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The Impacts of Flow Alterations To Crayfishes In Southeastern Oklahoma, With An Emphasis On the Mena Crayfish (*Orconectes menae*)

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**THE IMPACTS OF FLOW ALTERATIONS TO CRAYFISHES IN SOUTHEASTERN
OKLAHOMA, WITH AN EMPHASIS ON THE MENA CRAYFISH (*ORCONECTES
MENAE*) (FWS AGREEMENT NUMBER F11AF00031)**

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EXECUTIVE SUMMARY

Human activities can alter the environment to the point that it is unsuitable to the native species resulting in a loss of biodiversity. Ecologists understand the importance of biodiversity and the conservation of vulnerable species. Species that are narrowly endemic are considered to be particularly vulnerable because they often use specific habitats that are highly susceptible to human disturbance. The basic components of species conservation are 1) delineation of the spatial distribution of the species, 2) understanding how the species interacts with its environment, and 3) employing management strategies based on the ecology of the species. In this study, we investigated several crayfish species endemic to the Ouachita Mountains in Oklahoma and Arkansas. We established the spatial distributions (i.e., range) of the crayfish using Maximum Entropy species distribution modeling. We then investigated crayfish habitat use with quantitative sampling and a paired movement study. Finally, we evaluated the ability of crayfish to burrow under different environmental conditions in a controlled laboratory setting. Crayfish distribution at the landscape scale was largely driven by climate, geology and elevation. In general, the endemic crayfish in this study occurred above 300-m elevation where the geology was dominated by sandstone and shale, and rainfall totals were the highest compared to the rest of the study region. Our quantitative data indicated crayfish did not select for specific habitat types at the reach scale; however, crayfish appeared to continue to use shallow and dry habitat even as the streams dried. Movement by passive integrated transponder (PIT) tagged crayfish was highly variable but crayfish tended to burrow in response to drought rather than migrate to wet habitat. Controlled laboratory experiments revealed smaller substrate size (pebble) restricted crayfish burrowing more than larger substrates (cobble). We also found excess fine sediment restricted crayfish burrowing regardless of dominant substrate size. Our results suggest climate change and sedimentation resulting from land-use practices, combined with increased water withdrawals have the potential to alter crayfish distributions and affect persistence of some crayfish populations.

Background

Human-induced changes are altering the diversity of organisms that provide an array of benefits to society. Future predictions indicate biodiversity will comprise a few generalist species rather than the many unique species we see today (Vitousek, et al., 1997). Maintaining natural biodiversity is important because the native ecosystem provides benefits for the human population (Chapin, et al., 2000). These benefits, called ecosystem services, include air and water purification, natural resources, and climate and water-cycle maintenance (Hooper, et al., 2005). Biodiversity is important to maintain a properly functioning ecosystem that is able to provide natural services (Hooper, et al., 2005). For example, invasive vegetation that displaces native communities in the southwest is estimated to cost the public as much as \$230 million annually by reducing water availability and increasing flood damage (Sala, et al., 2000). Loss of the passenger pigeon *Ectopistes migratorius* is thought to have contributed to a rise in Lyme disease because the passenger pigeon regulated the abundance of Lyme disease-carrying rodents through competition (Chapin, et al., 2000). Marine fisheries that supply food for much of the world are not only more productive when there is high species richness, but also have a lower probability of collapsing than species poor ecosystems (Worm, et al. 2006). People worldwide have demonstrated interest in paying to preserve natural biodiversity and ecosystems, and Central American natural parks have generated as much as \$255 million from ecotourism (Nunes and van den Bergh, 2001). Dating back to the arrival of Polynesians on Pacific islands (1000 - 4000 years ago), humans have contributed to increased extinction rates (Pimm, et al., 1995). Extinctions caused by human activities are not limited to any taxa. Plants, invertebrates and vertebrates have all suffered increased extinction rates in the past 100 years (Pimm, et al., 1995), though aquatic fauna appear to be disproportionately affected (Jenkins, 2003).

Human land and water use has led to the alteration of stream channels and watersheds and cause unnatural environment for native species. Human alteration of the environment is the primary driver of the increase in extinction rate (Pimm, et al., 1995; Vitousek, et al., 1997). Humans alter the biological composition of the Earth via overexploitation and spreading of invasive species and by changing the natural land cover and exacerbating climate change (Vitousek, et al. 1997). Broad-scale changes in agriculture and urban land uses, including water use, are particularly problematic to aquatic systems (Chapin, et al., 2000; Jenkins, 2003; Xenopoulos, et al., 2005), and the increasing human population and global climate change will

likely exacerbate these degraded conditions (Smith and Tirpak, 1989; Sophocleous, 2000). Land-use activities alter the natural vegetation of the landscape and change the subsequent sediment regimes of aquatic ecosystems (Berkman, et al., 1986). Many land-use changes also alter the quantity and timing of water delivery to streams (Poff, et al. 1997) leading to direct changes in stream-water availability (LeMaitre, et al., 2002; Malmqvist and Rundel, 2002) and indirect changes in instream sedimentation (Rabeni and Smale, 1995; Pusey and Arthington, 2003) and the maintenance of channel units (Forsheim, Mount and Chin, 2008). Groundwater abstraction from the alluvial aquifer can reduce instream flows, but when taken from deeper aquifers can reduce the groundwater table leading to subsequent changes to the hyporheic zone of streams (Falke, Bestgen and Fausch, 2010). Reductions in water quantity within streams also reduce the dilution capacity of moving water and may result in anticipated and unanticipated water-quality concerns. Agricultural and urban areas are associated with nutrient fluxes in streams, often creating eutrophic and even hypoxic situations (Johnes, 1996; Wang, et al., 1997). Riparian buffers naturally mitigate some of the secondary impacts of land-use practices on streams (Karr and Schlosser, 1987); however, native riparian zones are also in decline (Naiman and Decamps, 1997). Heterogeneous instream habitat, often necessary for the persistence of lotic organisms (Klein, 1979; Freeman and Marcinek, 2006; Brewer and Rabeni, 2011; Brewer 2013) is often homogenized due to direct changes to streams (e.g., channelization and dam construction, Florsheim, et al., 2008) but also subsequent stream-morphological changes associated with broad changes in land use across catchments (Allan, 2004; Brewer and Rabeni, 2011). Recognition of the extent of catchment changes that alter lotic ecosystems has prompted targeted conservation efforts.

Because of the overall decline in stream conditions, conservation strategies are being developed or implemented that aim to protect regions with high levels of diversity and encompass a broader spatial and temporal extent than often previously considered. Areas with high levels of endemism are considered biological “hot spots” because changes to these areas are anticipated to have a disproportionate impact to diversity (Brooks, et al., 2006). These areas are particularly important because species in these regions often have narrow ranges and cannot readily disperse into more suitable habitats when their native habitat becomes altered and unsuitable for occupancy (e.g., climate change, Walther, et al., 2002, Stuart, 2004). One of the reasons these areas are targeted for conservation efforts is because of the relationship between

high rates of extinction and high level of endemism (Pimm, et al., 1995). For example, amphibians endemic to high-elevation streams account for the majority of new-amphibian additions to the list of species in decline (Stuart, 2004). Unsuitable conditions for native species often create conditions that allow non-native species to proliferate and can lead to extirpation of native species (Rahel, 2002). For example, the suppression of annual floods in the Colorado River has allowed invasive plant species and non-native trout *Oncorhynchus mykiss* to flourish and out-compete the native riparian vegetation and fish (Collier, Webb and Andrews, 1997). The challenges presented to endemic species have a much broader extent than previously considered (i.e., individual stream segments) and thus, conservation strategies have evolved to encompass broader spatial (Wiens, 2002; Allan, 2004) and temporal components (Ward, 1989). For example, the U.S. Fish and Wildlife Service has created landscape conservation cooperatives to help managers work toward a common goal and to promote cohesion of management efforts at a national scale. Researchers and managers have gained an appreciation for the importance of broad-scale conservation; however, conservation actions are likely to be most effective if we have a thorough understanding of the target species (Angermeier and Williams, 1994). To fully appreciate the needs of a species, the relationship between species and abiotic factors should be viewed at multiple scales to reveal emergent properties (Fausch, et al., 2002) that can thwart our best conservation efforts.

Crayfish are a sundry fauna that contribute substantially to aquatic diversity. Globally, there are more than 500 crayfish species representing 29 genera that display an array of life-history strategies (Taylor, 2002). Crayfish occupy a plethora of aquatic habitats that include rivers and lakes, wetlands, and sometimes simply the groundwater interface. For example, *Procambarus hagenianus* is a primary burrower that spends the majority of its life 0.9 - 4.5 m underground (Gherardi, 2002). Conversely, *Pacifiscus leniusculus* is native to lentic environments where it is considered to be a non-burrower (Gherardi, 2002). Crayfish occur on five of seven continents (Hobbs, 1988), but over 400 crayfish species occur in North America (Taylor, et al., 1996). Approximately half of North America's crayfish species are listed as species of conservation concern, with 15% listed as vulnerable, 14% listed as threatened, and 18% considered endangered (Taylor, et al., 2007). North American crayfish are at great risk because a high percentage of these crayfish are narrowly endemic and occur in areas with expanding human populations (Taylor, 2002). Like other freshwater organisms, crayfish

populations are threatened by habitat destruction, invasive species, pollution, and over exploitation (Taylor, et al., 2007).

Crayfish are economically and ecologically important components of stream ecosystems. Several crayfish species are cultivated for commercial use; however, the use of wild crayfish is still a large contributor of bait, food and pet trade in North America (Taylor, 2007). Over-exploitation has been cited as the reason for decline for one species, *Astacopsis gouldi*, but the introduction of non-native bait and aquarium species is considered the greatest threat to maintaining crayfish diversity (Taylor, 2007). Nonnative crayfish have been documented to alter the trophic web on every level (Twardochleb, Olden and Larson, 2013). Twardochleb, et al. (2013) reported nonnative crayfish to consistently and negatively affect primary producers (algae and macrophytes), other secondary producers (macroinvertebrates), and tertiary organisms (amphibians and fish). The wide spread effect of crayfish on other organisms is related to their behavior and ecology (Twardochleb, et al., 2013). Crayfish are responsible for a disproportionate amount of energy transfer in some ecosystems (Rabeni, 1992; Momot, 1995) and can serve as keystone species (Momot, 1978, 1995). Additionally, crayfish serve as forage for > 200 species, both aquatic and terrestrial (DiStefano, 2005). Finally, crayfish act as ecosystem engineers and create both forage and habitat for other invertebrates (Momot, 1995; Creed and Reed, 2004; Montemarano, Kershner and Leff, 2007). Clear-water, macrophyte-dominated Mediterranean wetlands were transformed into turbid phytoplankton-dominated systems after the invasion of *Procambarus clarkii* (Geiger, et al., 2005). Experimental manipulation of crayfish densities in New Zealand have been shown to significantly alter organic matter, accumulation of fine sediment and benthic invertebrate communities (Parkyn, Rabeni and Collier, 1997). Research and status monitoring of crayfish populations has increased in recent years likely due to an appreciation of their impact on lotic ecosystems.

Protecting aquatic organisms requires knowledge of the organism's spatial distribution and the ability of the species to respond to specific environmental perturbations. The spatial distribution of a species is important to the conservation of a species because it serves as a base line to compare future distributions and evaluate future conservation and management efforts (Horwitz, 1994). Ecologists strive to understand the habitat requirements of species in an effort to improve the success of conservation actions (Taylor, 2002). Habitat requirements, defined as

environmental features needed for species persistence, are often poorly understood (Rosenfeld 2003). At the most basic level, an understanding of the broad-scale constraints that act on populations (Poff, et al., 1997) is needed if we are to place requirements within an appropriate spatial context. Habitat use and selection within the geographic range provide little quantitative information on requirements, but are often needed to provide a foundation for experiments assessing mechanisms of change and habitat requirements in follow-up efforts. The notion of habitat requirements for populations is difficult to assess because only some habitats will limit a population at any time (Rosenfeld 2003) and behavioral modifications may be used by an organism to circumvent some perceived environmental disturbances (Hargis, Bissonette and David, 1998).

The Ouachita Mountain Ecoregion is a region with a high level of biodiversity including crayfishes; however little ecological information is known about these species (but see Bergey, Jones and Fenolio, 2004). The goal of this project was to provide the necessary foundation to conserve and manage *O. menae* and sympatric crayfish species (*Orconectes palmeri longimanus*, *O. leptogonopodus*, *O. saxatilis* and *Procambarus tenuis*). The project had two objectives:

1. Determine the distribution of *O. menae* and sympatric species at multiple spatial scales.
2. Identify responses of *O. menae* and sympatric species to seasonal drying or reduced flow in temporary and perennial streams.

The first objective identified the broad spatial constraints that act on these populations and should be helpful to identifying locations where populations may be present but have never been sampled. The coarse-scale features acting on crayfish populations place ecological limits on the suitability of habitats at more fine scales. Additionally, identifying important features at multiple scales allows us to view emergent properties (Stevenson, 1997) that may help elucidate important environmental features that are not used but can still be very important (e.g., Brewer 2013).

The second objective identified how these crayfish use habitat at finer scales within their distribution and how they move between habitats in response to stream drying. This objective provided insight to behavioral changes by crayfish in response to streamflow and how these

crayfish may respond to more intense drought periods as related to climate change. Finally, to make some predictions more broadly applicable to other locations and species, we also assessed how several important factors related to crayfish- substrate size, the addition of fine sediment, and water availability- might affect the fitness of crayfish populations and their persistence. Together, the information provided in this report will provide an important foundation to future efforts aimed at understanding the habitat requirements for endemic crayfish species.

OBJECTIVE 1.-DETERMINE THE DISTRIBUTION OF *O. MENAE* AND SYMPATRIC SPECIES AT MULTIPLE SPATIAL SCALES.

Introduction

Potential changes in climate are a major consideration for the future conservation and management of aquatic species. Climate change is expected to impact aquatic systems by altering stream-discharge patterns, increasing water temperatures, and increasing the frequency and intensity of drought and extreme storm events (Poff, 2002; Barnett, Adam, and Lettenmaier, 2005; Willy, et al., 2006). These changes to stream functioning are expected to increase the probability of invasion and the competitive ability of invasive species (Rahel and Olden, 2008), increase local extinctions (Maclean and Wilson, 2011) and reduce the distribution of many native species (e.g., Buisson and Grenouillet, 2009; Elith, Kearney and Phillips., 2010; Lyons, 2010). A reduction in suitable conditions is especially problematic for riverine species with limited dispersal capabilities (Woodward, et al., 2010) and particularly severe for endemic species with already diminutive distributions.

Regions with high levels of endemic species are considered "hot spots" for biodiversity (Brooks, et al., 2006); however, the status of many endemic species, including aquatic invertebrates, is poorly understood (Harding, 2003). Human-induced threats endanger aquatic invertebrates worldwide (e.g., pollutants, Cooper, 1993; habitat loss, Fahrig, 1997; land-use activities, Strayer, et al., 2003; non-native species introductions, Richardson and Whittaker, 2010; Wagner and Van Driesche, 2010), with these impacts likely to be exacerbated by climate change (Muhlfeld, et al., 2011). Further, organisms restricted to narrow geographic ranges – either naturally or through anthropogenic alteration – are particularly sensitive to cumulative

stresses (Smith and Tirpak 1989). The importance of conservation efforts for endemic species is recognized (Brooks, et al., 2006); however, our understanding of the distributional limits of these species and the factors that relate to those limits is inadequate.

Many crayfish species are restricted in distributions but still serve important functional roles in aquatic systems. Crayfish are a food source for hundreds of species (DiStefano, 2005), including sportfish populations (Rabeni, 1992). Additionally, crayfish consume large proportions of detritus, algae, and other invertebrates (Rabeni, 1992; Momot, 1995). In some aquatic systems, the biomass of crayfish exceeds that of all other benthic invertebrates (Rabeni, Gosset and McClendon, 1995). Further, the highest rates of secondary production occur in habitats likely impacted by alterations in streamflow (Brewer, DiStefano and Rabeni, 2009). These factors suggest changes in the distribution and abundance of crayfish via climate change have important implications for proper functioning of aquatic systems.

Species distribution models are a popular tool to predict a continuous probability surface from disparate sampled locations of organisms (Elith, et al., 2011). The major advantage of this modeling approach is that we are able to predict the likelihood of encountering a species at unsampled locations by examining the relationship among presence and a suite of environmental variables. Although many modeling programs are available, Maximum Entropy Species Distribution Modeling Software (MaxEnt; Phillips, Anderson and Shapire, 2006) and Genetic Algorithm Rule-set Production (GARP; Stockwell, 1992) are the most commonly used with MaxEnt tending to generate more conservative predictions (Peterson, Papes and Eaton, 2007). Although this approach has been mostly applied to terrestrial plants (Kumar and Stoltgren, 2009; Menon, et al., 2010) and birds (Peterson, Soberón and Sánchez-Cordero, 1999; Young, et al., 2009), it is increasingly used in aquatic ecology (e.g., Dominguez, et al., 2006; Chen, Wiley and McNyset, 2007; Hopkins and Burr, 2009). In this section, we used MaxEnt to predict the distribution of four endemic crayfish species in the Ouachita Mountains of Oklahoma and Arkansas, a region designated as a high priority for preserving freshwater biodiversity in the United States (Master, et al., 1998). We 1) predicted the current distribution of crayfish species using current and historic data points, 2) determined the landscape and in-channel factors related to the current distribution of crayfish species and 3) assessed how climate change might impact the future distributions of each species. We hypothesized that species whose current distribution

related more strongly to temperature and precipitation, or flow variables would be most susceptible to climate change.

Materials and Methods

Species distributions were modeled for four species of crayfish endemic to the Ouachita Mountains of Oklahoma and Arkansas: *Orconectes leptogonopodus*, *O. menae*, *O. saxatilis*, and *Procambarus tenuis*. Of the four species, *O. leptogonopodus* is the only species not listed as a species of special concern. *Orconectes menae* and *P. tenuis* are classified as vulnerable species whereas *O. saxatilis* is considered imperiled (Adams, Schuster and Taylor, 2010; Crandall, 2010; Schuster and Taylor 2010). *Orconectes saxatilis* is thought to be restricted to seven headwater tributaries of the Kiamichi River (Jones and Bergey, 2007).

Study Area

Our study area was located in the Ouachita Mountains of southeastern Oklahoma and southwestern Arkansas (Fig. 1). The Ouachita Mountains comprise a mixture of predominantly pine, oak, and hickory forest, and land-use practices consist primarily of agriculture, logging, ranching and recreation (Woods, et al., 2005). Streams in the area are generally confined within steep valleys and have boulder and cobble substrates (Splinter, et al., 2011). Streams in this region rarely reach third order (Strahler, 1957) before entering the main channels that exit the Ouachita Mountain region. Streams generally flow seasonally (December to May) and are reduced to intermittent pools and dry riffles during the summer and autumn months (Jones and Bergey, 2007).

Occurrence data

Occurrence data (presence locations) were obtained from three data sources. The Arkansas Game and Fish Commission provided historical-data collections (1934 to 2005), with the majority of data (85%) collected during the mid-1990's. The Oklahoma Biological Survey provided presence data from crayfish surveys conducted from 1992–2005, with most data (95%) collected from 2002–2005 (Jones, unpubl. data). We also contributed presence data collected via systematic sampling of 17 stream reaches during summer 2011 (see Objective 2 for sampling information). Combined, we used 50 occurrence points to construct species-distribution models for *O.*

leptogonopodus, 55 for *O. menae*, 17 for *O. saxatilis*, and 40 for *P. tenuis*. Because Maxent is especially well suited to deal with presence data (Philips et al., 2006), differences in collection methods were not thought to significantly influence the outcome of the models. Descriptions of sampling procedures used for data collected by the Oklahoma Biological Survey and Arkansas Game and Fish Commission, have been summarized in Jones and Bergey (2007), Robison (2001), and DiStefano (2003), respectively.

Environmental data

Coarse-scale variables, derived from existing geospatial data, were chosen as predictors to define the distributions of the four crayfish species. Variables were chosen to reflect environmental factors predicted to influence aquatic species distributions. For example, geology and climate are expected to be the most influential factors related to the distribution of aquatic organisms (Hynes 1975). We created a river network for the current study using the 1:100,000 digital stream network from the national hydrography dataset (USGS, unpubl. data, Accessed on 5/03/2012) as a foundation. Three catchments from the Mississippi drainage were merged to form a single extent that included the two major stream catchments of interest (Little River and Ouachita River; hereafter referred to as river network). The river network comprised 13,384 individual stream reaches. Landscape-scale climate and topography data were obtained from available sources (Table 1). Climate variables were chosen to represent seasonal (three months) trends and annual extremes within the study area. Specific topography variables were chosen due to potential influences on stream morphology. We created a flow-accumulation layer using ArcGIS 10 (Environmental System Research Institute Inc. Redlands, CA, USA), with the flow-direction raster provided by NHD Plus (USGS, unpubl. data). Appropriate data resolution for each environmental variable was chosen by considering 1) availability of different resolutions, and 2) how much variation occurred across the study area. Fine-scale resolution (30 m²) was chosen, when available, for layers representing environmental features with high variability across the study area (e.g., elevation); whereas, the available low resolution (1 km²) was deemed acceptable for layers representing environmental features with relatively low variability across the region (e.g., precipitation).

Species-distribution modeling

Current distribution – Occurrence data were imported into ArcGIS 10 and overlaid onto the river network. Each occurrence point was assigned geographically to the nearest reach within the network. Where multiple occurrence points existed for a single reach, we only kept one point to minimize undue influence on the model outcome caused by repeated sampling of the same locations (e.g., bridge access points). Wisz et al. (2008) recommended > 30 occurrence points be used to create a species-distribution model; however, accurate models have been created with as few as five presence locations using MaxEnt (Phillips, et al., 2006).

We used a vector-based approach in MaxEnt (MaxEnt 3.3.3k; Phillips, et al., 2006) to predict the current distribution of each crayfish species. Data were prepared in vector format rather than the traditional raster approach often used in species-distribution modeling (but see Elith, et al., 2008). The raster approach divides the study area into a grid where each cell is assigned a single probability-of-occurrence value. Multiple streams can occur within a single grid cell making the raster-based approach more error prone because a single value is assigned to multiple streams within the same grid (Elith, et al., 2008). Values were assigned based on a weighted average for continuous environmental data (weighted by length of section within a reach) whereas categorical data were weighted using the value of the longest segment within the reach. The default settings were used in MaxEnt (Phillips, et al., 2006) except for the maximum number of background points. The maximum number of points was set to 13,384 to match the background river network. The results from each model were spatially projected using ArcGIS 10.

