Co-occurring lotic crayfishes exhibit variable long-term responses to extreme-flow events and temperature

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Abstract: Crayfish serve critical roles in aquatic ecosystems as engineers, omnivores, and prey. It is unclear how increasingly frequent extreme-flow events and warming air temperatures will affect crayfish populations, partly because there are few long-term crayfish monitoring datasets. Using a unique 10-y dataset, we asked 1) whether recruitment of crayfishes in summer responded to extreme-flow events and air temperature during spring brooding and summer growing periods and 2) whether responses were similar among 3 co-occurring crayfish species. Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes were sampled in quadrats at 2 sites each in the Big Piney (1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA; $n = 3355$ 1-m^2 quadrats). We used zero-inflated generalized linear models to relate variability in quadrat-level age-0 counts to mean daily maximum air temperatures and flow metrics (variability, magnitude, and frequency of extreme high- and low-flow events). Species ranged from a small-bodied, abundant habitat generalist (Golden Crayfish) to large-bodied, uncommon habitat specialists (Ozark and Spothand crayfishes). Golden Crayfish occurred in higher-velocity habitats (riffles, runs) and had variable recruitment that increased during years with few spring and summer high-flow events and summers with lower flows and warmer temperatures. In contrast, annual recruitment variability of Ozark and Spothand crayfishes was low and explained by positive effects of cooler summers and by different flow metrics. Spothand Crayfish recruitment decreased in years with frequent spring and summer high-flow events, whereas lower summer minimum flow was the only flow metric that explained slight increases in Ozark Crayfish recruitment. Relationships with the preceding year's recruitment were quadratic for Ozark and Spothand crayfishes, suggesting potential density dependence at higher recruitment levels. Species-specific responses suggest that closely related crayfishes could respond idiosyncratically to changes in temperature and flow. Temperature- and flow-related disturbances may be key mechanisms mediating competition and, thus, may help maintain crayfish diversity. However, warming air temperatures and increasingly frequent extreme-flow events could disadvantage some species, thereby altering future crayfish assemblages.

Key words: climate change, crayfish, disturbance, habitat selection, hydrology, population dynamics, life history, species interactions, zero inflation

Crayfishes are among North America's most-imperiled freshwater taxonomic groups, with >½ of the 400 native species experiencing population declines (Taylor et al. 2007). Loss of crayfish diversity could significantly affect ecosystem function, given that crayfishes can comprise >½ of the invertebrate biomass in streams and lakes (Huryn and Wallace 1987, Momot 1995, Haggerty et al. 2002) and are consumed by >200 species (DiStefano 2005). Crayfishes play important

roles in aquatic food webs as both prey (DiStefano 2005) and consumers (Creed 1994, Nyström and Strand 1996, Dodds et al. 2000). Considered ecosystem engineers (Jones et al. 1997), crayfishes also modify aquatic habitats through burrowing and mobilization of streambed substrates (Statzner et al. 2003, Creed and Reed 2004) and can create habitat for endangered species, including snakes, toads, and dragonfly larvae (Bloomer et al. 2021). Despite the importance of crayfishes to freshwater ecosystems, ecologists lack information on fitness-based attributes of many crayfish species (Moore et al. 2013), impairing our ability to predict crayfish responses to environmental change and non-native species.

The effects of climate change are an important knowledge gap hampering development of conservation strategies for United States crayfishes (Taylor et al. 2019). Predicted future climate scenarios include fewer low-temperature events, higher frequencies and longer durations of heatwaves, and more-frequent intense-precipitation events (Pachauri and Meyer 2014). In the Midwestern US, these extreme climatic events are expected to alter stream baseflows (Ayers et al. 2019). Climate changes have already been linked to shifts in aquatic communities, and further effects are expected (Thomas 2010, Lynch et al. 2016, Palmer et al. 2017).

As ectotherms, crayfishes are highly sensitive to temperature. Westhoff and Rosenberger (2016) documented species-specific adaptations to different thermal regimes, including temperatures resulting in optimal growth, temperature thresholds resulting in decreased growth, and temperature gradients over which mortality rates varied. Crayfishes in Norwegian lakes had higher fecundity in warmer temperatures (Skurdal et al. 2011). Species with narrow thermal niches may have limited resilience, and a global assessment that used the International Union for the Conservation of Nature's trait-based assessment protocol classified 87 species of crayfishes as highly vulnerable to climate change (Hossain et al. 2018).

Hydrology may have even greater effects than temperature on lotic-crayfish species distributions (Krause et al. 2019). Different crayfishes specialize in a variety of stream sizes ranging from low-flow (low-discharge), intermittent headwaters to high-flow rivers (e.g., Flinders and Magoulick 2003, Herleth-King et al. 2015, Magoulick et al. 2017). Furthermore, crayfish species may differ in their ability to cope with both extreme high-flow (floods) and low-flow (drought) disturbances. High-flow events may act as pulse disturbances that increase mortality in stream-dwelling crayfishes (Light 2003, Parkyn and Collier 2004, Clark and Kershner 2011).

Annual recruitment (age-0 survival) is one of the most important vital rates determining crayfish population dynamics (Yarra and Magoulick 2018). Until relatively recently, standardized quantitative-sampling methods for age-0 crayfishes did not exist (DiStefano et al. 2003b). Instead, potential (egg counts inside ovaries) or realized (egg counts post-extrusion) fecundity were used as reproductive indices (Stechey and Somers 1995, Skurdal et al. 2011). However, by studying only fecundity, ecologists neglect influences of a myriad of biotic

and abiotic factors affecting post-hatch survival. For example, egg loss occurs during development from damage or detachment in swift currents, failure to fertilize, partial extrusion, pathogens and parasites, or predation (Prins 1968, Corey 1987, Muck et al. 2002b). Therefore, early life-stage mortality is likely a larger determinant of crayfish production than fecundity (Momot 1984).

Little is known about how habitat use and life-history traits dictate crayfish assemblage responses to disturbance. Morphological and behavioral adaptations, including body size (Clark et al. 2008), chelae size and shape (Perry et al. 2013), body posture (Maude and Williams 1983), and flow-dependent habitat selection (Clark and Kershner 2011), allow crayfishes to navigate the complex 3-dimensional forces imposed by flow (Statzner et al. 1988). Large-bodied crayfishes with less robust chelae are less successful at anchoring in habitats with high water velocities (Clark and Kershner 2011, Perry et al. 2013). Crayfishes may behaviorally adapt by dispersing to refuge habitats (Clark and Kershner 2011), although size-dependent interspecific competition for preferred habitats may preclude small-bodied species from accessing structurally complex, low-velocity refuge habitats already occupied by larger-bodied species (Rabeni 1995).

We examined recruitment dynamics of lotic crayfishes using a unique long-term dataset. We asked 1) whether age-0 densities in summer responded to extreme-flow events and air temperature during spring brooding and summer rearing periods and 2) whether responses were similar among 3 co-occurring crayfish species: Golden Crayfish (*Faxonius luteus* [Creaser, 1933]), Ozark Crayfish (*Faxonius ozarkae* [Williams, 1952]), and Spothand Crayfish (*Faxonius punctimanus* [Creaser, 1933]). Generally, we predicted that cool, wet years with frequent high-flow pulses in both spring brooding and summer growing periods would have strong negative effects on recruitment of all 3 crayfishes by increasing mortality in maternally attached and free-living age-0 crayfishes. However, we were unsure whether all species would respond similarly to flow and temperature variables. Golden crayfishes are small-bodied habitat generalists that could be more exposed to high flows by occurring in higher-velocity habitats, such as riffles and runs, during high-flow events. However, larger body sizes of both Ozark and Spothand crayfishes could predispose these species to displacement, even when occupying relatively protected structurally complex habitats. Further, we predicted hot, dry summer conditions would reduce habitat area and complexity, leading to increased competition (e.g., Corkum and Cronin 2004), thereby disadvantaging the smaller Golden crayfishes relative to larger-bodied Spothand and Ozark crayfishes.

