Ecology of crayfishes in the Ozark Highlands ecoregion of Oklahoma.

by

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Abstract

Crayfishes aid in the transfer of nutrients through aquatic ecosystems and are prey to many aquatic and terrestrial species. Although their importance in ecosystem dynamics is generally well recognized, information about the distribution and life-history for many species is unknown. My study objectives were 1) to determine habitat use by an assemblage of tertiary-burrowing crayfishes of the western Ozark Highlands ecoregion, and 2) assess the general life-history and microhabitat selection of *F. nana*, *F. macrus,* and *F. meeki brevis*. I used a hierarchical occupancy modeling framework to determine shared and species-specific physicochemical relationships for 7 *Faxonius spp*. All 7 crayfishes were generally associated with reaches of mid-order streams that had relatively wide and shallow channels and with the presence of Smallmouth Bass *Micropterus dolomieu*. *F. neglectus* and *F. virilis* are known invaders and were more tolerable of conditions indicative of local disturbance (i.e., increased pool habitat, soil with high runoff potential, high bank angles) than other native crayfishes. I sampled three creeks monthly to determine life-history patterns. I also assessed microhabitat use and habitat availability during spring and summer. On average, *F. nana and F. macrus* were smaller than *F. meeki brevis*. Reproductively active *F. nana* and *F. macrus* were observed in higher counts during late autumn and early spring, whereas *F. meeki brevis* appeared to have low levels of reproductively active individuals throughout the year. *F. meeki brevis* selected shallow microhabitats during spring and summer, whereas *F. nana* selected high-velocity microhabitats during the summer and low-velocity microhabitats during spring. My results indicate important species-specific habitat relationships and life-history patterns that will be beneficial to species status assessments. Moreover, the relationships associated with the known invaders may be useful for developing mitigation strategies in areas where they have become invasive.

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I. Introduction

Freshwater biodiversity, including crayfishes, is declining globally, and is attributed to a myriad of environmental factors. According to the International Union for Conservation of Nature (IUCN), more than 33% of all freshwater species need conservation (excluding species ranked as Data Deficient; IUCN 2021). The factors influencing this decline may be described by five broad categories; overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasive species (Miller et al. 1989; Didham et al. 2005; Dudgeon et al. 2006). Hogue and Breon (2022) found that habitat loss affected 88% and was the primary threat for 71% of threatened species on the IUCN red list (n = 20,784). For aquatic invertebrates such as crayfish and mussels, their small home ranges and limited dispersal mechanisms make them more susceptible to population decline (Collier et al. 2016).

Crayfishes are broadly distributed and play an important role in the trophic dynamics of aquatic systems. There are currently an estimated 644+ crayfishes globally (Lodge et al. 2012). Crayfishes are found on all continents except Antarctica, but most (360 species) are located in North America (Taylor et al. 2007; Lodge et al. 2012). Crayfishes are important to the transfer of nutrients through trophic levels and help regulate the benthic production available to fishes (Momot et al. 1978; Whitledge and Rabeni 1997; Reynolds et al. 2013). For example, (Huryn and Wallace 2006) estimated the Appalachian Book Crayfish *Cambarus bartonii* could convert 4-6% of annual leaf litter into fine particulate organic matter, thereby making it usable by other taxa (Creed and Reed 2004). Crayfishes also contribute largely to the diet of many popular sport fishes. For example, crayfish comprise over 60% of the annual diet for Smallmouth Bass *Micropterus dolomieu*, Rock Bass *Ambloplites rupestri*, and Shadow Bass *A. ariommus*

(DiStefano 2006). Although crayfishes are recognized as keystone species, studies documenting their basic ecology is lacking for many species (Moore et al. 2013; Richman et al. 2015).

The goal of my research was to improve our understanding of the distribution and habitat use of native crayfishes of the Ozark Highlands and adjacent ecoregions. My specific research objectives were to 1) determine the hierarchical habitat use by native crayfishes in Oklahoma streams, and 2) assess the general life-history patterns of three crayfishes of conservation concern (*F. nana nana*, *F. nana macrus*, and *F. meeki brevis*). Specifically, I determined their microhabitat selection, fecundity, reproductive timeline, and estimated age and growth patterns. These three species are of particular interest to natural resource agencies due to their lack of historical documentation and their presumed limited distributions.

Study area

My study area was centered in the Ozark Highlands Level-3 Ecoregion (hereafter Ozark Highlands, Environmental Protection Agency 2013) of Oklahoma (but see also Chapter 2). The Ozark Highlands drains 41,000 km^2 in the south-central United States including northeast Oklahoma, southeast Kansas, southern Missouri, and northern Arkansas. This ecoregion is characterized by limestone and dolomite lithologies and associated karst topography (Pflieger 1996). The ecoregion is relatively humid (104–125 cm of annual rainfall) with large tracts of oak-hickory-pine forest and many low gradient areas that were converted to pasture (Woods et al. 2005). Urban and agriculture land uses are rapidly expanding throughout this region (Petersen et al. 1998; Haggard 2010a; Scott et al. 2011). Approximately half of the agricultural lands are used for livestock production (Pickup et al. 2003). The reworking of historic floodplain deposits has created an excess of gravel supply in many Ozark Highland streams (e.g., Finley River, Martin and Pavlowsky 2013). Nonetheless, these streams are relatively clear under baseflow conditions and comprise typical riffle, run, pool morphologies (Brewer et al. 2007).

II. Hierarchical habitat use by native crayfishes in the Ozark Highlands of Oklahoma

Introduction

Dominant and aggressive native and non-native species outcompete other species, although the mechanisms are not well understood. Even species native to political boundaries may invade adjacent drainages or novel habitats but go unnoticed for a long time. These species are often highly adaptable and can thrive in a variety of conditions, which also allows them to quickly establish themselves in new environments. Although dominant and aggressive native species can play important ecological roles, they can also have negative effects on both other species in their native range or novel species when introduced outside their range. In particular, native crayfish assemblages have undergone significant changes following the introduction of non-native crayfishes (Lodge et al. 2000; Cruz et al. 2006); however, our understanding of the mechanisms associated with these changes is not well understood. There are several hypothesized displacement mechanisms including competition, differences in predation rates, disruption of reproduction, negative effects on growth and survival, and habitat alterations that favor one species (Butler and Stein 1985; Söderhäll and Cerenius 1999; Lodge et al. 2000; Perry et al. 2001; Fortino and Creed 2007; Taylor et al. 2007; Larson and Magoulick 2009). In some cases, the mechanisms may act synergistically and be related to a variety of different crayfish traits (e.g., environmental tolerances, Larson & Olden 2010). Although most species displacements occur in areas far removed from the native range of the invader, more recent evidence indicates that these introductions are not uncommon in nearby drainages where species invade and spread over several years. For example, DiStefano et al. (2002) examined life history differences among two native *Faxonius* crayfishes and *F. hylas*, the latter introduced from a nearby catchment. Likewise, Mouser et al. (2019) indicate invasion by *F. neglectus* into a cave system may have been facilitated by changes in reservoir elevation in the catchment. Our general lack of knowledge related to crayfish distributions, life histories (see also Chapter 3), and associations with environmental factors inhibit our ability to both be aware of invasions over smaller geographic areas and predict responses to invasions by species native to nearby drainages.

Hierarchical interactions among environmental factors are responsible for the observed heterogeneity and spatial arrangement of stream habitats that relate to both species' distributions and abundances. Coarse-scale factors such as climate, geology, and land use influence factors at finer spatial scales, such as water chemistry and substrate composition (Hynes 1975; Frissell et al. 1986; Tonn et al. 1990). Moreover, the relationships between biota and natural occurring conditions in catchments can change via interactions with human disturbances (Lammert and Allan 1999; Allan 2004). For example, Brewer and Rabeni (2011) show how land-uses in regions dominated by different lithologies and soils relate to changes in overarching population potential (i.e., densities) of riverine Smallmouth Bass *Micropterus dolomieu* in Missouri. Many landscape disturbances homogenize stream habitat, thus creating conditions tolerated by some species but not others (Byers 2002; Devictor et al. 2008; Nordberg and Schwarzkopf 2019). For example, Lee et al. (2017) found truncated Western Mosquitofish *Gambusia affinis* distributions related to increased velocities and macrophyte cover in areas dominated by agricultural land use. A majority of hierarchically structured studies focus on fish as the target taxa (e.g., salmonids (Beechie et al. 2008) Smallmouth Bass; (Miller and Brewer 2021), Smallmouth Bass and Largemouth Bass *M. salmoides* ; (Sowa and Rabeni 1995a), but has recently been applied to other taxa including crayfish (Westhoff et al. 2006; Magoulick et al. 2017; Mouser et al. 2018). Understanding the hierarchical interactions that shape ecosystems may lead to both conservation actions that meet the desired goal and improve our understanding of mechanisms (Wiens 1989; Stevenson 1997). However, biotic interactions are also important considerations and may also influence species distributions.

Investigations focused on understanding assemblage members and their relationships with physicochemical and biotic factors at multiple spatial scales are valuable to developing more meaningful conservation and management actions. The relationships with natural physicochemical conditions set an expected structure on distributions and improve our understanding of the conditions outside the range where introductions may be successful or how climate change may facilitate future distributions. Moreover, these investigations help facilitate an understanding of possible species traits based on ecological relationships (e.g., pelagic Great Plains minnows, Mollenhauer et al. 2022a). Lastly, the shared physicochemical associations among assemblage members provide some insight to how members may respond to specific threats (i.e., invasive species introduction and habitat loss).

Methods

Study area

In addition to sampling the Ozark Highlands ecoregion (see Chapter 1 Study Area), I also sampled across adjacent ecoregions to increase the variability in some coarse scale covariates. I sampled sites in the Boston Mountains and Central Irregular Plains ecoregions which transition from the Ozark Highlands to a more rolling hill and plateau topography dominated primarily by shale and sandstone lithologies (Woods et al. 2005). Streams in these regions are less likely to be spring fed and commonly comprise finer substrates (Splinter et al. 2010). Although climatic conditions are similar, some land-use practices (i.e., coal mining and urbanization) are more prevalent in these ecoregions than the Ozark Highlands (Woods et al. 2005).

Site selection

My sample sites were chosen haphazardly across the Ozark Highlands ecoregion and nearby drainages (Figure 1). Most stream access in the Ozark Highlands is privately owned and thus, required landowner permission. Each site comprised a sequence of riffle, run, and pool channel units following Rabeni and Jacobson (1993). Briefly, riffles were higher gradient areas with relatively coarse substrates, pools were depositional areas comprised of finer substrates and typically deeper water, and runs were transitional habitats with moderate velocities and depths and gravel to cobble substrates. Some sites also included off-channel habitats that comprised backwaters and forewaters (Rabeni and Jacobson 1993).

Sampling design and surveys

My study was set up in a multi-species, single season occupancy (MSOM) modeling framework. My season was defined as the relatively stable baseflow period that typically follows spring floods in the Ozark Highlands (i.e., late June through September) when species occupancy could be assumed closed. I sampled my sites (i.e., stream reaches, 20 times bankfull width, Rosgen 1996; Flosi et al. 2002) approximately three times (i.e., three surveys) during the season to evaluate both detection (through repeated surveys) and occupancy.

Crayfish sampling

Each crayfish survey used a combination of visual searches, seine hauls, and excavations during summer 2020-2022. Active searching was a combination of wading and snorkeling while capturing crayfish from each channel unit with hand nets. Search patterns followed the snorkeling methods of Miller and Brewer (2020). Briefly, my sample lanes (i.e., snorkeling and wading) were identified by dividing the channel longitudinally where lanes were narrower when water was shallow, comprised complex habitat, or had reduced visibility (Thurow et al. 2012). Observers searched in an upstream direction within their designated lane, overturning possible refuges (i.e., rocks, wood, tires, etc.) while collecting crayfish with hand nets (Vlach et al. 2010; Fulton et al. 2012). All crayfish were placed in a bucket on a shaded location of the streambank and identified after sampling each channel unit. Next, I kick seined in riffles and runs <1-m deep (Nolen et al. 2014), where one observer held a seine (1.5m x 1.75m, 3-mm mesh) perpendicular to discharge while the other person disturbed the substrate directly upstream of the seine. Observers then quickly pulled the seine through the area to collect any remaining crayfish (Mather and Stein 1993). In deeper-water or slackwater areas, observers pulled a beach seine (3 m x 1.75 m, 3-mm mesh) downstream in 10-m increments. Seine hauls were repeated until the entire length and width of the wadeable area was covered. Because some sites had dry stream sections during part of the baseflow period, I sampled crayfish in these areas by active searching and excavations(Jones and Bergey 2007; Dyer and Brewer 2018). I visually searched dry areas before conducting excavation plots. I then haphazardly placed a 1-m^2 plot in the streambed every 10 m where flow was interrupted (i.e., dry riffles and runs) and excavated each plot 30-cm deep while collecting crayfish (DiStefano et al. 2009).

I recorded the sex, reproductive form, and species of each crayfish sampled. I determined sex and reproductive form by gross examination of reproductive structures. Male crayfish were distinguishable by a pair of modified pleopods (i.e., gonopods) and female crayfish by the presence of a semen receptor (i.e., annulus ventralis). The reproductive status of male crayfish was recorded as form I (reproductive) or form II (non-reproductive). Form I males were distinguished by longer, more flexible, and feather like gonopods when compared to form II males (see Hobbs Jr. 1989; Pflieger 1996; Morehouse and Tobler 2013). Reproductively active females displayed either inflamed glair glands (i.e., swollen white ring near base of pleopods) or sperm plugs in the annulus ventralis (Mclay and van den Brink 2016). Field identification of crayfishes was based on morphological traits and multiple identification keys (e.g., Pflieger 1996; Morehouse and Tobler 2013). I made several vouchers of form-I males from each site for verification along with any species that could not be identified in the field. Vouchered crayfish were euthanized and placed in 70% ethanol for later laboratory analysis (Crandall 2016). All other crayfish were released near the sample location.

Physicochemical variables

I measured several covariates at multiple spatial scales that I hypothesized would relate to either crayfish detection or occurrence. Only covariates that remained relatively constant throughout the repeated visits (e.g., elevation) or were averaged across surveys (e.g., macrophyte coverage) were used as occupancy covariates, but detection covariates typically changed between visits (e.g., discharge) (MacKenzie et al. 2002). I quantified variables at three spatial scales (reach, segment, and catchment) to account for the nested hierarchy of riverine ecosystems (Hynes 1975; Frissell et al. 1986). Reach-scale variables were quantified at each site during my crayfish surveys. Stream segments were delineated using 2nd order stream (Strahler 1957) confluences where multiple reaches could be nested within segments. Catchment-scale variables were factors that set limits on species distributions (e.g., climate) and, in many cases, also constrain fine-scale variables (Stevenson 1997). For example, the lithology of the region dictates the natural pH ranges within the catchment (Hynes 1975), thereby affecting the successful hatch of species eggs (e.g., Fathead Minnows *Pimephales promelas*, Mount 1973). Catchment covariates were quantified over the area that drained to the downstream extent of each site (i.e., reach).

I quantified discharge and water clarity during each survey and the reproductive timing of crayfish to account for their possible effects on crayfish detection. During each survey, discharge was measured using the velocity-area method (Gordon et al. 1992). Water clarity may affect detection when actively searching for crayfishes and was quantified by horizontal secchi distance (see Magoulick 2004). Reproductive form is related to detectability of some crayfishes (Thorp and Covich 1991; Tierney et al. 2008; Larson and Olden 2016). Thus, I recorded the presence or absence of reproductive crayfishes (i.e., exhibiting sexual characteristics) during each survey.

At the reach-scale, I measured several abiotic and biotic variables that I hypothesized would influence the probability of crayfish occurrence (Table 1). I determined the proportion of channel units available in each stream reach. I estimated the proportion of each channel unit by measuring the average wetted width (3 evenly spaced measurements) and length using a measuring tape for distances <10 m and a laser range finder (Nikon Laser Forestry Pro) for distances >10 m. I then used the total area of each channel unit divided by the total area of the site to determine the proportional area of each channel unit. During each survey, I measured discharge (m^3/s) at a homogenous cross section of a run using the velocity-area method (Gordon et al. 1992). I then scaled the average discharge at each site by the corresponding drainage area to make it relative across sites. At the same cross section, I quantified the width-to-depth ratio (W:D) (Gordon et al. 1992). I measured water temperature approximately 0.5 m below the water's surface in a well-mixed and shaded area of a run. I quantified median substrate size (D50) at each site using a modified Wolman Pebble Count (Wolman M. G. 1954) following Fitzpatrick et al. (1998). Briefly, I measured the intermediate axis of approximately 50 substrate particles to determine the median particle size from all three surveys at a site (150 substrate particles from 3 surveys). Residual pool depth (RPD, 1.0 m) quantifies depth independent of discharge and was measured using the method of Lisle (1987) where downstream riffle crest depth was subtracted from the maximum pool depth. I measured RPD in the deepest available pool when multiple pools occurred in a single site. I visually estimated the percent vegetative cover and woody debris at each survey (Gordon et al. 1992) and averaged them across surveys for each summer (i.e., one measurement to represent each season). Bank erosion is related to increased sediment supply in streams (Rosgen 2001), but also creates undercut banks (bank angles <90°). Thus, I measured bank angle at a representative spot at each site by placing a field staff parallel to the bank and measuring the angle with a clinometer (Platts et al. 1983). Undercut banks were represented by angles > 90°. Lastly, I considered Smallmouth Bass present (1) at sites if they were sampled during at least one survey and absent (0) otherwise. Detection probability for Smallmouth Bass is relatively high using snorkeling and above water observations (Brewer and Ellersieck 2011) and was the method used to determine presence and absence of Smallmouth Bass.

I used GIS software (ArcGIS Pro 2.8.7, Esri 2021) and the National Hydrography Database plus V2 (NHD+; USGS 2016) to quantify covariates describing habitat, hydrography, and elevation at both the segment and catchment scales. I quantified sinuosity using the sinuosity index (SI = thalweg distance/straight line distance) described by Gordon et al. (1992) at the segment scale. Stream gradient (i.e., slope) was calculated as the change in elevation between the upstream and downstream extent of each segment divided by the downstream distance between the two points. I used a 10-m digital elevation model (NHD+) to determine elevation at the upstream and downstream extent of each segment and the Measurement Tool (ArcGIS Pro 2.8.7) to determine the distance (1.0 m) between the two extents. I measured elevation (1.0 m) every 10 m from the upstream to downstream segment extents to quantify the average elevation of each stream segment.

I hypothesized drainage area, geology, and soil composition would influence crayfish habitat use at the catchment scale (Table 1). Drainage area was the total land area (km^2) draining to the downstream extent of each reach. I delineated the drainage area for each site using the ArcGIS Pro watershed tool. I collected geological data from the U.S. Geological Survey's (USGS) National Geologic Map Database and determined proportional area of limestone in each catchment because is associated with basic pH levels and high concentrations of inorganic ions suitable for many crayfishes (Jay and Holdich 1981). I obtained soils data from the Natural Resources Conservation Service's Soil Survey Geographic database. I used these data to determine the proportion of hydrologic soil group D (HSGD) in each catchment.

I quantified landscape disturbance using a landscape disturbance index (LDI; Brown and Vivas 2005) modified by Mouser et al. (2018). LDI was calculated by multiplying the proportion of land use classes by a corresponding disturbance coefficient and summing the values. Coefficients were developed to describe landscape development intensity for land use classes and was later modified by Mouser et al. (2018) using National Land Cover Database (NLCD) classes. Coefficients rank each land use type on a scale of 1-10, where higher LDI values represent a more disturbed landscape. I determined the proportion of each NLCD land use class in a catchment and multiplied the proportions by the corresponding disturbance coefficient (Table 2). I then summed the values to calculate the LDI for each catchment.

Data analyses

I fit a MSOM for all crayfish species encountered in my study area. This approach estimates assemblage-level and species-level relationships in a single modeling framework (Dorazio et al. 2006). A MSOM is an extension of a single season occupancy model (MacKenzie et al. 2002) that uses detection data to simultaneously model the probability of detection (p) and the probability of occurrence (ψ) as a function of covariates at multiple spatial scales (i.e., reach, segment, and catchment). I used an occupancy model framework because it is efficient when monitoring species across a landscape (MacKenzie et al. 2006), and the robust design accounts for the imperfect detection (i.e., not detecting a species when it is present) common via most sampling gears (MacKenzie et al. 2002; Kéry and Schmidt 2008). Not accounting for imperfect detection can bias the underlying species-habitat relationships (Tyre et al. 2003; Gu and Swihart 2004; MacKenzie 2006). Additionally, the MSOM extension results in a composite analysis of the assemblage and provides more robust estimates of species-specific relationships (Russell et al. 2009; Zipkin et al. 2010).

In a MSOM framework, assemblage estimates are mean hyperparameters (μ) and species-specific coefficients are modeled as variation around μ (Dorazio et al. 2006; Kéry and Royle 2016). This framework is especially beneficial for including relatively rare species that would not have been included using more traditional frameworks. Occurrence and detection are assumed to follow a Bernoulli distribution. True occupancy state (z) for species i at site j is a latent variable, where z_{ij} = 1 if species i was detected at least once at site j or z_{ij} = 0 otherwise, and follows a Bernoulli distribution with the probability of occurrence ψ:

$$z_{ij} \sim Bernoulli(\varphi_{ij}).$$

Similarly, the probability of detection (y) follows a Bernoulli distribution:

$$y_{ijk} \sim Bernoulli(z_{ij} * \ p_{ijk}),$$

where y_{ijk} was conditional on the latent true occupancy (z) and detection probability (p).

There are 4 major assumptions to consider in occupancy modeling (MacKenzie et al. 2006; Bailey et al. 2014). Briefly, the assumptions are: (i) the occupancy state is “closed” (i.e., presence or absence of the species does not change during the season); (ii and iii) ψ and p are assumed constant across sites and surveys; and (iv) detection between sites is independent. I addressed the closure assumption (i) by sampling from July-October when streams are at relatively baseflow conditions and migrations related to reproduction in the assemblage should be minimal. I used covariates (i.e., habitat parameters) and grouping factors (i.e., random intercepts; (Wagner et al. 2006) to explain variation in ψ and p (ii and iii). Lastly, I addressed the site independence assumption (iv) by maintaining sites a minimum of 20x the average bankfull width apart so that sampling one site would not affect another site.

Prior to modeling, I first checked the distribution of my covariates and made any necessary transformations, tested for multicollinearity among covariates, and standardized all my continuous covariates. I plotted the frequency of each continuous covariate and applied a natural log transformation to right-skewed data (i.e., visibility, discharge, bank angle, W:D, drainage area, LDI, and HSGD) or made categorical transformations to highly bimodal data (i.e., cover, D50, limestone, and temperature). All categorical transformations were bivariate where: cover distinguished between the presence (1) or absence (0) of macrophytes or large woody debris at the site, median substrate size (D50) was (1) or was not (0) gravel (16-64 mm), limestone was present (1) or absent (0) in the catchment, and streams were classified as cooler (i.e., < 22 C°; 1) or warmer (i.e., > 22 C°; 0). I tested for multicollinearity among continuous covariates using a Pearson’s pairwise correlation coefficient (r). Because my detection (|r| = 0.35) and continuous occurrence covariates were not multicollinear (|r| < 0.58, Table 3), I retained them all for modeling. I also examined the independence of my categorical covariates by plotting their frequency of occurrence and they were also retained for modeling purposes. Lastly, I standardized my continuous covariates to a mean of 0 and standard deviation of 1 to improve model interpretation (Schielzeth 2010).