Future distributions – Climate data representing “future” conditions were obtained from the Community Climate System Model (Table 1), a model based on the fourth assessment report of the International Panel on Climate Change (IPCC). We integrated the “future” climate data with the aforementioned contemporary environmental variables (e.g., stream network, geology, soils) to make predictions about the future distribution of each crayfish species. Because precipitation and temperature data from the climate-change scenarios were based on a statistically down-scaled model, the resolution was not comparable to the current-distribution models (i.e., 4.5-km² in the future models and 1-km² in the current models). To compensate, we used the National Center for Atmospheric Research (NCAR) 20th century data (4.5-km² resolution; IPCC, 2001) and created a new set of models predicting current distributions for appropriate comparison (i.e.,

same spatial resolution) to the climate-change models. We anticipated the models using the 4.5-km² resolution data would not be as accurate as models created using the finer-resolution data but we wanted to have models to appropriately compare the relative effects of the climate scenarios.

There were four families of scenarios developed by IPCC; however, only the greenhouse gas emission predictions (GHG) were of interest in the current study. We were interested in the emission scenarios because changes in emission rates are predicted to influence precipitation patterns and water availability during already low-flow periods (e.g., drought severity) (Smith and Tirpak, 1989). We used three scenarios: A2, A1B, and B1, representing medium-high (19.6 – 34.5 Giga-tons of Carbon (GtC)), medium-low (13.5 – 17.9 GtC), and low (2.7 – 10.4 GtC) GHG emissions respectively. Each scenario predicts future GHG emission rates based on different combinations of population growth, energy-use, land-use, and technological advances (IPCC 2001).

Model validation and environmental-response curves

Variable-contribution analyses were used to determine the relative influence of each environmental variable to the model outcome and to identify variables appropriate for the development of response curves for current and future models. Two sets of statistics, percent contribution and permutation importance, resulted from variable-contribution analyses in MaxEnt. Percent contribution is the relative increase in model fit associated with each environmental variable, while permutation importance produces an indication in the loss in predictive power associated with the removal of the variable. The former may be more difficult to interpret given correlations among environmental variables included in the model. Maximum Entropy produces two types of response curves which indicate relative suitability of an environmental variable for a particular species. The appropriate choice of a response curve depends on the presence of collinear variables in a model. Extreme collinearity, or multicollinear variables, makes response curves difficult to interpret unless curves are developed without the inclusion of other variables. We conducted a Pearson's product-moment correlation procedure to identify those continuous variables that were multicollinear ($r > 0.65$). Statistical significance ($\alpha < 0.05$) was not used to determine multicollinearity because it simply identified collinear variables rather than extreme cases. Response curves represent the relative tolerance of each

crayfish to a particular environmental feature. Response curves were developed for variables that contributed to at least 70% of the predictive power (percent contribution) of the model. Curves were generated to represent responses to continuous data whereas responses to categorical data were represented by bar charts. Each curve or bar chart was examined to determine the relative suitability of the variable to the species under current and future distributions.

We used the cross-validation technique for small dataset recommended by Philips et al. (2006) to check the accuracy of the models. The cross-validation procedure excluded 10% of the occurrence data and then tested the proficiency of the model to predict the excluded data points. The cross-validation procedure was repeated 10 times for each model and the mean output was used to determine distribution probabilities and overall model performance. The accuracy of each model was determined using the Area Under the Curve (AUC) statistic generated by Receiver operating characteristic (ROC) analysis. An AUC close to one indicates a very accurate model.

In addition to the cross validation, we tested the accuracy of the models using quantitative field sampling conducted during summer 2012 (see objective 2). Ten streams in catchments adjacent to known occurrences were randomly selected. We sampled multiple channel units (a minimum of three riffles and pools) in each selected stream following methods described by DiStefano et al. (2003). Briefly, a 1-m² quadrat sampler, covered on three sides with 3-mm netting, was firmly placed and sealed on the stream bottom and all crayfish were swept downstream into an attached 1.0 x 0.5 x 1.2-m seine. We did not restrict our random selection of streams to those predicted by the models to contain particular species but simply chose from streams outside of the known presence locations.

Results

Species-distribution modeling

Current distributions – Models (1 km² resolution) predicted continuous distributions that extended beyond actual sampled locations (Fig. 2). Low probabilities of occurrences were predicted in several catchments where each of the four species had never been collected. Perhaps more importantly, three of four species were predicted to have a high probability of occurrence in individual streams that had never been sampled (*O. leptogonopodus*) and even entirely

separate catchments (*O. menae* and *P. tenuis*). However, the highest probability of occurrence was predicted where known individual species had previously been detected (> 66%). For each species, excluding *O. saxatilis*, streams west of current sampled locations appear to represent the highest chance of finding undetected populations, particularly in the Glover River drainage. The distribution model of *O. saxatilis* indicated there is only a small chance (< 33%) populations would be located outside of previously-sampled regions.

As expected, there were differences between the current-distribution models created using climate data at two different spatial resolutions (1 km² and 4.5 km²; Fig. 3). For three of four species (excluding *O. leptogonopodus*), the 1-km² models were more conservative than the models constructed using climate data with 4.5-km² resolution. For the most widely-distributed species, *O. leptogonopodus*, the coarse-resolution models predicted distributions similar to those predicted using fine-resolution data. The greatest difference in modeling results occurred when predicting the distribution of *O. saxatilis*. The 1-km² model predicted moderate-high probabilities of occurrence only at sampled locations and adjacent tributaries, whereas the 4.5-km² model predicted a low-moderate probability of occurrence across much of the Ouachita Mountain region. Although the models developed for *O. leptogonopodus* were similar in their predictions of distributional extent, the 4.5-km² climate data predicted overall lower occurrence probabilities than the 1-km² model (Fig. 3).

Future distributions – Comparable distributional changes associated with our climate-change models were observed for several species. Due to discrepancies in environmental data (e.g., resolution), only the 4.5-km² resolution models were comparable to future models. The two emission scenarios depicting moderate-high emissions, A1B and A2, produced similar results for each species (see A1B, Fig. 4). In all future scenarios, the distribution of *O. leptogonopodus* was predicted to expand across most of the study area with high probabilities of occurrence in the A1B scenario and a more conservative prediction for the low-emission scenario. The predicted distributions for *O. menae* and *O. saxatilis* were reduced to a small portion of the predicted range in the current model. In the A1B projection, *P. tenuis* was predicted to have its highest probabilities of occurrence in the western and northern catchments and low probabilities of occurrence in the southeast region of the study area. *Procambarus tenuis* was predicted to have a reduced range at low probabilities in the B1 scenario (Fig. 3, 4 and 5).

Model validation and environmental-response curves

Variable-contribution analyses for the current models indicate several important patterns in how environmental variables contributed to the species-distribution models. First, winter temperature appeared to be an important variable contributing to occurrence predictions of *O.*

leptogonopodus as it had the highest percent contribution (Table 2). In addition, the variable was still very important regardless of the order it was entered into the MaxEnt model (importance; Table 2). Likewise, soil composition contributed the most to the models predictive power for the species with the smallest distribution, *O. saxatilis*. However, winter temperature had substantially more impact on the accuracy of the final model as reflected by permutation importance (Table 2). Soil composition and elevation were the two factors that contributed the most to the model predicting the distribution of *P. tenuis*. These variables were also important to the distribution models for *O. leptogonopodus* and *O. saxatilis*. Important environmental variables related to the distribution of *O. menae* were soil and geology; however, winter precipitation had the highest permutation of importance based on the final MaxEnt model.

Variable-contribution results of the 4.5 km² and 1-km² resolution models were similar but indicated some minor differences. In all of the models, soil and geology were consistently important (represented in the top three variables) to the same species. Minor differences in the 4.5 km² and 1-km² resolution models included changes in the order of the variables. In addition, winter temperature in the fine-grain model was replaced by summer precipitation in the coarse-scale model for *O. leptogonopodus*. In *O. saxatilis* models, flow accumulation ranked third in coarse-resolution projection instead of elevation in the fine-resolution prediction. Land use was replaced by winter temperature in the *P. tenuis* models (1 km² and 4.5-km² models, respectively).

Pearson's product-moment correlations indicated some of the continuous variables used in our models were multicollinear ($r > 0.65$). Elevation was highly correlated with two precipitation variables: winter precipitation ($r = -0.77$), and winter temperature ($r = -0.80$). There were also several correlations among precipitation variables: summer precipitation and wet-season precipitation ($r = 0.66$); summer precipitation and dry-season precipitation ($r = 0.68$); and winter temperature and winter precipitation ($r = 0.68$).

Response curves were created to demonstrate how the occurrence probability would change as a single variable of interest was modified. All other variables were removed from each model before response curves or bar charts were developed because of the prevalence of correlated climate and elevation variables. Response curves were generated for continuous data whereas bar charts were used to represent categorical data. For example, the response of *O. saxatilis* to winter temperature indicated the species had the highest probability of occurrence between -4°C and -3°C (Fig. 6). The highest occurrence probability for *O. leptogonopodus* was associated with winter temperatures < -4°C. Elevation response curves for *O. menae*, *O. saxatilis* and *P. tenuis*, indicated high probabilities of occurrence (>66%) at altitudes > 300 m for the two *Orconectes* sp and > 400 m for *P. tenuis*. All four species also had high probability of occurrence in stoney-sandy loam soils (see example for *O. leptogonopodus*, Fig. 7). Additionally, areas with shale, novaculite and sandstone geology contributed significantly to high occurrences probabilities of *O. menae* and *O. leptogonopodus*. The model predicting the occurrence of *P. tenuis* was the only model to indicate land use was important. Land use, described as opened developed land, forest, and pasture, was indicated to have the highest likelihood of *P. tenuis* occurrence.

The cross-validation procedure indicated the models predicted omitted data points much better than would be expected at random. Receiver operating characteristic analyses indicated models generated for each species performed well in predicting omitted data points. The mean AUC associated with fine-grain current distribution models for *O. leptogonopodus*, *O. menae*, *O. saxatilis*, and *P. tenuis* was 0.95 (0.03 SD), 0.93 (0.04 SD), 0.98 (0.015 SD), and 0.93 (0.07 SD), respectively. Model performance was similar with coarse-resolution models: mean AUC was 0.91 (0.05 SD), 0.92 (0.6 SD), 0.97 (0.02 SD), and 0.95 (0.05 SD), respectively.

Field validation

Quantitative field sampling provided additional validation and areas for refinement related to our current-distribution models. Of the ten streams sampled, we detected *O. leptogonopodus* and *P. tenuis* in two streams of the Glover River Catchment. Additionally, *P. tenuis* was found in three tributaries of the upper Little River Catchment. The tributary where *O. leptogonopodus* was found was not predicted by the model; however, adjacent tributaries were predicted to have

moderate probabilities of occurrence. Two of three locations where *P. tenuis* was found during field sampling were predicted as areas with possible populations.

Discussion

Effective crayfish conservation requires knowledge of the distribution of species. Having a narrow range, in itself, puts some species at risk from potential threats, including invasive species, habitat alteration, and poor water quality (Taylor, et al., 1996; Lodge, et al., 2000; Jones and Bergey, 2007). Changes in distribution may signal a need for conservation action, but are difficult to assess for many crayfishes because of poorly known historic distributions. Occurrence patterns from museum records (Schuster, et al., 2008), gaps in current distribution (Horwitz, 1994), and absences in modeled potential distributions may signal range reductions. In contrast to range reductions, introduction and range expansion by non-native crayfish (and their accompanying diseases) is the single greatest threat to native crayfishes worldwide (Horwitz, 1990; Harlioğlu and Harlioğlu, 1996; Lodge, et al., 2000). Combining distribution patterns with habitat and other environmental data, including sympatric species, allows association of particular species with habitat conditions that can be helpful in modeling potential distributions (this objective, Fera and Faulkes, 2011), identifying invasion potential (Olden et al., 2011), and assessing factors affecting population change (Svobodová, et al., 2012). Despite the importance of documenting the distribution of crayfishes in the United States, our knowledge of the distributions of many crayfishes is poorly known (Larson and Olden, 2011) and funding for such endeavors is often inadequate (Taylor, et al., 2007).

Species-distribution modeling, like completed in the current study, is an excellent technique for identifying possible populations beyond sampled locations; however, this technique does not account for mitigating habitat factors, biotic interactions, or possible adaptations or behavioral modifications that might alter modeled predictions. Distributions are often defined using coarse-scale attributes (e.g., Brewer, et al., 2007; Chen, et al., 2007; Westhoff, Rabeni and Sowa, 2011) but there are numerous factors at finer-spatial scales that may ameliorate or exacerbate the realized distribution. For example, land-use changes may create unsuitable habitat at a coarse scale but stable riparian corridors may mitigate the negative inchannel effects locally (e.g., fish-assemblage response to deforestation; Lorion and Kennedy, 2009). Unintended biotic interactions, on the other hand, may result in distributions that contract

more extensively or rapidly than models may predict. For example, we predicted *O. leptogonopodus* had a moderate probability of expanding its range under a low-emissions scenario while three sympatric species were predicted to have a low probability of occurring anywhere within their original range. This expansion could be much more likely than we predicted or could occur at a larger spatial extent given other crayfish species are likely to be left with substantial amount of unsuitable habitat. Several other crayfish species in the Ouachita region occur at relatively low densities (see Objective 2) and it is unknown how these species may respond to the same climatic perturbation. Lindqvist and Hunter (1999) suggest r-selected crayfish are more successful invaders than k-selected species; however, the competitive nature of crayfish depends on the behavior of the species (e.g., feeding, predator avoidance, movements; Weis, 2010) and perhaps the level of ecosystem alteration (Westhoff, Rabeni and Sowa, 2011). Phenotypic adaptation is another strategy that species use to cope with changing climates (Bale, et al., 2002; Aitken, et al., 2008; Visser, 2008) and successful examples of this type of adaptation often relate to populations with high genetic diversity (e.g., Aitken, et al., 2008). Further, species may alter their temporal or spatial migration patterns in response to climate change (Walther, et al., 2002). Lack of basic ecological information, including how habitat use at finer-spatial scales constrains or enhances these populations, and an understanding of the competitive or adaptive abilities of these endemic species, makes it difficult to refine my predictions. However, the development of coarse-scale models such as in the current study provides an excellent foundation for how to approach examination of additional biotic and abiotic factors.

Coarse-scale environmental factors, such as significant variables in our distribution models, play a major role in the distribution of aquatic organisms because they constrain physicochemical processes at finer-spatial scales (Frissell, et al. 1986). The geology and soils within a catchment are known to influence the physicochemical character of the water (Hynes, 1975), influence runoff patterns following precipitation events (Beven, 2001), influence water infiltration rates (Smakhtin, 2001), and determine morphological characteristics of the streams (Knighton 1998). Geology has been shown to relate to the distribution of some crayfish species (e.g., France, 1992; Joy and Death, 2004; Westhoff, Rabeni and Sowa 2011) but not others (Westhoff, Guyot and DiStefano, 2006). However, few studies address crayfish distributions at coarse resolutions so the dearth of significant finding may relate simply to the lack of studies at this spatial scale. However, the relatively small distribution of many crayfishes and the lack of

fine-resolution geology layers may also be a contributing factor. While we did not find geology to be multicollinear with soils, soil types are often related to geology (Miller and Donahue, 1990). The relationship between crayfish distribution and soil composition may be due to its suitability for burrowing. Sandy loam is a coarse-grained soil that appears easily excavated by crayfish in this region (Dyer, personal observation). Constraints placed on these populations may relate to water capacity of the soil (see DiStefano, et al., 2009) given streams in this catchment are flashy and water availability is scarce during summer and autumn base-flow periods. Different tolerances of these endemic species to soil-water availability rather than instream water availability may provide insight to coexistence by several of these species as well as future distributional changes with predicted changes in climate patterns.

Elevation was important in determining distributions of several crayfish species. Elevation is related to stream gradient, which is associated with several abiotic and biotic factors within streams (Knighton, 1998; Nino, 2002). It is generally expected that higher elevation areas will have coarser substrates, higher water velocities, and a high diversity of aquatic habitats (Rosgen, 1996). Elevation also relates to stream size with higher elevations occurring in the headwaters and lower elevations in downstream systems. Headwater streams receive high loads of coarse organic material (Vannote, et al., 1980) which is a major food source for many crayfish (Momot, Gowing and Jones, 1978). Coarse substrates create large interstitial spaces in the stream bed which trap coarse organic matter (Parker, 1989) and serve as refuge for crayfish. In addition, headwater streams often have intermittent or temporary flow regimes that create an abundance of shallow-water habitat not suitable for predation by smallmouth bass (*Micropterus dolomieu*) and other centrarchid predators (Schlosser, 1987).

Land use was rarely related to distributional predictions by the models. We anticipated logging practices may relate to the current distribution of some of these species; however, *P. tenuis* was indicated to have a moderate (33% - 65%) probability of occurrence near opened developed land. Areas with open pasture also had a moderate probability of occurrence, but the highest probability of occurrence for the species was associated mixed forest which is the native land cover of the Ouachita Mountains. *Procambarus tenuis* appears to have a spotty distribution and occur in low densities (Bergey, Jones and Fenolio, 2004); however, they are not easily detected via traditional sampling techniques which may have skewed the relation between

occurrence and land-use parameters. This species burrows deeper in the substrate and earlier in the year than sympatric species and often seeks refuge under substrate > 500 mm in diameter and in zero-order streams (Dyer, personal observation). The International Union for Conservation of Nature considers the species as data deficient (Crandall, 2010) and as a result it is likely that our *P. tenuis* model would benefit from use of improved and efficient sampling techniques.

Combining species-distribution and global-climate models can help forecast potential range shifts in response to anthropogenic changes to environmental conditions (Hijmans and Graham, 2006; Yates and Bailey, 2010; Klamt, Thompson and Davis, 2011). The species in the current study showed varied responses to the emission scenarios, likely due to interspecific differences in tolerance to precipitation patterns. Although temperatures did increase in all climate-change scenarios, it is unlikely that temperature alone will exclude crayfish from the current range. Crayfish have tolerances for specific temperatures (though usually unknown), but they often inhabit areas with temperatures outside of their optimal thermal range (Sargent, et al., 2011). The changes in precipitation that result from an increase in average temperature are much more likely to have an impact on crayfish distribution. Crayfish occupying headwater streams have evolved to live in areas with natural disturbance; however, climate change in this region is anticipated to lead to extended drought periods and more intense precipitation events (<http://oklahomawatersurvey.org/?p=387>). More intense precipitation could increase stream bed scouring which could flush crayfish downstream and reduce detritus abundance (depending on channel configuration, etc). Precipitation is relatively high and, while fairly uniform across the Ouachita region, is somewhat higher near the headwaters (Negus, Fisher and Marston, 2006). With the exception of *O. leptogonopodus* and *P. tenuis*, other species were predicted to have a very low probability of occurrence in climate-change scenarios. The range expansion of *P. tenuis* in the A1B scenario is likely a result of collinearity between elevation and winter temperature (top two contributors respectively; Table 2). In the A1B scenario, precipitation amounts in the southeastern region are similar to areas where occurrence probabilities were high in our current model. However, the elevation of the southeastern region is < 100 m, whereas the species has the highest probability of occurrence where elevations are > 400 m. Both endemic and freshwater species are predicted to be vulnerable to climate change (Sala, et al., 2000; Xenopoulos, et al., 2005) because of already restricted ranges and limited dispersal opportunities. Our results agree with others (e.g., Daufresne, et al., 2004; Chessman, 2009) that response direction to climate

change is species specific. The Ouachita Mountain region is predicted to have warmer temperatures, prolonged droughts, and more intense precipitation events with global-climate change (Knapp et al., 2008). These changes are likely to negatively impact crayfish by reducing soil moisture, which crayfish depend on as refuge during seasonal droughts (DiStefano, et al., 2009).

Use of coarse or fine-resolution data can have different implications for modeling and ecological understanding (e.g., Wiens, 2002). Used alone, coarse-scale information may not reveal subtle, but important changes across an environment; however, an abundance of fine-scaled information may overwhelm the capacity of a model (Guisan, et al., 2007) or decrease the benefits of modeling to reducing field-sampling costs (Stoeckwell and Peterson, 2002). As a result, ecologists strive to reach a balance between data collection and identifying patterns that vary spatially and temporally. Guisan et al. (2007) evaluated the impacts of varying spatial resolution on model performance and found that while MaxEnt was one of the best techniques when using coarse-resolution data, the models degraded significantly under a 10-fold coarsening of resolution. Further, the authors suggested models with higher predictive power may be necessary to see the effects of scale. Differences in the grain of climate data had an impact on the predictions of our current-distribution models, with the fine-grain models projecting more conservative distributions than the coarse-resolution models. The 4.5-km² resolution models did predict all presence points that we gathered through field validation; however, it falsely predicted many high-probability areas that we were unable to validate during low-flow sampling. The 1-km² models predicted absences much more accurately than the coarse-resolution projection. Furthermore, significant field sampling has been completed targeting capture of *O. saxatilis* (Jones and Bergey 2007), and our fine-scale model more accurately represented their results than the 4.5-km² resolution model. Our results indicate that models of crayfish distributions that have high predictive power may benefit from use of fine-resolution environmental layers (i.e., field validation indicates these models were more accurate). This study also highlights the importance of field-validation procedures as suggested by Olden, Jackson and Peres-Neto, (2002).

The models developed for this portion of the report provide a framework for investigators to study anthropogenic impacts or other natural-habitat features on narrow-range endemic species. This study creates a framework for examining habitat features that may interact with the

coarse-scale factors found in the current study to influence distributions or population success. For example, in a period of increasing drought, we need to understand how soil composition, water withdrawals, and changes in climate patterns interact to determine changes in populations of crayfish. If some species are expected to expand their distributions with a changing climate, how do we expect stream systems to respond to changing distributions? For example, if *O. leptogonopodus* expands its distribution and other native species ranges constrict, will energy flow in these systems remain the same or will higher trophic levels respond differentially to these possible species replacements? Many of these questions require targeted studies that would benefit from a structured and targeted monitoring program.

Our models indicated the distribution of these endemic crayfish populations related primarily to coarse-scale features, primarily elevation, climate, geology, and soils. This information allows us to protect specific areas that are important to endemic crayfish, in addition to, prioritizing sampling efforts to monitor populations through time. Our model validation indicated the projected distribution either failed to predict or over predicted actual species locations. While we cannot expect models to be 100% accurate, we can better explain distribution with instream-environmental parameters and true absence data. Given the important role crayfish play in ecosystem dynamics, monitoring these populations would seem important to understanding changes in the function of stream systems over time. True absence data are rare, but a reasonable approximation could be achieved using targeted sampling that varies temporally and is designed to address specific conservation concerns (e.g., land-use changes, water withdrawals).

OBJECTIVE 2.- Identifying responses of *O. menae* and sympatric species to seasonal drying or reduced flow in temporary and perennial streams.