METHODS

We evaluated our predictions by investigating relationships between interannual variability in environmental conditions (discharge, temperature) and crayfish recruitment.

We used a unique 10-y dataset on age-0 densities of the 3 most-abundant crayfish species at 4 sites nested within 2 rivers, the Jacks Fork River (JFR) and Big Piney River (BPR), two 6th-order rivers in forested karst landscapes in the Ozark Plateau ecoregion in Missouri, USA (hereafter, Ozarks) (Fig. 1). Following field sampling, species identification, and assigning sampled crayfishes to age-class categories, we performed 2 separate analyses to model variation in crayfish recruitment at 2 spatial scales: 1-m^2 quadrats in sites ($n = 3355$ total quadrats across sites and years) and site scales (described below).

Crayfish surveys

We conducted fieldwork throughout summer months (June–September) at 2 sites/river (JFR: 1991–2001, BPR: 1992–2000). Both rivers are perennial, groundwater-fed, and have relatively stable base flows (Kennen et al. 2009). Both rivers also have well-defined riffle, run, and pool sequences with riffle and run substrates composed of gravel, pebble, and cobble, and sand and boulders more commonly occurring in deep bluff pools. Environmental conditions are similar in both rivers, even though BPR's watershed (area = 1955 km^2) is larger than JFR's (area = 1152 km^2). Mean flow (i.e., discharge) was 17.2 m^3/s (range = 2.4–648.5 m^3/s) in BPR (water y 1992–2000) and 13.9 m^3/s (range = 2.9–900.5 m^3/s) in JFR (water y 1991–2001). Mean daily maximum air temper-

ature was 18.8°C in BPR (1992–2000) and 19.3°C in JFR (1991–2001) (Fig. 2).

We used a 1-m^2 quadrat sampler (DiStefano et al. 2003b) to sample crayfishes. Field crews conducted between 58 and 117 quadrat samples (henceforth, quadrats) in each of the 4 sites each year (mean = 93 quadrats/site). Quadrats were apportioned by relative area of 5 habitat types at sites: riffle, run, pool, emergent aquatic vegetation patch (henceforth, vegetation), and backwater. Sampling efficiency of the quadrat sampler was high because of the ability to excavate substrates (10-cm depth) within the sampler's perimeter and flaps that sealed the sampler to the substrate, following the procedures detailed in Allert et al. (2012) and Engelbert et al. (2016). We identified (according to Pflieger 1996), counted, and sexed captured crayfishes and measured their carapace length (nearest 0.1 mm) from tip of rostrum to the posterior border of the thoracic region. Collected crayfish were retained temporarily in buckets of water and released after sampling each habitat unit.

Study species

Golden, Ozark, and Spothand crayfishes were categorized as least conservation concern or globally secure during the study dates (Adams et al. 2010a, b, c, NatureServe 2018). All species occurred in JFR, but only Golden and Spothand crayfishes occurred in BPR. Hubbs' Crayfish (*Cambarus*
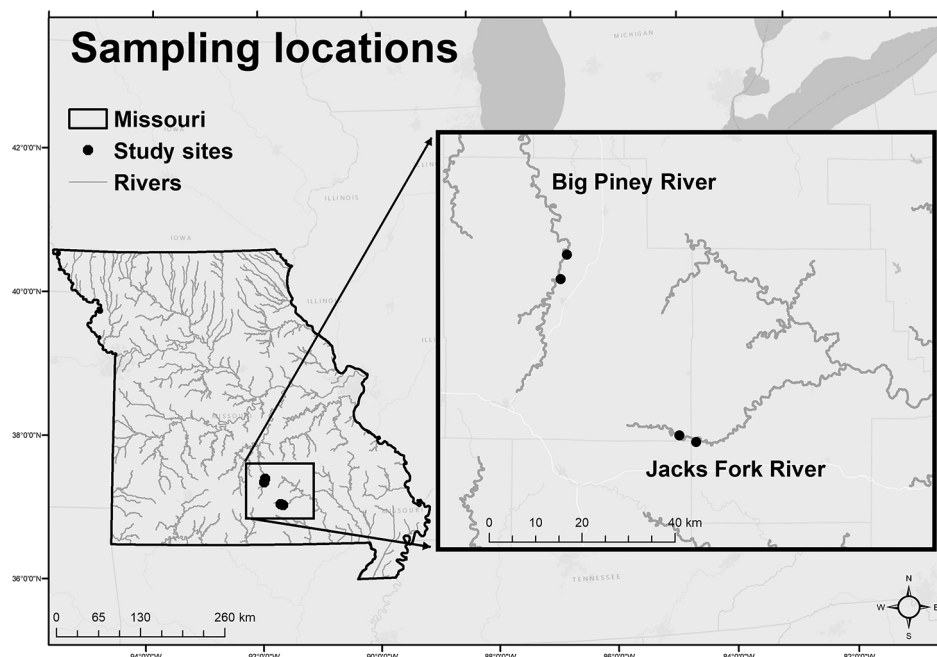

Figure 1. Sites sampled for Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes, June to September, in Big Piney (1992–2000) and Jacks Fork (1991–2001) rivers (Missouri, USA). Shapefile data from the Missouri Spatial Data Information Service Archive: rivers (https://msdis-archive.missouri .edu/archive/Missouri_Vector_Data/state/aquatic_gap/; file MO VST3) and state boundary (https://msdis-archive.missouri /archive/Missouri_Vector_Data/Administrative_Political_Boundaries/; file MO 2018 State Boundary).
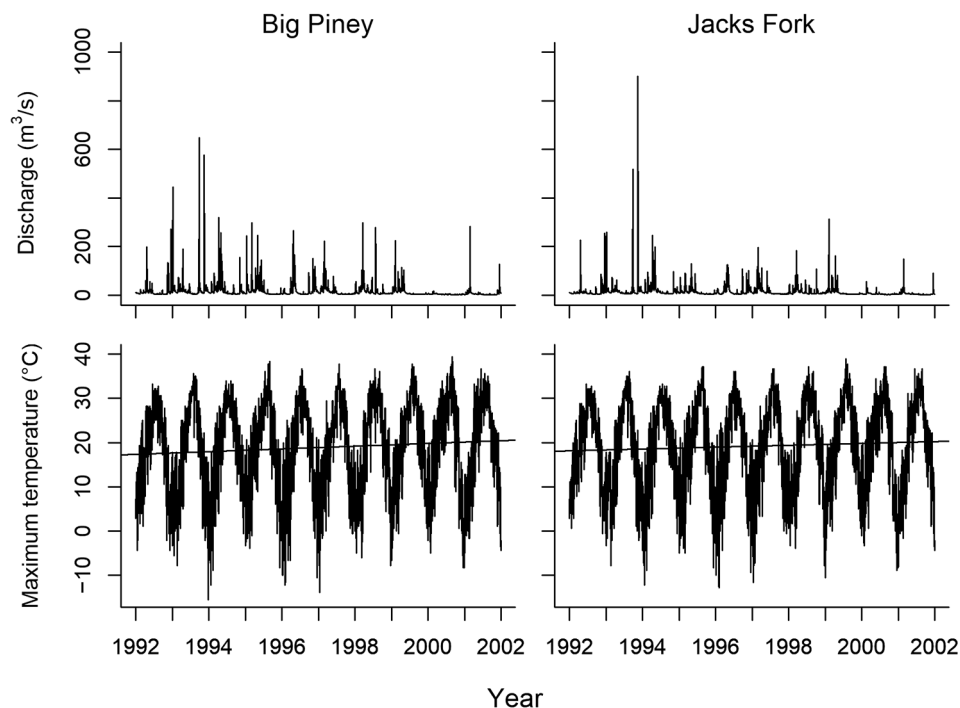
Figure 2. Mean daily flow (i.e., discharge; m³/s) and daily maximum air temperature (°C) for the Big Piney and Jacks Fork rivers (1992–2001; Missouri, USA). Data sources: flow data are from the United States Geological Survey (Big Piney: gage ID 06930000, Jacks Fork: gage ID 07066000); air temperature data are from the National Oceanic and Atmospheric Administration (Big Piney: station USC00234019, Jacks Fork: station USC00238184). Solid lines in the bottom panels indicate trends in maximum temperature over the study period in each river.