I modeled the variation in ψ and p as a function of my covariates. Species-specific coefficients for ψ, p, and relationships with occupancy covariates were modeled as deflections around the hyperparameter governed by a probability distribution (Dorazio et al. 2006; Kéry and Royle 2016). Detection relationships with covariates were assumed to be shared by the entire assemblage; thus, variation between species was not modeled to maintain simplicity on the detection side of the model. Because species that are prevalent across the study area often have a higher detection probability (Zipkin et al. 2009), I modeled the correlation between species detection intercepts θ_i, and species occurrence intercepts α_i by allowing them to be jointly distributed as $[\theta_i, \alpha_i \,|\Sigma] \sim N(0, \Sigma)$, where σ_θ^2 and σ_α^2 are the variance components for Σ, a 2x2 matrix with covariance $\sigma_{\theta\alpha}$ (Dorazio et al. 2006; Kéry and Royle 2008). The detection component of my model was structured as:

$$\mathrm{logit}(\mathrm{p}_{\mathrm{ijk}}) = \theta_i + \beta_1 \mathrm{x}_{\mathrm{jk},1} + \beta_2 \mathrm{x}_{\mathrm{jk},2} \ldots + \beta_N \mathrm{x}_{\mathrm{jk},N},$$

$$\text{for } i = 1,2\ldots i, \text{ for } j = 1,2\ldots j, \text{ for } k = 1,2\ldots k,$$

where $\mathrm{p}_{\mathrm{ijk}}$ is the probability of detecting crayfish i at site j on the k^{th} visit, θ is the detection intercept, and β_1 through β_N are the coefficients of covariates x_1 through x_N at site j on the k^{th} visit. I allowed the occurrence probability intercept to vary by 8-digit hydraulic unit code (HUC 8) units h (1 – 22) and sampling year y (2020, 2021, 2022) using a grouping factor (Gelman and Hill 2006; Wagner et al. 2006) to account my nested sampling design (i.e., psuedoreplication). I chose HUC 8 units because they distinguish portions of stream networks based on hydrologic or morphologic drainage area characteristics (Jones et al. 2022). The probability of occupancy was modeled as:

$$\mathrm{logit}(\varphi_{\mathrm{ij}}) = \alpha_i + \beta_{1\mathrm{i}}\mathrm{X}_{1\mathrm{j}} + \beta_{2\mathrm{i}}\mathrm{X}_{2\mathrm{j}} \ldots + \beta_{\mathrm{Ni}}\mathrm{X}_{\mathrm{Nj}} + \gamma_{ih} + \tau_{iy}$$

$$\text{for } i = 1,2\ldots i, \text{ for } j = 1,2\ldots j,$$

$$\beta_{ni} \sim Gaussian\ (\mu_{\beta_n}, \sigma_n^2), \text{ for } i = 7$$

$$\gamma_{ih} \sim Gaussian\ (0, \sigma_\gamma^2), \text{ for } h = 22$$

$$\tau_{iy} \sim Gaussian\ (0, \sigma_\tau^2), \text{ for } y = 3$$

where φ_{ij} is the probability that species *i* occupies site j, α is the occurrence intercept, $\beta_{1\mathrm{i}}$ - β_{Ni} are the coefficients of covariates X_1- X_N at site j for species i, γ is HUC 8 grouping factor, τ is the year grouping factor, μ is the assemblage mean hyperparameter, and σ is the variance of μ (i.e., how similar the relationship is among species).

I used the program JAGS (Plummer 2003) called from the statistical program R (v4.0.3, R Core Team 2020) using the package jagsUI (Kellner 2015) to fit a hierarchical Bayesian MSOM. I used vague priors from a normal distribution for coefficients and vague priors from a gamma distribution for the associated SDs (Kery and Royle 2016). I estimated posterior distributions using Markov chain Monte Carlo methods with 4 chains of 150,000 iterations with a 25,000 burn-in phase and thinning equal to 50.

I began by constructing a global model that contained all occurrence and detection covariates and the two grouping factors. Specifically, the global model had water visibility, discharge, and reproductive timing as detection covariates. I fit average bank angle, W:D, RPD, discharge, percent pool habitat, segment slope, segment elevation, segment sinuosity, drainage area, catchment scale LDI, and the amount of HSGD in the catchment as continuous occupancy covariates in the model. I also fit dominant substrate, cover, Smallmouth bass presence, water temperature, and limestone as categorical covariates (see covariate descriptions). I also included a quadratic term for drainage area because I hypothesized resources (i.e., proportions of channel units, food sources, substrates, Strahler 1957; Vannote et al. 1980) and disturbances (Stevenson 1997) may be limiting in relatively smaller and larger drainages. Lastly, the occurrence part of the model included year and HUC 8 unit grouping factors.

I then simplified the occupancy portion of my model by removing occurrence covariates that had coefficients with high uncertainty. I removed coefficients with endpoints of 95% highest density intervals (HDIs, Kruschke and Liddell 2018) that were greater than the absolute value of the mode (i.e., most likely value) in the posterior distribution for all species. When both endpoints of the posterior distribution are greater than the absolute value of the mode, there is little support for the strength or direction of the true relationship (Kruschke and Liddell 2018). For example, if the mode of the posterior distribution is 1.5 and the 95% HDI ranges from -3.0 to 3.0, it is plausible that the true relationship is stronger than the mode in the opposite direction, leading to a type I error (i.e., finding a significant relationship when there is not one). I removed average discharge, cover, water temperature, stream-segment sinuosity, and LDI because they did not meet my criterion. I did not remove any grouping factors.

I examined model fit using a Bayesian *p*-value from a posterior predictive check and convergence using the Brooks-Gelman-Rubin statistic ($\hat{R}$, Brooks and Gelman 1998). Briefly, for each iteration a new data set was simulated, and a Chi-square discrepancy value was used to compare the model to both the original and simulated data sets. The Bayesian *p*-value was then calculated as the mean of the posterior distribution of the difference between the two Chi-square discrepancy values (Kéry and Royle 2016). Bayesian *p*-values are a conservative measure of global lack-of-fit, where values near 0.5 indicate adequate fit and extreme values (i.e., <0.05 or

>0.95) are indicative of a lack-of-fit (Kéry and Royle 2016; Conn et al. 2018). Convergence (i.e., mixing of chains) was considered adequate if $\hat{R} < 1.1$ for all parameters (Brooks and Gelman 1998).

Results

Crayfish sampling

From 2020-2022, I sampled crayfishes from sites across the Ozark Highlands and surrounding ecoregions in Oklahoma. During the three summers, I compiled detection histories and habitat measurements from 249 surveys for seven crayfishes at 88 sites across 22 HUC 8 units and three ecoregions (Table 4). I sampled 68 sites in the Ozark Highlands ecoregion, 9 sites in the Boston Mountains ecoregion, and 11 sites in the Central Irregular Plains ecoregion.

As expected, the commonness of crayfishes varied by ecoregion (Table 5). *F. neglectus neglectus* (hereafter *F. neglectus*) was the most common crayfish species sampled and was detected during 215 surveys and at least once at 76 sites. The rarest crayfishes sampled were *F. palmeri*, which was detected at 6 sites and during 11 surveys; and *F. nais*, which was detected at 8 sites and during 8 surveys. The remaining crayfishes were detected during 32-105 surveys and at least once at 13-39 sites. Additionally, Smallmouth Bass was detected at least once at 41 sites and during 99 surveys. The commonness of all species was relatively similar in the Ozark Highlands and Boston Mountains ecoregions, with the exception of *F. nana macrus* (hereafter *F. macrus*) which was found only at sites in the Ozark Highlands. *F. virils* and *F. nais* were the only two species sampled in the Central Irregular Plains ecoregion.

Physicochemical variables

Reach scale habitat covariates varied across sites and ecoregions but were relatively similar among years (Table 6). The average stream gradient (~0.003) and sinuosity index (~

1.22) was similar among ecoregions. Sites in the Ozark Highlands and Boston Mountains ecoregion were relatively similar. Sites in these two ecoregions had similar pool depths (~ 0.87 m), average discharge (~ 0.30 m^3/s), and water visibility (~ 4.0 m) and had relatively larger drainage areas (~ 100 km^2) and lower landscape disturbance (LDI; ~ 2.00) compared to sites in the Central Irregular plains. Sites in the Central Irregular Plains Sites were located near Tulsa, OK and were more disturbed than those in the other two ecoregions (i.e., higher LDI, higher bank angles, and lower W:D). The physicochemical conditions did not vary much among sample years. Discharge and drainage area were the only two covariates that were noticeably different between years. The average discharge at my sites decreased over the sample years (2022, 0.09 m^3/s; 2021,0.20 m^3/s; and 2020, 0.41 m^3/s). Lastly, I sampled sites higher in the network in 2020 and moved to sampling larger streams in 2021 and 2022. (2020, 126 km^2; 2021, 72 km^2; and 2022, 39 km^2).

Data Analyses

My final model had appropriate model fit, adequate mixing of chains, and including the grouping factors accounted for variability among HUCs and sampling years. All modeled parameters successfully converged with a $\hat{R} < 1.001$ and an effective sample size >2000 suggesting the model had appropriate mixing of chains. Categorical covariates include the presence of Smallmouth Bass (absence as the reference), gravel dominated streams (no gravel as the reference), and the presence of limestone lithology (no limestone as the reference). Additionally, the standard deviation of grouping variables captured unexplained heterogeneity between HUC 8 units (0.48) and among sampling years (0.28).

The average detection probability for the assemblage was relatively high (0.87), but there were species-specific differences. Detection probability was lowest for *F. palmeri* (0.63) and highest for *F. neglectus* (0.98) (Table 7). Detection was negatively associated with water visibility, daily discharge, and reproductive timing (Table 8). However, all detection relationships were relatively weak.

My final model represented both shared relationships among the crayfish assemblage and species-specific relationships with occupancy covariates (Table 9). The variance parameter σ describes how similar shared relationships were among species, where a lower σ is indicative of a more similar relationship. The average probability of occurrence for the assemblage was 0.31 and, similarly to detection, was highest for *F. neglectus* (0.97) and lowest for *F. palmeri* (0.06) (Table 7). All species shared a positive relationship with W:D, the presence of Smallmouth Bass, and stream-segment slope. Species also shared a quadratic relationship with drainage area where occurrence probability was lowest in very small streams and rivers but higher in mid-sized drainages (Figure 2; Table 9). The relationship with W:D was similar among species but the effect size was greatest for *F. virilis* and *F. meeki brevis*. Most assemblage members were nearly equally likely (0.45 times as likely) to occur at sites with or without SMB, except *F. nais* and *F. nana nana* (0.12 times as likely). The positive relationship with segment slope was relatively strong for all species except *F. neglectus* (Figure 3). *F. neglectus* and *F. nana nana* (hereafter *F. nana*) had a weak quadratic relationship with drainage area, whereas all other species were more likely to occur in small to medium-sized streams (Figure 4). The direction and strength of relationships with all other covariates were species-specific (Figure 2; Table 9).

I found several differences in the strength and direction of species-specific relationships with all other covariates (Figure 2; Table 9). *F. neglectus* had relatively weak relationships with all covariates but was the most likely to occur in catchments with limestone lithology (Table 9). *F. virilis* was the only species that was positively related to bank angle and increasing amounts of pool habitat (Figure 2), but both relationships were relatively weak (Table 9). Additionally, *F. virilis* had a relatively strong negative relationship with stream elevation at the segment scale (Figure 5) and was the only species to have a strong positive relationship with the amount of HSGD in the catchment (Figure 6). *F. nais* and *F. palmeri* shared similar and relatively weak relationships with all covariates (Figure 2; Table 9). *F. macrus* shared similar relationships with *F. nais* and *F. palmeri* in most cases, except for being positively associated with gravel dominated streams, limestone in the catchment (Figure 2), and elevation (Figure 5). Occupancy by both *F. nana* and *F. meeki brevis* was positively related to RPD and elevation and negatively related to gravel-dominated reaches and increasing amounts of HSGD in the catchment (Figure 2). However, *F. nana* had a stronger relationship with elevation (Figure 5) and was positively related limestone in the catchment, whereas *F. meeki brevis* was negatively associated with limestone (Figure 2).

Discussion

Understanding how relationships differ among species or groups of species with similar traits is important for understanding their distributions. I found that the occurrence of known invaders (i.e., highly fecund species, larger body size, and increased environmental tolerance, Rabalais and Magoulick 2006; Larson and Olden 2010) was less dependent on local condition than other species. Specifically, *F. neglectus* and *F. virilis* are known invaders (Daniels et al. 2001; Larson et al. 2018; Magoulick et al. 2022) and known to invade novel habitats (Imhoff et al. 2012; Larson et al. 2018; Rodger and Starks 2020). *F. neglectus* was ubiquitous across my study area, whereas *F. virilis* favored increasing bank angles, increasing amounts of HSGD, and shallower pools. Although undercut banks (i.e., high bank angles) may provide habitat for some crayfishes (Parkyn and Collier 2004), it is also indicative of increased sedimentation and erosion.

Hydrologic soil group “D” is representative of soils with high runoff potential and increasing amounts of HSGD in the catchment is related to sedimentation at finer spatial scales (Doisy et al. 2005; Brewer et al. 2007). Associated siltation and shallower pools reduce habitat complexity (Matthews 1998; McIntosh et al. 2000) and the availability of larger substrates that provide shelter to many crayfishes (Stein and Magnuson 1976; Rabeni 1985; Clark et al. 2013). However, other crayfishes with much more restrictive ranges shared a strong positive relationship with pool depth and a negative relationship with bank angle and increasing amounts of HSGD. *F. nana* and *F. meeki brevis* are considered threatened by the American Fisheries Society due to their limited distributions (Taylor et al. 2007) and were strongly associated with reaches having deeper pool habitats, more stable bank conditions, and very little HSGD in the catchment. Collectively, this indicates that the latter species may be less tolerant of environmental perturbation, unlike *F. neglectus* and *F. virilis* that appear well adapted in habitats where other species do not thrive.

Biotic interactions may influence species distributions via several mechanisms and are often overlooked in distributional analyses. Biotic interactions such as competition, predation, and the spread of diseases may affect species distributions at fine (Connell 1961; Wiens 2011) and coarse spatial scales (Wisz et al. 2013; Clark et al. 2014). The ability of invasive crayfishes (i.e., species outside their native range causing ecological harm) to facilitate these interactions make their expansion one of the primary threats to native crayfishes (Larson and Olden 2010; Twardochleb et al. 2013) and a leading cause of extirpation in European crayfishes (Lodge et al. 2000). However, few studies have examined how the presence of a native species that is a known invader may affect the distributions of other sympatric crayfishes (James et al. 2015) (but see Mouser et al. 2018). Crayfishes that are known invaders may compete for resources (Hill and

Lodge 1994; Gherardi and Cioni 2004; Westhoff et al. 2006; Imhoff et al. 2012), spread diseases (Gil-Sánchez and Alba-Tercedor 2006; Bohman et al. 2006; Kozubíková et al. 2008), and alter trophic systems (Holdich 1999; Johnson et al. 2014). For example, the Spineycheek Crayfish *Faxonius limosus* has been extirpated from its native range in West Virginia (14 locations; Jezerinac 1995); the extirpation is related to perceived competition from the increasingly abundant and invasive Virile Crayfish *F. virilis* (Swecker et al. 2010). However, I found that *F. virilis* was able to exploit altered habitats but did not occur in less disturbed habitats, whereas *F. neglectus* was ubiquitous across my study area. The relatively strong relationships with local disturbances for *F. virilis* suggest that it may actually be a weak competitor and is only able to invade habitats that were not favorable for other native species. Thus, conservation and preservation of streams with known populations of imperiled crayfishes would likely reduce the risk of invasion by *F. virilis*.

Underlying soils and lithology are structuring variables for many species in this assemblage including the known invaders. Higher elevation streams are often associated with coarse substrates (i.e., not necessarily gravel) and higher water velocities (Knighton 1998). Mouser et al. (2018) also found that *F. nana* and *F. macrus* occurrences were positively associated with stream elevation. However, my model showed an opposite relationship by *F. neglectus*, *F. virilis*, and *F. meeki breivs*. These differences may be related to several factors. First, Mouser et al. (2018) used data from other studies that included a broader geographic area (i.e., higher elevations) and additional assemblage members which could certainly result in different relationships and broader range of elevations. Second, the authors used data from 2002-2015 and changes in assemblage relationships may have occurred over time. Streams in limestone dominated catchments are generally basic with abundant dissolved solids and rocky substrates (Jay and Holdich 1981; Brewer et al. 2007). Several studies have found that lithology is a structuring variable that influences the distributions of stream-dwelling crayfish (Westhoff et al. 2011; Magoulick et al. 2017). Results by Mouser et al. (2018) also show a strong relationship between limestone and the occurrence of *F. neglectus* and *F. virilis*. Like my study, the two species were not found together at sites, and they had opposite relationships with limestone lithology. It is unclear if the water chemistry associated with limestone is limiting to *F. virilis* or if one of the two known invaders is excluding the other.

Most crayfish were negatively associated with the increasing proportion of pool channel units at a site (i.e., except *F. virilis*), whereas all crayfish were positively associated with the presence of Smallmouth Bass. Habitat use at the channel unit scale is often species-specific (Flinders and Magoulick 2005). However, several studies have found that young-of-year and smaller crayfish often use shallower water with higher current velocities (Rabeni 1985; Englund and Krupa 2000) associated with riffles and runs, whereas larger crayfish (Clark et al. 2013) and gravid females (Mason 1970) may find shelter in low velocity pools and backwaters. Brewer et al. (2009) found that secondary production by stream dwelling crayfishes was generally higher in non-pool channel units. Thus, reaches dominated by a single habitat type may not support all life-history strategies or may result in lower production by some species. Similar distributions and habitat relationships observed by crayfishes and Smallmouth Bass are likely related to the predator-prey relationship (i.e., crayfish are the primary component of Smallmouth Bass diets, DiStefano 2006) and coevolution of the two in riverine systems. For example, Smallmouth Bass densities are negatively related to increasing pool habitat in a reach (Sowa and Rabeni 1995; Brewer 2013). Thus, as crayfish populations continue to decline, it is likely that populations of Smallmouth Bass and other popular sport fishes will also be affected.

My sampled assemblage shared an affinity for higher gradient streams in mid-sized drainages with relatively wide and shallow channels. These fluvial geomorphological processes relate to local conditions that may provide shelter and food sources for many crayfish. Channel scour in many Ozark streams is constrained by bedrock creating wide and shallow runs upstream and downstream of bluff pools (Rabeni and Jacobson 1993). These shallow areas likely provide shelter from predators, such as Smallmouth Bass, that often use bluff pool habitats (Brewer et al. 2007). Higher gradient streams in mid-sized drainages are generally associated with coarse substrates, and high benthic production (Vannote et al. 1980; Frissell et al. 1986; Knighton 1998) and may be favorable for many crayfish species. Streams with smaller drainage areas are associated with a higher frequency of flow intermittency (Vannote et al. 1980; Sabo et al. 2010) and the ability of crayfishes to burrow into the hyporheic zone limits the distribution of some species to more permanent streams (DiStefano et al. 2009; Yarra and Magoulick 2018). Larger drainage areas likely accumulate more sediment from upstream sources (Spaling and Smit 1995; Seitz et al. 2011) and may reduce the amount of shelter and coarse particulate organic matter available to crayfishes. Moreover, other studies have found that landscape disturbances often interact with stream size to influence the distribution of stream fauna (fish, Brewer and Rabeni 2011; crayfish, Mouser et al. 2018). There may be other factors affecting distributions related to water quality that I did not quantify. For example, degraded water quality related to poultry production has been a central debate in the Illinois River catchment (King and Richardson 2007; Haggard 2010b; Haggard et al. 2017) and may limit crayfish abundance in that river.

Given the relatively high detection of species, it was not surprising that covariate relationships were relatively weak. Snorkeling and visual observations of aquatic organisms are commonly impaired by visibility (Thurow et al. 2012). As discharge increases, our sampling gears become less effective (e.g., snorkeling, Larson and Olden 2016, seining, Magoulick et al. 2017). Lastly, several authors have observed difficulties sampling crayfish while reproducing (Thorp and Covich 1991; Somers and Green 1993) because crayfish commonly become less active and select shelter habitats (Mason 1970; Larson and Olden 2016). However, my detection relationships were relatively weak, likely because the probability of detection was relatively high using our sampling methods. This suggests that if a species is present at a site, my sampling methods are likely to detect them despite minor changes in baseflow conditions. The high probability of detection in my studies is likely related to my high sampling effort, where we sampled all possible areas of each site. Future projects in a similar stream system and under similar physicochemical conditions may focus sampling efforts on covering a larger geographic area (i.e., more sites) rather than repeated site visits. By sampling more locations fewer times, we would be more likely to detect other narrow range endemics assuming detection is also high for unsampled species. Alternatively, the extra time might be devoted to excavating dry streambeds or floodplains where burrowing species could be detected (DiStefano et al. 2009).

As is common with many ecological modeling approaches, there is a trade-off between precision and explanatory power that should be considered when using this modeling approach. In my modeling approach there is a trade-off between species-specific fit and the assemblage mean (μ) (i.e., coefficients shrink towards a central tendency, Dorazio et al. 2006; Kéry and Royle 2008). For example, I was able to make estimates for rarer species (e.g., *F. palmeri*), but this increased the uncertainty around estimates for more common species (e.g., *F. neglectus*). Additionally, because species-specific relationships are derived from μ, it is not possible to include multiple forms of a relationship (e.g., linear, polynomial, quadratic) that may vary by species. For example, the relationship with drainage area was not quadratic for *F. neglectus* and *F. nana*, but I was not able to model the relationship as linear for these two species and model it as quadratic for all others. However, I feel these trade-offs are reasonable given single-species analyses are unable to provide estimates for less common species (Zipkin et al. 2009) and more traditional multi-species models, where relationships are interpreted as differences from a reference species, would be more cumbersome and likely have similar fit issues (Mollenhauer et al. 2022b). Additionally, I recognize that all species do not experience the same range of physicochemical conditions. Thus, using the same range of simulated values likely extrapolated my predictions outside of the range of physicochemical conditions experienced by some species. However, this approach does allow me to directly compare relationships among the assemblage members.

