

River basin was the most common variable in the top interpretable abundance models and in the observed sampling data, which was not unexpected (Walls 2009; Budnick 2015). Estimated abundance and observed crayfish differed between basin for *P. acutus*, *O. maletae*, *P. vioscai*, and *P. natchitochae*, not but for *O. palmeri*. This suggests crayfish dispersal is more similar to freshwater fishes than other aquatic invertebrates. Fish are often more taxonomically similar within river basins, which has generally been interpreted to be the result of dispersal barriers between basins (e.g., Hughes et al. 1987; Matthews & Robison 1998; McCormick et al. 2000; Hoeinghaus et al. 2007; Kaller et al. 2013). Other aquatic invertebrates, specifically insects, are often quite similar among adjacent river basins, and become increasingly dissimilar over increasing overland distances (e.g., Corkum 1991; Feminella 2000; Gerritson et al. 2000; Rabeni and Dosy 2000; Sandin and Johnson 2000; Waite et al. 2000; Baselga et al. 2013; Kaller et al. 2013). Aerial dispersal by aquatic insects may be a partial explanation, however, not all insects disperse aerially and some species do use stream corridors for dispersal (Petersen et al. 2004; Lancaster & Downes 2013). Whereas some species of crayfish can move overland, not all

of them can make overland crossings, and those species than can make overland crossings only move over short distances (up to 2000m over easy terrain for *P. clarkii*) during times of high humidity and dew or rainfall (Cruz & Rebelo 2007; Ramalho & Anastácio 2015). Therefore, because crayfish dispersal is primarily aquatic, these results suggest that their biogeographic patterns are more aligned with fishes than other invertebrates and conservation actions should be more like fishes than other invertebrates, with watershed-based management.

Other stream conditions also contribute to crayfish abundance. Specific conductance affects the same two species as were also influenced by river basin and did not appear to influence *O. palmeri*. In these systems, specific conductance is primarily driven by calcium compounds (Garrison 1997, Johnson & Brown 2000; Budnick 2015), which crayfish require to maintain their exoskeletons (e.g. Huner et al. 1978; Edwards et al. 2015) and for neuromuscular control (Zucker 1974; Leib-Neri & Peterson 2014). Specific conductance had a positive association with abundance for *P. vioscai* and *P. natchitochae*, however, specific conductance did not exhibit any relationship with *O. palmeri*. This is an interesting difference between the two genera, and one of only two variables to show such a distinction between genera, along with stream width. Stream width influenced the abundance of the *Procambarus* group, *P. vioscai*, and *P. natchitochae*, though in different directions. *P. vioscai* appeared to occur more frequently in larger streams, whereas *P. acutus* and *P. natchitochae* were more associated with smaller headwaters. *O. malatae* was not affected by stream width. These stream size associations were consistent with the species descriptions (Walls 2009) and with other studies suggesting spatial segregation of other crayfish species across stream size gradients (e.g., Taylor 1983; Grubaugh et al. 1996; Joy & Death 2001). Therefore, given similar associations between crayfish with habitat components in this study with other studies, abundance of these crayfish species appeared to be



structured by similar biogeographic, calcium, and channel size parameters as other crayfish species.

Taken together and focusing on the meaningful transience values, without any other knowledge about a site, one would predict that *P. vioscai* was unlikely to colonize new sites and likely to leave sites over the study, suggesting that *P. vioscai* had some seasonal pattern of site use in these headwaters, which was not reported in a previous, but shorter duration, study for *P. vioscai* (Barcza 1994). Conversely, *P. natchitochae* was likely to colonize new sites and stay at sites already occupied. Again, a seasonal pattern may have been occurring. Whereas our data suggest seasonal movement in *P. vioscai* and *P. natchitochae*, there has been no evidence of it in the literature for these species. However, there is evidence for seasonal movement in other crayfish species (Hazlett et al. 1979; Ramalho & Anastácio 2015). For *P. vioscai*, relationships with dissolved oxygen and current velocity were weak. Low oxygen and low current velocity sites were slightly avoided and tended to be abandoned. *P. natchitochae* also appeared to avoid low dissolved oxygen sites; however, relationships between dissolved oxygen with site abandonment were unclear. In summary, both species demonstrated seasonality in site use and either clear or potential relationships with dissolved oxygen.