hubbsi [Creaser, 1931]) is also present in JFR at much lower densities and was not included in this analysis.

Life-history and habitat-selection information for adults from an early subset of this dataset (1991–1993) was previously reported by Muck (1997), Muck et al. (2002a, b), and DiStefano et al. (2003a) (organized in Table S1). Each species potentially reaches maturity and reproduces by its 1st autumn. However, large life-history and ecological differences exist among the 3 species, especially between Golden Crayfish vs Spothand and Ozark crayfishes. Golden Crayfish were most abundant, attained the smallest maximum size, had the smallest size at maturation, had the lowest realized fecundity, and grew the slowest relative to the other 2 study species. Further, Golden Crayfish exhibited the most generalized habitat selection patterns, with adults attaining the highest densities in riffles, runs, and pools. In contrast, Spothand Crayfish occurred at low densities, grew the fastest, had the highest fecundity, and attained the largest sizes. Ozark Crayfish also occurred at low densities and had intermediate growth and fecundity rates. Further, adult Spothand and Ozark crayfishes were habitat specialists and disproportionally selected emergent vegetation (mainly water-willow [*Justicia americana* L. Vahl]) patches, backwaters, and pools.

Age-class assignment

We used smoothed density plots constructed from carapace-length frequencies to distinguish size classes for each species (Fig. 3). We accounted for summer growth of age-0 individuals by placing moving breaks separating age-0 and age-0+ individuals between noticeable carapace-length frequency modes for each species and in each of the 4 sampling mo. Size classes are considered representative of age classes with an accuracy of ~80% in *Faxonius* crayfish species (DiStefano et al. 2016).

Data sources for flow and temperature metrics

We quantified flow and temperature metrics during 2 critical developmental periods for age-0 crayfishes: 1) spring brooding period (March–May), when eggs and age-0 instars are attached to adult females; and 2) summer (June–September), when post-brooding, free-living age-0 crayfishes grow most. Although crayfish sampling began in 1991 in JFR and 1992 in BPR, we did not begin modeling recruitment dynamics until 1992 for JFR and 1993 for BPR (see modeling approach below). We obtained daily maximum air temperatures for BPR (National Oceanic and Atmospheric Administration weather station near Houston, Missouri: USC0023 4019, 1993–2000) and JFR (weather station near Summersville, Missouri: USC00238184, 1992–2001). Some missing temperature data required us to fill 14% of daily temperature observations for BPR from a nearby (27 km away) weather station (Licking, Missouri: USC00234919). Similarly, a small percentage of daily temperature observations for JFR were filled with observations from nearby weather stations at
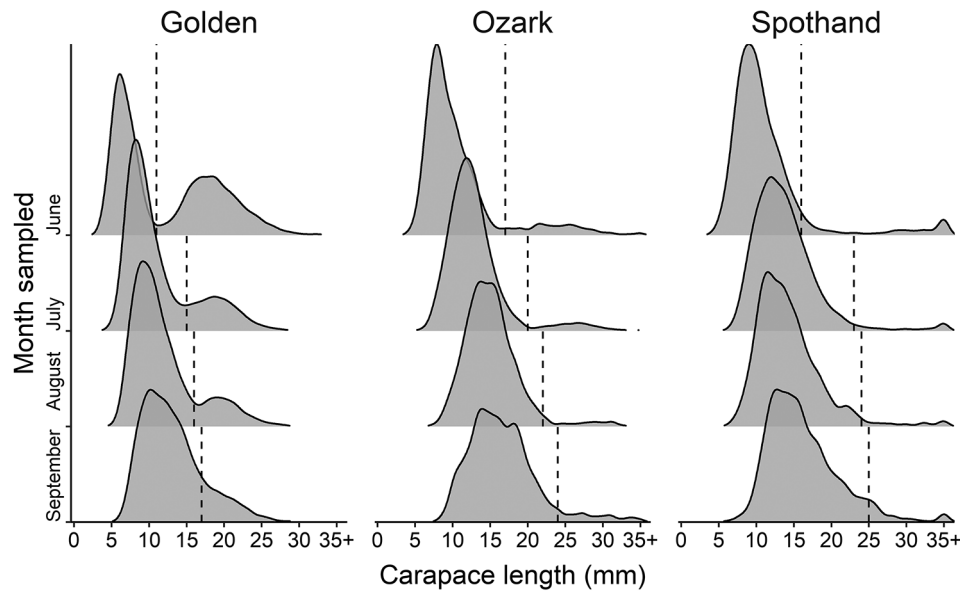
Figure 3. Carapace-length frequencies of Golden (*Faxonius luteus* [Creaser, 1933], *n* = 36,300), Ozark (*Faxonius ozarkae* [Williams, 1952], *n* = 8803), and Spothand (*Faxonius punctimanus* [Creaser, 1933], *n* = 12,264) crayfishes by month from the Big Piney (exempting Ozark Crayfish, 1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA). Individuals with carapace lengths < dotted vertical bar were classified as age 0.

Houston (36 km away, 5.8%) and Licking (51 km away, <0.01%), Missouri.

We obtained daily flow measurements from a combination of existing and computed daily flow data. We used daily flow data for BPR (United States Geological Survey gage ID = 06930000, Big Piney, Missouri) and JFR (gage ID = 07066000, Eminence, Missouri) from 1921 to 2017 (USGS 2016). Gage data were unavailable for BPR 19 September 1996 to 23 November 1999. Therefore, we used existing relationships between BPR and gages from nearby rivers with continuous flow records to predict missing flow data in BPR. Specifically, we trained a random forest model (Liaw and Wiener 2002) using 75% of available recent (1980–2017) daily flow data (7968 daily observations) between BPR (response variable) and daily flow at 4 nearby stream gages (predictor variables): JFR (gage ID = 07066000), Little Piney River (gage ID = 06932000), Gasconade River (gage ID = 06933500), and Meramec River (gage ID = 07013000). Then we used the model to predict daily flow data from the remaining 25% of daily flow records (2656 records). The Pearson's product-moment correlation coefficient between predicted and observed validation data was high ($r = 0.91$) and bias ([sum predicted daily flow – sum observed daily flow] / 2656 observations) was low (-0.65 m^3/s) relative to mean flow from the same timeframe (mean discharge = 15.65 m^3/s).