The way researchers examine crayfish relationships among riverscapes is changing and the results may be beneficial to developing more proactive conservation plans. Crayfish research has historically been conducted at a fine scale or on one or few focal species at a time (e.g., Larson and Magoulick 2011; Ishiyama et al. 2012; DiStefano et al. 2016). Although, more recent studies have investigated more coarse scale environmental relationships (Magoulick et al. 2017; Mouser et al. 2018; Krause et al. 2019) or have included multiple species (Johnston and Robonson 2009; Weinländer and Füreder 2012; Dyer and Brewer 2018). My modeling approach, however, is useful for identifying strategies that may benefit entire assemblages and allow for direct comparisons among assemblage members. For example, based on the relationships I found in my study, high conservation value could be placed on higher gradient and mid-sized streams; however, there must be recognition that the character of these sites is also a function of the upstream drainage. This approach is also beneficial for identifying how imperiled or known invaders species may be uniquely affected by changes to our riverscapes. My results indicate that increased sedimentation and erosion may result in habitats more favorable for known invaders. Those same conditions are negatively associated with Smallmouth Bass and native crayfishes. My results showed that poor land use practices and natural conditions related to sedimentation may bolster the spread of known invaders and that the benefits of conserving native crayfishes will likely extend to native sportfishes.

Table 1. Justification for covariates hypothesized to influence the occurrence of crayfishes. Scale is the spatial scale used to measure each covariate.

Scale	Covariate	Justification
Reach	Pool habitat	Crayfishes use areas where the proportion of channel units is adequate for survival of all life stages.[1, 2, 3]
	Discharge	Smaller crayfish species use shallow low velocity habitats found in lower discharge streams.[1, 4]
	W:D	Indicative of local disturbance where deep and wide channels tend to reflect erosion; thus, more tolerant species would use lower W: D ratios.[4, 5]
	Temperature	Thermal tolerance differ among crayfish species and water temperature is known to shape crayfish distributions.[6, 7, 8]
	Substrate	Smaller crayfishes can use more fine substrates for cover. [1, 9]
	RPD	Available pool depth during periods of low flow may make crayfishes more acceptable to predation.[9, 10, 11]
	Cover	Vegetation and woody debris provide cover for crayfishes.[12, 13]
	Bank Angle	Undercut banks tend to be associated with local disturbance but may also provide refuge for crayfishes.[14]
	SMB	Predators influence crayfish distributions and behavior but Smallmouth Bass have coevolved with crayfish in this region.[15, 16, 17]
Segment	Sinuosity	Crayfishes may use more sinuous streams due to the higher frequency of riffle-pool sequences.[18]

	Slope	High gradient streams are associated with increased velocity, larger substrates, and riffle habitats needed for reproduction, growth, and survival of crayfishes. [13, 19, 20]
	Elevation	Elevation is associated with microclimates, vegetation cover, and substrate sizes which relate to choice of successful traits (i.e., body size, thermal tolerances, etc).[7]
Catchment	Drainage area	Location in the network relates to multiple fine scale factors such as water volume, drying frequency, benthic production etc.[21, 22, 23]
	Limestone	Underlain lithology influences pH, springflow, stream morphology, and underlying soils and substrate composition which relate to hatch success, environmental tolerances.[24, 25, 26]
	HSGD	Associated with high runoff potential and which would likely be favored by more tolerant species.[27, 28, 29]
	LDI	Indicative of land-use disturbance which may lead to extirpation of sensitive species due to insecticide use (prevents molting) and increased runoff/sedimentation.[22, 30]

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Table 2. Landscape disturbance coefficients (LDI) for each of the National Land Cover Database (NLCD). See Mouser et al. (2018) for a complete explanation of how the coefficients were assigned to each class.

NLCD Class	LDI
Deciduous Forest	1
Emergent Herbaceous Wetlands	1
Evergreen Forest	1
Herbaceous	1
Mixed Forest	1
Open Water	1
Shrub/Scrub	1
Woody Wetlands	1
Developed, Open Space	1.83
Hay/Pasture	2.99
Cultivated Crops	4.54
Developed, Low Intensity	7.45
Developed, Medium Intensity	7.59
Developed, High Intensity	7.99
Barren Land	8.32

Table 3. Pearson’s pairwise correlation coefficients (r) for occupancy covariates. Variables include bank angle (BA), residual pool depth (RPD), width:depth ratio (W:D), discharge scaled by the drainage area (Q), percent pool habitat (Pool), slope (i.e., stream gradient) of the segment, average elevation of the segment, sinuosity of the segment, drainage area of the reach (DA), landscape disturbance (LDI), and the amount of hydrologic soil group “D” in the catchment (HSGD). Variables with a * indicate that they were log-transformed.

Variable	BA*	RPD	W:D*	Q*	Pool	Slope	Elevation	Sinuosity	DA*	LDI*	HSGD*
BA*	1.00										
RPD	-0.07	1.00									
W:D*	-0.38	0.09	1.00								
Q*	-0.06	0.19	0.03	1.00							
Pool	0.08	0.20	-0.16	-0.30	1.00						
Slope	-0.03	-0.22	-0.18	0.21	-0.11	1.00					
Elevation	-0.02	0.19	-0.05	0.27	-0.10	0.16	1.00				
Sinuosity	0.11	-0.04	-0.12	-0.05	0.03	-0.08	-0.02	1.00			
DA*	-025	0.39	0.45	0.18	-0.10	-0.58	0.11	-0.20	1.00		
LDI*	0.31	-0.23	-0.44	-0.11	0.18	0.00	-0.28	0.21	-0.58	1.00	
HSGD*	-0.06	-0.08	0.23	-0.29	-0.05	-0.21	-0.32	-0.04	0.04	0.20	1.00

Table 4. Crayfish sampling effort (i.e., number of sites and surveys) from 2020-2022 in the Ozark Highlands (OH), Boston Mountains (BM), and Central Irregular Plains (CIP) ecoregions. Sites were pool riffle sequences 20x times the average bankfull width and surveys were repeated sampling events that occurred at the same sites over time.

Ecoregion	2020 Sites	2020 Surveys	2021 Sites	2021 Surveys	2022 Sites	2022 Surveys	Total Sites	Total Surveys
OH	37	102	25	74	6	16	68	192
BM	6	18	3	9	0	0	9	27
CIP	1	1	4	12	6	17	11	30
Total	44	121	32	95	12	33	88	249

Table 5. Percent and number of sites and surveys where each species was detected by ecoregion: Ozark Highlands (OH), Boston Mountains (BM), and Central Irregular Plains (CIP).

Species	OH Sites	OH Surveys	BM Sites	BM Surveys	CIP Sites	CIP Surveys	Total Sites	Total Surveys
F. neglectus	99%	98%	100%	96%	0%	0%	86%	86%
	(67)	(189)	(9)	(26)	(0)	(0)	(76)	(215)
F. virilis	13%	9%	33%	33%	55%	37%	20%	15%
	(9)	(17)	(3)	(9)	(6)	(11)	(18)	(37)
F. nais	3%	3%	33%	30%	27%	20%	9%	8%
	(2)	(6)	(3)	(8)	(3)	(6)	(8)	(20)
F. macurs	19%	17%	0%	0%	0%	0%	15%	13%
	(13)	(32)	(0)	(0)	(0)	(0)	(13)	(32)
F. nana	53%	50%	33%	33%	0%	0%	44%	42%
	(36)	(96)	(3)	(9)	(0)	(0)	(39)	(105)
F. meeki brevis	26%	26%	22%	22%	0%	0%	25%	22%
	(20)	(50)	(2)	(6)	(0)	(0)	(22)	(56)
F. palmeri	6%	3%	22%	19%	0%	0%	7%	4%
	(4)	(6)	(2)	(5)	(0)	(0)	(6)	(11)
Smallmouth Bass	54%	46%	44%	37%	0%	0%	47%	40%
	(37)	(89)	(4)	(10)	(0)	(0)	(41)	(99)

Table 6. Mean, standard deviation (SD), minimum (Min), and maximum (Max) values for measured habitat factors used in the global model. Data are reported for sites in each ecoregion: Ozark Highlands (OH), Boston Mountains (BM), and Central Irregular Plains (CIP). RPD is residual pool depth, W:D is width-to-depth ratio, LDI is landscape disturbance index, and HSGD is the percent of hydrologic soil group "D".

Ecoregion	Covariate	Mean	SD	Min	Max
OH	Bank angle	27.31	12.73	3.5	57.33
	RPD	0.88	0.52	0.11	2.57
	W:D	35.38	19.51	7.98	102.83
	Pool habitat	47.20	21.80	0.00	89.90
	Discharge	0.34	0.50	0.004	3.42
	Visibility	4.79	2.54	1.1	11.4
	Slope	0.004	0.001	< 0.001	0.008
	Elevation	252.59	27.06	196.84	311.69
	Sinuosity	1.21	0.10	1.05	1.54
	Drainage area	107.68	121.88	11.54	769.74
	LDI	2.26	0.40	1.23	3.63
	HSGD	22.40	16.64	0.23	93.52
BM	Bank angle	24.55	10.14	9.00	45.00
	RPD	0.86	0.41	0.26	1.70
	W:D	39.60	19.65	15.46	83.47
	Pool habitat	54.29	21.71	24.30	88.83
	Discharge	0.26	0.26	0.002	0.88
	Visibility	3.48	2.43	0.76	7.71
	Slope	0.003	0.0005	0.002	0.004
	Elevation	201.67	18.05	177.05	245.40
	Sinuosity	1.16	0.05	1.09	1.28
	Drainage area	90.98	53.69	31.13	207.69
	LDI	2.00	0.36	1.34	2.55

	HSGD	45.29	27.34	0.17	74.60
CIP	Bank angle	39.68	18.75	24.16	92.50
	RPD	0.50	0.21	0.04	0.82
	W:D	23.14	17.46	7.43	65.13
	Pool habitat	57.50	20.89	32.88	90.51
	Discharge	0.045	0.05	0.00	0.17
	Visibility	1.22	1.31	0.10	4.48
	Slope	0.003	0.002	<0.001	0.007
	Elevation	194.40	9.72	178.56	209.16
	Sinuosity	1.28	0.10	1.13	1.41
	Drainage area	18.66	11.32	4.20	34.17
	LDI	5.96	1.32	2.21	7.36
	HSGD	65.65	34.80	8.80	100.00

Table 7. Species-specific detection and occupancy probabilities. The assemblage level detection probability was 0.87 and the occupancy probability was 0.31.

Species	Detection	Occupancy
F. neglectus	0.98	0.97
F. virilis	0.67	0.31
F. nais	0.87	0.07
F. macrus	0.86	0.09
F. nana	0.93	0.37
F. meeki brevis	0.91	0.29
F. palmeri	0.63	0.06
Assemblage	0.87	0.31

Table 8. Results from the detection side of my final model. Relationships are assumed to be shared by all species and are reported on the logit scale as the mode of the posterior distribution with the lower (Low) and upper (High) 95% highest density intervals.

Covariate	Mode	Low	High
Visibility	-0.190	-0.643	0.227
Discharge	-0.084	-0.505	0.276
Reproductive timing	-0.122	-0.789	0.553

Table 9. Results from the final model containing all retained occupancy covariates. Covariates (logits) are reported for all species and the assemblage average. The mode of the posterior distribution is reported with both the lower (Low) and upper (High) 95% highest density intervals. Variance is reported for assemblage mean relationships and is a measure of variability among species-specific relationships. Continuous covariates include bank angle, width-to-depth ratio (W:D), residual pool depth (RPD), the percent of pool habitat (Pool %), average elevation of the segment, stream gradient of the segment, the amount of hydrologic soil group "D" (HSGD) in the catchment, drainage area, and quadratic relationship with drainage area. Categorical covariates include the presence of Smallmouth Bass (absence as the reference), gravel dominated streams (no gravel as the reference), and the presence of limestone lithology (no limestone as the reference). HUC 8 and year were grouping factors and are reported as the standard deviation.

Covariate	Species	Mode	Low	High
Bank angle	*F. neglectus*	-0.137	-0.821	0.643
	F. virilis	0.054	-0.471	0.921
	F. nais	-0.228	-0.932	0.378
	F. macrus	-0.072	-0.558	0.554
	F. nana	-0.234	-0.782	0.264
	F. meeki brevis	-0.367	-1.069	0.119
	F. palmeri	-0.228	-0.962	0.39
	Assemblage	-0.173	-0.661	0.325
	Variance	0.286	0.014	0.937
W:D	*F. neglectus*	0.15	-0.475	0.716
	F. virilis	0.071	-0.607	0.576
	F. nais	0.191	-0.323	0.77
	F. macrus	0.149	-0.419	0.702

	F. nana	0.167	-0.35	0.709
	F. meeki brevis	0.298	-0.183	1.055
	F. palmeri	0.176	-0.428	0.843
	Assemblage	0.17	-0.271	0.636
	Variance	0.190	0.008	0.764
RPD	*F. neglectus*	0.189	-0.557	1.313
	F. virilis	-0.11	-1.029	0.473
	F. nais	0.101	-0.684	0.784
	F. macrus	-0.155	-1.028	0.388
	F. nana	0.357	-0.145	1.046
	F. meeki brevis	0.258	-0.211	0.85
	F. palmeri	-0.056	-1.106	0.557
	Assemblage	0.078	-0.507	0.582
	Variance	0.377	0.025	1.152
Pool	*F. neglectus*	-0.112	-0.681	0.762
	F. virilis	0.006	-0.505	0.816
	F. nais	-0.208	-0.81	0.418
	F. macrus	-0.402	-1.148	0.086
	F. nana	-0.296	-0.844	0.153
	F. meeki brevis	-0.22	-0.754	0.287
	F. palmeri	-0.304	-1.078	0.254
	Assemblage	-0.222	-0.674	0.259
	Variance	0.276	0.016	0.942
Smallmouth Bass	*F. neglectus*	0.669	-0.383	3.388
	F. virilis	0.495	-0.515	1.86
	F. nais	0.113	-1.815	1.144
	F. macrus	0.433	-0.545	1.498
	F. nana	0.16	-1.009	1.055
	F. meeki brevis	0.465	-0.426	1.51
	F. palmeri	0.489	-0.618	1.926
	Assemblage	0.409	-0.436	1.366

	Variance	0.426	0.019	1.830
Gravel	*F. neglectus*	0.076	-1.284	2.493
	F. virilis	-0.442	-1.809	0.927
	F. nais	-1.087	-3.372	0.23
	F. macrus	0.051	-1.158	1.842
	F. nana	-0.418	-1.684	0.807
	F. meeki brevis	-0.328	-1.537	0.917
	F. palmeri	-0.816	-2.927	0.5
	Assemblage	-0.422	-1.557	0.69
	Variance	0.738	0.035	2.200
Elevation	*F. neglectus*	1.141	-0.037	2.87
	F. virilis	-0.858	-1.853	-0.046
	F. nais	-0.979	-2.205	-0.014
	F. macrus	0.264	-0.421	0.972
	F. nana	0.965	0.268	1.744
	F. meeki brevis	0.305	-0.356	1.007
	F. palmeri	-0.764	-2.042	0.202
	Assemblage	0.015	-0.997	1.032
	Variance	1.038	0.473	2.198
Stream gradient	*F. neglectus*	0.601	-0.06	1.696
	F. virilis	0.352	-0.525	0.966
	F. nais	0.471	-0.22	1.137
	F. macrus	0.419	-0.34	1.056
	F. nana	0.604	0.024	1.468
	F. meeki brevis	0.515	-0.084	1.164
	F. palmeri	0.515	-0.219	1.371
	Assemblage	0.5	-0.037	1.103
	Variance	0.248	0.010	0.983
HSGD	*F. neglectus*	-0.878	-2.658	0.374
	F. virilis	1.356	0.154	2.999
	F. nais	0.034	-0.922	1.147

	F. macrus	0.259	-0.533	1.248
	F. nana	-0.815	-1.69	-0.087
	F. meeki brevis	-0.738	-1.516	-0.056
	F. palmeri	0.325	-0.792	1.822
	Assemblage	-0.063	-1.064	1.017
	Variance	1.001	0.385	2.222
Drainage area	*F. neglectus*	1.898	0.442	3.991
	F. virilis	-0.027	-1.186	1.116
	F. nais	-1.376	-2.988	0.007
	F. macrus	0.42	-0.731	1.619
	F. nana	2.082	0.964	3.448
	F. meeki brevis	0.226	-0.828	1.293
	F. palmeri	1.296	-0.11	2.968
	Assemblage	0.649	-0.672	2.082
	Variance	1.360	0.655	2.783
Drainage area^2	*F. neglectus*	-0.506	-1.134	0.173
	F. virilis	-0.479	-0.949	-0.011
	F. nais	-0.427	-0.961	0.169
	F. macrus	-0.619	-1.473	-0.186
	F. nana	-0.435	-0.919	0.185
	F. meeki brevis	-0.602	-1.273	-0.187
	F. palmeri	-0.616	-1.617	-0.129
	Assemblage	-0.53	-1.018	-0.14
	Variance	0.208	0.010	0.889
Limestone	*F. neglectus*	0.708	-0.981	3.336
	F. virilis	-1.549	-4.14	0.226
	F. nais	-0.025	-1.63	1.656
	F. macrus	0.29	-1.14	2.044
	F. nana	0.291	-0.987	1.728
	F. meeki brevis	-0.497	-1.899	0.727
	F. palmeri	-0.356	-2.434	1.332

	Assemblage	-0.145	-1.574	1.126
	Variance	1.046	0.087	2.615
HUC 8 SD	Assemblage	0.481	0.036	1.134
Year SD	Assemblage	0.280	0.011	1.559

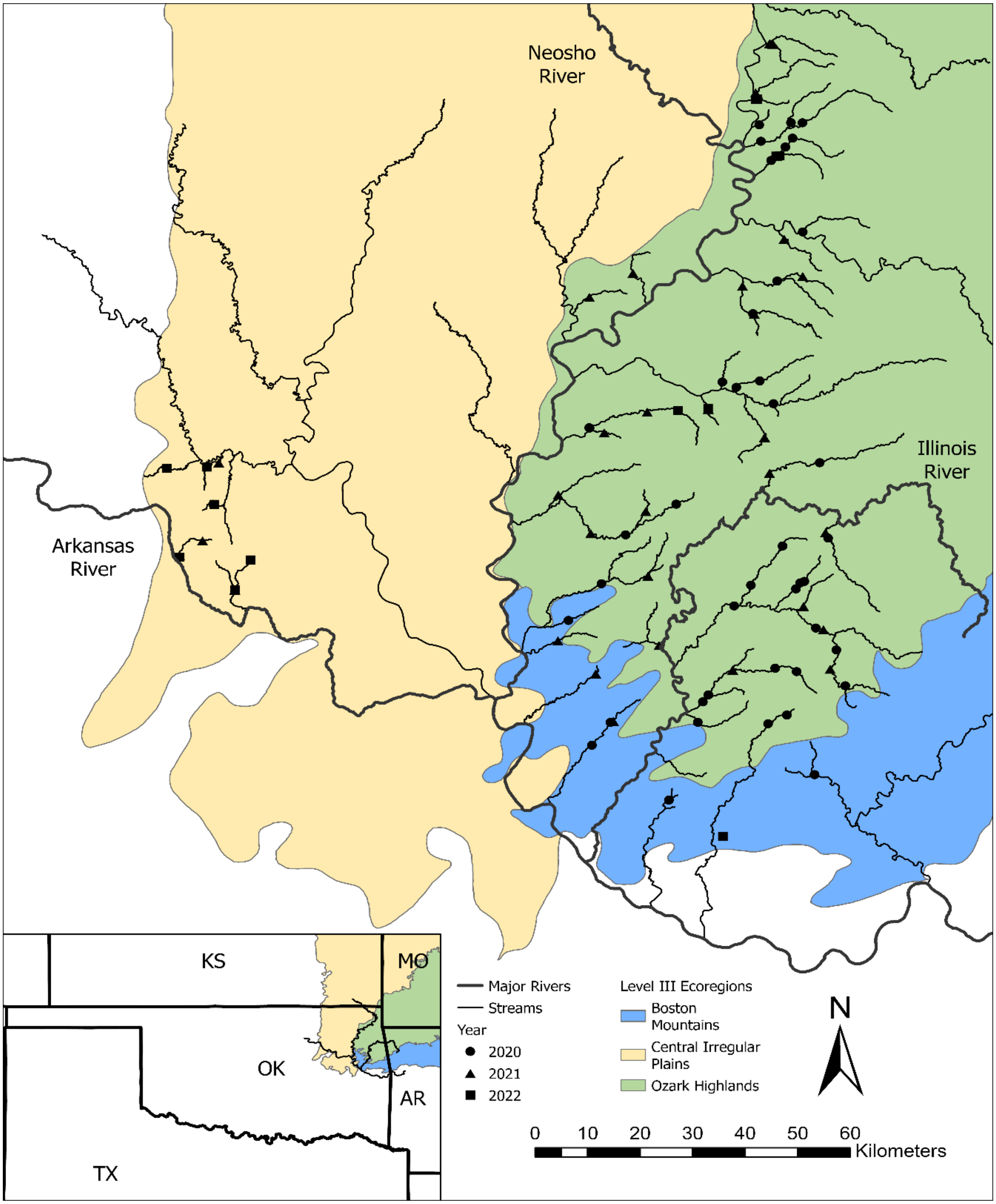

Figure 1. Map of sites sampled during 2020 (circles), 2021 (triangles), and 2022 (squares) in the Ozark Highlands (green), Boston Mountains (blue), and Central Irregular Plains (tan).