Introduction

Understanding how organisms are distributed at multiple spatial scales is an important prerequisite to developing appropriate conservation and restoration strategies. The relationship between organisms and environmental factors is rarely straightforward but rather set within the context of broad environmental constraints where different combinations of natural environmental features (e.g., geology) lead to different potential among populations (e.g.,

Brewer, et al., 2007). This phenomenon results because coarse-scale environmental features influence the relative suitability of habitat conditions to an organism at fine-spatial scales (Schlosser, 1995). Recognition of the interactions between landscape and more fine-scale habitat conditions allows conservation and restoration actions to be developed with full consideration of optimal or marginal conditions that may occur naturally within a species distribution (e.g., Brewer and Rabeni, 2011). Defining the suite of environmental conditions that leads to higher or lower abundances across spatial scales is rarely the focus of crayfish ecology, despite the importance of crayfish to the ecology of the ecosystems where they occur (e.g., trophic position and keystone species, Momot, 1995; Creed and Reed, 2004). Many crayfish species are narrowly distributed making them particularly susceptible to natural or human threats. Land-use practices affect water quality within a watershed and may alter environmental suitability for native organisms (Galloway and Hummon, 1991, Richards and Host, 1994). Additionally, global climate change is predicted to reduce water availability and extend drought periods (Smith and Tirpak, 1989).

Water withdrawals alter abiotic conditions and negatively affect the biotic and abiotic components of the stream ecosystem. Excessive water withdrawals may reduce groundwater availability, discharge variability and base-flow conditions leading to the loss of appropriate habitat for aquatic organisms (Poff, et al., 1997). As habitats and flow regimes become more homogeneous, native specialists are often replaced by generalist fish species (Freeman and Marcinek, 2006). Reducing natural variability in the flow regime may also allow invasive fish species to persist and displace native species via competition (Minckley and Deacon, 1991). Reduced natural discharges are also linked to reductions in species richness (Xenopoulos and Lodge, 2006). Decreases in base flows can negatively affect recruitment and are thought to be a major limitation to steelhead *Oncorhynchus mykiss* populations (Grantham, et al., 2012). Additionally the influx of groundwater to streams acts as a thermal refuge and without it fish populations are at risk of heat stress (Waco and Taylor, 2010).

Land-cover manipulation alters runoff and sediment conditions in streams (Poff, et al., 1997). In urban areas, land is paved or otherwise developed and made less permeable to precipitation. As a result, surface runoff reaches the stream faster following precipitation events leading to flashy hydrographs and the reduced infiltration rates that reduce groundwater availability needed to maintain base-flow conditions (Klein, 1979). In altered watersheds, non-

point source pollution becomes more prevalent (Wang, et al., 1997). Excess sediment is considered one of the leading causes of stream impairment (Waters, 1995). Excess sediment degrades habitat and water-quality conditions and leads to a loss in biodiversity (Lenat, 1984). Excess sediment fills interstitial spaces in the stream bed and alters substrate composition leading to changes in primary and secondary production (Lenat, 1984, Goddard et al. 2008). Biota in altered ecosystems tends to shift to species more tolerant to environmental stressors (Klein, 1979).

Much of the existing ecological information on crayfish populations in the Ouachita Mountain region is either based on anecdotal evidence or does not account for varying spatial scales. Williams (1954) described *Orconectes leptogonopodus* (Hobbs, 1948) as common in small to medium, clear, permanent streams with rapid flow and rocky substrates. This species is considered stable because it is locally abundant (Taylor, et al., 2007; Bergey, Jones, and Fenolio, 2004). *Orconectes menae* (Creaser, 1933) is thought to inhabit shallow pool margins and swift runs of clear, rocky, perennial streams in the uplands of the Ouachita Mountain ecoregion (Williams, 1954; Robison et al., 2009). The species is listed as threatened because it occurs in low abundances where found (Taylor, et al., 2007; Bergey, Jones and Fenolio, 2004). *Procambarus tenuis* is the least studied of the three species. The International Union for Conservation of Nature categorized the species as data deficient (Crandall, 2010). In the U.S., the species is listed as vulnerable because it is rare within its range (Bergey, Jones and Fenolio, 2004; Taylor, et al. 2007; Robison and McAlister, 2008). *Procambarus tenuis* occupies small (1st and 2nd order; Strahler, 1957) spring-fed streams and cool, clear, perennial streams where it excavates shallow, simple burrows or seeks shelter under rocks (Jones and Bergey, 2007; Robison and McAllister, 2008). Previous work on *P. tenuis* was largely based on qualitative sampling. Abundance estimates derived from these qualitative samples are largely speculative (but see Jones and Bergey, 2007). Quantitative sampling that did occur was restricted to the upper portion of the Kiamichi River in Oklahoma. Although general information related to habitat use for each of these species is provided, the descriptions are vague and do not explicitly characterize the spatial significance of those habitats (e.g., some habitat types may only be important in certain areas of the watershed).

Despite studies documenting relationships between aquatic species and habitat, little is known about the mechanistic responses of organisms to human-induced changes that occur

within habitat (e.g., stream drying or excess sediment). Aquatic organisms are able to respond to some level of alteration using morphological and behavioral adaptations. Phenotypic plasticity is a common response to habitat alteration (Candolin, 2009). Fransen (2011) showed that there are significant morphological differences between stream and reservoir populations of red shiner *Cyprinella lutrensis*. Plasticity in reproductive behavior is another common mechanism (Candolin, 2009). The brassy minnow *Hybognathus hankinsoni* is dependent on backwater habitat for reproduction; however, during drought periods, the species will spawn in vegetated margins of the main channel (though reproductive success is reduced) (Falke, et al. 2010). Crayfish that inhabit headwater streams burrow into the hyporheic zone when streams begin to dry (Flinders and Magoulick, 2003). Crayfish along with other macroinvertebrates are resilient and able to rapidly recolonize areas where drought has reduced the fish population (Dorn, 2008).

The ranges of the species considered in this study were delineated in the first objective and climate and soils were particularly important. For Objective 2, we 1) assessed the importance of reach, and microhabitat factors that relate to the distribution of these species within their range during the drying season using discrete sampling and via recapture of tagged individuals, and 2) we conducted a laboratory component to examine the response of crayfish to stream drying under controlled substrates and with the addition of fine sediment. We hypothesized these species were not restricted to perennial streams, due to limited availability of these conditions in the region. We anticipated crayfish would seek out the deepest stream habitats as the streams dried throughout the summer. Finally, we hypothesized that the ability of crayfish to burrow would be negatively impacted by fine sediment and fitness would be reduced under these circumstances.

Materials and Methods

Study Area

Discrete and quantitative sampling of crayfish was completed on thirty reaches (three riffle-pool sequences in length) of twenty-five streams in the Little River Catchment of the Ouachita Mountain Ecoregion (Fig. 8). Dominant geology in the Little River Catchment comprises sandstone and shale. The landscape is a mixture of hardwood and coniferous forest and land-use practices include recreation (e.g., horseback riding), logging and poultry or cattle agriculture (Woods, et al., 2005). The Ouachita National Forest is located in the northeast portion of the

catchment and encompasses much of the headwaters of the Mountain Fork River. Streams within the Ouachita National Forest are somewhat protected from agriculture and timber-harvest practices of private industry (Woods, et al., 2005).

Crayfish were tagged and relocated on two streams within the Mountain Fork Catchment (Fig. 8). Cucumber and Beech creeks are headwater streams that originate in the uplands of the Ouachita National Forest (elevation ~ 600m). Beech Creek flows into the Mountain Fork River, whereas Cucumber Creek terminates at the confluence of Eagle Creek upstream of the Mountain Fork River. All streams occur above 300-m elevation and have mean slopes of approximately 19 and 14 m/km for Cucumber and Beech creeks, respectively. These streams typically experience elevated flows November - May and low flows June - October (USGS gage number 07338750).

Field sampling and habitat delineation

Crayfish were sampled using a quantitative gear similar to DiStefano et al. (2003). A 1-m² quadrat sampler was constructed using 2.5-cm² angle iron and 3-mm nylon netting (Fig. 9). Our quadrat differed from the one described by DiStefano et al. (2003) because we removed the bottom crossbars and instead used angled supports between the legs and top crossbars. The quadrat had a 15-cm weighted skirt around the bottom that was used to seal the gear to the streambed using surrounding cobble. Our design was better suited for the conditions of the Ouachita Mountains by allowing a better seal with the coarse substrate that is common in the region. This is particularly important because making a good seal with the substrate influences efficiency of this gear (Williams, et al., 2014). Once the quadrat was sealed to the streambed, coarse substrate was removed from the interior of the sampler to an approximate depth of 15 cm while water was swept downstream into the bag seine. In dry channel units, each quadrat was excavated and searched to a depth of 30 cm. Sampled crayfish were identified to species and gender, measured for carapace length (CL, 1.0 mm) and weighed (0.1g). Crayfish that were too small to identify in the field (5 mm – 10 mm CL) were preserved in 10% formalin and later identified in the lab. Additionally, we created voucher specimens of one adult male, one adult female and one juvenile male of each species (vouchers are held in the Oklahoma Cooperative Fish and Wildlife Research Unit laboratory). Crayfish that were not preserved were returned to the channel unit from where they were sampled.

Channel units (e.g., riffles) were sampled systematically and haphazardly throughout each sample reach. We sampled three replicates of each channel unit. Pools were channel units with low gradient and water-column velocities < 0.1 m/sec, and riffles had water-column velocities > 0.1 m/sec and a moderate to high gradient. Additional channel units sampled were: runs (transition areas of low gradient but with velocities > 0.1 m/sec), vegetated patches (shallow-water areas having > 2 m² of emergent vegetation) and backwaters (depositional areas with no upstream surface-water supply). Dry stream bed separating pools was considered a dry channel unit. A minimum of one sample was taken per channel unit; however, two to three subsamples were taken haphazardly in each channel unit when channel units were large enough to accommodate multiple subsamples.

Microhabitat parameters were measured at each quadrat location prior to collecting the crayfish since sampling altered the characteristics of the habitat. Substrate was classified visually using the modified Wentworth scale (Cummins, 1962). We used four substrate classes, bedrock, boulder and cobble (> 64 mm), pebble and gravel ($64 - 4$ mm) and fine sediment (< 4 mm). Depth (m) and average water-column velocity (0.6 of depth, m⁻¹s⁻¹) were measured in the center of each sampled quadrat. Velocity was measured using an electromagnetic flow meter (Marsh McBirney, Fredrick, Maryland).

In addition to quantitative sampling, we tagged crayfish and tracked them in May and June 2013 to assess habitat use and movement as streams dried. Densities can be very useful; however, they only provide information on habitat use at a point in time. By tagging and tracking crayfish, we were able to understand what habitat is most useful to crayfish as streams dry and how they can use behavior modifications to avoid harsh conditions.

Microhabitat patches were delineated using a cell system to describe the habitat used by crayfish. First, we marked a 400-m reach as the core study area (Fig. 10). We placed rebar stakes every 10 m or at obvious changes in streambed morphology or habitat (i.e., channel unit boundaries or bedrock outcrops). Each stake indicated a transect that was perpendicular to the direction of streamflow. Habitat was classified by channel unit: riffles, runs, pools, backwaters, and edgewater. Edgewater differed from the previous channel-unit description because we considered both vegetated and non-vegetated regions when assessing movements. Edgewater were shallow habitats along the wetted perimeters where velocities were much lower than the

surrounding stream area. We delineated cells (microhabitat patches) within each transect based on changes in substrate, depth or average water-column velocity. More cells were delineated in heterogeneous habitats, whereas, fewer cells were used in areas of homogenous habitat. Habitat measurements were taken in the center of each cell. We recorded average depth and water-column velocity (based on three measurements) and substrate composition in each cell as previously described.

Crayfish tagging

Crayfish used in the tagging study were captured using a backpack shocker (Smith-Root Co., Vancouver, WA), kick seine, and hand-searching methods. At each site, we began sampling at the 300-m transect and worked upstream until we reached the 200-m transect. All captured crayfish that met the minimum-size criteria (see below) were tagged and released back into the habitat patch from where they were captured. By tagging crayfish between the 200-m and 300-m transects, we left a 100-m buffer downstream and a 200-m buffer upstream to minimize crayfish emigration from the study area.

Crayfish were tagged with passive integrated transponder tags (PIT; Oregon RFID, Portland, OR, USA). We used 12-mm half duplex PIT tags because of the small size of *O. menae* (mean CL = 22 mm) and because half duplex tags are less susceptible to environmental noise than full duplex tags (http://www.oregonrfid.biz/index.php?main_page=page&id=31&zenid=hmmfth0f3gm11ijmo sisu15rc3, Accessed: 12/18/13). Bubb et al. (2002) determined crayfish with CL > 25 mm suffer low mortality rates when tagged using 12-mm PIT tags. Carapace length, measured from the anterior-most point of the rostrum to the posterior of their carapace, is roughly equal to 50% of the total length of the crayfish. In the lab, we found *O. menae* as small as 22 mm CL could be successfully tagged; however, *O. p. longimanus* needed to be at least 25 mm CL. In a 48 day tag-retention pilot study, mortality and growth rates did not significantly differ between tagged and untagged crayfish (Brewer and Dyer, unpublished data). Mortalities were due to cannibalism following a molt. Crayfish were tagged by creating an incision with a 12 gauge needle and inserting the PIT tag by hand, interior of the right-side walking legs and laterally along the carapace (Fig. 11). The insertion point of the PIT tag varied slightly between male and female crayfish due to interference of male gonopods (Fig. 11). Before releasing crayfish, we recorded

the unique PIT tag code, the cell where they were captured, CL, weight, species, gender, and reproductive form for males. After tagging, crayfish were left undisturbed for at least one week before trying to relocate them.

Crayfish were relocated using a backpack PIT tag reader and a portable pole-mounted antenna (hereafter referred to as antenna; Oregon RFID, Portland, OR, USA). We began searching for crayfish at the most downstream-mapped transect (400-m transect) and worked upstream. While sweeping the antenna slowly side to side, we walked transects that were 2- m apart and parallel to the downstream mapped transect (hereafter referred to as pass). We continued working upstream until we reached the 150-m mapped transect. If a tag was detected between the 200-m and 150-m mapped transects, we continued to scan until we had gone 50 m without a single detection regardless of recapture rates. We did not consider recapture rates in the survey protocol because the read range of the antenna was limited to approximately 30 cm and crayfish could escape redetection by burrowing into the streambed. Thus, continuing to search the streambed during some periods would not have improved recapture rates. We recorded the location of redetected tagged crayfish as the occupied habitat patch. We also counted the number of passes made within each mapping transect and further described the location of the tagged crayfish by the pass number and whether it was upstream or downstream of the antenna operator. Recording the pass number allowed us to be more accurate in our description of crayfish location (to the nearest m).

Crayfish that had a total range < 10 m or had not moved > 2 m in the final weeks of the study were thought to be deceased. On August 7, we relocated PIT tags that had not recently moved and attempted to recover the tagged organism or PIT tag. We relocated the tags with the antenna and then hand searched the stream bed for the tag. If we were not able to recover the tag, we removed the large substrate and all crayfish (CL > 20 mm) from the area and then rescanned the searched region. If a PIT tag was redetected after all adult crayfish were removed, we assumed the tagged crayfish was deceased.

Laboratory study design

Crayfish (Mena crayfish *Orconectes menae*, western painted crayfish *O. palmeri longimanus*, Kiamichi crayfish *O. saxatilis* and Ouachita crayfish *Procambarus tenuis*) were collected from the field and allowed to acclimate to laboratory conditions. Crayfish were acclimated to

laboratory conditions for approximately one week (never less than 3 days). Crayfish were held in three flow-through circular tubs where they were fed frozen fish, invertebrates and algae pellets ad libitum. Water chemistry was monitored daily and water temperature was allowed to fluctuate with the temperature of the laboratory.

Twelve experimental chambers were constructed following the design of Stoeckel, Helms and Cash (2011). Our chambers were wider than those used by Stoeckel et al. (2011) to accommodate larger substrate (Fig. 20). Additionally, we did not include the foraging area above the burrowing chamber. The chamber walls were constructed of clear acrylic sheets. Supply and drain pipes were connected approximately 15 mm from the bottom of the chamber. We used 12-mm polyvinyl chloride pipe to construct an external stand pipe that allowed us to manipulate water level within the chamber. The external stand pipe also allowed us to maintain a constant water supply to simulate hyporheic flow through the substrate. We placed 1.5-mm mesh in front of the supply and drain openings inside of the chambers and on top of the chambers in an attempt to prevent crayfish escape.

Experimental chambers were randomly selected to be filled with one of two sizes of substrate that was collected from Cow Creek in the Ouachita Mountains of Oklahoma. First, fine gravel (4 - 8 mm diameter) was placed along the bottom of each chamber to a depth of approximately 1.5 cm. Fine gravel provided a buffer to distribute the weight of the large substrate on the acrylic chamber bottom. Each chamber was then filled with the appropriate substrate treatment (cobble or pebble) to a depth of 40cm: six chambers were filled with cobble substrate (64 mm - 250 mm diameter) and six were filled with pebble substrate (32 mm -64 mm diameter). The substrate treatment assigned to each chamber remained unchanged for the duration of the study.

Crayfish demographics were measured and then each crayfish was randomly assigned to a treatment tank. Individuals were not reused in multiple trials. Crayfish were identified to species and gender was recorded. We also measured carapace length (CL, mm) and weighed (0.1 g) each crayfish prior to the experiments.

Water-withdrawal experiment (Experiment 1).- Experiment 1 was designed to assess the burrowing abilities of the crayfish during water withdrawals and to evaluate impacts on crayfish fitness. Experimental chambers were filled to the top with water so there was 5 cm of water

above the surface of the treatment substrates. Crayfish were allowed two days in the treatment chamber to acclimate before water-level treatments were applied to the chambers. Crayfish were given five days to respond to each water-level manipulation before being carefully excavated from the chambers. At the time of excavation, crayfish burrowing depth (cm) and weight (to the nearest 0.1 g) were recorded.

We assigned one of four water-level reduction treatments to each experimental chamber. The four water-level treatments were: 1) no water reduction (control), 2) 5-cm reduction below the substrate surface, 3) 15-cm reduction below the substrate surface, and 4) all water removed except for the saturated fine gravel at the bottom of the chamber (Table 6). We randomly assigned one of the four water-level reduction treatments to each individual chamber while stratifying by substrate treatments to ensure each substrate had all four treatment groups. Each water-level treatment and substrate group combination was replicated at least six times. Four crayfish were not recovered from the chambers at the end of the trials. We assumed the crayfish escaped through the drain pipe. Data from the trials with missing crayfish were not included in the analyses.

Sedimentation experiment (Experiment 2).-Experiment 2 assessed the effects of excess sediment on the burrowing ability and fitness of crayfish during dewatering. Fine sediment (≤ 2 mm diameter) was obtained from the Ouachita Mountain ecoregion by collecting substrate and using a 2-mm sieve to separate out the fine sediment. Richards and Bacon (1994) indicate that sediment particles < 2 mm are generally considered problematic for benthic organisms.

One of three sediment treatments was randomly applied to each chamber. Sediment treatments were based on the average volume of interstitial space for chambers containing either cobble or pebble substrate. One sediment treatment served as the control with no sediment added to the substrate. The remaining sediment treatments were distinguished by adding sediment volume equal to 45% or 90% of the average interstitial-space volume for each substrate treatment (cobble or pebble, Table 6). The fine sediment was added when the tanks were dry and then each tank was filled with water. We added water from the supply pipe located at the base of the chamber so the sediment distributed throughout the substrate by gravity rather than being washed completely to the bottom. At the end of each trial, the fine sediment was thoroughly washed from each chamber, allowed to dry, and then collected for use in the next

trial. Each sediment and substrate-treatment combination was replicated eight times. One crayfish was not recovered from the chamber at the end of the sediment trials and on two other occasions sediment clogged the drain pipes preventing the water from draining correctly. Data associated with these three occasions were not used in our analyses.

Each trial was performed by first incorporating fine sediment, then adding the study crayfish, completing the trial and finally excavating the crayfish. After fine sediment was added to the chambers, a 24-h period was allowed for the sediment to settle and distribute in each chamber. At the end of the settling period, one crayfish was randomly selected and added to each experimental chamber while the water level remained 5 cm above the substrate surface. Crayfish were allowed 24 h to acclimate before water-level reduction was applied. The water-level reduction was constant across all sediment treatments and was reduced by approximately 43.5 cm over a 24-h period during each trial. Crayfish were left undisturbed for five days and then were carefully excavated. Burrowing depth (1.0 cm) was measured and crayfish were weighed (0.1 g) after the fine sediment was gently removed from the exterior of the crayfish with a dry paper towel.

Data analyses

Age estimation.-Carapace length that distinguishes juveniles and adults of these species has not been well established so all crayfish were included together in the habitat analyses. Length-frequency histograms suggest the upper limit for juvenile CL is between 13 mm – 17 mm CL for *O. menae* (n = 120) and *O. leptogonopodus* (n = 218), and lab data indicate *O. p. longimanus* males are sexually mature by the time they reach approximately 20 mm CL (Dyer, unpublished data). *Orconectes saxatilis* is a crayfish endemic to the Ouachita Mountains and similar in size to *O. menae* and *O. leptogonopodus*. Jones and Bergey (2007) used 16.5 mm CL as the upper limit for *O. saxatilis* to be considered juveniles. Additionally, *O. p. longimanus* was used in the Jones and Bergey (2007) study and they determined 22.4 mm CL to be the cut-off between juveniles and adults. *Procambarus tenuis* has not been captured in large enough quantities to speculate on an upper-size limit for juveniles. Due to the uncertainty of what size should be considered adults and the fact that Jones and Bergey (2007) observed similar proportions of

crayfish densities in different habitats between adult and juvenile crayfish, we did not distinguish ontogeny in our analyses.

Habitat. Decision tree models were used to determine the relationship between crayfish densities and the suite of habitat factors measured at each site. We used decision tree analysis associated with the RPART package (version 3.1; Therneau and Atkinson, 2002) in R (version 2.15.1; R Development Core Team, 2012). Decision tree models are a non-parametric statistical technique, capable of modeling many types of data (linear and nonlinear, Brewer, et al. 2007), and are particularly well-suited to deal with continuous and categorical data (Venables and Kuhnert, 2005). These models are especially useful for identifying different sets of environmental conditions that allow persistence of an organism (Brewer, et al. 2007). In a decision tree model, the data are split into groups based on specified splitting criteria. Two common splitting criteria are used: recursive partitioning (Classification) and analysis of variance regression (ANOVA). We used the ANOVA method because our response variable was continuous (crayfish densities) and the classification method (recursive partitioning) is better suited for binomial data (De'ath and Fabricius, 2000). Analysis of variance was used to model splits in several predictor variables and the model with the best fit (based on R^2) was chosen (Therneau and Atkinson, 2012). Further splits were then preformed on the subsets of data resulting from the previous split. Once there were no longer any splits that improve the fit of the model by a predefined complexity parameter, the model was complete (Venables and Kuhnert, 2005; Therneau and Atkinson, 2012).