Modeling framework

We modeled variation in age-0 crayfish counts/quadrat to account for sampling timing and fine-scale environmental

processes that could affect crayfish densities throughout each year's sampling period. For example, accumulated mortality could result in fewer age-0 crayfishes from beginning (June) to end (September) of summer sampling, or mismatches between counts and environmental processes could arise if crayfish sampling preceded extreme-flow or extreme-temperature events occurring later in summer. Modeling densities also required us to control for other processes potentially affecting quadrat-level counts, including habitat selection and interspecific interactions, while accounting for spatial and temporal dependencies within the hierarchical dataset.

We used a 7-step modeling workflow to control for influential processes unrelated to temperature and flow, assemble a minimally correlated suite of candidate flow and temperature explanatory variables, and select the best-supported combination of variables explaining recruitment dynamics (Fig. 4). Several processes often create more absences in ecological count data than are predicted by traditional count distributions (e.g., Poisson, negative binomial; Wenger and Freeman 2008). For example, even though we were interested in the influence of flow and temperature on crayfish recruitment, an excessive absence of age-0 crayfishes in a quadrat could arise from placing a quadrat in non-suitable habitats. Consequently, we used zero-inflated negative binomial models to model excessive absences in age-0 count data. In zero-inflated negative binomial models, multiple processes are modeled via 2 distributions: 1) a binomial distribution (hereafter, binomial component) that models the probability of excessive absences within quadrats and 2) a negative binomial

| 1 | Base count model | **Fixed effects** • Calendar date • River (L, P) or site (O) | **Random effects** • Year • Site (L, P) |

| 2 | Binomial model | **Fixed effects** • Calendar date • River (L, P) • Habitat index • Species interactions | **Random effects** • Year • Site (L, P) |

| 3 | Density dependence | **Relationship with previous year** • No relationship • Linear relationship (density independence) • Quadratic relationship (density dependence) | |

| 4 | Flow & temperature | **Brooding** • Flow variability • Median flow • High-flow events • High-flow duration • Mean daily max. temp. | **Growing** • Flow variability • Median flow • High-flow events • Low-flow events • Low-flow duration • Mean daily max. temp. |

| 5 | Scale dependency | **Brooding** • High-flow events (>75, 90, 95, 99 pctl) • High-flow duration (1, 3, 5, 7-d max.) | **Growing** • High-flow events (>75, 90, 95, 99 pctl) • Low-flow events (<25, 10, 5 pctl) • Low-flow duration (1, 3, 5, 7-d min.) |

| 6 | Model screening | **Variables removed** • Variation inflation factor > 5 • Pairwise r > 0.70 | |

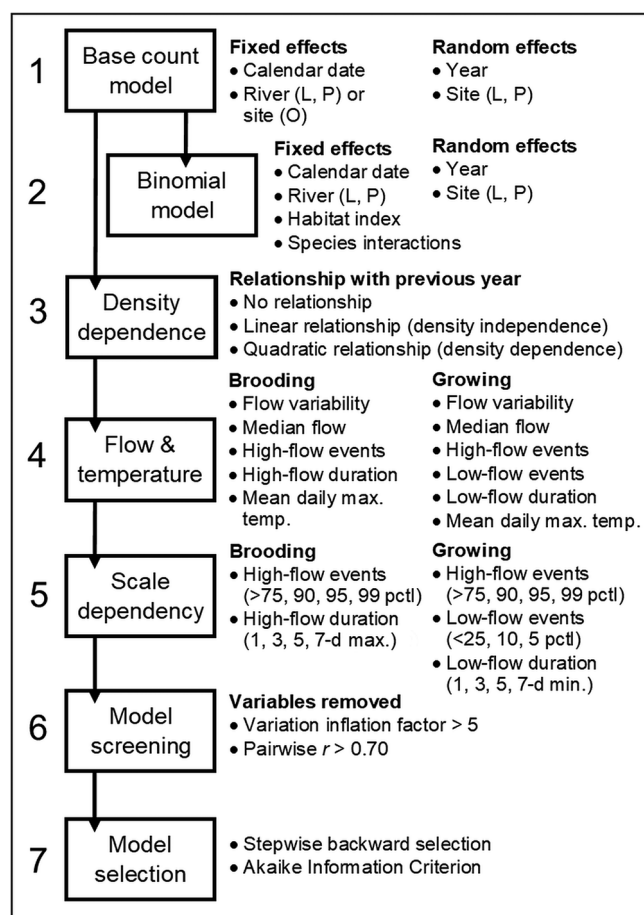| 7 | Model selection | • Stepwise backward selection • Akaike Information Criterion | |

Figure 4. Analytical workflow for modeling densities of age-0 crayfish/1-m² quadrat sample for Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes in Big Piney (exempting Ozark Crayfish, 1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA). Zero-inflated models used a binomial distribution to model probability of excessive 0 counts (i.e., excessive absences) caused by spatial and temporal grouping variables and covariates for potential species interactions among congeneric crayfishes and habitat types surrounding quadrats. Non-excessive 0 counts and counts >0 were modeled with a negative binomial distribution based on spatial and temporal grouping variables and covariates that included density dependence and temperature and flow variables. Brooding months = March to May, growing months = June to September, L = Golden Crayfish, O = Ozark Crayfish, P = Spothand Crayfish, mean daily max. temp. = mean daily maximum air temperature, pctl = percentile.

distribution (hereafter, count component) that models count data without excessive absences but with estimated true 0 counts. Thus, we isolated variation in counts created by processes at broader spatial and temporal scales (e.g., disturbance events, annual environmental conditions) by modeling excessive absences within quadrats based on fine-scale processes including habitat selection and potential interspecific interactions. We used the package *glmmTMB* (Brooks

et al. 2017) in R (version 4.0.4; R Project for Statistical Computing, Vienna, Austria) to implement all zero-inflated negative binomial models.

At each step we evaluated support among competing models based on the model with the lowest Akaike's information criterion (AIC). We centered and standardized all continuous or integer predictors with the equation $(x - \bar{x}) / sd(x)$ to minimize model-convergence issues and make magnitudes of fixed effects directly comparable. In step 1, we accounted for the hierarchical grouping structure of the dataset by treating river (BPR, JFR) as a fixed effect and site as a random effect (for Golden and Spothand crayfishes) nested within river within count and binomial-model components. There were only 2 sites for Ozark Crayfish, so for that species we treated site as a fixed effect. Temporally, we included calendar day (1 January = 1, 30 September = 273), and we included year as a random effect in both count and binomial-model components to account for potential grouping structure of multiple observations within the same year.