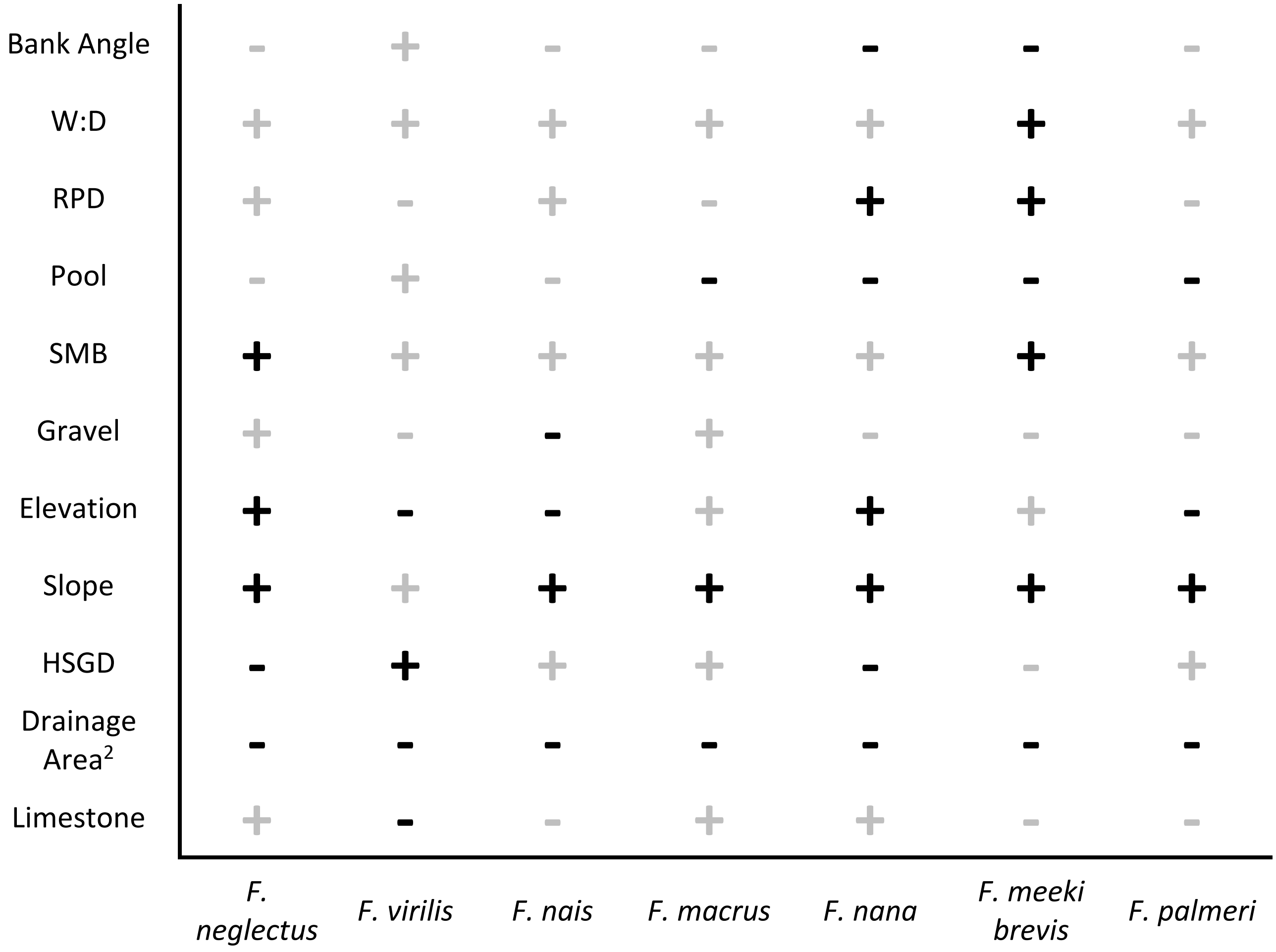

Figure 2. Direction of relationships between occupancy covariates included in my final model and all species. W:D is width-to-depth ratio, RPD is residual pool depth, Pool is the percent of pool habitat at the reach scale, SMB is Smallmouth Bass presence, Slope is the gradient of the stream segment, and HSGD is the amount of hydrologic soil group "D" in the catchment. Covariates with relationships that had adequate support (i.e., 95% HDI < |mode|) are shown in black and all others in grey.

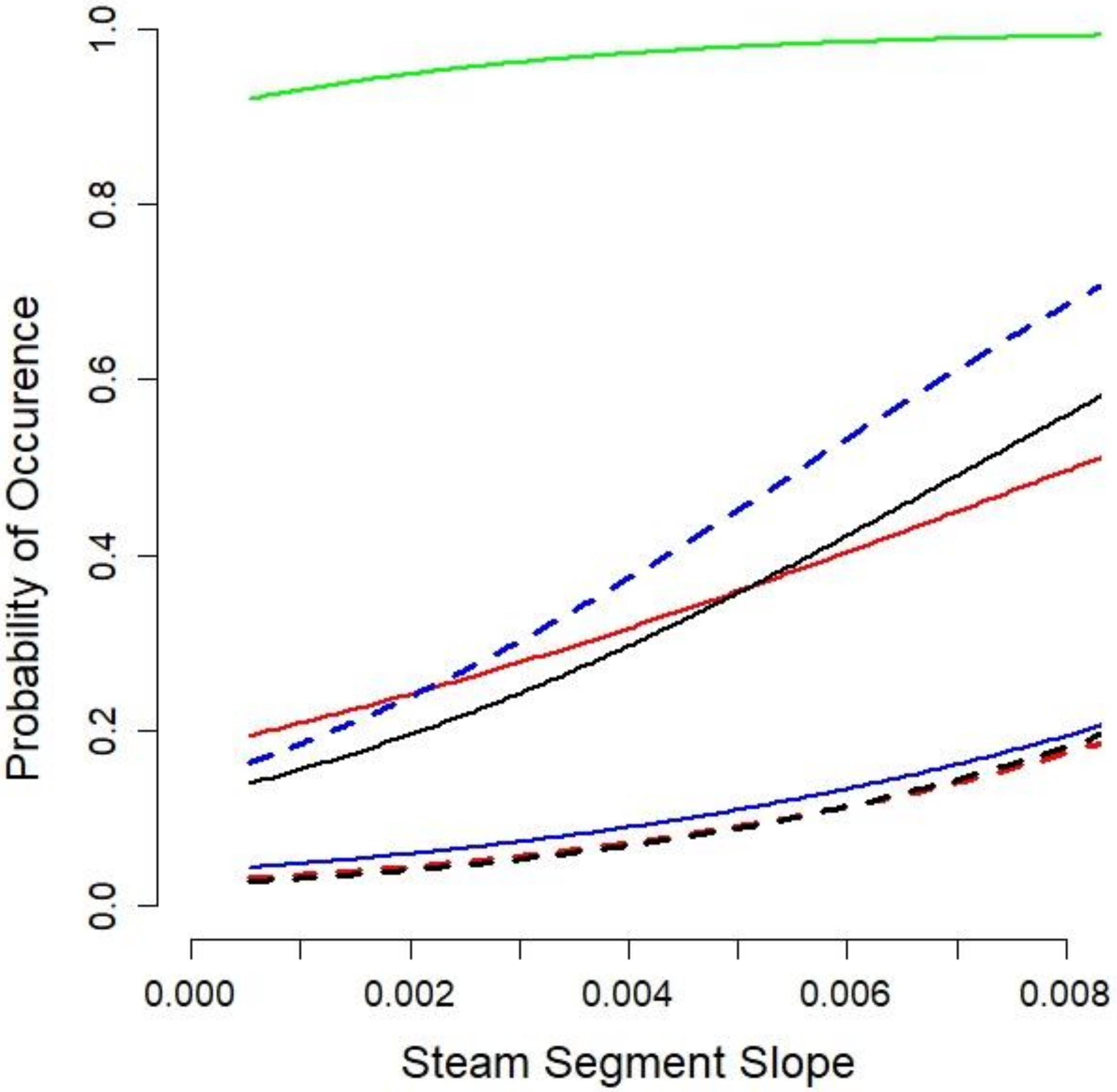

Figure 3. Relationships between probability of occupancy and slope (i.e., stream gradient; m) of the stream segment modeled as deviations from the assemblage average for all species: *F. neglectus* (solid green), *F. virilis* (solid red), *F. nais* (dashed red), *F. macrus* (solid blue), *F. nana* (dashed blue), *F. meeki brevis* (solid black), and *F. palmeri* (dashed black). See Table 9 for uncertainty around estimates.

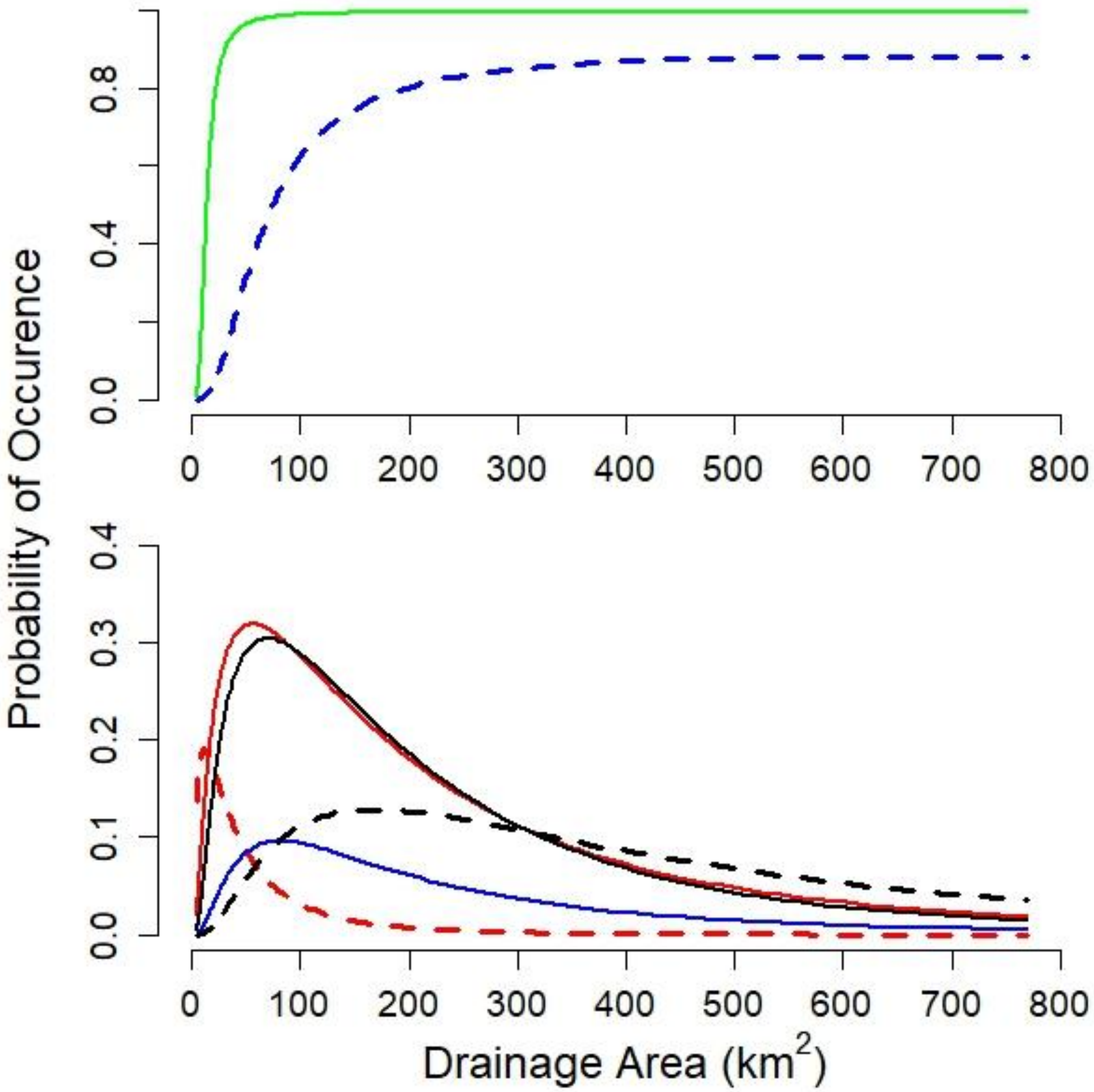

Figure 4. Quadratic relationships between probability of occupancy and drainage area (km^2) modeled as deviations from the assemblage average for: (top panel) *F. neglectus* (solid green) and *F. nana* (dashed blue); and (bottom panel) *F. virilis* (solid red), *F. nais* (dashed red), *F. macrus* (solid blue), *F. meeki brevis* (solid black), and *F. palmeri* (dashed black). See Table 9 for uncertainty around estimates.

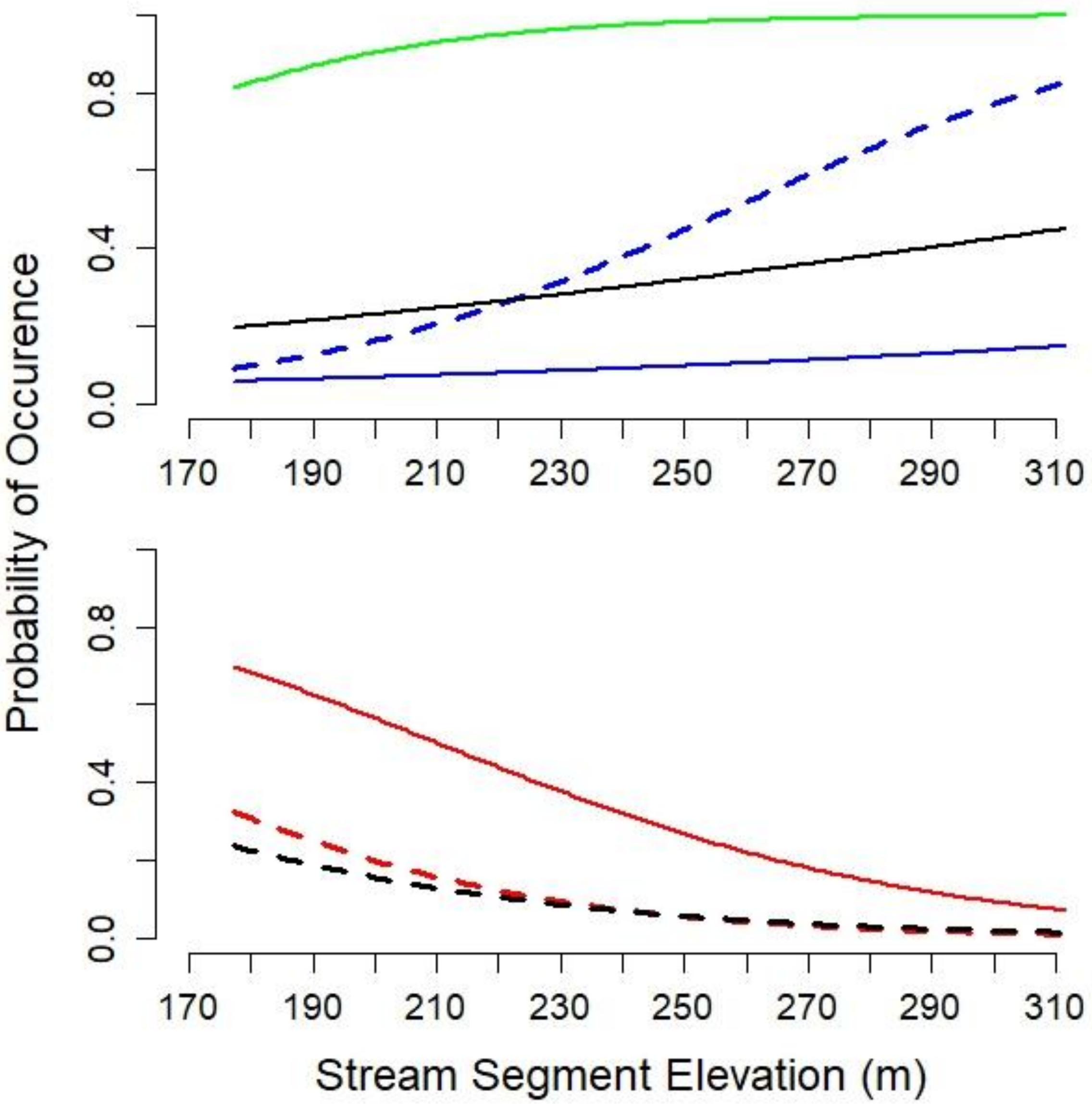

Figure 5. Shared positive (top panel) and negative (bottom panel) relationships between probability of occupancy and elevation (m) of the stream segment modeled as deviations from the assemblage average for: *F. neglectus* (solid green), *F. macrus* (solid blue), *F. nana* (dashed blue), and *F. meeki brevis* (solid black); and *F. virilis* (solid red), *F. nais* (dashed red), and *F. palmeri* (dashed black). See Table 9 for uncertainty around estimates.

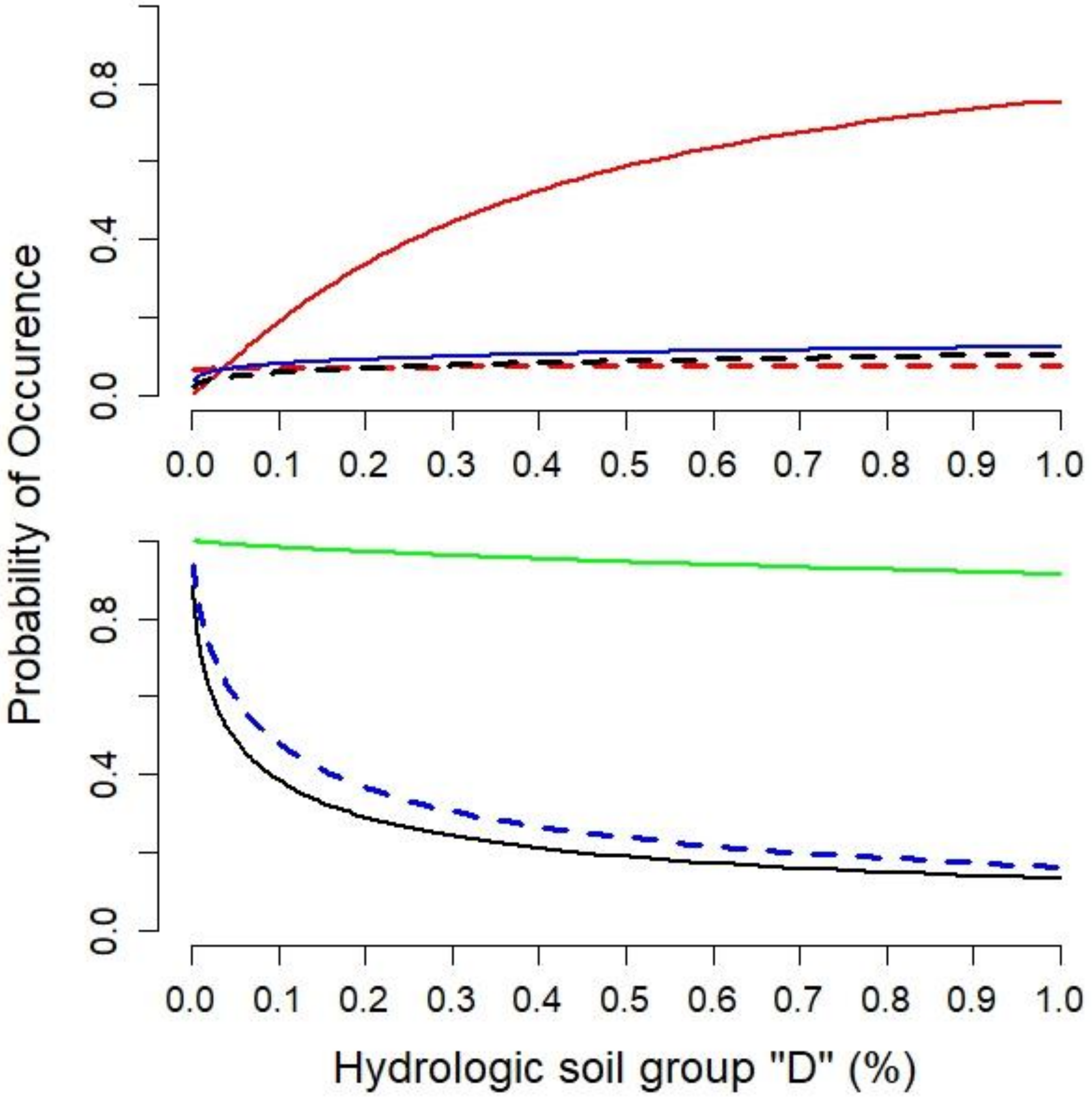

Figure 6. Shared positive (top panel) and negative (bottom panel) relationships between probability of occupancy and hydrologic soil group “D” (%) in the catchment modeled as deviations from the assemblage average for: *F. virilis* (solid red), *F. nais* (dashed red), *F. macrus* (solid blue), and *F. palmeri* (dashed black); and *F. neglectus* (solid green), *F. nana* (dashed blue), and *F. meeki brevis* (solid black). See Table 9 for uncertainty around estimates.

III. Life-history patterns and seasonal microhabitat selection by three crayfishes of conservation concern (*Faxonius nana*, *F. macrus*, and *F. meeki brevis*).

Introduction

An understanding of species-habitat associations and life history (i.e., fecundity and growth) is lacking for many crayfishes, yet forms the basis of many conservation and management efforts. The ICUN considers more than 20% of all freshwater species to be data deficient, meaning there is inadequate information to make a direct or indirect assessment of extinction risk (ICUN, 2021). For crayfishes, life-history data are lacking for an estimated 88% (305) of crayfishes in the United States and Canada. Understanding general life-history traits (i.e., age, maturation, egg production, egg size) provides important information on survival and reproductive potential (Holden and Raitt 1974; Panfili et al. 2002), helps guide life-history specific management strategies (e.g., the addition of substrate to mitigate habitat loss, Beechie et al. 2010; Stratton and DiStefano 2021), and improves our understanding of how crayfishes may influence or be influenced by predators or invasive species (Moore et al. 2013). For example, Roberts et al. (2008) examined River Otter *Lontra canadensis* seasonal diets, including crayfishes and fishes, to better understand the target population size in Missouri streams, USA. However, in many regions, we are lacking the necessary data to make these linkages between crayfishes and their key predators, including important sportfish populations.

Accurate age estimation often is a key parameter to properly managing populations. The use of calcified structures is common for many aquatic species, but a verified structure has yet to be identified for crayfishes or other crustaceans. With no verified ageing methods, age estimations for crustaceans are done using length-frequency analyses (Mclay and van den Brink 2016). Length-frequency data are useful but require a large sample size, are biased by sampling gear inefficiencies (e.g., certain size classes, France et al. 1991), and cannot differentiate between fast and slow growing individuals (Kilada et al. 2012). However, relatively recent research indicates gastric mill ossicles, comprising the food grinding structures, may be a viable option (Leland et al. 2015; Kilada and Ibrahim 2016; Leland and Bucher 2017). Some studies indicate the structure cannot be used for ageing because the gastric mill is shed during molting (Vatcher et al. 2015; Sheridan and O'Connor 2018; Becker et al. 2018), but calcein grow-out studies indicate some temporal band formation on these structures are retained through the molting process (Leland et al. 2015; Mouser et al. 2020). Moreover, daily bands appear to occur in *F. n. neglectus* juveniles, and also align with length-frequency histograms except for individuals estimated to be longer lived (Mouser et al. 2020). The usefulness of each ossicle in age determination varies by species and research has focused mainly on larger crustaceans (i.e., crabs, Ibrahim and Kilada 2015; Crook et al. 2018 lobsters, Leland and Bucher 2017) including some crayfishes (Leland et al. 2015; Mouser et al. 2020). Management would benefit from improved age estimates to better evaluate population demographics over time. For example, it is currently difficult to evaluate changes to crayfish populations when non-native fishes are introduced (e.g., Rainbow Trout, Reynolds 2011) or when previously extirpated animals are reintroduced into areas where the habitat has changed over time (e.g., River Otters, Roberts et al. 2008).

Resource selection (i.e., where use exceeds availability, Manley et al. 1993) by crayfishes is important for understanding how species meet their life-history requirements, how species are sympatric with other crayfishes, and how crayfishes alter behavior when occurring with novel species. At the most basic level, resource selection provides key information to understand how species meet their survival requirements (Manly et al. 1993). For example, fine-scale microhabitat selection may affect the ability of two species to coexist (Grossman and Freeman 1987). Competition may result if two species have overlapping resource needs, and the oppressor may shift niches or decline in abundance (Garvey et al. 1994; Hill and Lodge 1994). The latter situation is important as the frequency of invasive crayfishes has increased over time and considered a major threat to native crayfishes (Lodge et al. 2000, 2012; Pintor et al. 2008). Thus, understanding habitat associations of native species may help biologists identify species with increased risk of competition in case of invasion (see also Chapter 2). Lastly, understanding overlap in use of some resources by multiple species may be useful for identifying possible surrogate species (Stratton and DiStefano 2021).