Decision-tree modeling consisted of three steps. First, we “grew” an exhaustive tree using a small complexity parameter (cp), a predefined value that must improve the R^2 value in order to be considered for the model (Therneau and Atkinson, 2012). A 10-fold cross-validation procedure was used to determine the error rate for each split made by the model. The more trees created, the lower the error rate; however, too many splits increase the possibility of misclassification or over fitting (Venables and Kuhnert, 2005). We then pruned the tree to a point where the lowest-error rate occurred without the risk of misclassification. We used the cp of the lowest-error rate to prune our trees because the models tended to over fit when the tree was still relatively small. Once the tree was pruned, we checked the accuracy of the model by

assessing the correlation between the input data and the fitted data using Spearman's rank test (Venables and Kuhnert, 2005).

Movement.-Data analyses of PIT-tagged crayfish were restricted to crayfish recaptured a minimum of four times and those that moved at least 10 m. We made these restrictions to reduce bias from incomplete data and expelled tags. With the exception of missing data from equipment failure or difficulties from weather, crayfish with > 40% recapture rates had no more than one week between recaptures. Crayfish with total ranges < 10 m were suspected to be deceased. To verify that these crayfish were not just sedentary, we relocated the sedentary tags on August 7 by the methods previously described.

We used an ANOVA to determine if some crayfish (species, gender, or size) moved greater distances than others. Data were combined from all streams due to limited sample numbers, particularly by species, in individual streams. Our response variable was total longitudinal distance moved (by individual). The main effects in the model were: species, gender and CL. Because adult *O. p. longimanus* grow to greater lengths than *O. menae*, we expected CL and species to violate the independence assumption associated with ANOVA (Zuur, et al. 2009). We tested the assumption using ANOVA with CL as the response variable and species as the main effect (considered significant at $\alpha \leq 0.10$). If the model was significant, we rejected the assumption of independence and instead created two ANOVA models with either species or size and gender as main effects. Residuals were assessed for normality using q-q plots. If normality was not approximated, we applied log transformations to the response variable to normalize the residuals. If the overall ANOVA model was significant, we used paired t-tests with Bonferroni adjustments to determine differences within groups (Field, Miles and Field, 2012).

We used a graphical approach to assess patterns in crayfish movement related to changes in discharge. We tracked crayfish movements over a limited number of discharge events and had a relatively low sample size of tagged crayfish in each stream so statistical analyses were inappropriate. We instead plotted the average weekly movement of crayfish in each stream against discharge. Plots were created by combining all crayfish movements unless species was significant in the ANOVA models previously described.

Habitat selection by crayfish was assessed over different time periods by determining if differential use occurred in available habitat. Available habitat was determined by examining the water depth of habitat patches. Each habitat patch was classified as deep (> 0.4 m), intermediate (0.1 - 0.4 m) or shallow (< 0.1 m). Time intervals over the entire sampling period (May through August) were classified as early, mid and late periods based on major changes in stream-discharge patterns. Frequency of use and availability histograms were created for each time period to indicate how crayfish selected habitat (where use was greater than availability, Rosenfeld, 2003) over time (corresponding with wet and dry periods). The early season was characterized by the beginning of the study (May 5, discharge (Q) ~ 5 m³/s) to a major precipitation event on June 1, where the Mountain Fork discharge peaked at 64 m³/s. The mid-season related to a time interval where flows were receding from the June 1 spate and a moderate precipitation event on June 20 contributed to elevated flows ($Q = 2 - 7$ m³/s; Fig. 12). The late-season related to a point in time when flows were $0.2 - 2.0$ m³/s and streams began to lose surface-water connectivity to the end of the study period (July 24) when a rainfall event restored streamflows ($Q = 14$ m³/s).

Laboratory experiments.-The response variables in our analyses were: burrowing depth and percent change in weight (hereafter referred to as Δ weight). Burrowing depth was measured (1.0 cm) from the surface of the substrate to the approximate lowest point of the crayfish. We calculated Δ weight as the percentage change from the beginning to the end of the study. Weight change was used as an indicator of crayfish fitness. Crayfish that had Δ weight < 0 were considered to have reduced fitness (i.e., growth).

We completed several preliminary assessments of the data to determine if a covariate would be appropriate to include in the analyses. We were concerned that the different CLs of crayfish used might have influenced the results of my analyses. We used two-way analysis of variance (ANOVA) to determine if the mean of the covariate significantly differed between substrate and treatment groups ($\alpha \leq 0.1$) (Miller and Chapman, 2001). Additionally, we conducted a Pearson product-moment correlation coefficient test to determine if there was a significant linear relationship between crayfish size and each response variables (Field, Miles and Field, 2012). Because a covariate reduces statistical power by adding a degree of freedom, the covariate must be at least moderately correlated ($r > 0.4$) with the response variable to be

beneficial (Porter and Raudenbush, 1987). After determining if a covariate was appropriate, we developed two ANOVA models for each objective.

The assumptions of ANOVA were assessed for each developed model. Normality (distribution of residuals) was assessed using a graphical representation of the data in a Q-Q plot. If data did not approach normality, a series of transformations (log, arcsin, rank) was attempted and then data were reexamined. Homogeneity of variance was assessed with Bartlett's test. All models were created using R (version 2.15.1; R Development Core Team, 2012) and considered significant at $\alpha \leq 0.1$.

The first two models were used to examine the results of the water-level reduction experiment. The first model examined the response of crayfish burrowing depth to each water-level treatment (burrowing depth = water-level treatment). This model used only data where pebble was the substrate treatment. Data from the trials using cobble substrate were omitted because all crayfish were able to burrow to 40 cm in each replication thereby creating the equivalent of a constant in an ANOVA model with no variance. Therefore, to determine whether individual water-level treatments differed between the substrate classes, we completed a simple ANOVA using data from the pebble treatments and then calculated the F statistic for each water-level treatment. This was done by subtracting the mean from pebble experiments in water-level treatment_i from the mean in cobble experiments in water-level treatment_i and then dividing the difference by the standard error of the pebble experiments in water-level treatment_i. We then calculated P-values from the resulting F-statistics. The second model examined Δ weight of crayfish relative to substrate, water-level treatment, and the interaction of substrate and water-level treatment. We used paired t-tests with Bonferroni adjustments to assess where significant differences occurred given the overall models were significant (Field, et al. 2012).

Two additional ANOVA models were developed to assess the results of the sedimentation experiments. The response variables were the same as with the water-level treatment trials: burrowing depth and Δ weight. The first model examined the burrowing depth of crayfish related to two main effects: substrate (pebble or cobble) and sediment (45% or 90% filled). We also included an interaction between substrate and sediment as we anticipated the effects of fine sediment additions would vary depending on the size of interstitial space in each treatment. The first model examined was: burrowing depth = substrate + sediment treatment + substrate*sediment treatment. The second model examined Δ weight of crayfish related to the

same main effects and interaction as used in the previous model (substrate, sediment treatment, and substrate*sediment treatment). If the overall model was significant ($\alpha \leq 0.1$), we used a paired t-test with a Bonferroni adjustment to assess where significant differences occurred (Field, et al. 2012).

Results

Quantitative field sampling

We collected 448 quadrat samples in the Little River Catchment in southeast Oklahoma (Table 3). *O. p. longimanus* occurred at the highest density (4.63 crayfish per m²) and *O. menae* at the lowest density (1.63 crayfish per m²). *Procambarus tenuis* was the rarest and it was found in only 7% of samples (25 of the 378) within its geographic range. *O. leptogonopodus* occurred at the highest density of the Ouachita Mountain endemic crayfish (3.32 crayfish per m²) but was still fairly rare within its distribution (detected in only 11% of samples within its range, Table 3). *Orconectes menae* was found in 17% of samples and *O. p. longimanus* was found in 36% of samples.

We used the complexity parameter for the lowest-error rate to prune the regression trees. Pruning resulted in relatively small regression trees because models tended to over-fit after a few splits. *Orconectes leptogonopodus* had the smallest tree with only one split and a complexity parameter (cp) of 0.03. The lowest cp used was *O. p. longimanus*, the model with the lowest accuracy. The lowest error rate for *O. p. longimanus* was achieved at a cp = 0.02. Complexity parameters for *O. menae* and *P. tenuis* were 0.03 and 0.04, respectively. The *P. tenuis* model had four split and it was the largest.

In general, our regression tree models predicted shallow depths (< 0.1 m) to have the highest densities of crayfish. The *O. menae* model was the only model not to have depth as the first split in the model; however, dry and run channel units (usually shallower than other channel units) were predicted to have the highest densities in the first split (Fig. 13). Water depth was the first significant variable found for the other three species. Depths < 0.09 m, 0.1 m and 0.01 m were predicted to have the higher densities than the deeper areas for *O. p. longimanus* (Fig. 14), *O. leptogonopodus* (Fig. 15), and *P. tenuis* (Fig. 16), respectively.

Substrate composition and channel unit accounted for additional splits in the models predicting densities of crayfish. The second split in the *O. menae* model was made in the cobble and boulder substrate category and areas with > 27% cobble and boulder were predicted to have lower densities of *O. menae*. However, areas with > 27% cobble and boulder were still predicted to have densities four times greater than other channel units in the first split (Fig. 13). Split in substrate variables comprised the majority of the *P. tenuis* model and indicating that a variety of substrates are useful to the species (Fig. 16). Splits in channel unit were made to further describe *O. p. longimanus* densities. Run channel units were predicted to have the highest densities of *O. p. longimanus* (4.83 crayfish per m²) in the shallow habitats (Fig. 14).

Overall, regression tree accuracy, defined as the correlation between predicted densities and the original data, was limited for some species. The most accurate models were the *P. tenuis* and *O. menae* models ($r_s = 0.34$ and 0.32 , respectively). The model developed to predict *O. p. longimanus* densities was the weakest predictor ($r_s = 0.05$) followed by the *O. leptogonopodus* model ($r_s = 0.20$).

Crayfish movements and habitat use

We tagged a total of 101 crayfish (60 *O. menae*, 28 *O. p. longimanus* and 13 *P. tenuis*) and tracked them over a period of 81 days. Weekly resampling events were attempted on 11 occasions during the study; however, weather and technical difficulties resulted in nine and ten successful samples on Cucumber and Beech creeks, respectively. We were able to detect 80 of the tagged crayfish at least once during the study, but only 48 crayfish that were redetected on four or more occasions and met the criteria for inclusion in our analysis. Field validation of non-moving crayfish (range < 10 m or had moved < 2 m in the previous three weeks) resulted in the exclusion of an additional 17 crayfish due to either tag expulsion or mortality. Two *P. tenuis* were redetected four or more times and they were both determined to be dead during our field validation.

We included 31 crayfish in our analysis to determine whether there were significant differences in total crayfish movement (distance in m) between species, gender or size. As anticipated, crayfish size and species were not independent of one other ($F_{1,29} = 20.02$, $P < 0.01$), so we completed two separate ANOVA models (total movement = size (CL) * gender; total

movement = species * gender). A log transformation of total distance moved was required in each model to normalize residuals. No significant differences in movements were detected in either model related to the main effects of species, size (CL), or gender (Table 4 and Table 5).

Crayfish displayed similar movement trends between streams, but there was a lot of variability in movement distance between individuals. However, some patterns emerged in weekly crayfish movement related to stream discharge. The ten crayfish included in the Beech Creek analysis showed a peak in movement following high flows on June 1. On average, crayfish movement declined with the hydrograph in late June; however, as stream flows increased in July there was an increase in average crayfish movement but with substantial variation (Fig. 17). Eight crayfish in Cucumber Creek displayed the greatest movement following the June 1 rain event and increased movement on average throughout the remainder of the study period (Fig. 18). Overall, the mean total distance moved by individuals in all streams combined was 67 m (range: 14 - 158 m). In each week, there were many crayfish that moved very little (< 5 m); however, extreme weekly movements were obvious. An individual crayfish in Cucumber Creek moved 72 m and an individual in Beech Creek moved 108 m. Mean weekly movements of individual crayfish in Cucumber Creek ranged 5 - 33 m, but on average crayfish moved approximately 15 m per week. On average, mean weekly distances moved by individuals in Beech Creek were just over 10 m (range: 4 - 18 m).

Habitat availability differed in each stream. Deep habitat (> 0.4 m) was rare in both streams. Shallow habitat (< 0.1 m) was the most prevalent in Cucumber Creek whereas the medium habitat (0.1 – 0.4 m) occurred at the highest frequencies in Beech Creek.

Crayfish movement affected habitat selection during different time periods and appeared to be related to changes in discharge. In Cucumber Creek, crayfish were observed more frequently in the habitats with medium depth in the early season and more crayfish appeared to move out of the shallow habitat and into the medium habitat as the streams dried (Fig. 19). In Beech Creek, crayfish used medium and shallow habitat in proportion to availability (Fig. 19). In the mid-season when streamflow was elevated, some *O. menae* moved out of the moderately deep habitat and into the shallow habitat as streams began to dry again. *O. menae* then dispersed into the medium and shallow habitats at frequencies similar to what was observed in the early season. The opposite trend was observed for *O. p. longimanus* in Beech creek. *Orconectes p.*

longimanus moved into the moderate depth habitat during high flows (mid-season), rather than into shallow habitat as *O. menae*. Both species used habitat relative to the availability before and after the mid-season.

Laboratory Experiments

Analyses indicated use of a covariate (CL) was not necessary in our models. In both of the experiments, CL of crayfish was not significantly different between substrate and treatment (water-level $F_{3,47} = 1.33$, $P = 0.28$ or sediment $F_{2,45} = 1.56$, $P = 0.22$). Further, Pearson's product-moment correlation coefficient test indicated that $r < 0.4$ in all combinations of response variables and CL. The strongest correlation found was in the water-level treatment experiment where CL was negatively related to burrowing depth ($r = -0.34$). The correlation between CL and Δ weight was weak ($r = 0.01$). In the sediment experiments, CL was negatively and weakly correlated with burrowing depth ($r = -0.19$) and Δ weight ($r = -0.20$).

Preliminary analyses suggested some transformation would be needed to meet the assumptions of ANOVA. Results of the Q-Q plots suggested violation of the normality assumption for several models. The model examining crayfish burrowing depth related to water-level treatment in the pebble substrate was the only model examined that did not require a transformation to normalize residuals. Data for the other three models were rank transformed prior to development of the ANOVA models. Computing the F-statistic from ranked data is mathematically similar to the traditional ANOVA although the resulting statistic is an approximation of the true value (Conover and Iman, 1981). Further, multiple comparisons procedures are more powerful when using ranked data associated with non-normal populations (Conover and Iman, 1981). Bartlett's test indicated the assumption of homogeneous variance between treatments was violated with untransformed data. After transforming the data, this assumption was met by all analyses: 1.) Depth = water-level treatment ($k^2 = 0.2$, $df = 3$, $P = 0.98$), (substrate not included; see methods), 2.) Δ weight (ranked) = substrate ($k^2 = 1.26$, $df = 1$, $P = 0.26$), water-level treatment ($k^2 = 2.50$, $df = 3$, $P = 0.48$), 3.) Depth (ranked) = substrate ($k^2 = 0.02$, $df = 1$, $P = 0.89$), sediment treatment ($k^2 = 3.97$, $df = 2$, $P = 0.14$), 4.) Δ weight (ranked) = substrate ($k^2 = 0.80$, $df = 1$, $P = 0.37$), sediment treatment ($k^2 = 1.65$, $df = 2$, $P = 0.44$).

The overall ANOVA model examining the effects of pebble substrate and water withdrawal on crayfish burrowing depth was not significant ($F_{3,22} = 1.29$, $P = 0.30$); however,

there were significant differences between the substrate treatments (Fig. 21). Subtracting the mean values from the pebble treatment by the values for each cobble treatment suggested there were significant differences between substrate size in treatments one, two and four ($F_{1,47} = 4.93$, $P = 0.03$; $F_{1,47} = 4.42$, $P = 0.04$; $F_{1,47} = 3.52$, $P = 0.07$, respectively) where finer substrate related to reduced burrowing depths in crayfish (mean burrowing depth: cobble = 40 cm; pebble = 21.5 cm).

The ANOVA examining Δ weight and the main effect of substrate (Fig. 22) was significant ($F_{1,42} = 9.52$, $P < 0.01$); however, water-level treatment was not ($F_{3,42} = 2.00$, $P = 0.13$). More importantly, the interaction between substrate and water-level treatment was significant ($F_{3,42} = 2.35$, $P = 0.09$) suggesting the effects of water-level treatment on fitness depended on the substrate. The post-hoc test showed differences between the control and the most severe water-level treatment (treatment four) combined with pebble substrate ($P = 0.01$). All other treatment and substrate combinations were not significant ($P > 0.1$). In the pebble substrate, water-level treatment four had the greatest mean Δ weight.

The ANOVA model with burrowing depth as the response variable (Fig. 23) indicated that the main effects of substrate and sediment treatments were each significant ($F_{2,41} = 65.99$, $P < 0.01$ and $F_{1,41} = 7.99$, $P < 0.01$ respectively). The interaction of substrate and sediment treatment was not significant ($F_{2,41} = 1.48$, $P = 0.24$). As with Experiment 1, crayfish burrowing depth was greater in the cobble substrate of the control sediment group when compared to pebble ($P = 0.02$) (Fig. 23). However, there were no significant differences between burrowing depth of crayfish in the two substrate treatments within the two remaining fine-sediment treatments (45% and 90%). Mean burrowing depth was reduced with increasing amounts of fine sediment. The reduction in burrowing depth was significantly different between all cobble and sediment treatments ($P < 0.01$). However, in the pebble substrate, only the 90% sediment treatment was significantly different from the control ($P < 0.01$).

The final ANOVA model indicated that Δ weight was not significantly affected by substrate ($F_{1,41} = 1.35$, $P = 0.25$; Fig. 24), sediment treatment ($F_{2,41} = 0.72$, $P = 0.50$) or the interaction of substrate and sediment treatment ($F_{2,41} = 0.14$, $P = 0.87$; Fig. 24). These results suggest sediment does not significantly reduce crayfish fitness as measured by weight loss in this study. However, variation in weight loss was substantial within and among treatments and increased in the most severe sediment treatment group.

Discussion

This is the first study to address reach-scale habitat use of three of these species using quantitative collection methods. *Orconectes saxatilis*, a state-listed endangered species that occupies the headwaters of the Kiamichi River was previously investigated quantitatively (Jones and Bergey, 2007). Jones and Bergey (2007) captured *O. p. longimanus* and *P. tenuis*; however, *P. tenuis* was rarely encountered and the authors did not include the species in the habitat-use analysis. Jones and Bergey (2007) found *O. p. longimanus* to occur at high densities and that pool habitats were used more often than other channel units. Our models indicated that runs yielded higher densities of *O. p. longimanus* than all other channel units. An explanation for the discrepancy between this study and that of Jones and Bergey (2007) is because of the paucity of run channel units sampled on the Kiamichi River. Other qualitative studies have focused on *O. menae* (Robison, et al., 2009) and *P. tenuis* (Robison and McAllister, 2008). Habitat descriptions in these studies were vague. Suitable substrate composition was described as rock and rubble and it was suggested that both species occurred in spring-fed headwater streams (Robison and McAllister, 2008; Robison, et al., 2009). In the current study, spring-fed streams were rare and we were able to detect both species in dry habitats of intermittent streams, and as we hypothesized these species were not restricted to spring-fed streams.

The regression tree models in this study showed low levels of accuracy which may be attributed to the scale that the data were collected (i.e., channel unit and microhabitat) and low habitat heterogeneity within the sampled reaches. The low accuracy of the *O. p. longimanus* and *O. leptogonopodus* models indicates that these species did not consistently occur at higher densities in specific habitats, contradicting our hypothesis. Boulder, cobble and pebble substrates accounted for > 70% of all substrates measured at each site. These substrate sizes are known to be suitable for many crayfish (Nyström, et al., 2006) and substrate composition is known to drive crayfish abundances at reach scales and more coarse scales (Nyström, et al., 2006; Usio, 2007). However, if the majority of a reach comprises suitable substrate, it is reasonable that crayfish would not select specific habitat patches within the reach which would contribute to low model accuracy. Froude number and water velocity are also related to crayfish densities at the microhabitat scale (Rabeni, 1985; Distefano, et al., 2003; Wooster, Snyder and

Madsen, 2012). We included water velocity in our models; however, the vast majority of our samples were in either dry habitat or depositional areas with limited flow. In addition to substrate composition, velocity was also relatively homogenous. Channel unit and depth were the most significant predictors and the most diverse within the study reaches. Run and dry channel units were predicted to have the highest densities. These channel units were generally the more shallow habitats available. Water depth was the best microhabitat predictor in our model. Some crayfish use deeper water to escape terrestrial predators (Englund and Kruppa, 2000), but crayfish in this study appeared to be selecting shallower habitat. Fish common to our study area (e.g., Smallmouth Bass *Micropterus dolomieu*) are more efficient predators in deeper-water habitats (Schlosser, 1987). It is possible that crayfish selected shallow habitats to avoid aquatic predators and used coarse substrate as refuge from terrestrial predators (Lodge and Hill, 1994; Nyström, et al., 2006).

Low abundances and patchy occurrences of crayfish may contribute to the low prediction rates of our regression tree models. *Orconectes menae* and *P. tenuis* are known to have spotty distributions and occur in low abundances (Bergey, Jones and Fenolio, 2004). Our data support this claim; however, *O. leptogonopodus* also has a patchy distribution (at least in Oklahoma) although it occurs at greater abundances than *O. menae* and *P. tenuis*. Low abundances of crayfish may be related to the intermittent nature of Ouachita Mountain streams. These streams predictably have low availability of aquatic habitat during certain periods. When compared to streams of the Ozark Highlands, low abundance of Smallmouth Bass in Ouachita Mountain streams was attributed to intermittent flow and fewer nutrients (Balkenbush and Fisher, 1999). Dorn and Wojdak (2004) found that crayfish can reduce the dissolved oxygen levels by consuming filamentous algae. It is possible that the intermittent habitats in the Ouachita Mountains cannot support forage and oxygen requirements of high densities of crayfish throughout the year.

Gear efficiency could also contribute to estimated low crayfish densities. Larson, et al. (2008) measured the efficiency of the quadrat sampler in riffles and found that it was relatively efficient (69%) but other channel units were not evaluated. Discrepancies between snorkeling and SCUBA observations and quadrat samples provide some evidence that the quadrat sampler is less efficient in deep habitat (> 1 m) and around large boulders (DiStefano, et al., 2003).