In step 2 we identified the best-supported model structure for the binomial-model component by evaluating whether excessive absences of each crayfish species within quadrats were explained by counts of interspecific crayfishes and habitat selection strength for a given habitat type (i.e., channel-unit type). Presence of interspecific crayfishes could deter a given species from using a quadrat (i.e., positive effect on probability of excessive absences) or signify a quadrat with mutually suitable resources for multiple crayfish species (i.e., negative effect on probability of excessive absences). We calculated a selectivity index of habitats that were disproportionately selected by each species by dividing relativized frequency distributions of habitats occupied by relativized frequency distributions of habitats sampled. Habitats with selectivity ratios >1 were disproportionately selected by a given species (Fig. 5). Golden Crayfish exhibited the most general habitat-selection patterns but slightly selected run, pool, and vegetation habitat types. Golden Crayfish did not disproportionally select riffles, but the species was the most likely to occur in riffles among the 3 species. Ozark Crayfish exhibited stronger habitat-selection patterns and disproportionately selected run, pool, vegetation, and backwater habitats. Finally, Spothand Crayfish were the most selective species and disproportionately selected low-velocity habitats including pools, vegetation, and backwaters. We accounted for habitat selection by including the selectivity index value (i.e., ratio of habitat type used to habitat-type availability) as a covariate in the binomial-model component. We quantified potential interspecific interactions as the sum of individuals for each interspecific species within a quadrat (separate effects for each interspecific species) or a single effect for the sum of interspecific individuals within a quadrat regardless of species. For example, the candidate predictors in the binomial-model component explaining excessive absences of Golden Crayfish in quadrats included separate
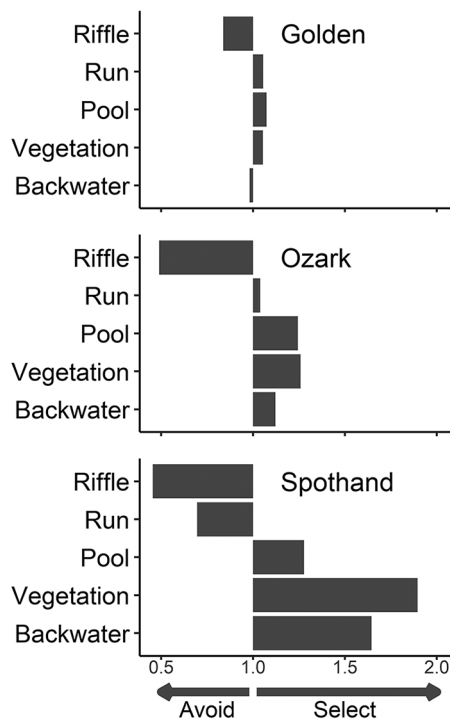
Figure 5. Selection of 5 habitat types by age-0 Golden (*Faxonius luteus* [Creaser, 1933], *n* = 3355 quadrats), Ozark (*Faxonius ozarkae* [Williams, 1952], *n* = 1861 quadrats), and Spothand (*Faxonius punctimanus* [Creaser, 1933], *n* = 3355 quadrats) crayfishes in Big Piney (exempting Ozark Crayfish, 1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA), June to September. Selectivity index values are ratios of proportions of quadrats occupied by age-0 crayfish vs proportions of quadrats sampled by habitat type. Values >1 reflect disproportional habitat selection, whereas values <1 reflect habitat avoidance.

counts of Ozark and Spothand crayfishes (2 effects) or the sum of Ozark and Spothand crayfish individuals within quadrats (1 effect).

In step 3 we examined whether recruitment depended on the preceding year's recruitment, with densities from initial years of 1991 and 1992 used to predict recruitment in 1992 and 1993 for JFR and BPR, respectively. We compared a model without a preceding-year recruitment term with 2 model formulations containing preceding-year recruitment terms: 1) a model with a single term for the previous year's mean site-level density of age-0 crayfishes/quadrat and 2) a 2nd formulation with a quadratic term for mean site-level density of age-0 crayfishes/quadrat. Crayfishes can be highly territorial and aggressive (Corkum and Cronin 2004), which might result in density-dependent recruitment if resources are limited at high densities and manifest as a quadratic spawner–recruit relationship among years.

In step 4 we selected a candidate set of flow and air temperature variables to explain recruitment dynamics. We characterized flow regimes in each river during brooding and growing periods by central tendency (median), magnitudes (highest and lowest single or multi-day flow), variability (coefficient of variation), and frequencies of high-flow and low-flow events (Table 1). We characterized air temperatures as mean daily maxima from spring brooding and summer growing periods. We included interactions between air temperature and river because rivers vary slightly in size, and both rivers are groundwater influenced, which could affect thermal linkages between air and water (Westhoff and Paukert 2014). Predictor variable inputs during summer growing period were calculated leading up to the day of sampling to avoid mismatches between sampling date and environmental conditions. For example, if sampling occurred 1 July, flow and temperature variables during the summer growing period were calculated between 1 June and 1 July (Table 1).

Although we generally expected lower recruitment after frequent and prolonged extreme flows, we were unsure of specific flow magnitudes and durations to define extreme-flow events. This scale-dependency issue is common with spatial and temporal data and is often mitigated by using multiple thresholds spanning spatial and temporal scales to calculate metrics (McGarigal et al. 2016). Therefore, in step 5 we calculated maximum flows separately during spring brooding and summer growing periods and minimum flows during summer growing periods at 1-, 3-, 5-, and 7-d durations. Similarly, for high-flow frequencies, we summed days during spring brooding and summer growing periods separately with flows >75th, 90th, 95th, and 99th percentiles from water years (1920–2017) and days with flows <25th, 10th, and 5th percentiles for low-flow frequencies during the summer growing period. We retained the best-supported threshold within each flow-hypothesis category for each species for step 6.

Flow data are often correlated (Olden and Poff 2003), so in step 6 we used 2 criteria to screen highly collinear variables. First, we removed variables with variation inflation factors >5. Then we calculated pairwise correlation coefficients among remaining variables and removed the least-supported variable from highly correlated ($r > 0.70$) pairs.

Finally, in step 7 we began with a global model that included all remaining complementary variables and then sequentially eliminated variables via stepwise backward model selection. Although we limited predictor variables to those that we hypothesized would influence crayfish recruitment, stepwise model selection was necessary because of the large number of candidate flow and temperature predictors. Each stepwise-regression step consisted of the following: 1) iteratively dropping single variables associated with fixed effects from the count-model component, 2) calculating AIC for each model, and 3) dropping the least-supported variable from further continuation before continuing to the next step. Stepwise selection ended when no additional terms could be dropped without raising AIC. We report pseudo-R^2 terms for estimated variation in the

Table 1. Candidate predictor variables included in zero-inflated negative binomial models to explain variation in age-0 Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes in 1-m^2 quadrat samples in Big Piney (1993–2000, exempting Ozark Crayfish) and Jacks Fork (1992–2001) rivers (Missouri, USA). Terms in the count-model component explain counts (non-excessive 0 counts and >0 counts). Terms in binomial-model component explain excessive absences in quadrats generated by fine-scale processes (habitat selection, species interactions). Q = flow (m^3/s), B = spring brooding period (March–May), G = summer growing period (June–September), L = Golden Crayfish, O = Ozark Crayfish, P = Spothand Crayfish, # = placeholder for varying durations or percentiles for a given metric.