Population estimates were low at all sites, and errors were generally higher than the estimates, except for *O. palmeri* and sometimes *P. vioscai*. *P. natchitochae* was widespread and comparatively very numerous during sampling, yet population estimates exhibited wide errors. Possibly, these errors may be attributable to sampling conditions, as it was usually deep and turbid where *P. natchitochae* was found, resulting in large adjustments from the detection model or the disparity between large local abundance and zero detections increased variability. In either case, a better understanding of *P. natchitochae* abundance patterns will require additional

effort. Previous crayfish studies have published a wide variety of crayfish population estimates, usually somewhere between 0.5 and 2 crayfish per m<sup>2</sup> (Abrahamsson & Goldman 1970; Matthews & Reynolds 1995). If one assumes that the traps sampled a small area already sampled by the electrofishing, our density estimates can be calculated by our abundance estimates divided by the width of the stream multiplied by 100. Density estimates would be smaller than other studies, even if one only counted the area sampled by electrofishing. The largest density estimate would be 0.015 crayfish per m<sup>2</sup>. This number might be increased slightly, if all species were estimated together, and counted all crayfish, regardless of total length. However, estimates would still be miniscule compared to other studies. *O. palmeri* was estimated to have a population of 1.19 per 100m at all sites, because none of the measured habitat variables influenced it. This is likely because *O. palmeri* is a widespread species with many subspecies and may be tolerant of many habitats (Penn 1957; Payne & Price 1981; Walls 2009). It is possible for it to occur in many places at low numbers, and potentially become an invasive species in more places (Sargent et al. 2011). Although not directly comparable to other studies, these estimates and the observed data suggest that despite being in the endemic range of these species, these crayfish species are not numerous in these streams supporting the general contention of Taylor et al. (2007).

Notably, although reported from the region (Walls 2009), *P. tulane* and *P. kensleyi* were only sampled in one site, and *O. lancifer* was not detected. Budnick (2015) reported *O. lancifer* in surveys of 50 sites within the Calcasieu, Red, and Vermillion-Teche River basins, which were generally west and south of this study. Kaller et al. (2015) found none of these species in a survey of 22 sites in the Sabine, Red, and Calcasieu River basins, which again were west of this study. Taken together, sampling of 94 sites in the South Central Plains ecoregion generally corroborates the distributions in Walls (2009) suggesting sharp biogeographic delineations of

these endemic species among river basins. Moreover, the rarity of these crayfish highlight the conservation concerns for these species.

These findings are useful for crayfish conservation because it can direct conservation and restoration efforts. These efforts should prevent inter-basin connections that would facilitate the spread of species beyond their natural range and put some species at risk. Conversely, intra-basin connections should be increased and barriers reduced to expedite the dispersal of species within their own basin and open up for habitat for colonization. This habitat should be available in a variety of stream widths, as some species prefer headwaters and some prefer larger streams. Specific conductance is primarily driven by underlying geology and, therefore, is difficult to influence, except by agriculture and urbanization (e.g., Ometo et al. 2000; Daniel et al. 2002; Roy et al. 2003; Conway 2007). Moreover, the relationship between specific conductance with crayfish abundance differs among species, suggesting a diversity of specific conductance ranges may be the target. To promote *P. natchitochae* *P. vioscai*, and, by congeneric association, *P. acutus*, higher levels of specific conductance should be maintained. Current velocity should also be maintained for *P. vioscai*, and flow can also help maintain dissolved oxygen for *P. natchitochae*. Whereas only *O. maletae* is officially classified as anything other than “least concern” of the species modeled, many of these species are restricted to waterways of only one river basin in a few states (Taylor et al. 2007; Walls 2009; Budnick 2015), and apparently have small populations and different ecologies. The spread of more aggressive species or change in habitat management could easily change the status of some of these species, and the function of these streams. It is likely that we would not know about a reduction in particular species until they were near extinction.

In summary, the insights into population abundance and transience suggest a few overarching findings. First, frequencies of occurrences and estimates of population abundance were generally low, which was consistent with the limited distribution and the consensus conservation concern for these species (Taylor et al. 2007; Walls 2009). Additional sampling for more robust population estimation should focus on increasing recaptures by reducing sampling sites and increasing sampling frequency or focus on unmarked methods, as in this study, increasing the number of sites with similar sampling frequency. Second, abundance appeared to be influenced by logical and manageable habitat parameters. The segregation of species by river basin was known, and this study reinforces the importance of preventing intra-basin exchange. Interestingly, the differing relationship with specific conductance between *Procambarus* and *Orconectes* species suggests an opportunity for conservation and habitat segregation between the genera. Third, the lack of recaptures that were not attributable to tag loss and the high estimates of site transiency suggest that these species of crayfish are more mobile, move at larger scales possibly following some seasonal pattern, or into other habitats (e.g., onto the floodplain) than previously believed. In combination, these findings suggest opportunities for conservation of endemic crayfish species.

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## **VITA**

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