The Meek's Short Pointed crayfish *Faxonius meeki brevis*, Midget crayfish *F. nana nana* (hereafter *F. nana*), and Neosho Midget crayfish *F. nana macrus* (hereafter *F. macrus*) are three crayfishes that currently lack life-history information and are considered of conservation concern. Taylor et al. (2007) compiled conservation status rankings from the American Fisheries Society and the Network of National Heritage Programs for North American crayfishes. The American Fisheries Society classified *F. meeki brevis* as threatened, *F. nana* as threatened, and *F. macrus* as stable. The Network of National Heritage Programs classified *F. meeki brevis* as imperiled, *F. nana* as vulnerable, and *F. macrus* as "apparently secure." Taylor et al. (2007) also listed the criteria for the below stable classifications of *F. meeki brevis* and *F. nana* as having a "restricted range." Lastly, species status assessments would benefit from providing general ecological data for listing considerations for data poor species (Richman et al. 2015; Stratton and DiStefano 2021).

The basic information available on *F. meeki brevis*, *F. nana*, and *F. macrus*, indicates they use similar habitats and have similar reproductive patterns but are simply distributed in different drainages. They are considered tertiary burrowers and found in relatively clear, cool, permanent streams dominated by gravel and cobble substrates (Morehouse and Tobler 2013). Although little is known about the fecundity or reproductive patterns of *F. nana* and *F. meeki brevis*, they are assumed to follow similar reproductive patterns to *F. macrus* and other *Faxonius* species in this region (Pflieger 1996; Morehouse and Tobler 2013). Historic collections compiled by Morehouse and Tobler (2013) indicate that *F. nana* is endemic to the upper Illinois River drainage, *F. macrus* to the Neosho River drainage, and *F. meeki brevis* is endemic to both drainages. These inferred similarities suggest these species are vulnerable to similar threats, but that inference may simply be related to the lack of available ecological information.

Endemism by *F. meeki brevis*, *F. nana*, and *F. macrus* may put them at risk to displacement by more dominant congeners. The Ringed Crayfish *F. neglectus neglectus* (hereafter *F. neglectus*), is commonly found in the same drainages and thought to negatively affect other imperiled crayfishes (Magoulick and DiStefano 2007; Imhoff et al. 2012; Nolen et al. 2014). Crayfish can be aggressive competitors, and oppressed species commonly disperse to areas with lower abundances (Bovbjerg 1953). Thus, the ability of *F. neglectus* to expand its niche may put populations of sympatric species that are presumed inferior competitors (i.e., *F. nana, F. meeki brevis, F. macrus*) at risk of decline (Flinders and Magoulick 2005; Rabalais and Magoulick 2006; Imhoff et al. 2012). For example, the Coldwater Crayfish *F. eupunctus* and Hubbs' Crayfish *Cambarus hubbsi* were historically abundant in the West Fork of the South Fork Spring River (Pflieger 1996), but more-recent surveys indicate they were extirpated (Magoulick and DiStefano 2007). Although the mechanism related to this extirpation is unknown, *F. neglectus* was introduced into this system between 1984–1998 and has now become the most abundant species (Magoulick and DiStefano 2007). *F. neglectus* is documented to invade novel habitats within its native range (e.g., caves, Mouser et al. 2019) and thus, understanding how the species interacts with other native species is advantageous.

Consequently, the goal of my third thesis chapter was to better understand the life history of *F. meeki brevis*, *F. nana*, and *F. macrus*. Specifically, my study objectives were to 1) document the reproductive timing, age distribution, and length-frequency of each species, and 2) determine microhabitat selection by the three species. Collectively, these findings will be useful for developing conservation strategies (i.e., species status assessments) for the three focal species.

Methods

Site Selection

I haphazardly selected 7 stream reaches (20x bankfull width) along Tyner Creek, Lost Creek, and Peacheater Creek within the Ozark Highlands ecoregion (see description in Chapter 1) (Figure 1). These streams were identified in cooperation with the Oklahoma Department of Wildlife Conservation due to known populations of the target species. Specific reaches were selected based on permission to access privately owned lands. Some reaches were sampled multiple times, but under different physicochemical conditions.

Crayfish sampling

Crayfishes were sampled using seining, visual observations, and trapping during the sample season (see Microhabitat and Life History below). First, two observers sampled crayfishes using a series of kick seines (1.5m x 1.75m, 3-mm mesh) in turbulent water (e.g., riffles). Next, I visually searched or snorkeled for crayfishes in calm waters (i.e., typically pools and runs). Two observers began at the downstream end of each reach and sampled using each gear as appropriate (e.g., seins were not used in areas with woody debris). In areas suitable for kick seining (i.e., shallow, higher velocities, and turbulent), one observer held a seine while the other disturbed the area directly above the seine inside a $1m^2$ plot. Active searching followed the procedures outlined in Chapter 2. Briefly, two observers snorkeled or walked in a systematic search of the area while flipping rocks and other debris to locate and capture crayfishes. A numbered flag was placed as close as possible to the original capture location (i.e., within one meter, Dyer and Brewer 2018) to later measure microhabitat use and quantify available habitat (see next section). Minnow traps (42cm x 22cm, 5cm opening) were also used to collect crayfish only during life-history sampling. I set 10 traps overnight in deeper available pools in an attempt to catch individuals that may be more active during that time or under-represented due to gear bias.

Microhabitat use and availability

I quantified microhabitat use by measuring five physicochemical parameters at each target species' location (i.e., at each numbered flag) during baseflow conditions during the spring and summer of 2021 and 2022. Specific water depths and current velocities are typically chosen by crayfishes and related to energy expenditure, feeding habits, or habitat partitioning (Rabeni 1985; Gherardi et al. 2001; Benvenuto et al. 2008). Therefore, I measured water depth (0.1 m) using a meter stick and average water-column velocity (0.6 of depth) using a Marsh McBirney flow meter (Gordon et al. 1992). Westhoff and Rabeni (2013) found that crayfishes select habitats that provide cover relative to their body size. I visually estimated the percent composition of substrate classes in each plot using a modified Wentworth scale (Bovee 1978). Substrate classes were (diameter in parentheses) silt and sand (< 2 mm), gravel (2-16 mm), pebble (17-64 mm), cobble (65-256 mm), boulder (> 256 mm) and bedrock or clay hardpan (0 mm). Bedrock varied in size but was represented by large unbroken sheets of bedrock, whereas clay hardpan was very fine clay particles that were embedded to form large continuous areas. I also estimated the percent area covered by woody debris and macrophytes, because these areas provide shelter from heigh velocities or from predators in low velocity areas (Rabeni 1985; Ishiyama et al. 2012).

I systematically determined microhabitat availability in each reach to quantify habitat selection. Availability was quantified on the same day that I sampled microhabitat use to ensure it adequately reflected available conditions. I quantified microhabitat availability by measuring microhabitat conditions (described above) at 1-m intervals along transects spaced 5-m apart starting at the downstream end of each reach. At each transect location, I placed a 1 m^2 plot on the water's edge and worked across at 1-m intervals perpendicular to streamflow, until the plot was no longer fully submerged on the opposite side. The next transect began on the opposite bank to ensure habitat conditions available were represented in my availability measurements. This process continued until availability was quantified throughout the sample reach.

Microhabitat selection

I used a logistic regression to determine habitat selection (i.e., where habitat use exceeds availability) by *F. meeki brevis*, *F. nana*, and *F. macrus* using program R. I used a use versus availability approach (Manly et al. 1993) where all availability samples were assigned a 0 and all habitat use samples assigned a 1. Absences are not considered in this model framework and occupied sites are treated as a subset of the available points (Boyce et al. 2002). Logistic regression is only useful in evaluating habitat selection if the results are interpreted correctly (Keating and Cherry 2004; Johnson et al. 2006). Estimates from these models are indicative of relative selection probability and not a true selection probability (i.e., coefficients are estimates of selection strength, not selection probability; Johnson et al. 2006; Northrup et al. 2013; Wolf et al. 2019), but relative selection probability estimates are useful because they represent selection patterns proportional to true probability estimates (Johnson et al. 2006).

I made any necessary transformations to my covariates and tested for multicollinearity among my continuous covariates before standardizing them. Depth and velocity data were right skewed; thus, I applied a log transformation. Substrate composition and the proportion of macrophyte and woody debris present were bimodal and thus, were transformed into categorical covariates. I quantified substrate by assigning each plot a 1 if 100% of the composition was “moderate” (i.e., gravel and cobble) and 0 in all other cases. I combined the proportion of macrophytes and woody debris into a single categorical variable “cover”, where plots with any macrophytes or woody debris was assigned a 1 and 0 otherwise. I used a Pearson’s pairwise correlation coefficient (r) to test for multi-collinearity between depth and velocity. Depth and velocity were not severally correlated in any of the species models ($|r| < 0.33$) and thus, were retained in all models. I also examined the independence of my categorical covariates by plotting their frequency of occurrence and they were also retained for modeling purposes. I then standardized depth and velocity to mean of 0 and standard deviation of 1 to improve model interpretation (Schielzeth 2010).

I used categorical and continuous covariates to model patterns in spring and summer microhabitat selection for each species. Categorical covariates were binary variables where a reference category was coded as 1 and the other as 0 (i.e., summer =1 and spring = 0). I fit a separate model for each species because habitat available to one species was not always available to the others. I fit the resource-selection functions using logistic regression:

$$logit(Y_i) = \beta_0 + \beta_1 X_{i,1} + \beta_2 X_{i,2} \ldots + \beta_N X_{i,N}$$

where Y is the relative probability of use at microhabitat plot *i*, β_0 is the model intercept, β_1 through β_N are the coefficients of covariates X_1 through X_N. The covariates considered in my *F. nana* and *F. meeki brevis* models were depth, average water-column velocity, substrate, cover, season, and stream, whereas stream and season were not included in my *F. macrus* model.

I used a multi-step selection process to remove non-significant covariates (Wolf et al. 2019) and examined binned residuals plots to assess model fit. I determined the significance of each covariate using the 90% confidence intervals (CI). Covariates with CIs that overlap 0 were treated as non-significant and removed from the model. I began by fitting a global model that included an interaction between seasons (spring and summer) and all orthogonal covariates ($|r| < 0.33$). I first removed any seasonal interaction that was not significant. I then refit my model including only significant seasonal interactions and habitat covariates as linear, fixed effects. I then removed any fixed effect that was either not significant or was not associated with a retained interaction. Lastly, I fit a final model that included only significant seasonal interactions and linear effects. Additionally, I assessed model fit using a binned residuals posterior predictive simulation, where approximately 95% of residuals falling the error bounds suggest adequate fit (Gelman and Hill 2006). This process was repeated for developing resource selection models for each of the three species.

Life history

I collected ≈50 crayfishes monthly to examine general life-history patterns. I collected crayfishes via hand collection (i.e., visual observations to locate and capture), seining, and trapping. I recorded the species, sex, reproductive form, and total carapace length (TCL) from all sampled crayfishes. The species, sex, and reproductive form was determined as described in Chapter 2. The TCL is the distance (1.0 mm) from the tip of the rostrum to the base of the carapace. I measured TCL with a pair of vernier calipers. Any crayfish that suffered mortality during sampling was vouchered in 70% ethanol for use in ageing analyses. In addition to the 50 crayfish used for ageing, I vouchered an additional 10 females of each species per month to examine fecundity patterns.

I estimated crayfish ages using both length-frequency histograms and quantifying bands on the gastric mills. I used the TCL measurements from collected individuals to construct a length-frequency histogram (France et al. 1991) to estimate age classes for each species using a traditional framework. Age estimates from length-frequency histograms were also used as a comparison to ages estimated using the gastric mill ossicles (hereafter ossicles). The gastric mill is a calcified food grinding structure in the foregut of crustaceans made up of 5 major ossicles (Figure 2): mesocardiac ossicle, paired zygocardiac ossicles, and paired pterocardiac ossicles (Caine 1974; Felgenhauer and Abele 1985). Ossicles were processed and aged following methods of Leland et al. (2015), Leland and Bucher (2017), and Mouser et al. (2020). Briefly, each crayfish was dissected to remove the gastric mill. I rinsed out any stomach contents with water and used scissors to disarticulate each of the 5 ossicles. I then used forceps and dissection probes to remove any excess stomach tissue or organic material attached to the ossicles. Each ossicle was then rinsed and air dried for at least 24 h before mounting them in epoxy resin. I used an isomet low speed saw to make an approximately 200-µm wide cross section of each ossicle. Paired zygocardiac and pterocardiac ossicles were sectioned transversely at the midpoint and the mesocardiac ossicle was sectioned longitudinally approximately 200 µm off center (Leland et al. 2015). I sanded each cross section using 800-2000 grit sandpaper until the cross section was approximately 100-µm wide or the endocuticular boundary and growth bands were clearly visible (approximately 3-5 min). I then used thermoplastic cement or clear acrylic nail polish to mount the cross sections on glass slides where paired ossicles (i.e., zygocardiac and pterocardiac) were mounted on the same slide.

Two readers independently examined each cross section to estimate the putative age of each crayfish by ossicle type. A small amount of mineral oil was placed on each ossicle to increase the readability of bands before examination (Mouser et al. 2020). Readers used a microscope to count the number of growth marks (i.e., a broad light-colored band followed by a dark narrower band) past the cuticular boundary (i.e., boundary between the endo- and exocuticular layers; Figure 3). Each band past the endocuticular boundary was interpreted as 1 year in age (i.e., 0+, 1+, 2+, 3+; Leland et al. 2015). The outermost growth mark was only counted if a sufficient amount of material was deposited after the band (Leland and Bucher 2017). For paired structures mounted on the same slide, the reader examined both cross sections and decided on a single age estimate for the ossicle type. Independent readings of each ossicle were used to determine precision between readers. The two readers determined a consensus age estimate where there was disagreement. The two readers were able to reach consensus in all cases; thus, all ossicles were retained for analyses.

I constructed a length-frequency histogram (France et al. 1991) with 1-mm size bins and used the Bhattacharya method (Bhattacharya 1967) to determine age classes for each species (Mouser et al. 2020) using the R package TropFishR (Taylor and Mildenberger 2017). This method uses modal progression to estimate growth by the mode shifts in a length-frequency histograms. Normal distributions were identified from the overall length-frequency distribution where each distribution represents a cohort (i.e., age class) (Gayanilo and Sparre 2005). After identifying the distributions, the left most distribution was removed from the overall distribution, and the process was repeated until only one distribution remained. A separation index (SI) was calculated to measure the degree of separation between cohorts where a SI <2 describes a cohort that is not distinguishable from other cohorts (Sparre 1998; Gayanilo and Sparre 2005). I then compared the age estimates using the length-frequency analysis to estimates provided by counting gastric mill bands on each ossicle.

I estimated precision and bias associated with each ossicle to determine the ossicle that best reflected age for each species. I determined the mean CV and percent reader agreement of age estimates for each ossicle (Campana et al. 1995). I then used the Evans-Hoenig test of symmetry (Evans and Hoenig 1998) to compare age estimates from the length-frequency analysis and age estimates from the ossicles. I used the Evans-Hoening test of symmetry because it is more powerful than traditional tests (Evans and Hoenig 1998; Mouser et al. 2020). Additionally, I constructed age bias plots to determine any over- or underestimation of age estimates between ossicles and the estimates provided by length-frequency histograms (Campana et al. 1995).

Females vouchered during monthly sampling were used to determine patterns in female reproductive strategies. First, I quantified the number of eggs and average egg size for each crayfish. I removed and counted the number of eggs in the ovarian sac (ovarian eggs) or attached to the abdomen (pleopodal eggs). I only considered eggs that were well individualized with cortical crypts formed (Pârvulescu et al. 2015) as countable ovarian eggs to avoid variation between the number and size of eggs during oogenesis (Nakata and Goshima 2004). Then, I measured the diameter (0.01 mm) of the 10 most round eggs from each crayfish using a microscope and a digital micrometer (Muck et al. 2002).

Morphological measurements from collected individuals were used to quantify reproductive (i.e., size at maturity, reproductive timing, fecundity, and egg size) characteristics.

Size at sexual maturity was quantified as the size (TCL) where 50% of the individuals were in reproductive form (L50, King 1995; Skúladóttir 1998) using a Bayesian logistic regression with 10,000 iterations in the "sizeMat" package (Torrejon-Magallanes 2020) in program R. I used a subset of crayfish larger than the smallest reproductively active individual to describe the reproductive timing of each species by plotting the proportion of reproductively active adults collected each month. I quantified potential and realized fecundity by determining the average number of ovarian and pleopodal eggs. I determined the average pleopodal and ovarian egg sizes using the ten most round eggs. I then used a simple linear regression with an alpha of 0.05 to determine the relationship between TCL and egg size and count (Stechey and Somers 1995).

In addition to reproductive patterns, I determined the sex ratio and age structure of each species. I quantified sex ratio simply as the proportion of males to females sampled. The age structure of the populations was determined using the relative frequency of crayfish in each age class (Neumann and Allen 2007) using estimates from the gastric mill ossicle that provided the most precise estimates.

Results

Crayfish sampling

I sampled 5,615 crayfish during my monthly life-history and microhabitat sampling combined. I sampled 2,683 during monthly life-history sampling, though I was unable to sample during December and January because of harsh winter conditions and April because of a flood pulse. I sampled 2,932 individuals during microhabitat sampling. Sampling across my target species indicated *F. nana* was the most abundant (n=4,030), following by *F. meeki brevis* (n=1,001) and *F. macras* (n= 584).

Microhabitat use and availability

F. macrus observations were limited to Lost Creek, whereas the other two species occurred in both Peacheater and Tyner creeks. *F. macrus* occurred in 181 use plots in Lost Creek. Both *F. nana* and *F. meeki brevis* occurred in more plots in Peacheater Creek (*F. nana* = 605, *F. meeki brevis* = 73) compared to Tyner Creek (*F. nana* = 596, *F. meeki brevis* = 58). All species were found in fewer microhabitat plots during the spring. F. macrus was relatively less common during the spring than during the summer (0.03, spring = 6, summer = 175) compared to *F. nana* (spring = 202 summer = 999) and *F. meeki brevis* (spring = 43 summer = 88).

Available habitat was somewhat different among the reaches of streams I sampled (Table 1). Lost Creek was a little deeper (average depth, 0.31 ± 0.22 m) and with somewhat faster water (average velocity, 0.39 ± 0.28 m/s) compared to other streams (Table 1). However, maximum depth was greatest in Peacheater Creek (1.35 m) followed by Tyner (1.50 m) and Lost creeks (1.16 m), respectively. The proportion of plots with cobble and pebble substrate was similar among streams (Table 1). The percentage of microhabitat plots with cover present was higher at Tyner (19%) and Peacheater (13%) creeks compared to Lost Creek (6%).

Microhabitat selection

The final model for *F. macrus* included main effects for cover, depth, substrate, and velocity (Table 2) and had adequate model fit (Figure 4). The ratio of used to available microhabitat samples in this model was 1:7 respectively. However, I did not include covariates for stream or season because *F. macrus* was only observed at Lost Creek and only 6 times during spring sampling. *F. macrus* was 1.86 times as likely to select microhabitat plots without cover compared to those with cover. Additionally, *F. macrus* selected shallower depths and substrates other than gravel and cobble. However, these relationships were relatively weak.

The final model for *F. meeki brevis* included an interaction between depth and season and main effects of substrate, velocity, and stream (Table 3). The ratio of used to available microhabitat samples in this model was 1:13 respectively *F. meeki brevis* selected shallower depths during the spring than during the summer (Figure 5). *F. meeki brevis* was less likely to select habitats dominated by gravel and cobble substrates and more likely to select microhabitats with high velocities; however, these relationships were relatively weak. Additionally, they were more likely to select habitats at Peacheater rather than Tyner creek. The binned residuals plot was indicative of adequate model fit (Figure 6).

Interactions between season and all fixed effects were kept in the final model for *F. nana* (Table 4). The ratio of used to available microhabitat samples in this model was 1:1.4 respectively I found that *F. nana* selected low velocity habitats during the spring and high velocity habitats during the summer (Figure 7). *F. nana* generally selected microhabitats at Peacheater Creek more than Tyner Creek, shallow depths (Figure 8), no cover, and substrates other than gravel and cobble. I also found that F. nana selected lower velocities and were less likely to select microhabitats with cover and mid-sized substrates during the spring compared to the summer. The binned residuals plot was indicative of adequate model fit (Figure 9).

Life-history

Although the precision of age estimates obtained by each ossicle type varied by species, age estimates from the mesocardiac ossicle were generally the most precise. Percent reader agreement and percent reader agreement ± 1yr was similar across all ossicles and species (Table 5). Age estimates obtained using the pterocardiac ossicle were the most precise for *F. macrus* (mean CV = 11.11%) and *F. meeki brevis* (mean CV = 14.94%). However, the pterocardiac ossicle had the highest mean CV (mean CV = 15.71%) across all species, and the sample size relatively lower due to difficulties processing the structure (i.e., the ossicles were often too small to process) (Table 5). Age estimates obtained from the mesocardiac ossicle had the lowest mean CV (14.12%) and thus, were used in comparisons with age estimates obtained using a length-frequency analyses.

Age estimates obtained using the gastric mill (i.e., mesocardiac ossicle) were generally similar to estimates made by the length-frequency analysis (LFA). LFA estimates indicated the presence of three year classes for all species, whereas gastric mill estimates indicated four year classes in *F. nana* and *F. meeki brevis* and three year classes in *F. macrus*. For all species, agreement between the two methods decreased as age increased, however no estimates were more than 1 yr different (Table 6). The Evans-Hoenig test of symmetry showed that there was a difference between the two methods for *F. macrus* ($X^2 = 9.8$, $P = 0.001$) but not for *F. nana* ($X^2 = 0.04$, $P = 0.83$) and *F. meeki brevis* ($X^2 = 2.8$, $P = 0.08$). Moreover, age bias plots indicated that the mesocardiac ossicle generally underestimated age compared to LFA for age-2 *F. macrus.* However, this was the only difference between the two methods that was significantly different from 0 (Figure 10).

Size (TCL) at maturity estimates differed among the three species (Table 7). *F. meeki brevis* was larger, on average (mean TCL = 17.22 mm +/- 5.70), than *F. nana* (mean TCL = 13.61 mm +/- 3.93) and *F. macrus* (mean TCL = 13.44 mm +/- 3.36) and as expected had the largest length-at-maturity estimate (L50 = 28.71 mm TCL, 95 % HDI = 27.6, 30.17). Interestingly, *F. nana* had an L50 estimate (L50 = 26.61 mm TCL, 95 % HDI = 25.01, 28.69) that was much larger than *F. macrus* (L50 = 18.05 mm TCL, 95 % HDI = 17.04, 19.72) even though they had similar TCL averages.