Variable	Description	Abbreviation	Scale	Period
Count-model component				
Day	Date beginning on 1 Jan (d 1) to 30 Sep (d 273)	–	Day	–
Density dependence	Mean quadrat density at site in previous year	–	Site	–
River	Either Big Piney (reference level) or Jacks Fork	–	River	–
Site	Random effect; site nested within river (4 total sites)	–	Site	–
Year	Random effect 1992–2001	–	Year	–
Flow variability	Coefficient of variation of mean daily Q	B or G CVQ	River	B, G
Median flow	Median daily Q	B or G MedQ	River	B, G
High-flow days	Days with Q >75th, 90th, 95th, 99th percentiles	B or G HF$_{\#}$	River	B, G
High-flow duration	Maximum Q for 1, 3, 5, and 7 d	B_MaxQ$_{\#d}$	River	B
Low-flow days	Days with Q <25th, 10th, 5th percentiles	G_LF$_{\#}$	River	G
Flow minima	Minimum Q for 1, 3, 5, and 7 d	G_MinQ$_{\#d}$	River	G
Air temperature (°C)	Mean daily maximum air temperature	B or G Temp	River	B, G
Air temperature (°C) × River	Interaction between air temperature and river	B or G Temp × River	River	B, G
Binomial-model component				
Day	Date beginning on 1 Jan (d 1) to 30 Sept (d 273)	–	Day	–
River	Either Big Piney (reference level) or Jacks Fork	–	River	–
Site	Random effect; site nested within river (4 total sites)	–	Site	–
Year	Random effect; year from 1992 (y 1) to 2001 (y 11)	–	Year	–
Habitat	Habitat selectivity index for habitat type sampled	Habitat	Quadrat	–
Species interactions	Count of interspecific individuals in quadrat; terms included separate effects for each interspecific species or sum of interspecific individuals in quadrat	L, O, P	Quadrat	–

count-model component explained solely by fixed effects (marginal p-R^2) and fixed + random effects (conditional pR^2) (Nakagawa et al. 2017)

Benefits of quadrat-level modeling of crayfish counts included integrating influential processes at multiple scales while controlling for fine-scale mismatches between summer sampling dates, temperature, and flow regime. However, influential temperature and flow variables at the site level are likely more intuitive for managing these species. Therefore, we used negative binomial mixed-effects models to perform a complementary analysis of among-year variation in age-0 crayfish abundances summed across quadrats at sites. All models treated year as a random effect, included an offset of quadrats/site and year to account for uneven sampling effort, and, because of low sample size, were limited to the following fixed effects: river (only for Golden and Spothand crayfishes), site-level densities in previous year, and a single effect for 1 flow or temperature variable/model.

RESULTS

Species varied considerably in density, ubiquity, and among-year variation patterns in age-0 recruitment. Field crews collected 36,300 Golden, 8803 Ozark, and 12,264 Spothand age-0 crayfishes across 3355 quadrats. Generally, the smaller-bodied species with the most generalized habitat-selection patterns (Golden Crayfish) occurred at the highest densities and had the most variable recruitment among years. For example, Golden Crayfish recruits varied between 4.8 to 19.6 crayfishes/quadrat among years (Fig. 6) and were most ubiquitous among species (present within 77–97% of quadrats). In contrast, age-0 Ozark and Spothand crayfishes occurred at lower mean densities (Ozark Crayfish = 2.2–7.6 crayfishes/quadrat, Spothand Crayfish = 0.6–10.0 crayfishes/quadrat) and in lower percentages of quadrats (Ozark Crayfish presence within quadrats = 70–88%, Spothand Crayfish = 25–74%). Age-0 Spothand Crayfish mean densities were also much lower in JFR (1.8/quadrat) than in BPR (6.0/quadrat).
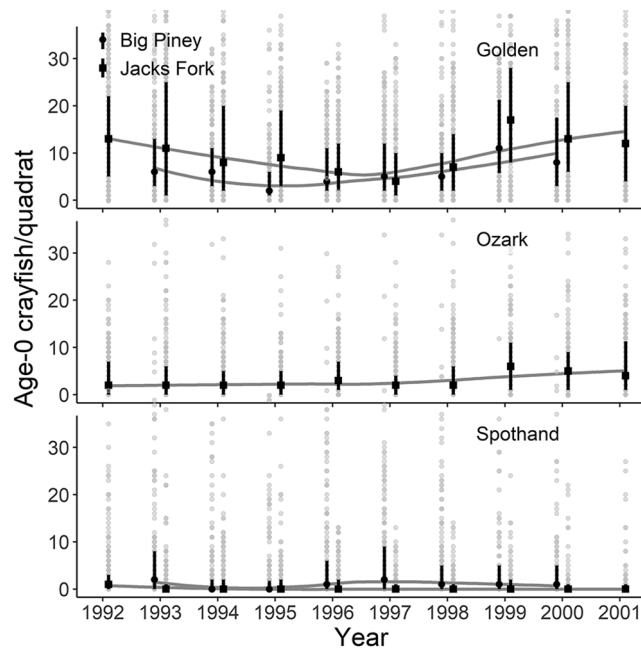
Figure 6. Median (black symbols) and 25th to 75th percentiles (black bars) of age-0 counts of Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes/1-m² quadrat sample in Big Piney (exempting Ozark Crayfish) and Jacks Fork Rivers (Missouri, USA), June to September. Gray dots are counts from individual quadrats. Counts >35 individuals were included in trend calculations but omitted from figures.

Flow and temperature patterns were similar between rivers and generally characterized by an early series of high-flow years and cooler temperatures followed by low-flow years and warmer temperatures (Fig. 2). For example, there were 244 high-flow events between 1992 and 1996 in which flows exceeded the 95th percentile for water years on record for a given river, whereas only 69 such days occurred across both rivers from 1997 to 2001. There was also a trend from early to later years in mean daily maximum air temperatures (Fig. 2). Correlations between year (1992–2001) and mean daily maximum air temperatures indicated air temperatures increased slightly from early wet years to later drier years (BPR, $r = 0.75$; JFR, $r = 0.52$).

Modeling excessive absences within quadrats (binomial-model component)

The main purpose of the binomial-model component was to explain variation driven by processes at the quadrat level, thereby isolating variation explained by processes at broader spatiotemporal scales (e.g., annual flow metrics and temperatures). Best-supported models for each species indicated that habitat-selection patterns and densities of congeners explained excessive absences within quadrat samples (Table 2). The probability of excessive absences in quadrats decreased in habitats that were disproportionally selected, meaning many 0 counts resulted from quadrat placement in habitats with low suitability (effect ± SE of habitat selectivity index on probability of excessive 0 counts for Golden Crayfish = -0.61 ± 0.11, Ozark Crayfish = -1.09 ± 0.12, Spothand Crayfish = -1.70 ± 0.11; see Table S2 for effect sizes of best-supported model for each species). Note that for binomial components of zero-inflated models, negative estimated effects indicate higher probabilities of crayfish presence in a quadrat. The probability of excessive absences also decreased in quadrats with increasing densities of other congeneric crayfishes. Thus, occurrences of congeneric species in quadrats may indicate habitat types that were suitable for lotic crayfishes in general or other mechanisms or resources facilitating cohabitation. The best-supported model explaining Spothand Crayfish excessive absences in quadrats included separate effects for Ozark (-0.97 ± 0.23) and Golden (-0.55 ± 0.11) crayfishes, and the model for Ozark Crayfish included separate effects for Spothand (-5.94 ± 1.71) and Golden (-3.29 ± 0.51) crayfishes. In contrast, the best-supported binomial-model component for Golden Crayfish included only a single congeneric effect that summed counts of Ozark and Spothand crayfishes (-15.6 ± 3.72), indicating these 2 congeners affect excessive absences of Golden Crayfish in quadrats similarly. Altogether, excessive absences in quadrats for each species decreased in more suitable habitats for a given species and in quadrats with higher densities of congeners.