Habitat > 1-m deep was rare (1 %) but large substrate sizes were common in my study areas. The quadrat sampler is more efficient at sampling crayfish in low-water velocities compared to seining methods (Williams, et al., 2014). The relationship between larger substrate size and efficiency has not been quantified but we suspect densities of these crayfish were conservative in our study due to possible gear bias related to larger substrates.

The use of PIT tags for marking crayfish has been explored in recent years and has several advantages over other tagging methods. Other studies have used non-electronic mark and recapture (Gherardi, Barbaresi and Salvi, 2000; Pillotto, et al., 2008) and radio tags (Bubb, et al. 2004). Non-electronic mark and recapture techniques require the crayfish to be recaptured and handled to verify the location. This is heavily influenced by chance and often low recapture rates are problematic (e.g., Gherardi, et al., 2000). Radio-telemetry tags have high recapture rates and do not require handling of the crayfish for detection, but they are large and because they are externally mounted to the crayfish, the tag is lost when the crayfish molts. Further, even the smallest radio tags are too large for many crayfish species (Bubb, et al., 2002). Passive integrated transponders are a better choice for small crayfish but are not without limitations. Crayfish size is limited to crayfish > 25 mm CL when using 12-mm PIT tags (Bubb, et al., 2002) and tag loss and mortalities can be an issue for some species (Black, Herleth-King and Mattingly, 2010). Westhoff and Seivert (2013) reported 57% mortality in *O. hylas* tagged with 12.5-mm PIT tags. In a field study, Black, et al., (2010) were only able to detect 17% of PIT tagged crayfish multiple times over a 1.5 week study. In this study, 31% of tagged crayfish were alive throughout the study and we recaptured them more than four times. We determined that 17% of the tagged crayfish perished during the study. One of the deceased crayfish appeared to have moved 94 m upstream between the time it was determined to be dead and the previous detection. We speculated that this tag was moved upstream and re-deposited by a predator. Fifty-two percent of crayfish disappeared from the study area and it is unknown whether they perished, were washed downstream, were removed by predators, were undetectable due to burrowing depth, or simply left the study reach. It is likely that predation plays an important role in lost crayfish because they are an important food source to > 200 other species (Distefano, 2005).

Despite low recapture rates, other studies have documented crayfish movements and their results were comparable to our findings. Bubb, et al. (2006) PIT tagged 406 *Pasifastiscus leniusculus* and tracked them over a 15-day period. The tagged *P. leniusculus* moved both upstream and downstream; however, the greatest distance moved was downstream. Similarly, the greatest movements we detected (> 100 m) were in the downstream direction. Bubb, et al. (2006) speculated that upstream movement was truncated by a waterfall. Similarly, upstream movement in Beech Creek was likely prevented by a steep bedrock riffle. However, in Cucumber Creek, crayfish moved relatively long distances both upstream and downstream. Westhoff and Rabeni (2013) used PIT tags to assess habitat selection relative to proximate and reach-scale habitat availability by two Ozark Highland crayfish species. The authors were able to achieve a large sample size (307 crayfish) to apply discrete choice models. In their study, substrate composition, vegetative cover that aided concealment, and channel unit were the best predictors of habitat selection (Westhoff and Rabeni, 2013). We were able to document the importance of channel units to crayfish selection of habitats and like Westhoff and Rabeni (2013), crayfish appeared to use runs over riffles; however, we attributed this to the disproportionate availability of runs in our study reaches. Dukat and Magoulick (1999) found higher predation rates on riffle-dwelling *Cambarus hubbsi* than the more generalist species *O. marchandi*. Predation rates were similar for each species in the riffles indicating that crayfish were less susceptible to predation in runs and pools. The importance of particular channel units is likely to vary by species, ecoregion, and with ontogeny (Brewer, et al. 2009).

This study is unique from other PIT tag studies because we related crayfish movement to changes in streamflow patterns. However, a similar study was conducted by Momot (1966) in an intermittent stream in south-central Oklahoma using non-electronic mark and recapture methods. He reported the majority of crayfish to migrate upstream while the water was flowing. Upstream movement was attributed to the need for crayfish to recolonize after being washed downstream by scouring floodwaters. In this study, crayfish movement did appear to increase following a flood; however, crayfish displayed both up and downstream movement patterns during the different time intervals of the study. Two crayfish in Beech Creek moved upstream toward the steep bedrock barrier after week June 17 (mid-season). One of the crayfish reached the barrier by June 24 then moved downstream to a deep, low-velocity run the following week (July 2) where it remained until the end of the study. The other crayfish moved upstream steadily after

June 17 and did not reach the barrier until the final week of the study (July 24). In contrast, the most extreme movement (108 m) was in the downstream direction and occurred between June 10 and June 24.

We hypothesized that crayfish would move toward deeper habitats as streams dried; however, we observed variation in crayfish use of moderate and shallow depth habitat. DiStefano, et al. (2009) reported crayfish to persist in the hyporheic zone during drought despite the presence of intermittent pools. The authors indicated some crayfish moved to deeper habitats as streams dried, but many crayfish remained in the shallow habitats. Covich, Crawl and Scatena (2003) documented densities of freshwater shrimp to increase as intermittent pool size decreased. This seemed to indicate that the shrimp were moving to remain in the water. Distefano, et al. (2009) did not observe an increase in crayfish densities in pools during the drought season suggesting that many crayfish use the hyporheic zone or some other refuge rather than pools. Reasons for crayfish to select the hyporheic zone over deeper habitats may be related to predator avoidance (Englund, 1999). Fish predation is a major source of crayfish mortality and can influence crayfish movement (Englund, 1999). In Cucumber Creek, tagged crayfish tended to move into the deeper habitat in each time interval, but in Beech Creek crayfish moved into the shallow habitat during the mid-season. Anecdotally, we suspect predators may account for this difference because we detected Smallmouth Bass and Green Sunfish *Lepomis cyanellus* during elevated flows in Beech Creek but not in Cucumber Creek. Likewise, Englund (1999) reported increased movement of crayfish out of pools when green sunfish were introduced. The large substrate in the streams likely provided refuge from terrestrial predators while in the shallow habitat. Conclusions of previous work on crayfish response to drying period relied on inferences made by observed shifts in abundance. Jones and Bergey (2007) showed that *O. saxatilis* abundances increased in pools during the dry period indicating that the species may migrate to or become restricted to deeper habitats during the dry season. The results in our movement study support the idea that some crayfish move to deeper habitats; however, discrete sampling analyzed using regression trees indicated both shallow and dry habitats support relatively high densities of crayfish.

Adult and juvenile crayfish may be affected differently by stream drying. Habitat use can differ between age classes for some species (Wooster, et al., 2012) but not others. For example,

O. saxatilis (the closest relative to *O. menae*) and *O. p. longimanus* juveniles occur at similar proportions to adults in pools and riffles (Jones and Bergey, 2007). Drought in streams has been shown to lead to lowered abundances of adult crayfish while juvenile abundances appear unaffected or even increase (Taylor, 1988). Momot (1966) concluded that adult crayfish in intermittent streams suffer high mortality rates during the dry period and the young-of-year account for the brood stock the following year. We had difficulties capturing adult crayfish to tag until early May. This could be an artifact of high adult mortality during the dry season. Unfortunately, we did not conduct seasonal quantitative sampling to support this hypothesis and were not able to separate juveniles and adults during summer sampling. More information on basic life-history attributes by many narrow-range endemic crayfish would be beneficial to improving our understanding of crayfish ecology.

We hypothesized that the pebble substrate would be more difficult for crayfish to burrow into than the cobble substrate. This prediction was true in the treatments without fine sediment; however, fine sediment had a similar effect on burrowing depth regardless of the substrate size. Other crayfish have been recorded to have impaired burrowing ability in sand, e.g., *Procambarus fallax* failed to initiate burrows in sandy substrate in 98 of 100 trials (Dorn and Volin, 2009). Additionally, we hypothesized that smaller substrate would lead to greater weight loss in the pebble substrate and sediment. As with the previous hypothesis, our predictions were accurate in the absence of sediment. Crayfish weight change was highly variable in the sedimentation experiment and we believe this to be a result of the sediment providing moisture to the crayfish throughout the trial.

Excess fine-sediment in streams has been documented to negatively affect many different groups of aquatic organisms. Alexander and Hansen (1986) demonstrated through field experimentation that sediment loads can reduce the abundance of brook trout *Salvelinus fontinalis*. The reduced abundance of brook trout was thought to be a result of lowered recruitment and changing streambed habitat (Alexander and Hansen, 1986). Macrophytes and invertebrates are negatively affected by increasing sandy substrates due to the instability of the streambed (Nuttall, 1972). Lenat (1984) found that areas where agricultural runoff was poorly managed macroinvertebrate taxa richness decreased. In general, streams where runoff was poorly managed had more erosion and the substrate became sandier (Lenat, 1984). Jones and Bergey (2007) suggested anecdotally that absence of an endangered crayfish *O. saxatilis* was

likely related to land-use changes outside of the Ouachita National Forest where much of their study was conducted. The national forest service uses the best logging practices and prevents agriculture in the Ouachita National Forest reducing excess sediment loads in streams (personal observation).

These experiments indicated substrate size and excess sediment impacted the ability of crayfish to reach a simulated hyporheic zone. The results of the burrowing depths in the control treatments of the sedimentation experiment were comparable to the most severe treatment in the water-level reduction experiment. In general, both experiments suggest that pebble substrate prevented crayfish from reaching the reduced water level more so than the larger cobble substrate. Dorn and Trexler (2007) found that *Procambarus alleni* and *P. fallax* suffered mortality from desiccation when they failed to reach the hyporheic zone in slough environments. Additionally, Dorn and Trexler (2007), reported larger crayfish to burrow deeper into the peat and marl substrates of the everglades. Gherardi (2002) surmised that soils with large particles impede the construction of permanent burrows and that free water is essential for burrowing. There was no relationship between crayfish size and burrowing depths in either substrate size in this study. Perhaps, in the absence of fine sediment, small crayfish were better able to slip through the interstitial spaces of the pebble substrate; whereas, large crayfish had the strength to maneuver into the interstitial spaces in the pebble and reach water levels of 35cm and 25cm. In the sedimentation experiments, however, crayfish had to both maneuver between the rock substrate and excavate fine sediment. The cobble substrates were not an issue for crayfish burrowing depth in the treatments without sediment, so crayfish in cobble substrate only had to excavate fine sediment to burrow. These results strongly suggest that excess fine sediment inhibits burrowing depth in both cobble and pebble substrates.

There are several correlative studies that suggest burrowing is related to substrate factors. DiStefano et al. (2009) found that during the drought season, *O. williamsi* and *O. meeki meeki* use dry habitat with cobble and boulder substrate; however, these crayfish were also able to burrow into sand and fine gravel. DiStefano et al. (2009) indicated that crayfish found in fine sediment and above the subsurface-water level were in moist chambers. The fine sediment in our experiment mostly comprised sand and sand appears to be more difficult for crayfish burrowing compared to peat and marl (Dorn and Volin, 2009). This observation is likely related to the lack of cohesion of sand particles (Dorn and Volin, 2009). Dorn and Volin (2009)

reported greater burrowing success by crayfish when vegetation roots helped stabilized the substrate.

Biologists often relate an animal's body size to its fitness because size can influence susceptibility to predation and environmental stressors and its ability to consume resources (Werner and Gilliam, 1984). Because mortality and growth were not strongly related, Hill and Lodge (1999) used mortality divided by growth as a fitness metric to measure responses to interspecific competition between *O. rusticus*, *O. virilus* and *O. propinquus*. As with Hill and Lodge (1999), we were not able to detect a strong relationship between survival and weight loss. Dorn and Volin (2009) attributed crayfish weight loss to stress from drying when water levels were reduced and our observations generally agree. All mortalities in the water-level experiment had $\geq 12\%$ weight loss, but in the sedimentation experiments only 44% of mortalities experienced any weight loss. This suggests that Δ weight may not have been the best predictor of crayfish fitness in the sediment trials. Deceased crayfish were often found moist indicating that desiccation was not the cause of death as in the water-level reduction experiments. Fine sediment can reduce dissolved oxygen in streams and cause damage to organic tissue (Kemp, et al., 2011). Fine sediment in the interstitial spaces of coarse substrate can block fresh-source water and lead to hypoxic conditions in the hyporheic zone (Malcolm, et al. 2008). Similarly, we were not able to simulate hyporheic flow in the sedimentation experiments because the sediment prevented the water from draining at the same rate that water was being added. It is possible that hypoxia or gill abrasion could have accounted for crayfish mortalities; however, we did not determine the actual cause of death.

Our trials lasted one week and may have contributed to the variability in Δ weight that we observed. Hill and Lodge (1999), Dorn and Trexler (2007) and Dorn and Volin (2009) experiments ranged from one to two months. Our experiments may have benefited from longer trial periods especially since Ouachita Mountain ecoregion streams may experience dry periods of five months (Jones and Bergey, 2007). Our week long trials were not long enough to reliably measure crayfish growth and increased crayfish weight was likely due to foraging in the holding tanks prior the experiments. Based on our experiments we cannot speculate on whether crayfish would continue to grow after several weeks in the substrate. We attributed a reduction in Δ weight to desiccation in the trials without sediment, (consistent with Dorn and Volin, 2009), and our trial lengths were long enough to measure weight loss in desiccated crayfish. Longer trials

and greater sample sizes would have generated better growth and mortality data which could be applied as a more reliable measure of fitness.

Crayfish often excavate burrows into the hyporheic zone to find water and escape drought (Gherardi, 2002; Distefano, et al. 2009); however, it is not uncommon for crayfish to survive for a period of time without water (McMahon, 2002). In humid conditions, *Cherax* spp. and *Procambarus clarkii* have been reported to survive for 28 days above in burrows above the water table (Huner, 1989; McMahon and Stuart, 1999). But when relative humidity is reduced to 50%, *P. clarkii* may suffer mortality in as few as three days (McMahon, 2002). The physiology of crayfish gills allows sufficient oxygen and carbon-dioxide exchange to occur in air (McMahon, 2002). However, nitrogen and salts have been reported to accumulate in a crayfish's body in the absences of water submersion (McMahon, 2002). This can disturb the ionic and acid-base balance within the crayfish's body and impede bodily functions (McMahon, 2002).

Comparing burrowing abilities with environmental alterations is a first step to predicting how human alteration may affect natural aquatic ecosystems. Additional, studies are needed to test the desiccation tolerance of these crayfish under controlled environmental conditions (i.e., temperature and humidity), and physiochemical properties in the hyporheic zone in Ouachita streams that may or may not be impacted by human land use. For this objective, we show the potential of sedimentation to impact the ability of crayfish to burrow and the importance of burrowing to crayfish persistence. Excess sediment can be detrimental to an aquatic ecosystem, but healthy upland land use can limit erosion and appropriate riparian regions can buffer excess sediment loads (Osborne and Kovacic, 1993). We do not, however, know much about the ability of crayfish to disperse to more suitable habitat if sedimentation creates unsuitable local conditions. The movement section of this objective was limited in scope to the drying season and under conditions with limited sedimentation levels. Even if crayfish can move considerable distances, unsuitable local conditions for native crayfish may create conditions that allow invasion by non-native species and alter trophic dynamics. Water withdrawals have the potential to be more problematic for management because groundwater levels are not easily restored without *a priori* regulation, most often with water-conservation efforts (Wollmuth and Eheart, 2000). The current best management practices are to restore and maintain native riparian buffers, regulate water withdrawal during already low-flow periods, and prevent non-sustainable groundwater withdrawals.

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Table 1. Environmental variables used to create species-distribution models. A season is defined as three months of a year. Data sources are free and may be accessed at the web sites indicated below. Data resolution is provided below.

Variable	Source	Resolution
Soil	www.soildatamart.nrcs.usda.gov	lat: 0.0000001 long:
Composition (%)		0.0000001 (vector)
Geology	www.datagateway.nrcs.usda.gov	1:100,000 scale
Rock type (%)		(vector)
Land-use	www.datagateway.nrcs.usda.gov	30 m ² (vector)
Warmest season	www.worldclim.org/bioclim	1 km ²
temperature (°C)		
Coldest season	www.worldclim.org/bioclim	1 km ²
temperature (°C)		
Wettest season	www.worldclim.org/bioclim	1 km ²
precipitation (mm)		
Driest season	www.worldclim.org/bioclim	1 km ²
precipitation (mm)		
Warmest season	www.worldclim.org/bioclim	1 km ²
precipitation (mm)		
Coldest season	www.worldclim.org/bioclim	1 km ²
precipitation (mm)		
Elevation	www.horizon-systems.com/nhdplus/data.php	30 m ²
Stream order (Strahler)	www.horizon-systems.com/nhdplus/data.php	data base table
Flow accumulation	Arc GIS Tools	N/A
January temperature (all	gisclimatechange.ucar.edu	4.5 km ²
scenarios 2099)		
August temperature (all	gisclimatechange.ucar.edu	4.5 km ²
scenarios 2099)		
January precipitation (all	gisclimatechange.ucar.edu	4.5 km ²

scenarios 2099)

August precipitation (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km ²
July precipitation (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km ²
March precipitation (all scenarios 2099)	gisclimatechange.ucar.edu	4.5 km ²
Stream network	www.horizon-systems.com/nhdplus/data.php	1:100.000 scale

Table 2. The contribution (%) and permutation of importance (importance) (%) for significant environmental variables for four crayfish species. The contribution is a summation of the regularized gain in all iterations for each variable; whereas, the permutation importance reflects the effect, of randomly permuting the variables, on training area under the curve.

Variable	<i>O. leptogonopodus</i>		<i>O. menae</i>		<i>O. saxatilis</i>		<i>P. tenuis</i>	
	Contribution	Importance	Contribution	Importance	Contribution	Importance	Contribution	Importance
Soil content	6.9	13.9	20.3	15.0	45.9	2.8	32.9	49.3
Elevation	5.5	15.8	35.4	0.4	16.1	4.1	44.8	17.9
Geology	8.4	0.1	21.1	7.4	0.4	0.2	0.2	0.1
Land-use	0.7	1.2	3.5	2.8	5.0	0.9	8.2	7.3
Stream order (Strahler)	1.6	3.2	2.4	1.9	1.2	0.2	1.0	1.2
Flow accumulation	0.2	0.7	0.8	0.9	2.7	0.5	3.0	4.6
Summer temperature	0.1	0.0	0.4	0.2	0.4	0.2	1.1	6.0
Winter temperature	71.8	52.1	0.4	1.7	17.6	87.0	1.5	5.1
Summer precipitation	0.8	0.5	0.4	5.5	0.0	0.0	0.0	0.0
Winter precipitation	0.0	0.0	9.6	61.0	7.5	0.0	4.2	3.1
Wet season precipitation	3.4	12.4	0.1	0.3	0.0	0.0	0.7	4.8
Dry season precipitation	0.6	0.0	5.6	2.8	3.0	4.1	2.4	0.5

Table 3. Quantitative samples taken within each species range. Crayfish indicates the number of each species captures in the respective samples and samples with crayfish are the number of samples that contained each species.

Species	Samples	Crayfish	Samples with crayfish
<i>Orconectes menae</i>	263	75	46
<i>O. palmeri</i>	448	745	161
<i>longimanus</i>			
<i>O. leptogonopodus</i>	336	126	38
<i>Procambarus tenuis</i>	378	25	14

Table 4. Analysis of variance table showing the degrees of freedom (df) sum of squares (Sum Sq) mean squared error (Mean Sq) F-statistic (F value) and the P-value (Pr (>F)) of the total distance moved by individual crayfish.

Equation: Log(Total distance) = Species + Sex + Species:Sex

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Species	1	0.78	0.78	1.91	0.18
Sex	1	0.10	0.01	0.02	0.88
Species:Sex	1	0.42	0.42	1.03	0.32
Residuals	27	11.08	0.41		

Table 5. Analysis of variance table showing the degrees of freedom (df) sum of squares (Sum Sq) mean squared error (Mean Sq) F-statistic (F value) and the P-value (Pr (>F)) of the total distance moved by individual crayfish.

Equation: $\text{Log}(\text{Total distance}) = \text{Length} + \text{Sex} + \text{Length:Sex}$

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Species	1	0.11	0.11	0.25	0.62
Sex	1	0.47	0.47	1.08	0.31
Length:Sex	1	0.01	0.01	0.02	0.90
Residuals	27	11.71	0.43		

Table 6. Treatments applied to experimental chambers in water-level reduction and sedimentation experiments. Water-level reduction treatments (experiment 1) are described as the depth of the water-level reduction below the substrate in centimeters (cm). Sediment treatments (experiment 2) are described as L of sediment added to the chamber. Cobble and pebble substrate treatments are represented on separate rows because the volume of sediment added for each treatment differed between substrate size.