I found similar patterns in reproductive timing between *F. nana* and *F. macrus*, whereas a different pattern was observed for *F. meeki brevis* (Figure 11). The majority of *F. nana* and *F. macrus* were in reproductive form during late autumn and early spring. However, the decline in the proportion of reproductively active individuals during the summer months was less so in *F. nana* than in *F. macrus*. Alternatively, the proportion of reproductively active *F. meeki brevis* was relatively low and more consistent throughout the seasons. The proportion of reproductive *F. meeki brevis* was lowest in November (0.00), whereas it was quite high for both *F. nana* (0.55) and *F. macrus* (0.74).

I estimated fecundity and built regression models relating count and diameter of ovarian eggs to TCL for *F. nana* and *F. macrus.* However, too few *F. meeki brevis* (n = 3) females with ovarian or pleopodal eggs were sampled to perform these analyses. Pleopodal and ovarian egg sizes were similar in both *F. nana* and *F. macrus* (Table 8), where average pleopodal egg size was near 2 µm and the average ovarian egg size was approximately 1 µm. *F. nana* had an average of 49 (± 19) pleopodal eggs and 53 (± 24) ovarian eggs and *F. macrus* averaged 42 (± 23) pleopodal eggs and 51 (± 23) ovarian eggs. I found a significant positive relationship between TCL and the number of ovarian eggs for both *F. nana* (*p-value* < 0.05) and *F. macrus* (*p-value* = 0.01) (Table 9; Figure 12). I also found a significant relationship between TCL and ovarian egg size for *F. nana* (*p-value* = 0.02); however, this relationship was not a significant for *F. macrus* (*p-value* = 0.72) (Table 9; Figure 12).

The sex ratio and age structure of *F. nana* and *F. macrus* were more similar than *F. meeki brevis*. Females were more abundant than males for all species (Table 7). Sex ratios (M:F) were similar in *F. nana* (1:1.26; M = 1697, F = 2155) and *F. macrus* (1:1.24; M = 254, F = 315), however the ratio of *F. meeki brevis* was relatively more biased towards females (1:1.86; M =

317, F = 592). The age structure of *F. nana* and *F. macrus* comprised primarily age 1 crayfish and the percentage in each age class generally decreased as age increased (Table 10). Whereas age 2 crayfish made up the greatest percentage of the sampled *F. meeki brevis* population.

Discussion

My results contribute to the growing literature about the life histories and habitat associations of crayfishes. This information is lacking for a large majority of crayfishes (Resh and Rosenberg 2010; Moore et al. 2013) and is often inferred for data-limited species using data for sympatric or closely related species (e.g., Hobbs Jr. 1989; Pflieger 1996). Although identifying life-history patterns for closely related species may help develop conservation strategies that benefit multiple species, making non-data-driven inferences may lead to poor management of species assumed to share similar traits. For example, my results show similarities and differences in the life-history patterns and the microhabitat selection among three commonly associated crayfishes.

I found differences in the selection of water velocities between two sympatric species (i.e., *F. nana* and *F. meeki brevis*) that likely relates to the differences observed in their reproduction patterns. *F. nana* selected high velocity microhabitats during the summer and low velocity areas during the spring, whereas there was no relationship between velocity and microhabitat selection for *F. meeki brevis*. I also found that reproductive activity in *F. nana* was highest during the spring and lowest during summer, whereas reproductive *F. meeki brevis* were found throughout the year. The use of lower velocity habitats during reproductive periods is common in many crayfishes (Pflieger 1996; Longshaw and Stebbing 2016). Reproductively active crayfish use chemical cues during mating (Belanger and Moore 2006; Aquiloni and Gherardi 2007; Berry and Breithaupt 2010) and to reduce cannibalism of offspring (Figler et al.

1997; Mathews 2011). Higher-velocity habitats may dilute these chemical cues below detection thresholds (Moore and Crimaldi 2004) making lower-velocity habitats important during reproductive periods. Thus, the reproductive timing of crayfishes should be considered before altering flow regimes.

Although the strength of the relationships varied among species and between seasons, all crayfishes in this study were more likely to select relatively shallow microhabitats. Larger crayfish generally use deeper habitats than smaller crayfish and this relationship has been observed in lotic (e.g., Creed 1994) and lentic ecosystems (e.g., Litvan et al. 2010) including those in caves (e.g., Mouser et al. 2022). Shallow-water habitats are commonly associated with larger substrates and likely provide shelter from predators, especially for smaller crayfishes (DiStefano et al. 2003; Flinders and Magoulick 2007; Longshaw and Stebbing 2016). However, Clark et al. (2013), found that crayfish survival was higher in shallow pools and riffles regardless of body size, Interestingly, *F. meeki brevis* had the strongest selection for shallower depths, given it has a relatively larger body size than both *F. nana* and *F. macrus*. This too may be related to the prolonged reproductive strategy by *F. meeki brevis* due to the increased predation risk associated with molting (Brewis and Bowler 1983). Additionally, *F. nana* and *F. meeki brevis* selected shallower water depths during the spring. This was not surprising because crayfish, like many poikilotherms, are less active when exposed to cooler temperatures (Crawshaw 1983; Withers 1992; Bubb et al. 2002) and likely to seek shelter in shallower water. I was unable to sample enough *F. macrus* during the spring to model seasonal differences in microhabitat selection. However, Pflieger (1996) found that *F. macrus* behaves more similar to *Cambarus spp.* than other *Faxonius spp*. and spends much of their time in cavities beneath rock or tunnels in gravely substrates. Difficulties detecting the species during the spring suggest that they may select habitats that are difficult to sample using our gears (Somers and Green 1993; Richards et al. 1996). Thus, detection by these species may not be high in all seasons of interest.

All the crayfish in my study were negatively associated with cover (i.e., macrophytes and woody debris) at the microhabitat scale, and these findings may be related to the presence of a known invader *F. neglectus*. Macrophytes and woody debris provide shelter from higher velocities and predators and are associated with high amounts of detritus and macroinvertebrates that are the primary food source for many crayfish (Jordan et al. 1996; DiStefano et al. 2003; Flinders and Magoulick 2007). These areas are often dominated by smaller or juvenile crayfish (Momot and Gowing 1983; DiStefano et al. 2003; Flinders and Magoulick 2007). Thus, I hypothesized that *F. nana* and *F. macrus* would select these areas due to their relatively smaller sizes. However, larger crayfish are often thought to outcompete smaller crayfish by excluding them from shelters when the resource is limited (Hill and Lodge 1994; Gherardi and Cioni 2004) regardless of species identity (Larson and Magoulick 2009). For example, Rabeni (1985) found that when either *F. luteus* or *F. punctimanus* were at least 1-mm larger than the other, the larger crayfish occupied the shelter more than 80% of the time. *F. neglectus* is known to be invasive in many drainages across North America (Daniels et al. 2001; Magoulick and DiStefano 2007; Imhoff et al. 2012), and its success as an invader is often attributed to it relatively large body and chelae (Rodger and Starks 2020; Magoulick et al. 2022). Additionally, Gore and Bryant (1990) found that adult *F. neglectus* were associated with macrophyte beds, whereas juveniles were found primarily in cobble substrates. Although I did not record habitat use by *F. neglectus* in this analysis, occupancy is high across my study area (see Chapter 2) and may have excluded my target species from microhabitats where cover was present. There may be intricacies associated with different life stages or gender that I did not examine here (Rabeni 1985; Gore and Bryant

1990; Usio and Townsend 2002; DiStefano et al. 2003). Additionally, future studies examining the behavioral interactions between *F. neglectus* and other native species would improve our understanding of these patterns.

Using gastric mill ossicles to estimate the age of crayfishes may be more efficient than the more commonly used length-frequency analysis (LFA) (Reynolds 2002). In addition to requiring a relatively smaller sample size (France et al. 1991), using gastric mill ossicles to age crayfish allows researchers to differentiate between faster- and slower-growing individuals and compare results between populations and years (Kilada et al. 2012) that is not possible using LFA. Additionally, I found that disagreement between the two methods was generally greater for older aged crayfish (see also Mouser et al. 2020) and LFA estimates are known to be less accurate for older aged individuals (France et al. 1991). I found that age estimates between the two methods were generally similar and only differed for age-2 *F. macrus*. Mouser et al. (2020) also found a general agreement between the two methods using the paired zygocardiac ossicles to age *F. neglectus*. However, longevity estimates were lower using LFA (i.e., 3 yr) than using the gastric mill (i.e., 4 yr). Kilada and Ibrahim (2016) also observed an extra year class using the gastric mill to age Blue Swimmer Crabs *Portunus pelagicus* compared to LFA, whereas Mouser et al. (2020) found that LFA underestimated longevity by 4 yr when ageing with the gastric mill (i.e., 6 vs 10 yr) for the longer-lived *F. neglectus*.

I recommend using the mesocardiac ossicle when estimating the age of *F. nana*, *F. macrus*, and *F. meeki brevis*. The utility of different ageing structures is often species-specific (Campana 2001) and each ossicle has been recommended for ageing in at least one other study (e.g., zygocardiac, Kilada and Ibrahim 2016; pterocardiac, Gnanalingam et al. 2019; mesocardiac, Kilada et al. 2012). However, difficulties extracting the pterocardiac (i.e., the smallest ossicle) ossicle may limit its use for ageing smaller crayfishes. Mouser et al. (2020) also reported difficulties using this structure due to its relatively small size. Furthermore, use of the pterocardiac ossicle for ageing crayfish has only been recommended by Leland et al. (2015) for *Cherax quadricarinatus*, which is relatively larger than most *Faxonius* species. Additionally, gastric mill ageing research has been conducted primarily on invasive non-native and aggressive native crayfishes (e.g., *F. neglectus*, Mouser et al. 2019; *C. quadricarinatus*, Leland et al. 2015; *Procambarus clarkii*, Leland et al. 2011). Thus, future research on band formation and the usefulness of the gastric mill for ageing would benefit from a focus on other native, less aggressive crayfishes. This may provide a better understanding of how traits differ between less aggressive and more competitive crayfish populations, particularly when there may not be enough individuals to develop meaningful LF histograms.

F. nana and *F. macrus* may breed early in the winter as is common in other *Faxonius spp.* at this latitude (Riggert et al. 1999; Muck et al. 2002; DiStefano et al. 2019); though, *F. meeki brevis* had a different pattern. Pflieger (1996) observed a similar pattern for *F. macrus* in Missouri, USA. *F. meeki brevis* showed a more continuous reproductive pattern throughout the year. Although reproductively active male crayfish have been observed year-round in other crayfishes (Riggert et al. 1999; Mouser et al. 2019), a peak in reproductive activity was still apparent; however, this was not observed in *F. meeki brevis*. Additionally, DiStefano et al. (2019) cautions against using sperm plugs to identify reproductive activity in females, as this trait may not be as common in *Faxonius spp.* as once thought (e.g., DiStefano et al. 2002; Larson and Magoulick 2008).

There were few differences in size in maturity and fecundity estimates, and fecundity estimates and sex ratios were as expected given our current understanding of crayfishes.

Although *F. nana* and *F. macrus* were relatively similar in size, maturity was observed in smaller individuals of *F. macrus*. The smallest *F. macrus* observed by Pflieger (1996) was ~20-mm total length, which is consistent with my results given TCL is approximately half of the total length. Alcorlo et al. (2008) found that size-at-maturity was negatively associated with population density for *P. clarkii* and may be the case for *F. macrus* which seemed to occur in lower densities than *F. nana* and *F. meeki brevis*. Additionally, *F. macrus* was the only species that I sampled that was able to reproduce in the first year of life. Realized fecundity and average egg sizes for *F. macrus* and *F. nana* were well with the range reported by Mabery et al. (2017) who compiled fecundity and egg size data for 19 *Faxonius spp.* from 26 studies. They also found no differences in the number or size of pleopodal eggs between the imperiled *F. quadruncus* and invasive *F. hylas*. Sex ratios in *Faxonius spp.* are commonly biased towards males during the spring and females during the mid- to late-summer (Flinders and Magoulick 2005; DiStefano et al. 2019; Hartzell 2020). A majority of my microhabitat sampling occurred during the mid- to late-summer and thus, may explain the female biased sex ratios I observed in all of my species.

My results show that using sympatry or phylogenetics to make inferences about the life history and habitat association of other crayfishes may lead to conservation actions that do not meet the intended goals. For example, life-history information for *F. meeki brevis* and *F. nana* reported by Morehouse and Tobler (2013) was based primarily on Pflieger (1996) descriptions for *F. macrus*. However, I found several differences in the life histories and selection of microhabitats among these three species. Although I recognize the difficulty of examining the life histories of every species, it would be beneficial to tie variation in traits or trait probabilities to groups of species to better address our uncertainty in conservation actions. Life-history studies are valuable and arguably a missing link in our ability to complete species status assessments or develop meaningful options for species recovery (Taylor et al. 2019). Moreover, understanding the resilience of different species to invasive species would be improved if we improved our understanding of crayfish traits, particularly those that influence the accuracy of population models and can be linked to specific behaviors. Differentiating the mechanisms associated with species declines can be difficult. However, if we have information on both reproduction and habitat selection, then we can develop experiments that directly address the species' response. For example, Larson et al. (2009) found that the native *F. eupunctus* was less tolerant of stream drying than the invasive *F. neglectus*, whereas Larson and Magoulick (2008) reported few differences in the life histories between the two species. However, less is known about how different life-history strategies relate to species' responses. For example, overlap in habitat use when two species have similar reproductive patterns may lead to population declines by the lesser competitive species when resources are limited, whereas species with different reproductive patterns that use the same habitat may be able to persist. Future studies including species with different life histories and habitat associations may allow us to ascertain how certain traits respond to disturbances and may lead to more efficient and successful conservation of data limited species.

Table 1. Summary of available microhabitat at Tyner, Peacheater, and Lost creek. N is the number of microhabitat plots sampled, depth (1.0 m) and velocity (1.0 m^3/s) are reported as mean ± SD and range (min – max), substrate is the number of microhabitat plots comprised of 100% gravel and cobble, and cover is the number of microhabitat plots where cover was present.

Stream	N	Depth	Velocity	Substrate	Cover
Tyner	1055	0.24 ± 0.20 (0.01 – 1.50)	0.16 ± 0.16 (0.00 – 1.07)	699	198
Peacheater	655	0.26 ± 0.23 (0.01 – 1.35)	0.11 ± 0.13 (0.00 – 0.75)	382	87
Lost	1319	0.31 ± 0.22 (0.01 – 1.16)	0.39 ± 0.28 (0.00 – 1.37)	878	86

Table 2. Regression coefficients and associated lower- and upper confidence intervals from the final microhabitat selection model for *F. macrus*. Cover and substrate were categorical variables where cover absent and substrate not comprising 100% gravel and cobble in the microhabitat plot were the reference nodes.

Covariate	Coefficient	Lower CI	Upper CI
Depth	-0.39	-0.52	-0.26
Velocity	0.14	0.006	0.29
Cover	-1.89	-3.34	-0.90
Substrate	-0.34	-0.59	-0.08

Table 3. Regression coefficients and associated lower- and upper confidence intervals from the final microhabitat selection model for *F. meeki brevis*. Categorical covariates were: cover, where no cover present was the reference; substrate, where substrate not comprising 100% gravel and cobble was the reference; season, where spring was the reference; and stream, where Peacheater Creek was the reference. This model also included an interaction term between depth and season (Depth:Season).

Covariate	Coefficient	Lower CI	Upper CI
Depth	-1.60	-1.96	-1.25
Season	0.18	-0.17	0.58
Velocity	1.46	1.23	1.71
Substrate	-0.38	-0.69	-0.08
Stream	-1.00	-1.31	-0.70
Depth:Season	1.73	1.30	2.16

Table 4. Regression coefficients and associated lower- and upper confidence intervals from the final microhabitat selection model for *F. nana*. Categorical covariates were: cover, where no cover present was the reference; substrate, where substrate not comprising 100% gravel and cobble was the reference; season, where spring was the reference; and stream, where Peacheater Creek was the reference. Seasonal interactions with covariates are indicated by Covariate:Season.

Covariate	Coefficient	Lower CI	Upper CI
Depth	-0.97	-1.21	-0.75
Season	0.31	0.04	0.58
Velocity	1.38	1.15	1.63
Cover	-0.57	-1.09	-0.08
Substrate	-1.20	-1.53	-0.87
Stream	-0.69	-0.83	-0.56
Depth:Season	0.52	0.29	0.76
Velocity:Season	-0.46	-0.72	-0.21
Cover:Season	0.74	0.21	1.30
Substrate:Season	0.52	0.16	0.89

Table 5. Number of mesocardiac and paired zygocardiac and pterocardiac gastric mill ossicles used to determine the percent reader agreement (Agreement), percent reader agreement within 1 year (± 1 yr), and mean coefficient of variation of age estimates for *F. nana*, *F. macrus*, and *F. meeki brevis*.

Ossicle	Species	Number	Agreement	± 1 yr	Mean CV
Petro	*F. nana*	49	48.9 (24)	91.8 (45)	17.55
	F. macrus	9	66.6 (6)	100 (9)	11.11
	F. meeki brevis	64	51.5 (33)	93.5 (61)	14.94
	All Species	122	51.6 (63)	94.2 (115)	15.71
Zygo	*F. nana*	180	61.6 (111)	93.8 (169)	13.68
	F. macrus	64	54.6 (35)	95.3 (61)	14.98
	F. meeki brevis	108	50.0 (54)	96.2 (104)	16.46
	All Species	352	56.8 (200)	94.8 (334)	14.99
Meso	*F. nana*	160	59.3 (95)	95.6 (153)	13.54
	F. macrus	58	58.6 (34)	100 (58)	13.10
	F. meeki brevis	105	50.96 (53)	99.0 (103)	15.57
	All Species	323	56.5 (182)	97.5 (314)	14.12

Table 6. The mean total carapace length (TCL), standard deviation (SD), and separation index (SI) of age classes determined using a length-frequency analysis (LFA). Also reported are the number of crayfish in each age class aged via the mesocardiac ossicle from the gastric mill (Number), percent agreement with LFA estimates (Agreement), and the percent agreement within 1 year of the LFA estimate (± 1 yr).

Species	Age	TCL	SD	SI	Number	Agreement	± 1 yr
F. macrus	1	7.71	1.04	4.4	13	100	100
	2	14.76	2.12	3.0	37	51.3	100
	3	20.19	1.47	-	3	33.33	100
F. nana	1	11.50	2.70	2.49	80	86.2	100
	2	17.60	2.18	3.10	72	86.1	100
	3	24.12	2.01	-	6	66.6	100
F. meeki brevis	1	10.40	1.24	4.2	30	100	100
	2	20.26	3.44	3.2	60	66.6	100
	3	28.03	1.35	-	8	62.5	100

Table 7. The sample size (N) used to determine the mean ($\bar{X}$), standard deviation (SD), minimum (Min), and maximum (Max) total carapace length (TCL); size-at-maturity (L50) from a bootstrapped regression and the associated 95% highest density intervals (L50 HDI); and sex ratio (M:F) for *F. nana*, *F. macrus*, and *F. meeki brevis*. Parameters with “Repro” were calculated using a subsample of only reproductively active individuals.

Parameter	*F. nana*	*F. macrus*	*F. meeki brevis*
N	4030	584	1001
$\bar{X}$ TCL (mm)	13.61	13.44	17.22
SD TCL (mm)	3.93	3.36	5.70
Min TCL (mm)	<4	<4	6
Max TCL (mm)	28	22.3	32.1
Repro N	551	134	49
$\bar{X}$ Repro TCL (mm)	15.45	14.78	23.10
SD Repro TCL (mm)	2.60	1.67	3.36
Min Repro TCL (mm)	10	10	15
Max Repro TCL (mm)	28	20	29
L50 (mm)	26.61	18.05	28.71
L50 HDI (mm)	25.01, 28.69	17.04, 19.72	27.60, 30.17
Sex Ratio	1:1.26	1:1.23	1:1.86

Table 8. Mean, standard deviation (SD), minimum (Min), maximum (Max), and sample size (N) for fecundity-related parameters for *F. nana* and *F. macrus*. Parameters included potential fecundity (i.e., number of ovarian eggs; PF), realized fecundity (i.e., number of pleopodal eggs; RF), ovarian egg diameter (OED, mm), pleopodal egg diameter (PED, mm), TCL of individuals with ovarian eggs (O TCL), and TCL of individuals with pleopodal eggs (P TCL). Sample size (N) for PF, RF, O TCL, and P TCL was the number of individuals and N for OED and PED was the total number ovarian or pleopodal eggs.

Species	Parameter	Mean	SD	Min	Max	N
F. nana	PF	53	24	10	134	16
	RF	49	19	29	85	4
	OED (mm)	1.06	0.34	0.42	1.95	190
	PED (mm)	2.10	0.25	1.51	2.57	40
	O TCL (mm)	16.52	2.97	11.12	23.51	16
	P TCL (mm)	16.16	2.25	13.37	19.35	4
F. macrus	PF	51	23	15	99	66
	RF	42	23	18	70	6
	OED (mm)	1.14	0.19	0.71	1.59	71
	PED (mm)	2.19	0.3	1.81	2.77	600
	O TCL (mm)	15.51	2.14	10.9	21.15	66
	P TCL (mm)	14.27	1.51	12.02	16.27	6

Table 9. Model coefficients, standard error (SE), adjusted R^2, and *p-value* from the linear regression model relating the number of ovarian eggs (i.e., potential fecundity, PF) and average ovarian egg diameter (OED) and total carapace length (TCL; mm) for *F. nana* (N = 66 females) and *F. macrus* (N = 16 females).

Species	Model	Coefficient	SE	Adjusted R^2	*p-value*
F. nana	PF	5.22	0.77	0.40	$5.7e^{-9}$
	OED	0.03	0.01	0.07	0.01
F. macrus	PF	5.72	2.31	0.25	0.02
	OED	-0.008	0.02	-0.06	0.72

Table 10. Relative percentage and number of crayfish in each age class for *F. macrus*, *F. nana*, and *F. meeki brevis* using age estimates from the mesocardiac ossicle.