Variation in age-0 densities (count-model component)

Among-year recruitment dynamics of all 3 species were related to extreme-flow events, air temperature, and previous year's recruitment (Table 3, Fig. 7). High multicollinearity (variation inflation factors > 5, $r \geq 0.70$) prevented

Table 2. Variables within zero-inflated (binomial) component of zero-inflated negative binomial models explaining age-0 densities of Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes in 1-m² quadrat samples in Big Piney (1993–2000, exempting Ozark Crayfish) and Jacks Fork (1992–2001) rivers, June to September (Missouri, USA). Parameter estimates are in Table S2. Year and Site are treated as random effects. sum(O, P) = single effect containing sum of Ozark and Spothand crayfishes in quadrat, L = sum of Golden Crayfish in quadrat, O = sum of Ozark Crayfish in quadrat, P = sum of Spothand Crayfish in quadrat.

Species	Effects
Golden	River + Day + Habitat + sum(O, P) + Year + Site
Ozark	Day + Habitat + L + P + Year
Spothand	River + Day + Habitat + L + O + Year + Site

Table 3. Number of parameters (K) and evaluation criteria for zero-inflated negative binomial models explaining age-0 counts of Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes in 1-m^2 quadrat samples in Big Piney (1993–2000, exempting Ozark Crayfish) and Jacks Fork (1992–2001) rivers (Missouri, USA), June to September. Models are from backward selection beginning with a global model. Models are ranked by lowest Akaike information criterion (ΔAIC) and greatest model weight (w_i). Marginal pseudo-R^2 values (M pR^2) and conditional pseudo-R^2 values (C pR^2) reflect variation explained in the count model solely by fixed effects and fixed + random effects, respectively. Lower-order terms and main effects are implicit when higher-order terms and interactions are printed. Parameter estimates for the best-supported model are in Table S2. See Table 1 for variable abbreviations. LL = log-likelihood, w_i = is the probability of a model being the best-supported model among the candidate model set.

Count-model effects	K	LL	ΔAIC	w_i	M pR^2	C pR^2
Golden Crayfish						
River, Day, Density$_{t-1}$, B_HF$_{95}$, G_HF$_{99}$, G_LF$_{25}$, G_MinQ$_{1d}$, G_Temp, Site, Year	19	−10,935.2	0.0	0.62	0.20	0.24
River, Day, Density$_{t-1}$, B_HF$_{95}$, G_HF$_{99}$, G_LF$_{25}$, G_MinQ$_{1d}$, B_Temp, G_Temp, Site, Year	20	−10,935.2	1.8	0.23	0.20	0.24
Day, Density$_{t-1}$, B_HF$_{95}$, G_HF$_{99}$, G_LF$_{25}$, G_MinQ$_{1d}$, G_Temp, B_Temp × River, Site, Year	21	−10,935.1	3.7	0.10	0.20	0.25
Day, Density$_{t-1}$, B_HF$_{95}$, G_HF$_{99}$, G_LF$_{25}$, G_MinQ$_{1d}$, B_Temp × River, G_Temp × River, Site, Year	22	−10,935.1	5.7	0.04	0.20	0.25
Day, Density$_{t-1}$, B_HF$_{95}$, B_CVQ, G_HF$_{99}$, G_LF$_{25}$, G_MinQ$_{1d}$, B_Temp × River, G_Temp × River, Site, Year	23	−10,935	7.6	0.02	0.20	0.24
River, Day, Density$_{t-1}$, Site, Year (ecological null)	14	−11,001	121.5	<0.01	0.10	0.16
Ozark Crayfish						
Day, Density$^2_{t-1}$, G_MinQ$_{1d}$, G_Temp, Year	14	−4510.7	0.0	0.40	0.10	0.11
Day, Density$^2_{t-1}$, G_HF$_{90}$, G_MinQ$_{1d}$, G_Temp, Year	15	−4510.1	0.9	0.26	0.10	0.14
Day, Density$^2_{t-1}$, B_HF$_{75}$, G_HF$_{90}$, G_MinQ$_{1d}$, G_Temp, Year	16	−4509.6	2.0	0.15	0.11	0.14
Day, Density$^2_{t-1}$, B_HF$_{75}$, G_HF$_{90}$, G_MinQ$_{1d}$, B_Temp, G_Temp, Year	17	−4508.8	2.4	0.12	0.12	0.15
Day, Density$^2_{t-1}$, B_HF$_{75}$, G_HF$_{90}$, G_LF$_{10}$, G_MinQ$_{1d}$, B_Temp, G_Temp, Year	18	−4508.7	4.0	0.06	0.12	0.15
Day, Density$^2_{t-1}$, B_HF$_{75}$, B_CVQ, G_HF$_{90}$, G_LF$_{10}$, G_MinQ$_{1d}$, B_Temp, G_Temp, Year	19	−4508.5	5.8	0.02	0.12	0.15
Day, Density$^2_{t-1}$, Year (ecological null)	12	−4523.3	21.2	<0.01	0.07	0.12
Spothand Crayfish						
Day, Density$^2_{t-1}$, B_HF$_{95}$, G_HF$_{90}$, B_Temp × River, G_Temp × River, Site, Year	22	−6025.3	0.0	0.62	0.19	0.23
Day, Density$^2_{t-1}$, B_HF$_{95}$, G_HF$_{90}$, G_LF$_{25}$, B_Temp × River, G_Temp × River, Site, Year	23	−6025.2	1.8	0.25	0.20	0.24
Day, Density$^2_{t-1}$, B_HF$_{95}$, G_HF$_{90}$, G_LF$_{25}$, G_MinQ$_{3d}$, B_Temp × River, G_Temp × River, Site, Year	24	−6024.8	3.1	0.13	0.20	0.24
River, Day, Density$^2_{t-1}$, Site, Year (ecological null)	16	−6057.0	51.4	<0.01	0.16	0.25

testing median flows in both seasons, high-flow maxima in both seasons, and flow variability in summer. Hence, support for these variables was not examined in models containing multiple flow and temperature variables. However, Tables S3 (quadrat level) and S4 (site level) list support for models with individual flow or temperature variables.

Best-supported models of Golden Crayfish recruitment dynamics indicated recurrent extreme-flow events during spring brooding and summer growing periods adversely affected recruitment (Akaike weight [w] = 0.62, marginal pR^2 = 0.20, conditional pR^2 = 0.24; Table 3). Specifically, recruitment decreased with increasing numbers of high-flow events in spring (B_HF$_{95}$, −0.23 ± 0.05), and high-flow (G_HF$_{99}$, −0.05 ± 0.02) and low-flow (G_LF$_{25}$, −0.09 ± 0.03) events in summer. Recruitment also decreased with higher summer minimum flows (G_MinQ$_{1d}$, −0.11 ± 0.04) and increased with warmer summer mean daily maximum temperatures (0.19 ± 0.03), indicating Golden Crayfish recruitment benefits from warmer, drier summer growing periods (Fig. 8). Finally, Golden Crayfish recruitment was positively related to previous year's recruitment via a single 1st-order effect (0.05 ± 0.03; Fig. 9).