Experiment	T1 (control)	T2	T3	T4
Water Reduction	0cm	5cm	15cm	38.5cm
Sediment (Cobble)	0L	9.67L	19.4L	NA
Sediment (Pebble)	0L	9.25L	18.45L	NA

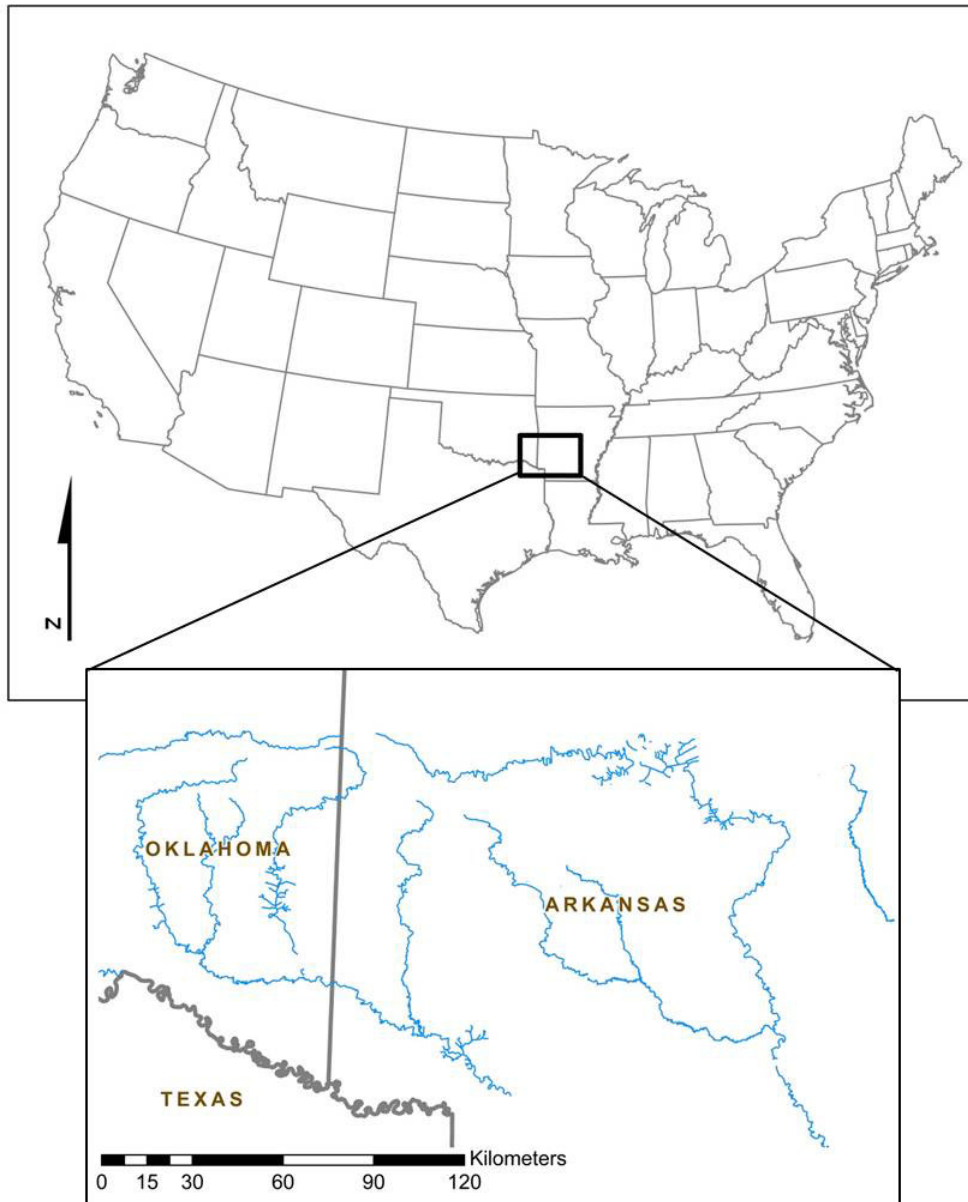


Figure 1. Map indicating the Ouachita Mountains of Oklahoma and Arkansas, USA. Only major rivers are depicted for simplicity and include (from the northeast to southwest): Kiamichi, Little, Ouachita and the Saline rivers.

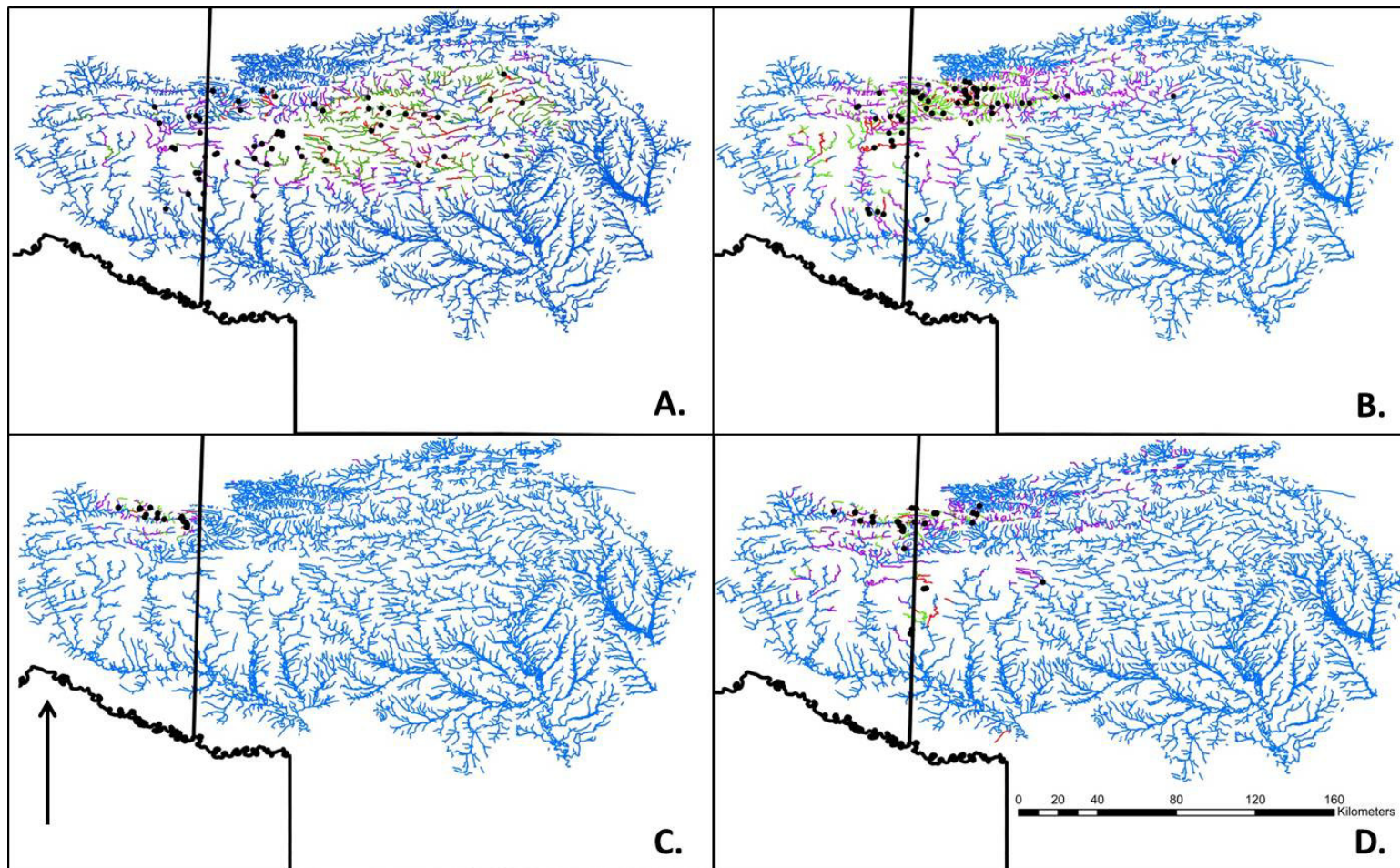


Figure 2. Current predicted distributions based on 1-km² resolution data for A.) *O. leptogonopodus*, B.) *O. menae*, C.) *O. saxatilis*, and D.) *P. tenuis*. Probabilities of occurrence are indicated by: blue <10%; purple 11% -32%; green 33%-65 %; and red $\geq$ 66%. Occurrence points are indicated by black dots.

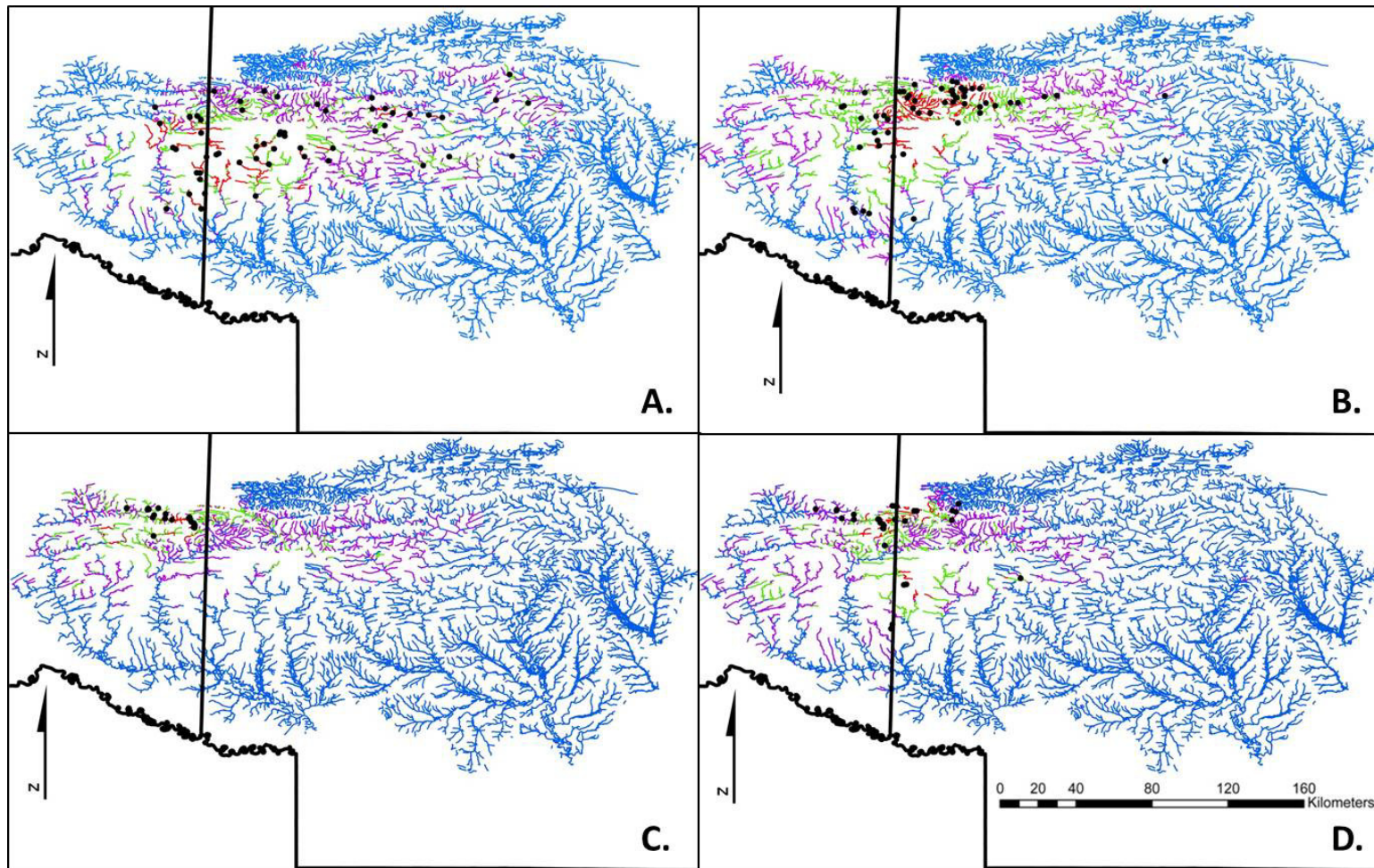


Figure 3. Current predicted distributions based on 4.5-km² resolution data for A.) *O. leptogonopodus*, B.) *O. menae*, C.) *O. saxatilis*, and D.) *P. tenuis*. Probabilities of occurrence are indicated by: blue <10%; purple 11% -32%; green 33%-65 %; and red ≥ 66%. Occurrence points are indicated by black dots.

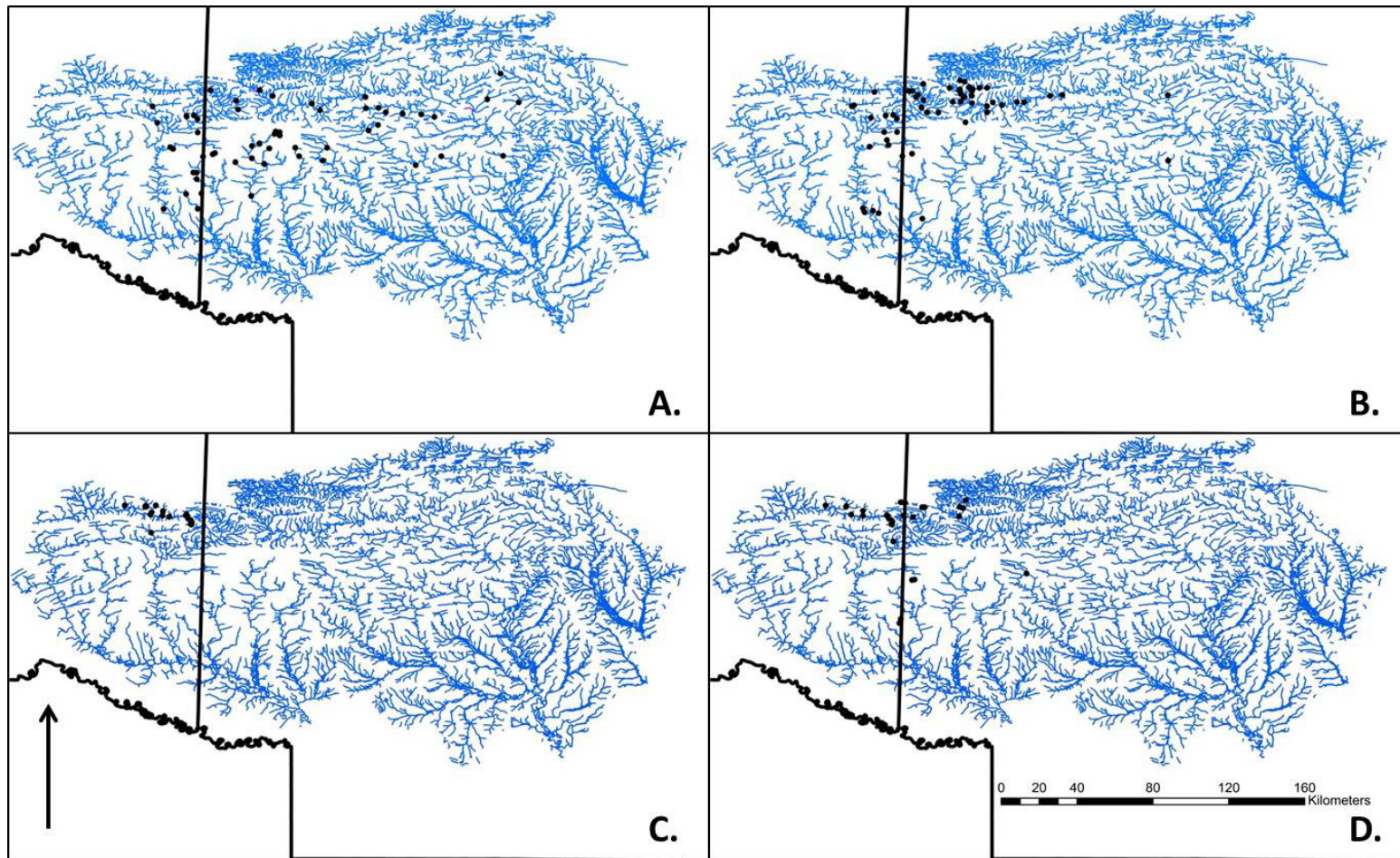


Figure 4. Future predicted distributions based on a high-emission scenario (A1B). Species distributions are represented by panels: A.) *O. leptogonopodus*, B.) *O. menae*, C.) *O. saxatilis*, and D.) *P. tenuis*. Probabilities of occurrence are indicated by: blue <10%; purple 11% -32%; green 33%-65 %; and red $\geq 66\%$. Occurrence points are indicated by black dots.

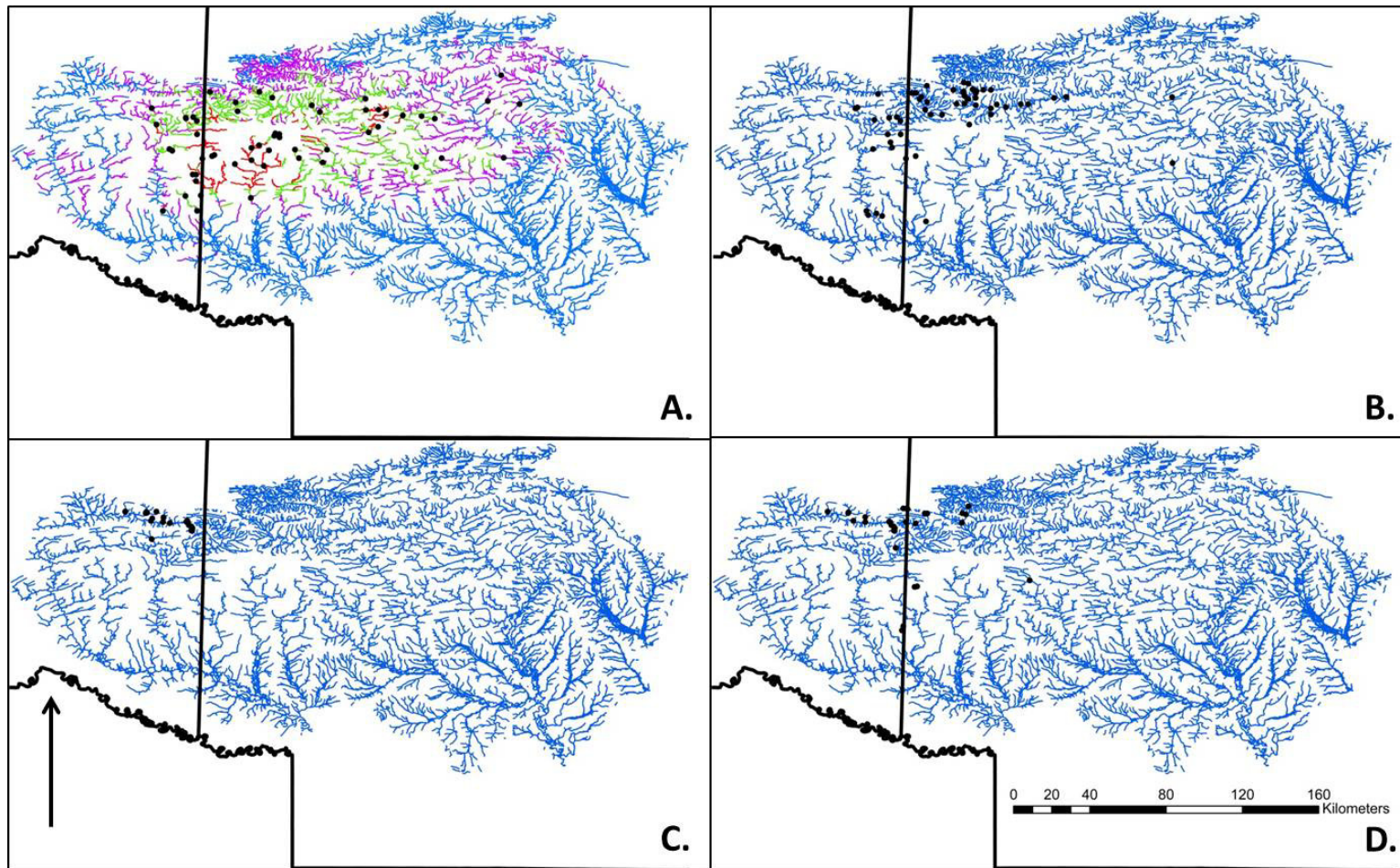


Figure 5. Future predicted distribution based on a low-emission scenario (B1). Species distributions are indicated in panels: A.) *O. leptogonopodus*, B.) *O. menae*, C.) *O. saxatilis*, and D.) *P. tenuis*. Probabilities of occurrence are indicated by: blue <10%; purple 11% -32%; green 33%-65 %; and red $\geq 66\%$. Occurrence points are indicated by black dots.

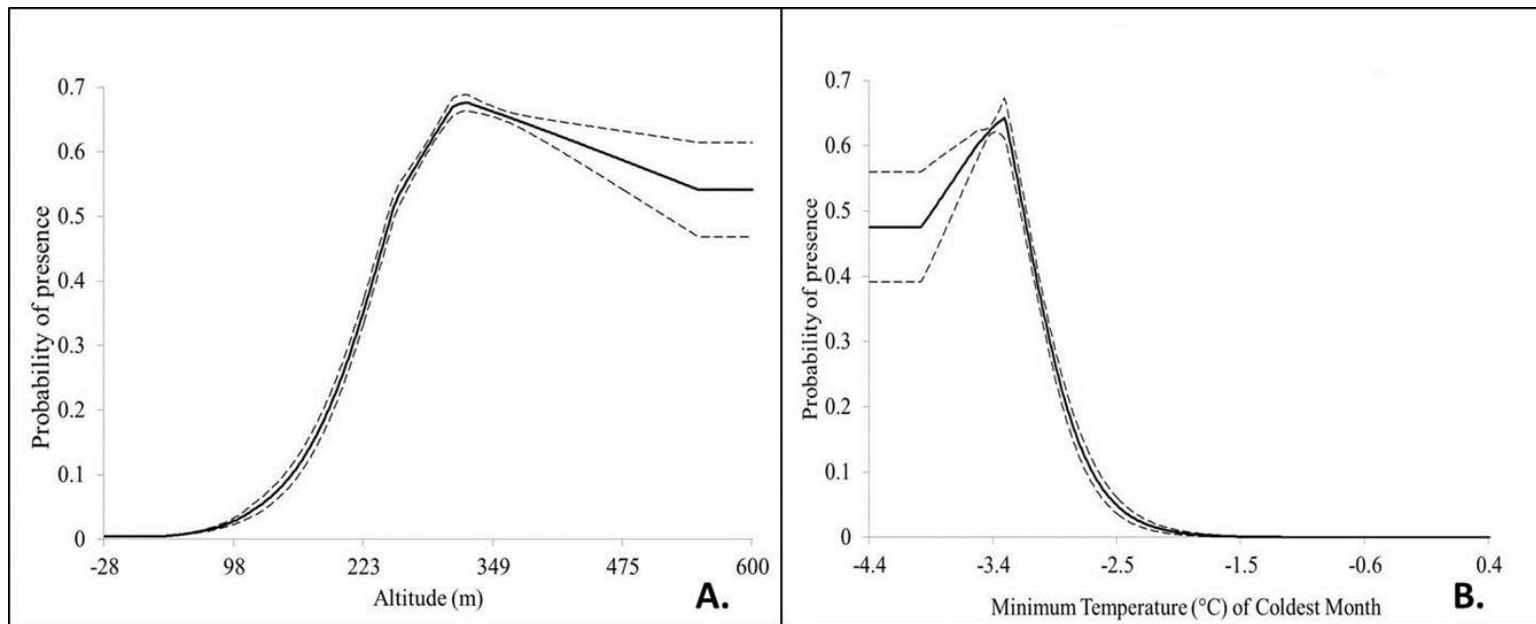


Figure 6. Response curves indicating the relationships between *O. menae* and elevation and between *O. saxatilis* and winter temperature.