Species	<1 yr	2 yr	3 yr	4 yr
F. macrus	53.4	39.7	6.9	0
	(31)	(23)	(4)	(0)
F. nana	49.4	43.8	6.3	0.6
	(79)	(70)	(10)	(1)
F. meeki brevis	41.0	47.6	9.5	1.9
	(43)	(50)	(10)	(2)

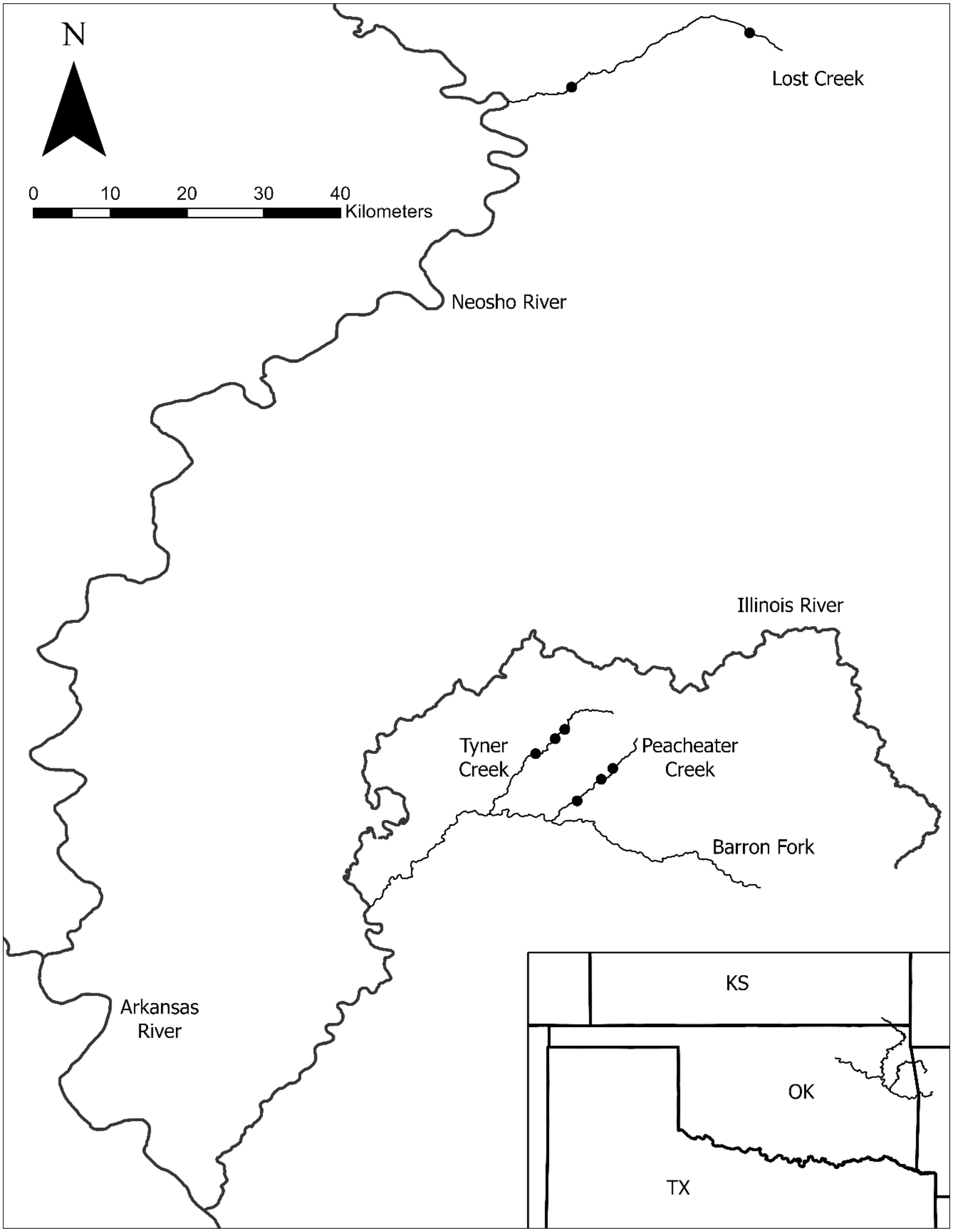

Figure 1. Map sites (points) sampled to determine microhabitat selection and life history patterns for *F. nana*, *F. macrus,* and *F. meeki brevis*. Some sites were sampled multiple times under different physicochemical conditions.

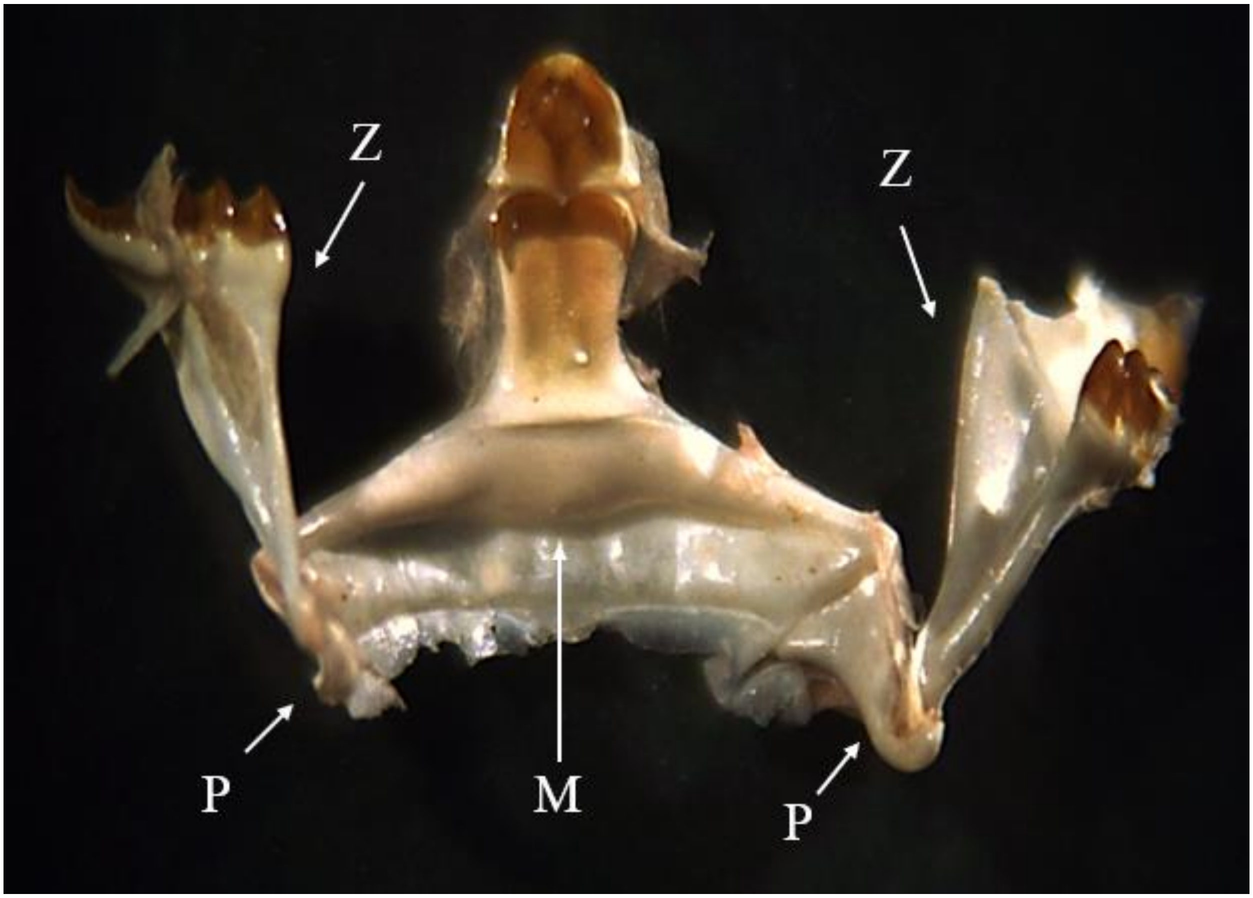

Figure 2. The gastric mill from a *F. nana* after the stomach tissue has been removed and before disarticulation of the ossicles. The gastric mill consists of 5 ossicles; mesocardiac ossicle (M), paired zygocardiac ossicles (Z), and paired pterocardiac ossicles (P).

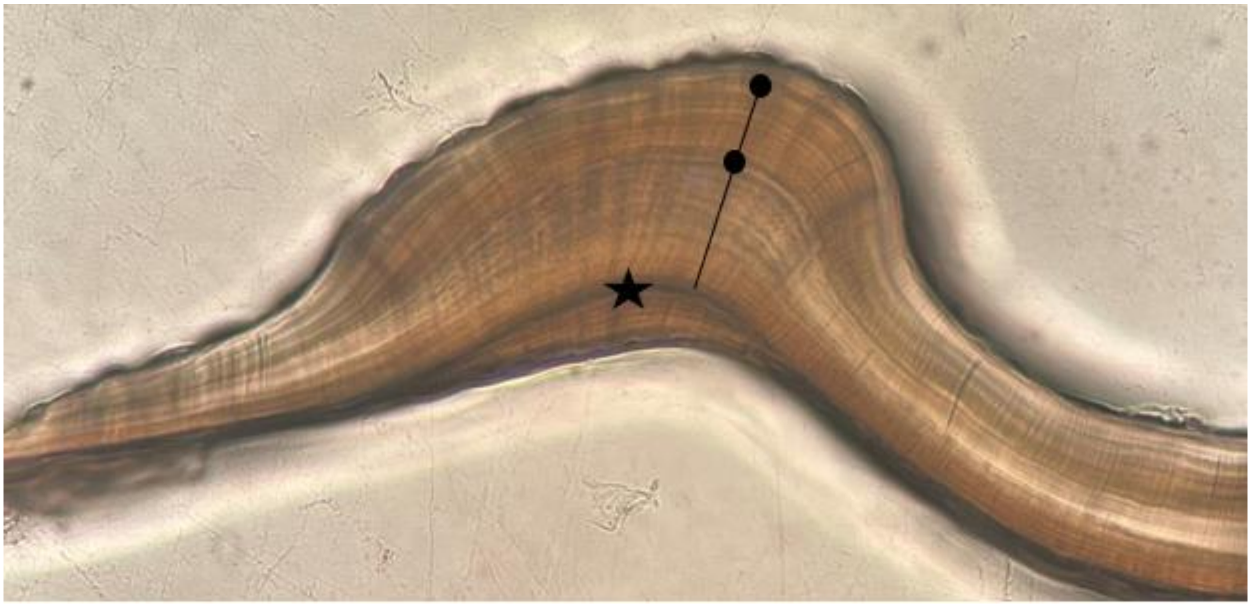

Figure 3. Section of the mesocardiac ossicle from an estimated 2yr old F. nana. The star indicates the endocuticular boundary and the black circles mark growth bands.

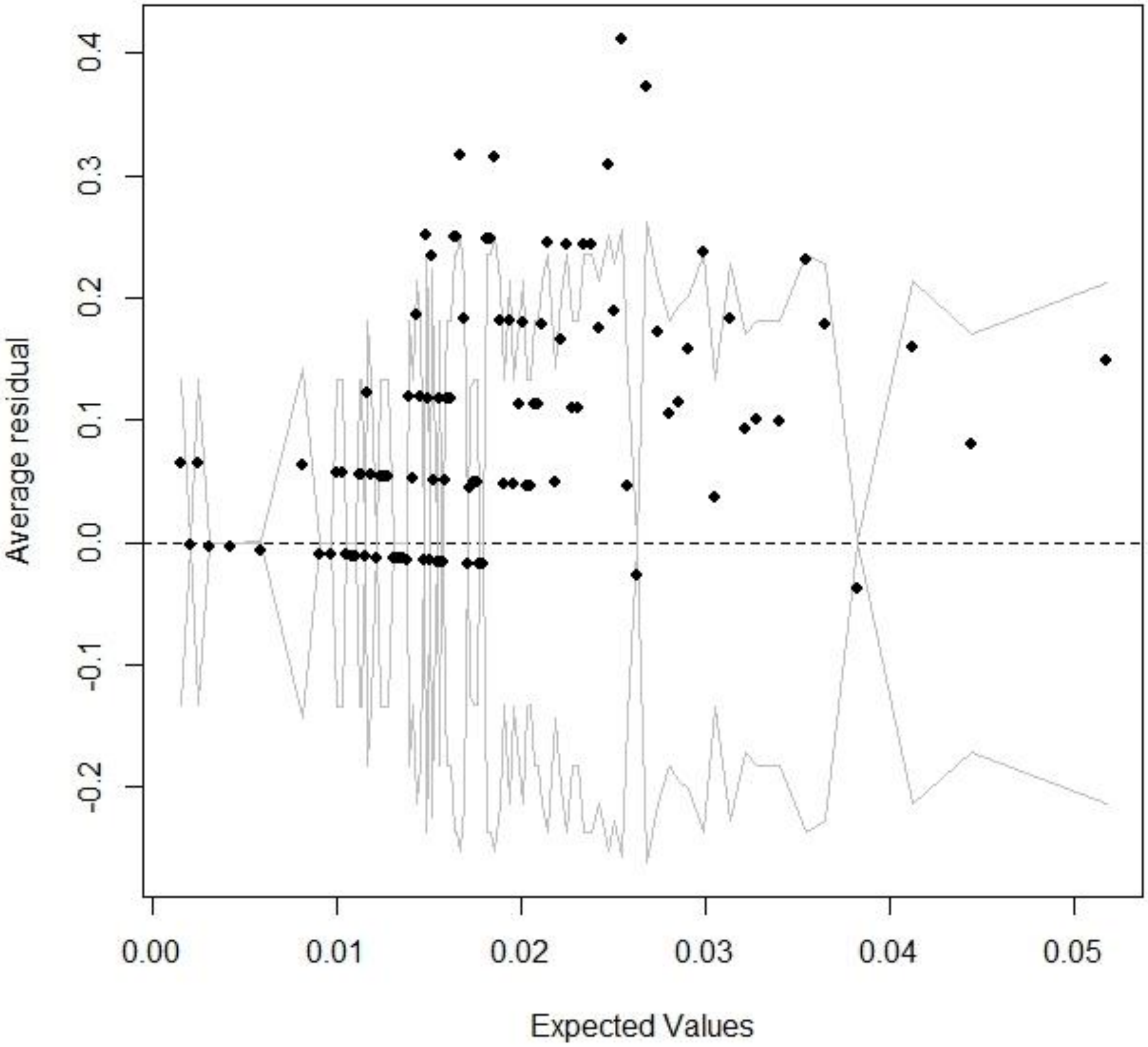

Figure 4. Binned residuals plot for my microhabitat selection model for *F. macrus* showing adequate fit. Gray lines are the theoretical error bounds and black points are the binned residuals.

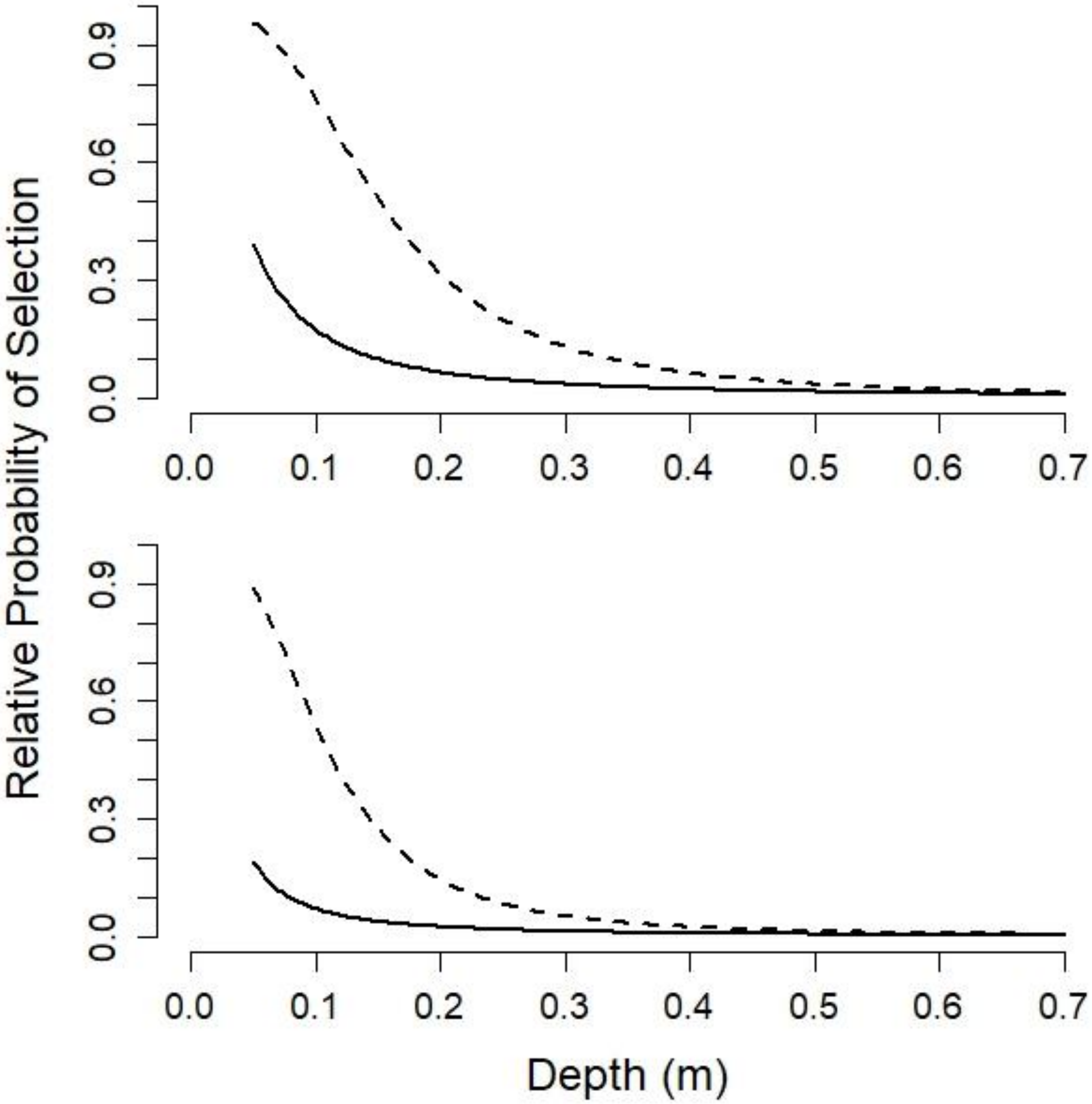

Figure 5. Model predicted relative probability of selection of depth (1.0 m) by *F. meeki brevis* during the spring (dashed line) and summer (solid line) at Peacheater Creek (top panel) and Tyner Creek (bottom panel). See Table 3 for uncertainty around these estimates.

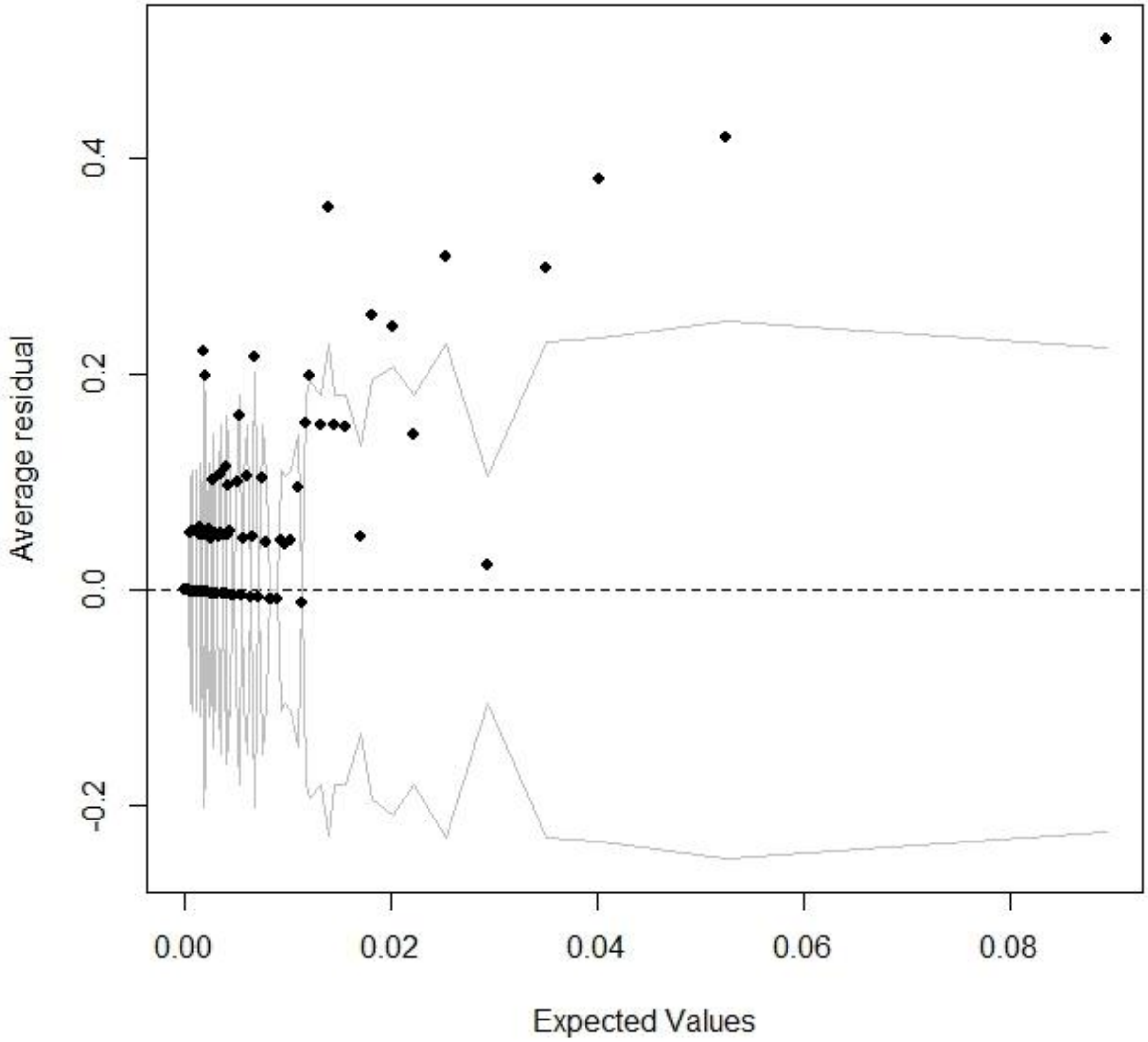

Figure 6. Binned residuals plot for my microhabitat selection model for *F. meeki brevis* showing adequate fit. Gray lines are the theoretical error bounds and black points are the binned residuals.