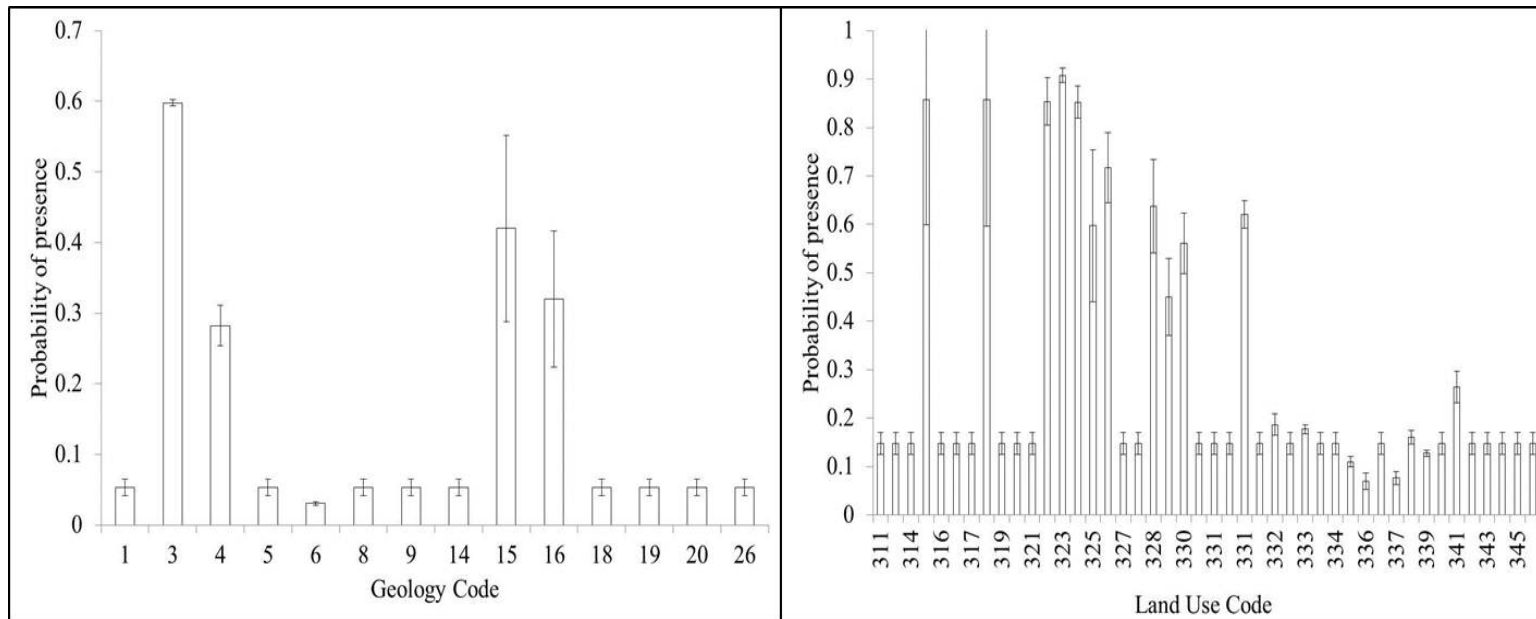


Figure 7. Response graphs of the relationships between geology classes and *O. leptogonopodus* and between land-use classes and *P. tenuis*. Numbers along the x-axis represent a combination of lithophilic classes and land-use practices

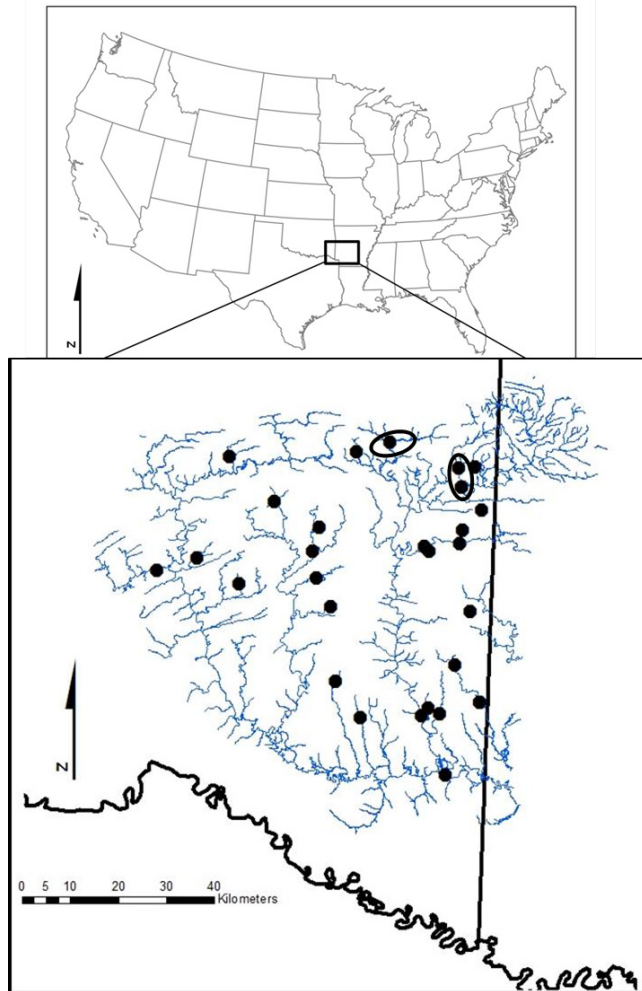


Figure 8. Location of quantitative sampling points and movement study reaches. From west to east the streams are: Little, Glover and Mountain Fork rivers. Quantitative sampling locations are indicated as black dots, whereas, the black dots surrounded by open ovals indicate movement-study reaches.

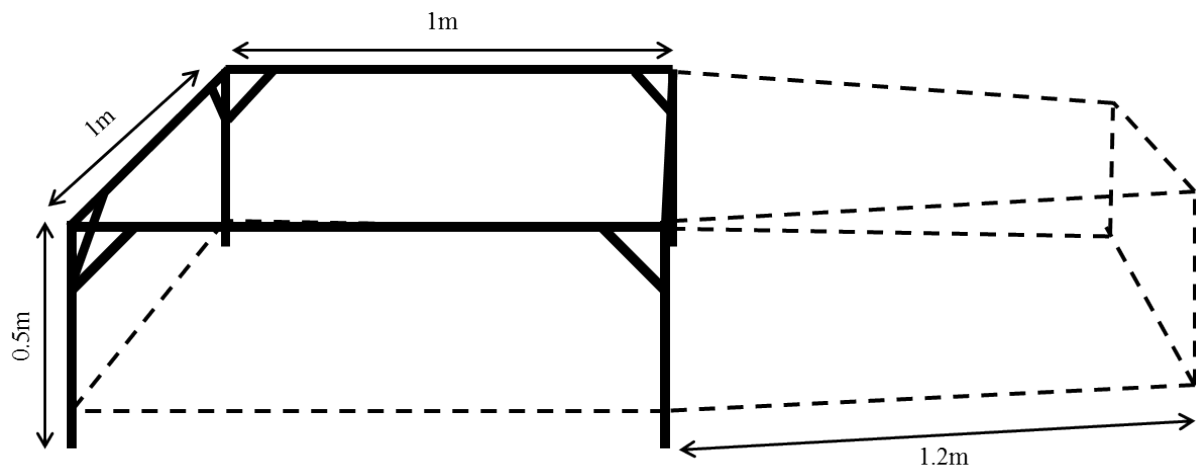


Figure 9. Quadrat sampler used in quantitative sampling. The steel frame is represented by solid black lines and the outline of the netting is displayed as dashed lines.

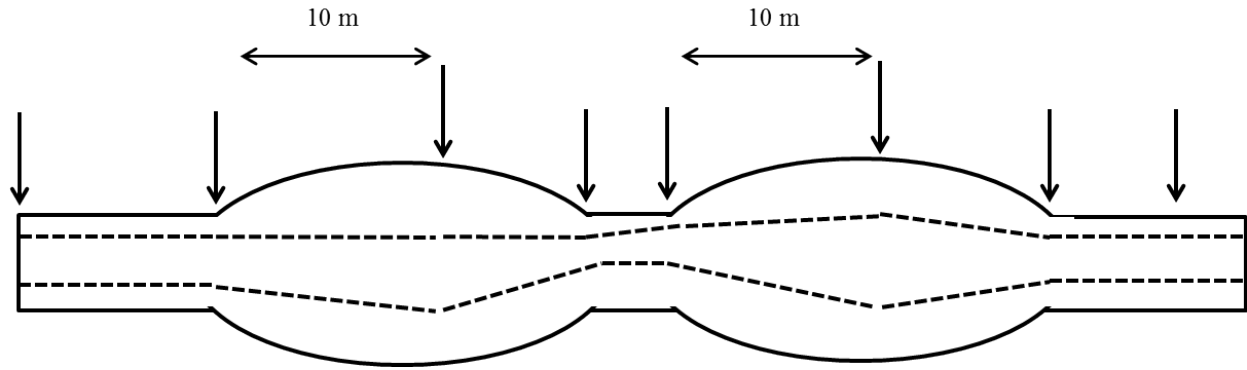


Figure 10. Stream mapping system used in the crayfish movement study. The black lines and curves represent a hypothetical pool-riffle sequence. The arrows represent transect markers along the stream bank. Transect markers were placed at obvious changes in channel unit (e.g., pool or riffle), substrate composition or stream depth. When habitat was homogenous for > 10 m, additional transects were added so that the greatest interval between transects was 10 m. The dashed lines represent cell boundaries. Cell boundaries were described as left, center and right and were recorded as distance from the transect marker. Intersections of the cell boundaries and the transect lines (running perpendicular to stream flow) delineated habitat patches within the stream.



Figure 11. Male *Orconectes menae* being tagged with a 12-mm half-duplex passive integrated transponder. The dashed line indicates the insertion point on female crayfish.

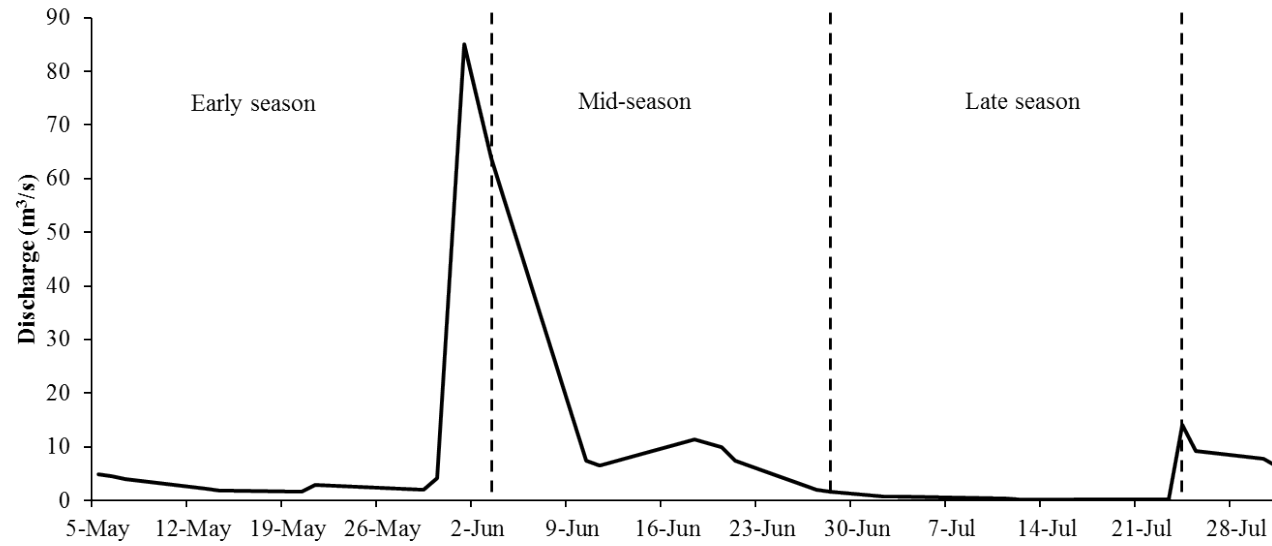


Figure 12. Discharge on the upper Mountain Fork during the crayfish tracking period (May 5 - July 24, 2013). The vertical dashed lines delineate the early, mid and late time intervals.

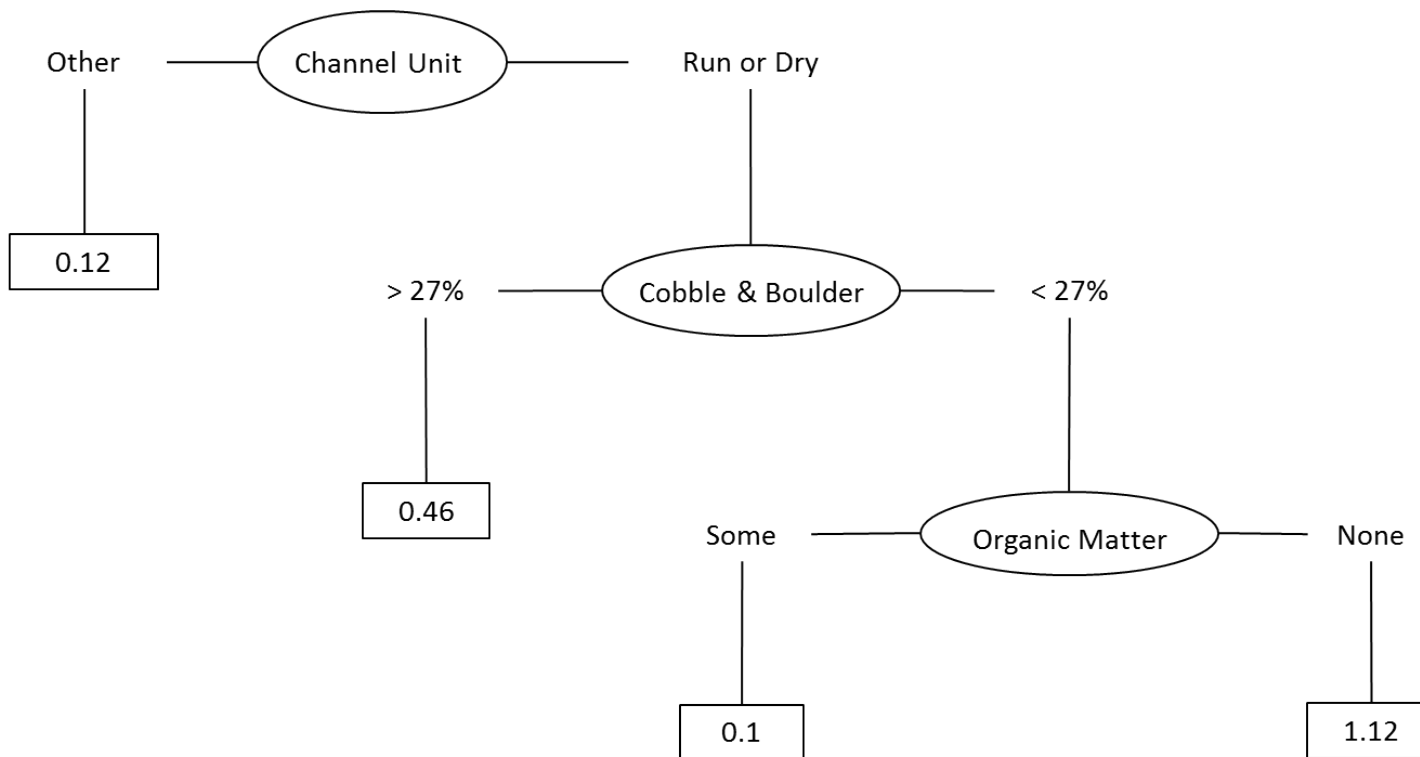


Figure 13. Regression-tree model predicting densities of *Orconectes menae*. The ovals represent environmental variables that were split to predict densities. To the left of the oval is the category within the environmental variable predicted to have the lower density. To the right is the split within the environment variable predicted to have the higher density of crayfish. The rectangles indicate terminal nodes and the numbers within them are the predicted crayfish densities in the conditions leading to the node.

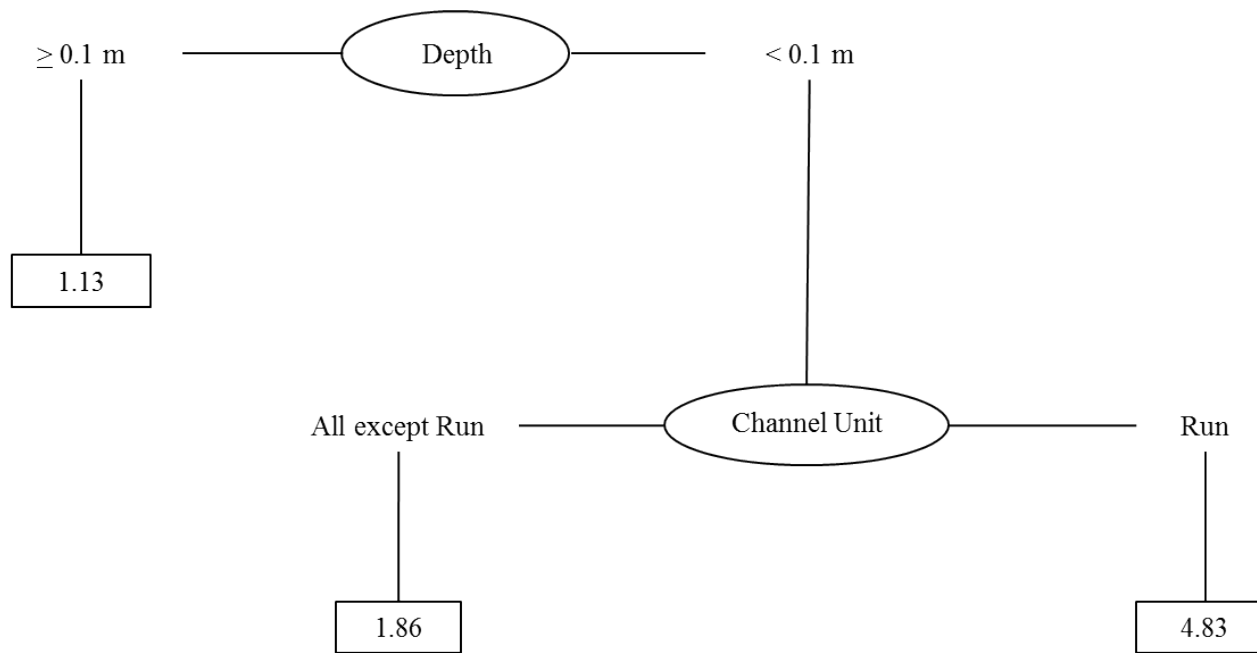


Figure 14. Regression-tree model predicting densities of *Orconectes palmeri longimanus*. The ovals represent environmental variables that were split to predict densities. To the left of the oval is the category within the environmental variable predicted to have the lower density. To the right is the split within the environment variable predicted to have the higher density of crayfish. The rectangles indicate terminal nodes and the numbers within them are the predicted crayfish densities in the conditions leading to the node.

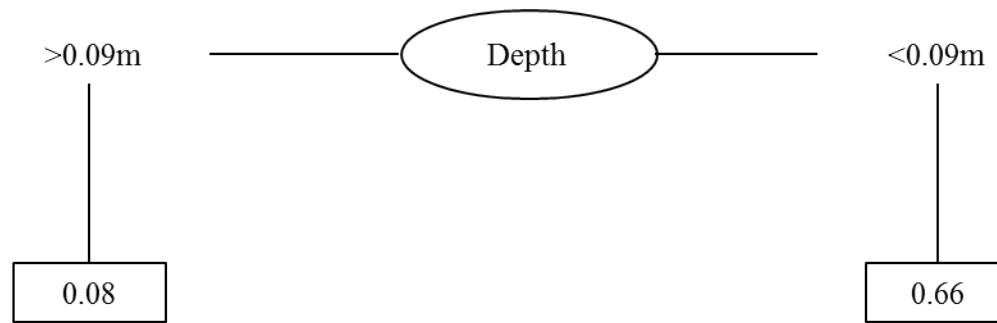


Figure 15. Regression-tree model predicting densities of *Orconectes leptogonopodus*. The ovals represent environmental variables that were split to predict densities. To the left of the oval is the category within the environmental variable predicted to have the lower density. To the right is the split within the environment variable predicted to have the higher density of crayfish. The rectangles indicate terminal nodes and the numbers within them are the predicted crayfish densities in the conditions leading to the node

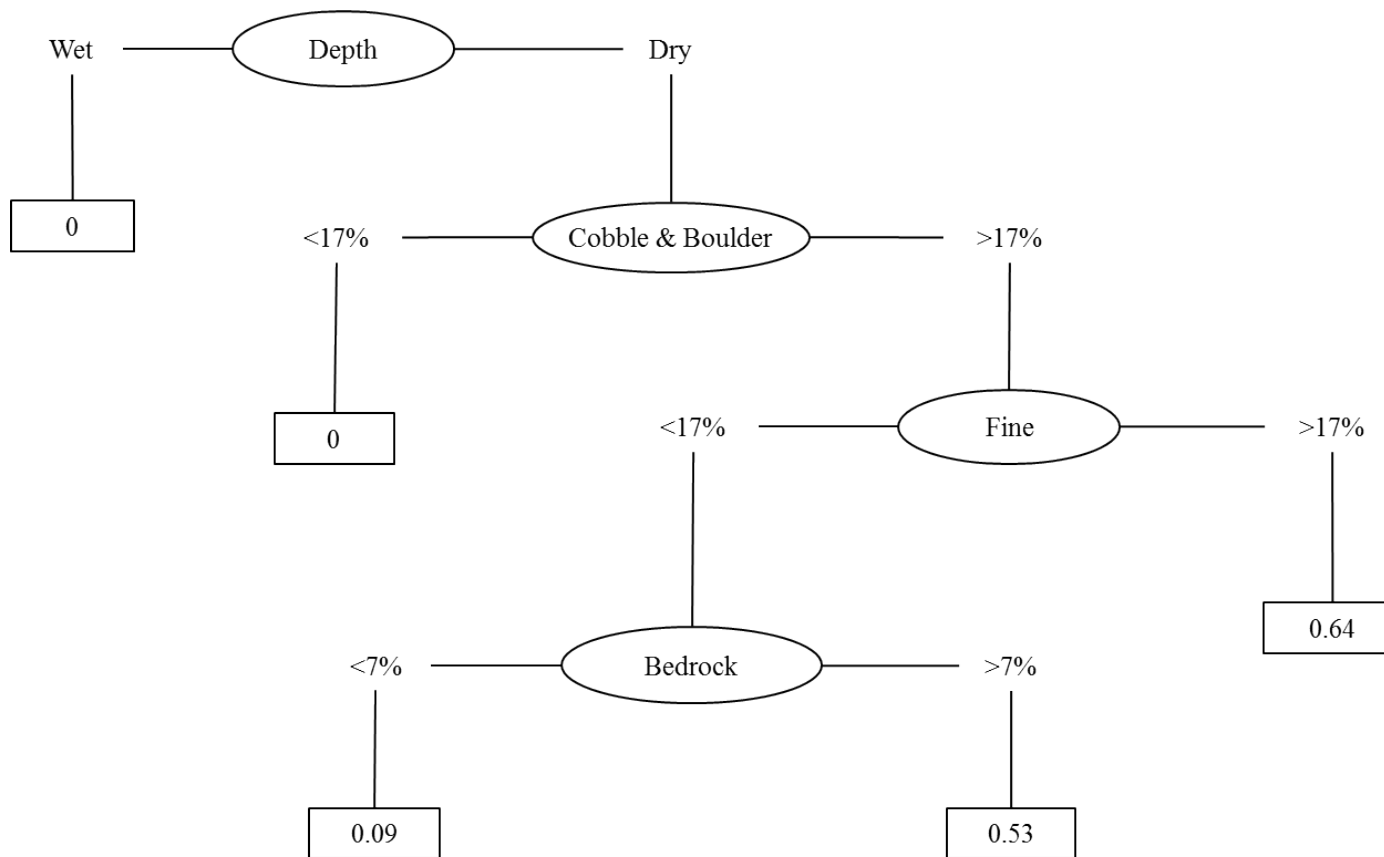


Figure 16. Regression-tree model predicting densities of *Procambarus tenuis*. The ovals represent environmental variables that were split to predict densities. To the left of the oval is the category within the environmental variable predicted to have the lower density. To the right is the split within the environment variable predicted to have the higher density of crayfish. The rectangles indicate terminal nodes and the numbers within them are the predicted crayfish densities in the conditions leading to the node.