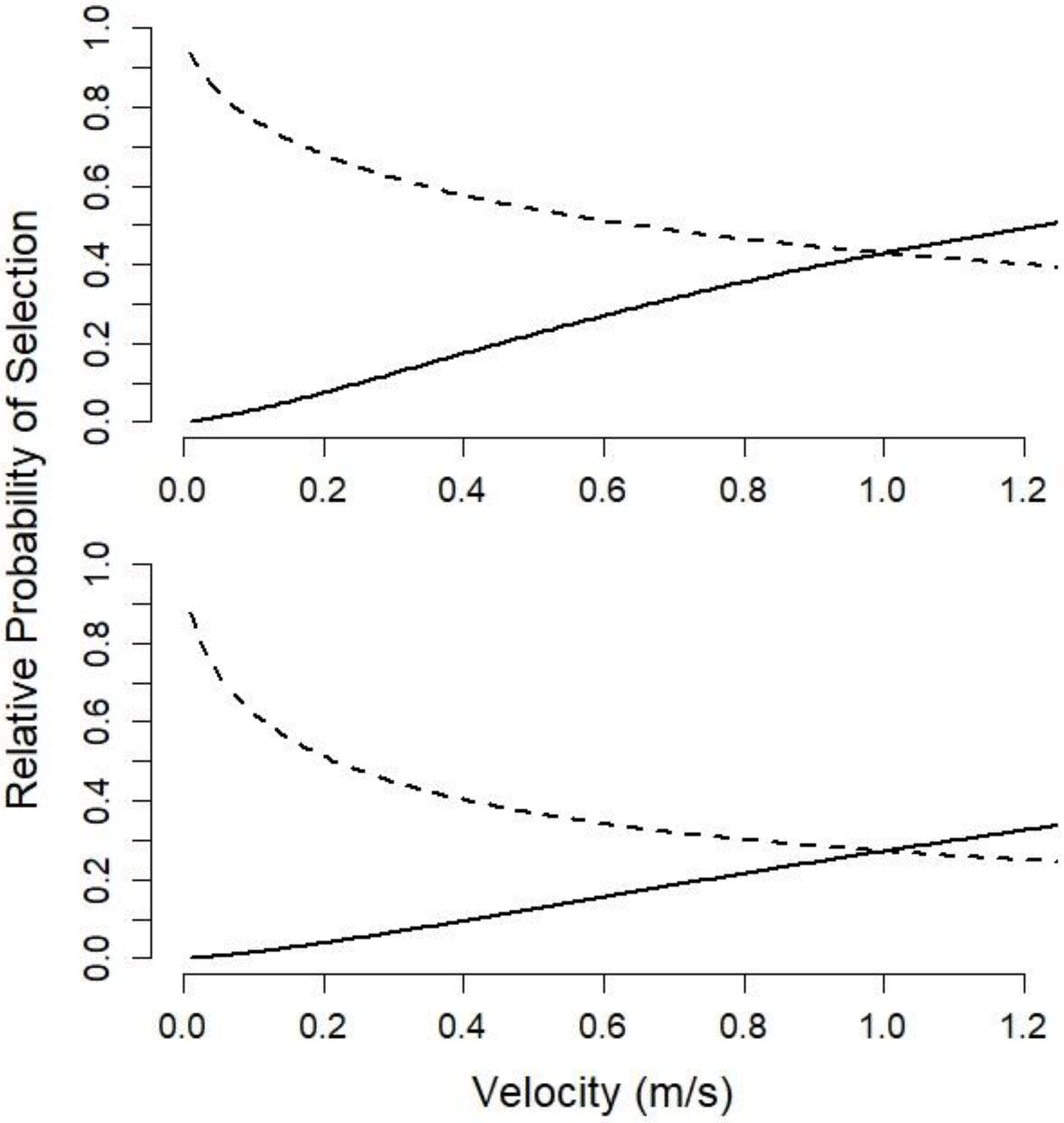

Figure 7. Model predicted relative probability of selection of water velocity (1.0 m/s) taken 0.6 depth from the bottom by *F. nana* during the spring (dashed line) and summer (solid line) at Peacheater Creek (top panel) and Tyner Creek (bottom panel). See Table 4 for uncertainty around these estimates.

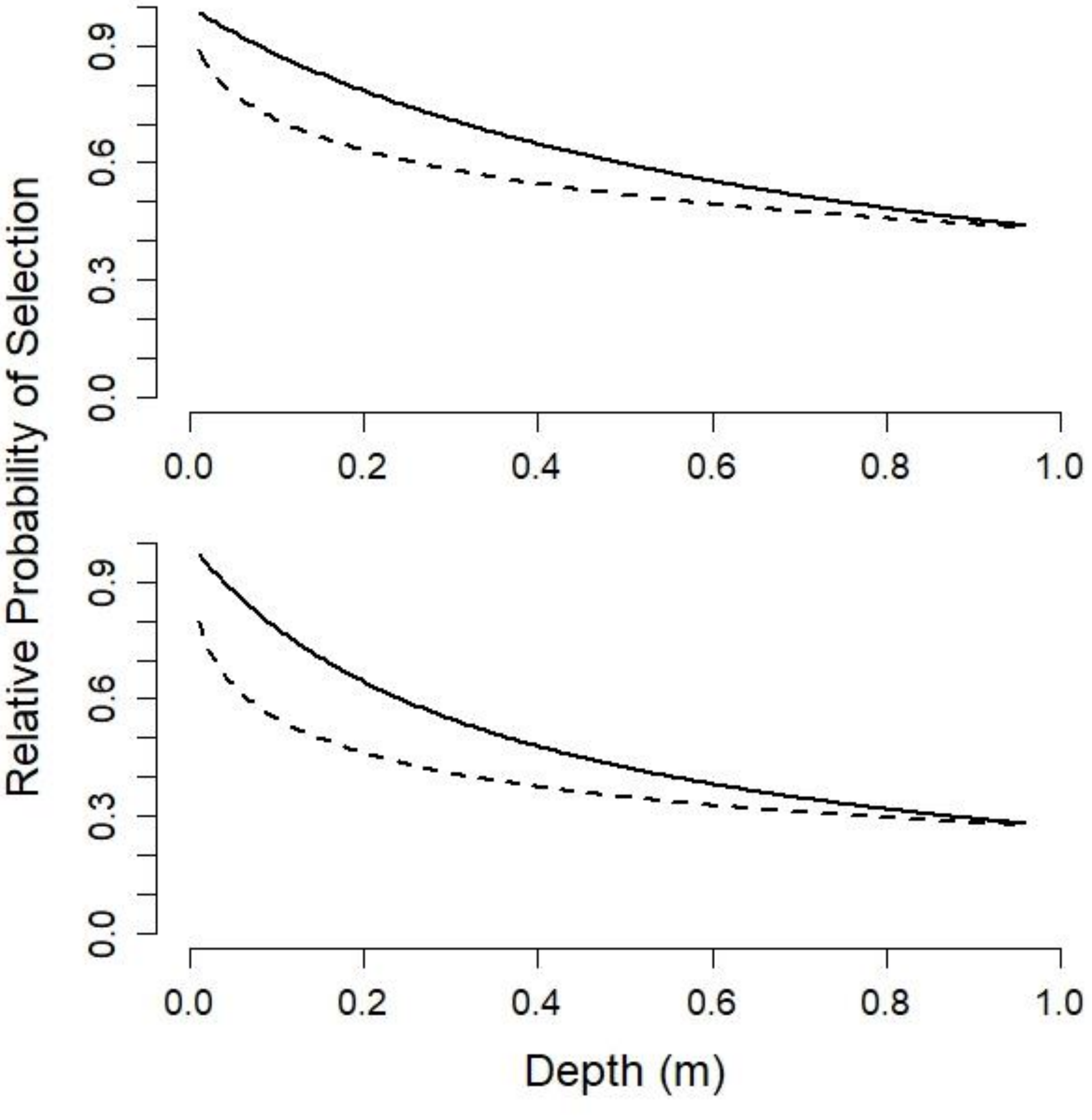

Figure 8. Model predicted relative probability of selection of depth (m) by *F. nana* during the spring (dashed line) and summer (solid line) at Peacheater Creek (top panel) and Tyner Creek (bottom panel). See Table 4 for uncertainty around these estimates.

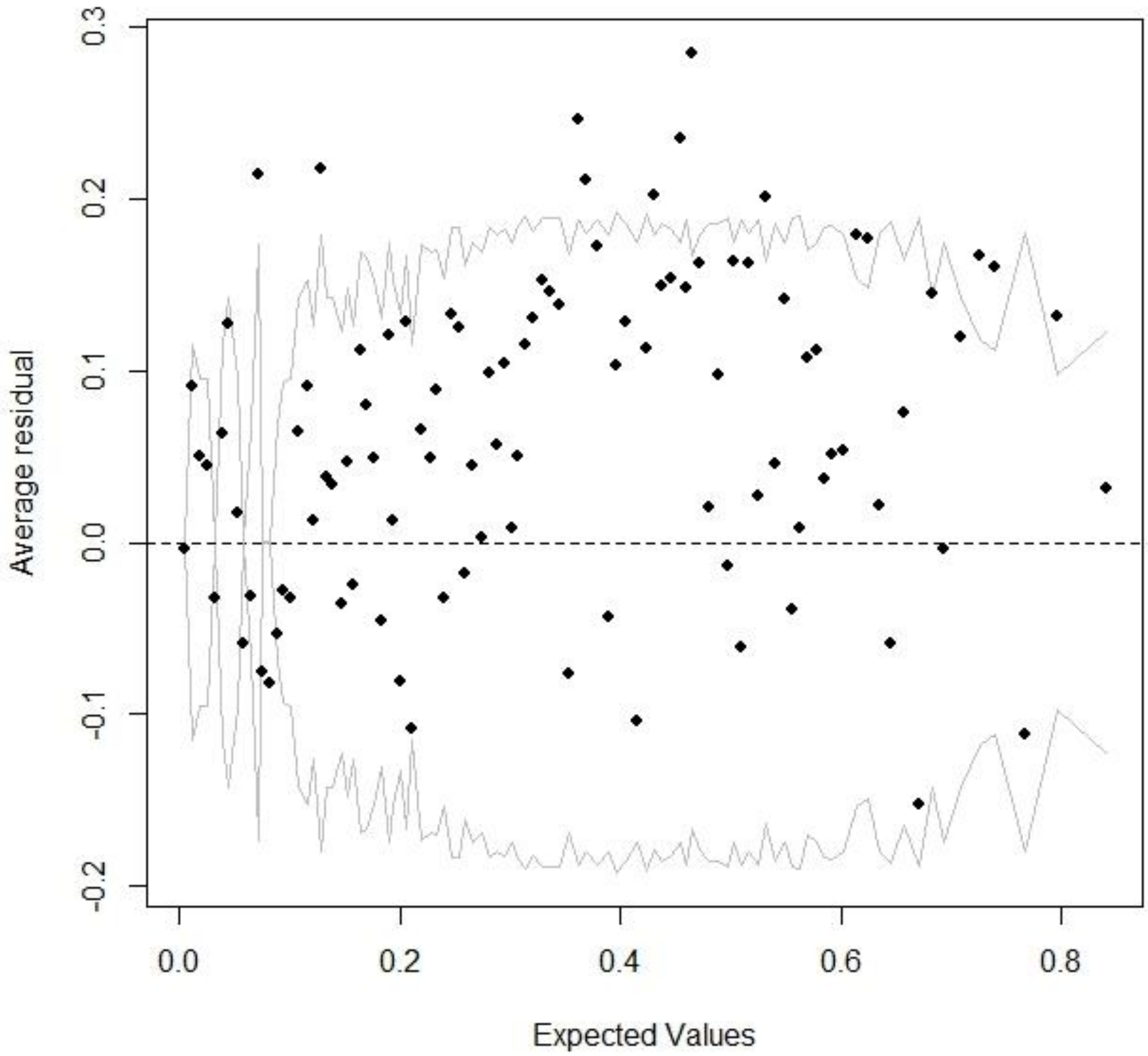

Figure 9. Binned residuals plot for my microhabitat selection model for *F. nana* showing adequate fit. Gray lines are the theoretical error bounds and black points are the binned residuals.

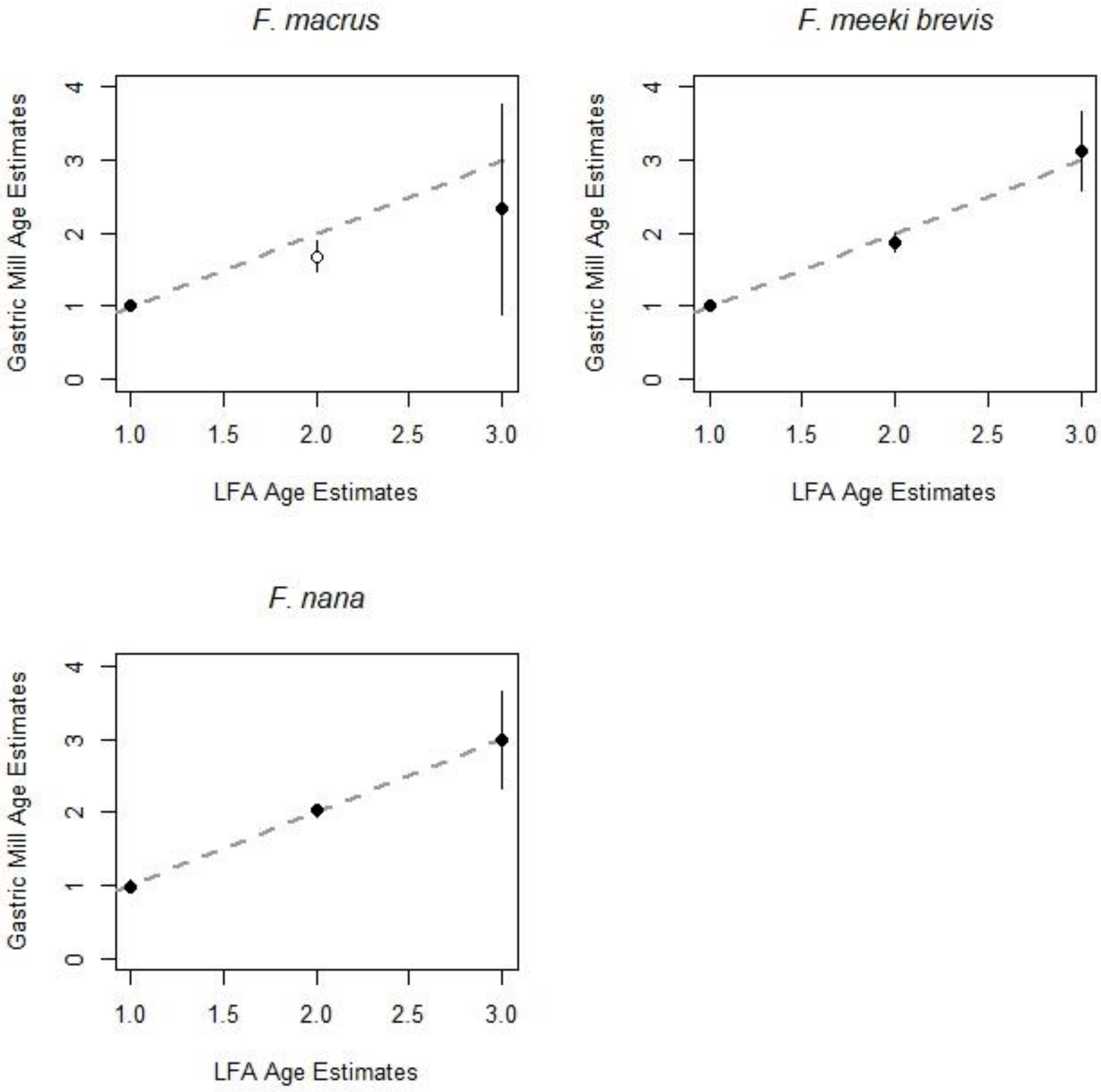

Figure 10. Agreement between age estimates using the mesocardiac ossicle of the gastric mill and length-frequency analysis (LFA) for *F. macrus* (top left panel), *F. meeki brevis* (top right panel), and *F. nana* (bottom left panel). The dashed line shows agreement between the to estimates, points are the mean age via the gastric mill (open = disagreement, closed = agreement), and vertical lines show the 95% confidence intervals around the mean.

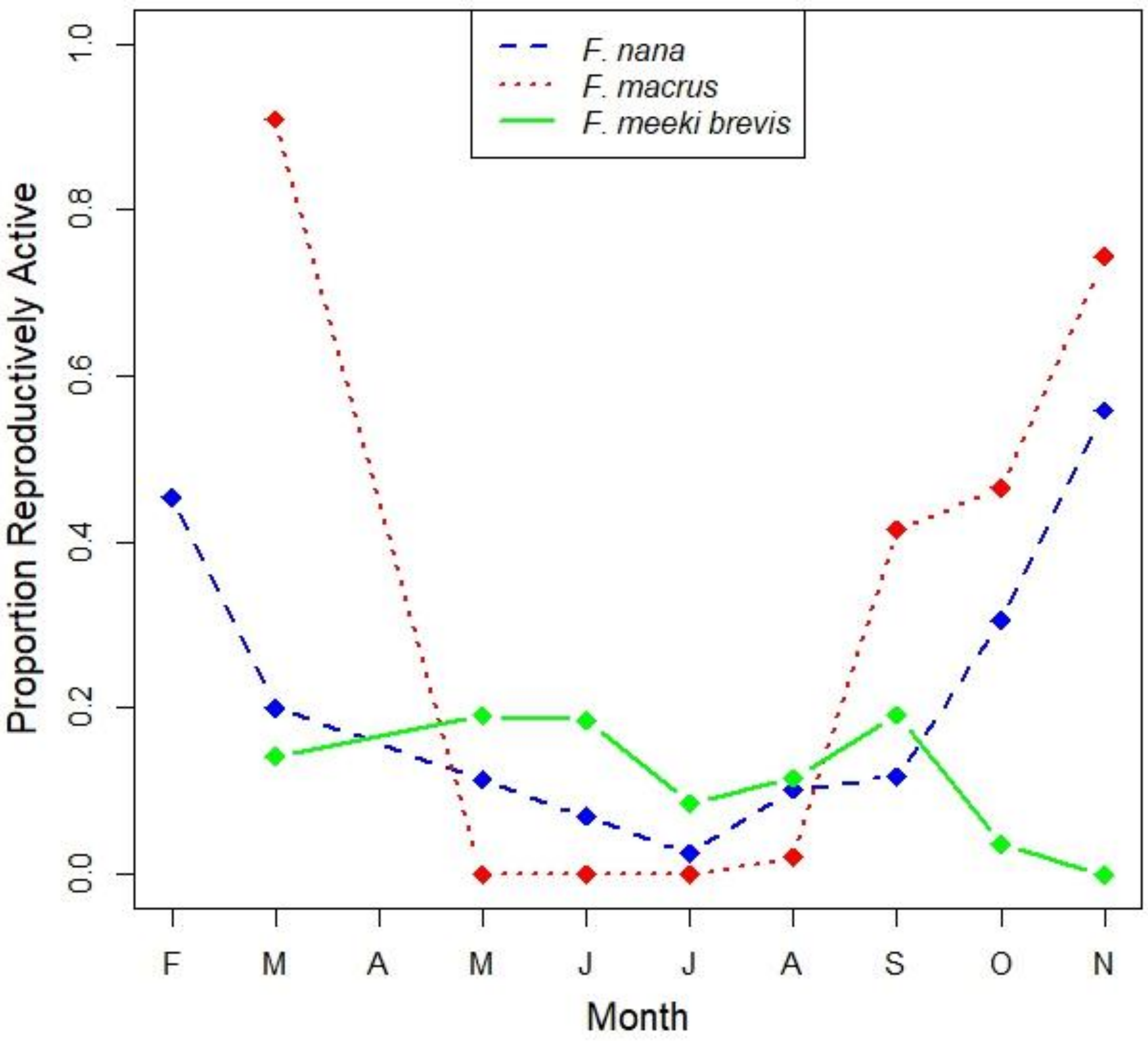

Figure 11. Proportions of reproductively active individuals by month for *F. nana* (blue; dashed line), *F. macrus* (red; dotted line), and *F. meeki brevis* (green; solid line).

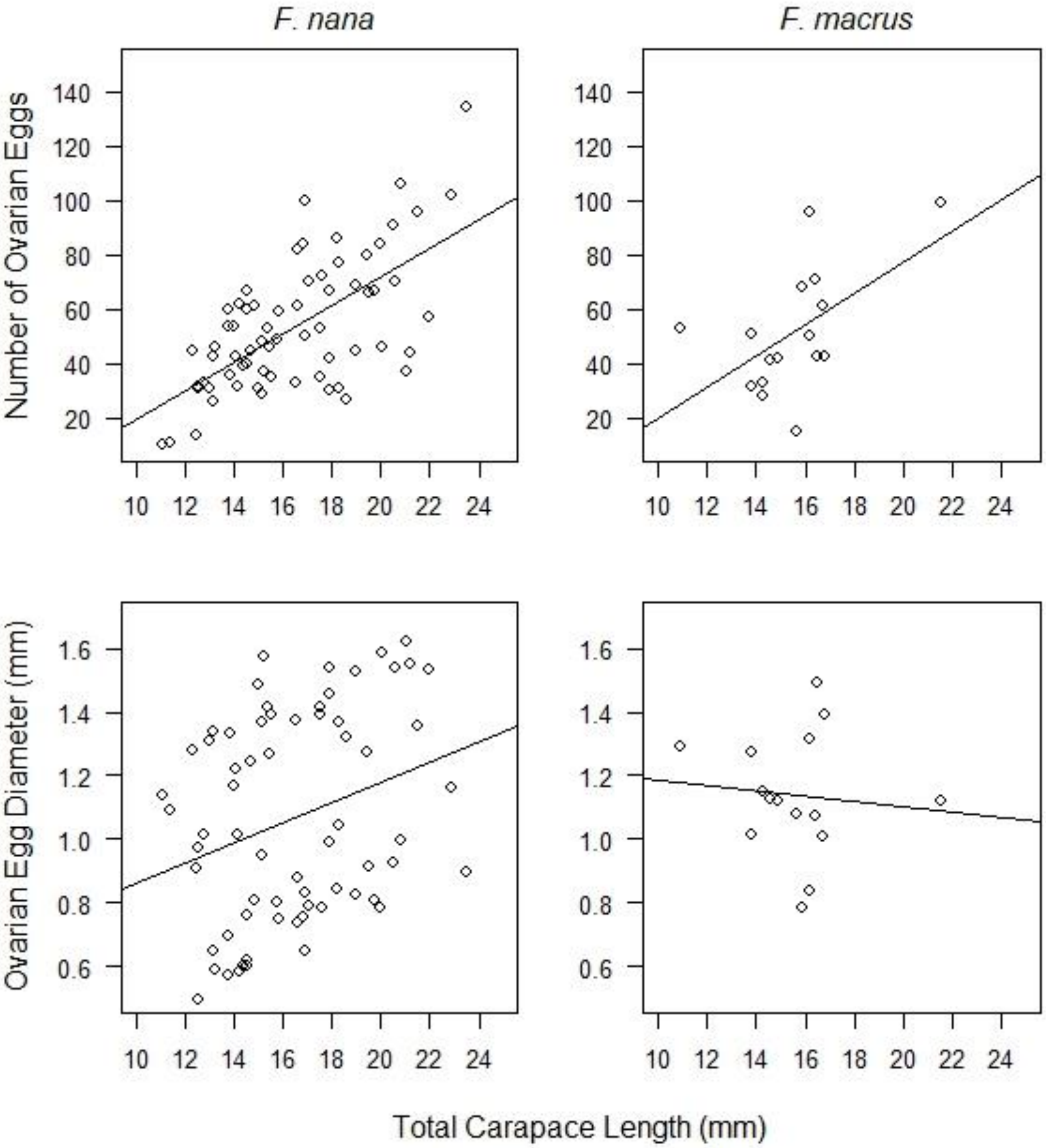

Figure 12. Simple regression relationships between total carapace length (TCL; mm) and potential fecundity (i.e., number of ovarian eggs; top panels) and between TCL and ovarian egg diameter (mm; bottom panels) for *F. nana* (left panels) and *F. macrus* (right panels). Regression coefficient estimates are provided in Table 9.

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