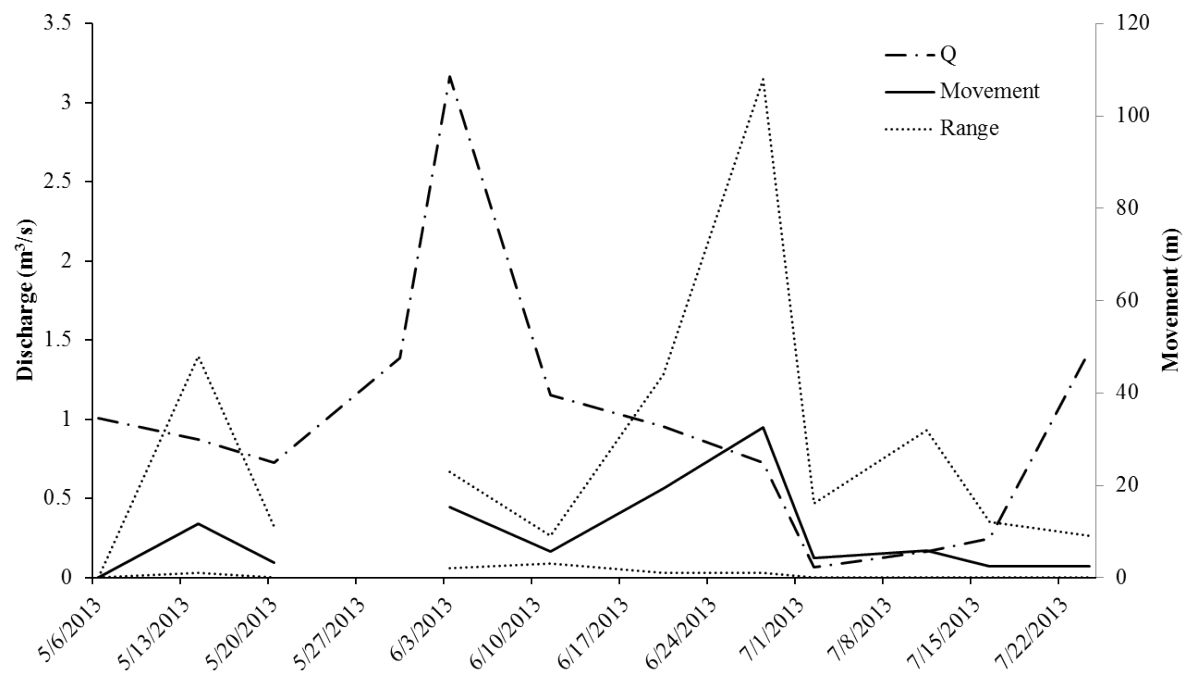


Figure 17. Relationship between stream discharge and crayfish movement on Beech Creek. The dash-dot line represents stream discharge whereas; the solid line represents average movement of crayfish detected in the corresponding week. The fine dotted lines represent the minimum and maximum distances moved by crayfish at each sampling period.

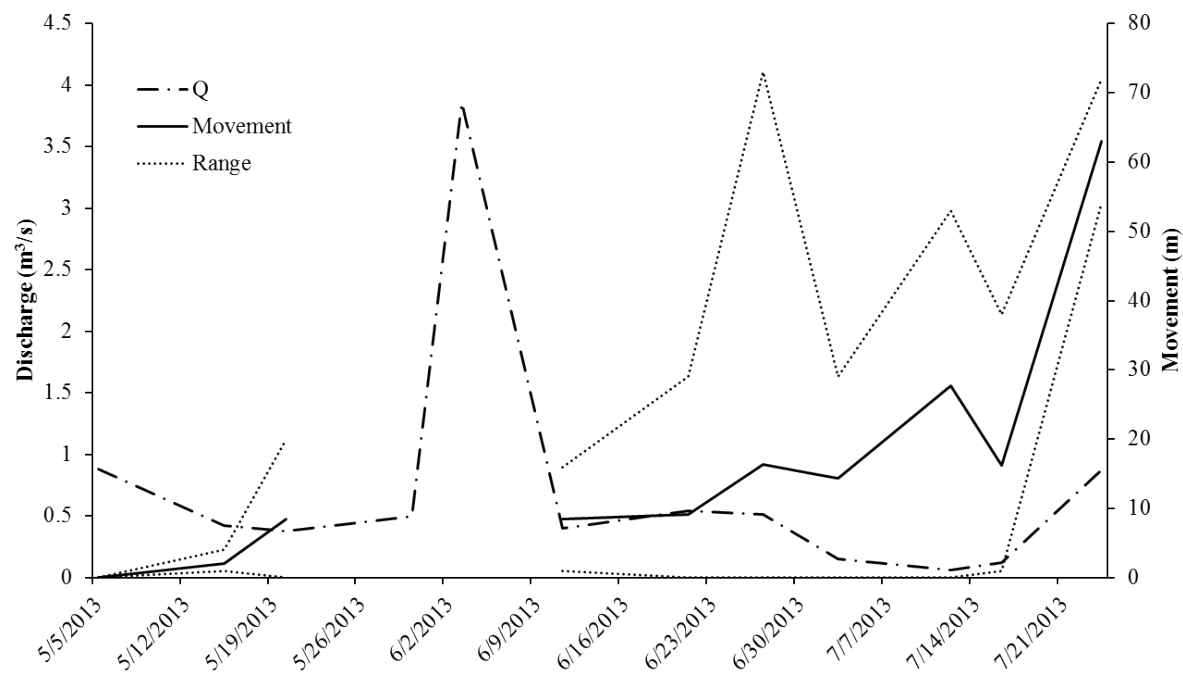


Figure 18. Relationship between stream discharge and crayfish movement on Cucumber Creek. The dash-dot line represents stream discharge whereas; the solid line represents average movement of crayfish detected in the corresponding week. The fine dotted lines represent the minimum and maximum distances moved by crayfish at each sampling period.

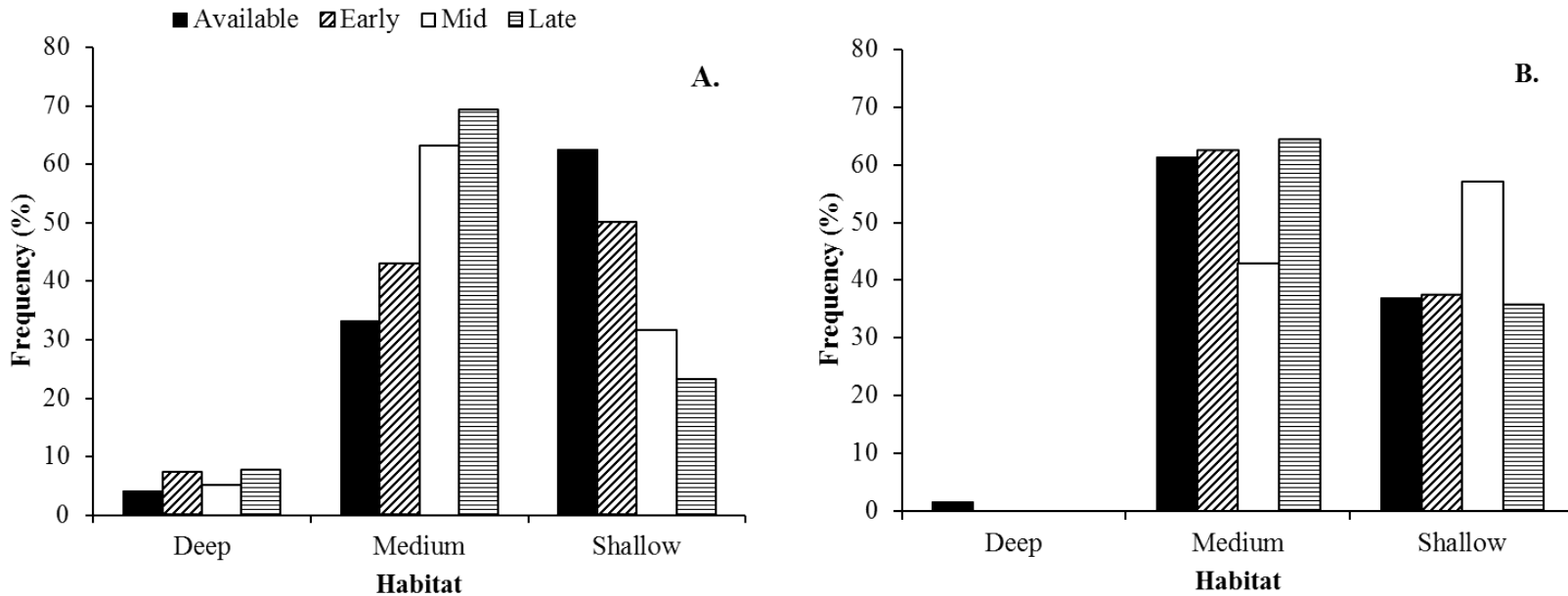


Figure 19. Habitat use by *Orconectes menae* relative to habitat availability in A.) Beech Creek and B.) Cucumber Creek. Habitat availability is shown as black bars whereas, the other bars indicate the frequency crayfish were observed in each habitat during different time periods (early, mid, or late). Bars with diagonal lines indicate the early season (May 5 - June 3), hollow bars represent the mid-season (June 4 - June 28) and bars with horizontal lines depict the late season (June 30 - July 24). Habitats were defined as deep (> 0.4 m), medium (0.1 - 0.4 m) and shallow (< 0.1 m).

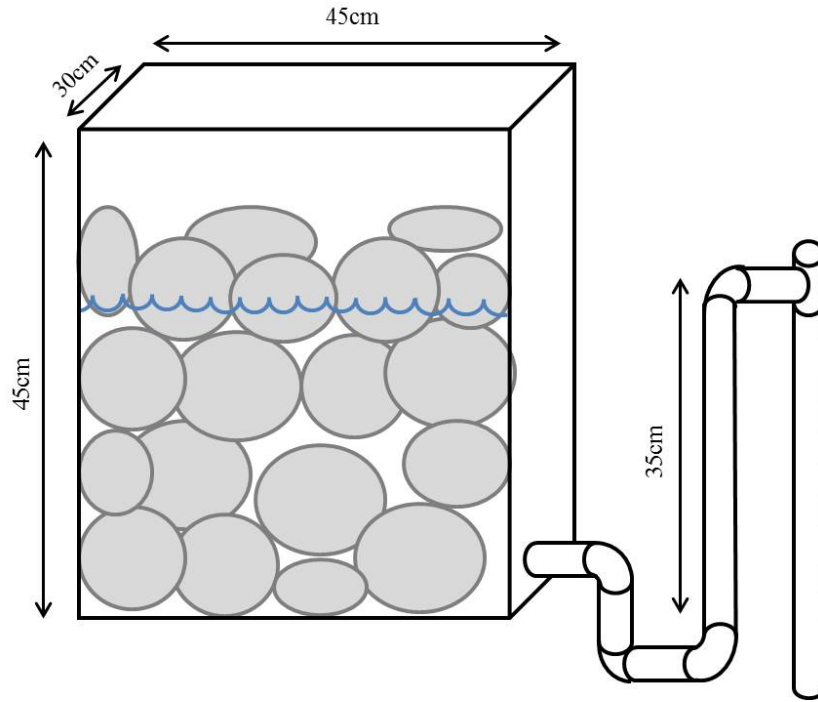


Figure 20. Front view of burrowing chambers used in laboratory experiments. Outflow pipe is located at the bottom right of the chamber, substrate is represented by gray circles, and the water level is shown as a wavy line within the chamber. The length of the vertical portion of the outflow pipe was adjusted to control the water level. The illustrated water-level line depicts water-level treatment two where the water was reduced to a depth of 35cm. The height of the outflow pipe is equivalent to the water depth because the height of the pipe regulates water depth within the chamber.

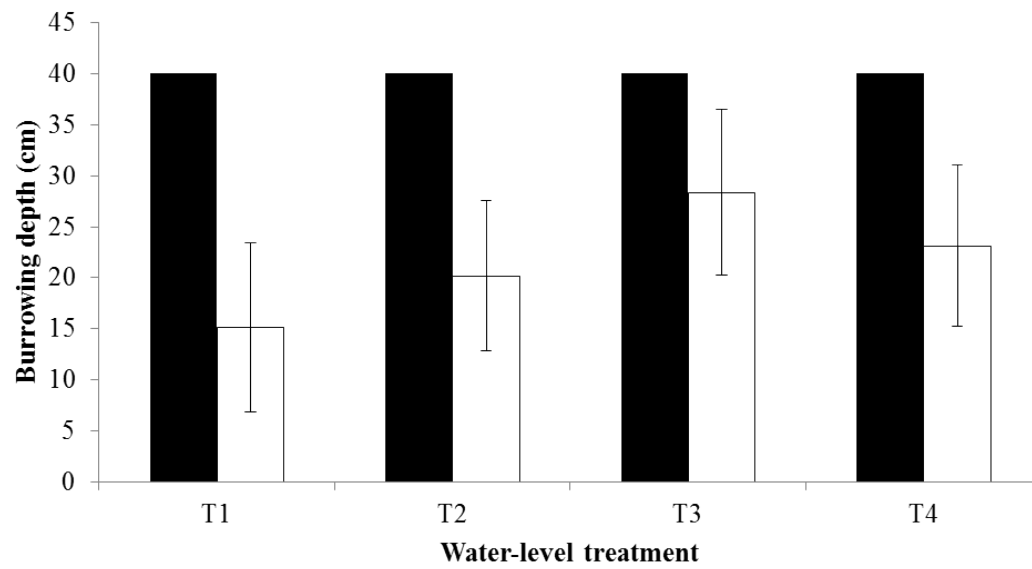


Figure 21. Relations between burrowing depth (mean $\pm$ 90% confidence limits), and water-level treatment with two substrate sizes: cobble in black bars and pebble in white bars. Water-level treatments are listed on the x axis: T1 = 45cm depth (control), T2 = 35cm depth, T3 = 25cm depth and T4 = 1.5cm depth (complete water reduction).

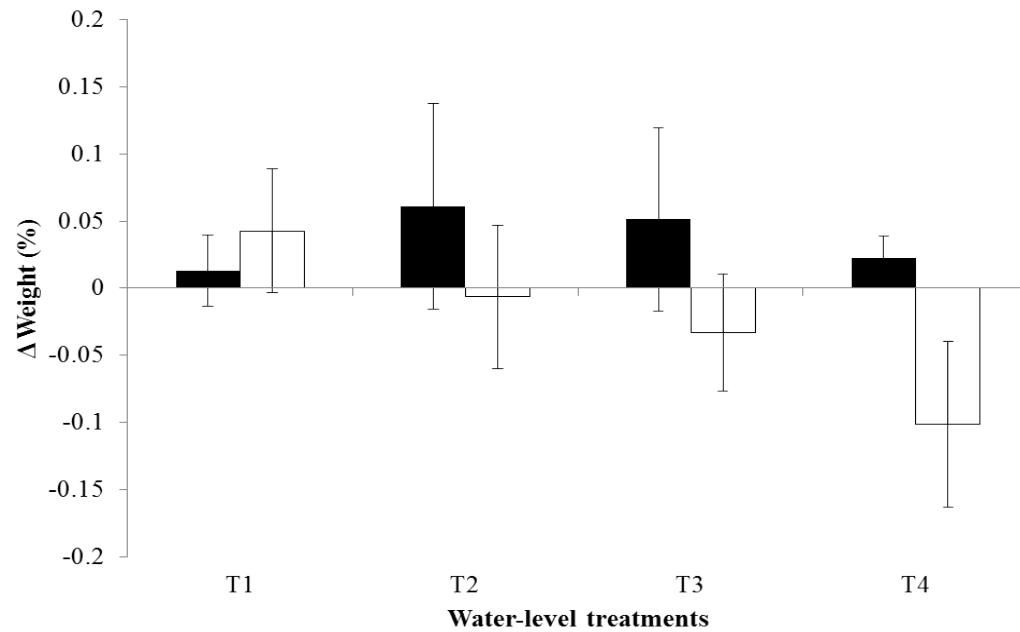


Figure 22. Relations between percent change in weight (mean $\pm$ 90% confidence limits), and water-level treatment using two substrate sizes, cobble (black bars) and pebble (white bars). Water-level treatments are: T1 = 45cm depth (control), T2 = 35cm depth, T3 = 25cm depth and T4 = 1.5cm depth (complete water reduction).

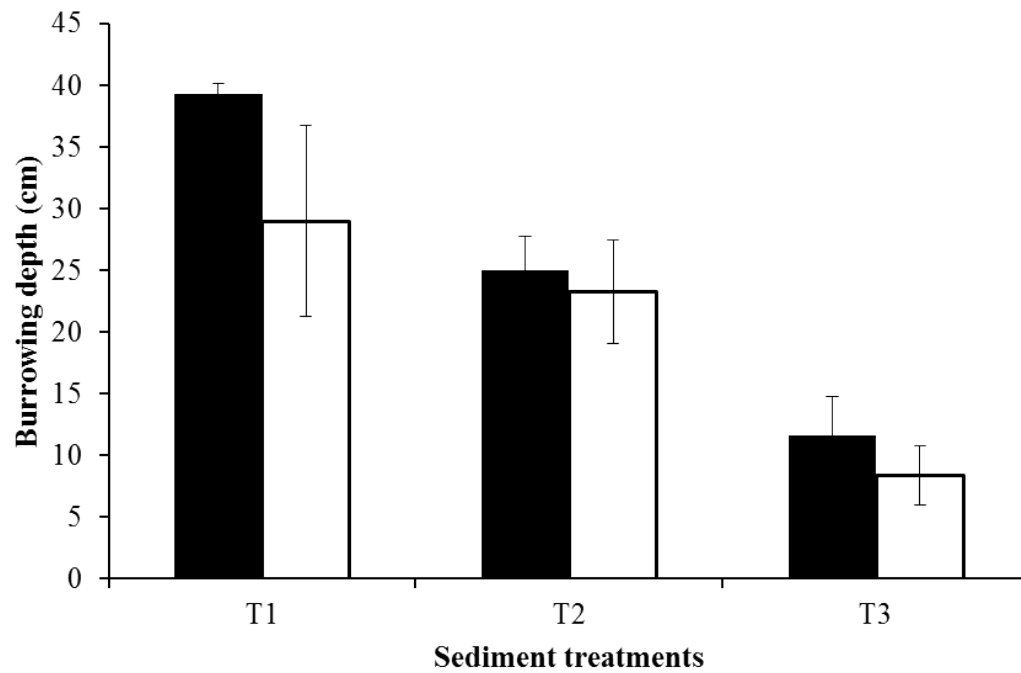


Figure 23. Relationship between mean burrowing depth ($\pm$ 90% confidence limits), substrate and sediment treatment. Sediment treatments are listed along the x axis: T1 = 0 L of sediment (control), T2 = 9.5 L (Interstitial spaces were 45% filled with fine sediment) and T3 = 19 L (interstitial spaces were 90% filled with fine sediment). The cobble substrate treatment is indicated by black bars and the pebble substrate is indicated by white bars.

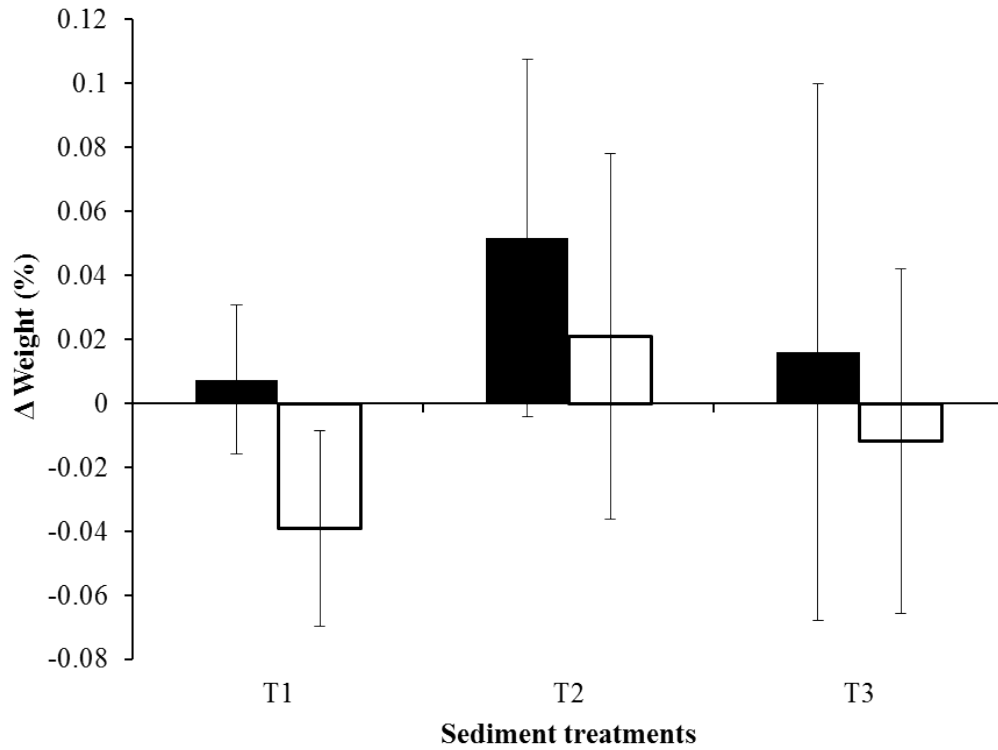


Figure 24. Relationship among mean percent change in weight ($\pm$ 90% confidence limits), substrate and sediment treatment. Sediment treatments are listed along the x axis: T1 = 0L of sediment (control), T2 ~ 9.5L of sediment and T3 ~ 19L of sediment (interstitial spaces were 90% filled with fine sediment). The cobble substrate treatment is indicated by black bars and the pebble substrate is indicated by white bars.