The best-supported model for Ozark Crayfish explained a lower percentage of variation and included fewer effects than the best-supported model for Golden Crayfish (w = 0.40, marginal pR^2 = 0.10, conditional pR^2 = 0.11 Table 3).
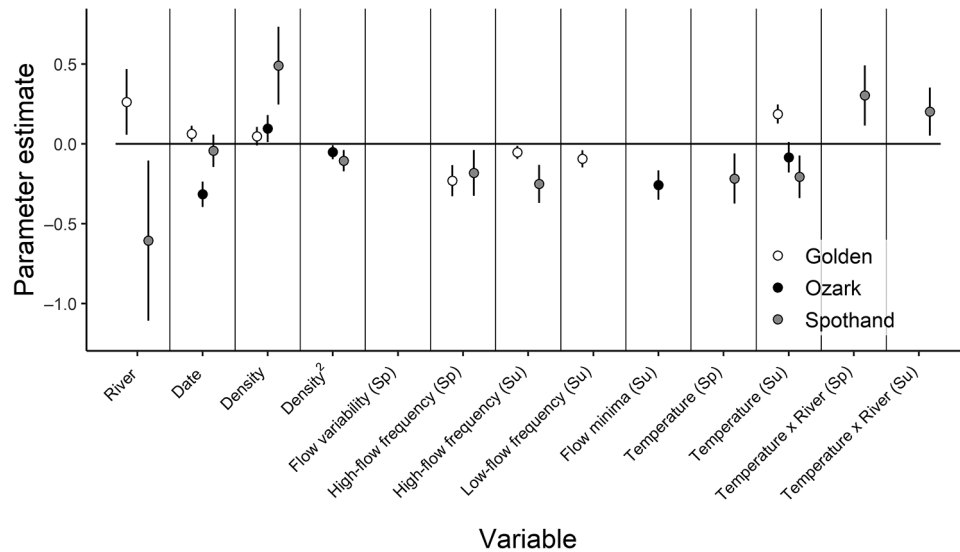
Figure 7. Parameter estimates (±95% CIs) of best-supported zero-inflated negative binomial models explaining variation in age-0 counts of Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes/1-m² quadrat sample in Big Piney (exempting Ozark Crayfish, 1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA), June to September. Continuous predictor variables were centered and standardized, and parameter estimates are on a linearized scale. A lack of a parameter estimate for a variable and species indicates that variable was removed from the initial global model during stepwise backward model selection (e.g., flow variability). The initial global model for Ozark Crayfish did not include a river effect because Ozark Crayfish only live in 1 study river. Sp = spring, Su = summer.

Ozark Crayfish recruitment increased with decreasing summer minimum flows (G_MinQ$_{1d}$, -0.26 ± 0.05), but unlike Golden Crayfish, Ozark Crayfish recruitment decreased with higher mean daily summer thermal maxima (-0.08 ± 0.05; Fig. 8). Finally, Ozark Crayfish recruitment was related to the previous year's recruitment by a quadratic density term, revealing that recruitment may be density-dependent (Fig. 9).

Best-supported models for Spothand Crayfish indicated recruitment dynamics were particularly sensitive to spring (B_HF$_{95}$, -0.18 ± 0.07) and summer (G_HF$_{90}$, -0.25 ± 0.06) high-flow events ($w = 0.62$, marginal p$R^2 = 0.19$, conditional p$R^2 = 0.23$; Table 3). Warmer spring mean daily maximum temperatures were strongly negatively associated with recruitment in BPR but slightly positively associated with recruitment in JFR, indicating river-specific features mediate effects of air temperature (Fig. 8). An interaction between summer mean daily maximum temperatures and river was also supported, with predicted negative effects of temperature on recruitment being much larger in BPR than JFR (Fig. 8). Like Ozark Crayfish, Spothand Crayfish recruitment was related to the previous year's recruitment at low densities via a weak quadratic relationship (Fig. 9).

None of the best-supported models explaining recruitment dynamics were identical, but we identified commonalities among species (Fig. 7). For example, recruitment of Golden and Ozark crayfishes was higher in summers with lower flow minima, whereas recruitment of Golden and Spothand crayfishes decreased with increasingly frequent high-flow events. Further, Ozark and Spothand crayfishes might be negatively affected by warmer summer daily maximum air temperatures and exhibit signs of density-dependent survival among years.

Low sample sizes limited model complexity for the complementary analysis explaining recruitment dynamics at the site level, but several models were still better supported than ecological null (i.e., baseline) models that included only grouping variables. Moreover, best-supported models at the site level explained much higher percentages of variation in recruitment (marginal p$R^2 = 0.47$–0.67, conditional p$R^2 = 0.62$–0.70; Table S4). Flow and temperature variables within best-supported models at the site level were similar to those included in best-supported models at the quadrat level, although specific flow thresholds sometimes varied. For example, Golden Crayfish recruitment at sites decreased after frequent high-flow events in spring (B_HF$_{95}$) and summer (G_HF$_{75}$). Spothand Crayfish recruitment decreased with frequent high-flow events in spring (B_HF$_{95}$), and with warmer summer maxima air temperatures (G_Temp). Similar to findings at the quadrat level, Ozark Crayfish recruitment increased after summers with lower summer flow minima (G_MinQ$_{1D}$). However, unlike in the best-supported quadrat-level model, Ozark Crayfish recruitment at the site level decreased in years with frequent high-flow events in summer (G_HF$_{75}$). Despite not being included in the best-supported model at the quadrat level, a negative effect for frequent high-flow events in summer (G_HF$_{90}$) was included in
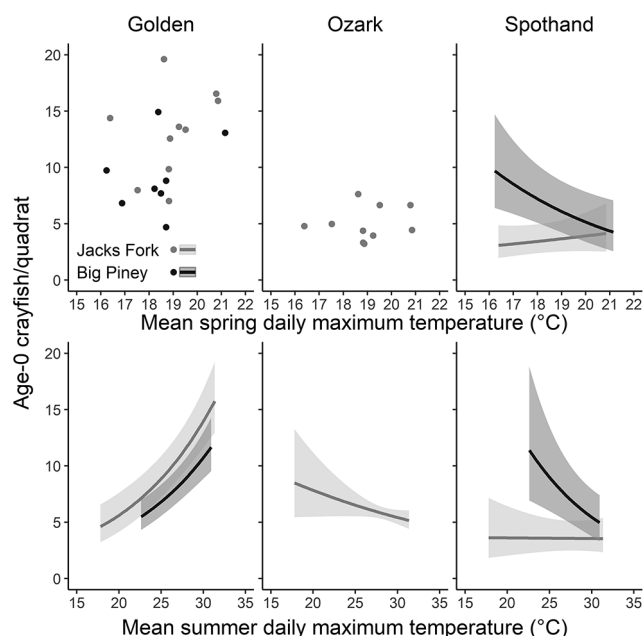
Figure 8. Predicted effects (±95% CIs) of mean daily maximum temperatures during crayfish brooding (March–May) and growing (June–September) periods on age-0 Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes in 1-m² quadrat samples in Big Piney (exempting Ozark Crayfish, 1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA). Averages were used as inputs for non-temperature terms in models. Predictions span observed ranges of densities within each river. Points depict mean densities/quadrat and, for models without temperature effects, temperatures/site and year.

the 2nd-best model at the quadrat level for Ozark Crayfish, which had moderate support ($w = 0.26$; Table 3). Taken together, analyses explaining recruitment dynamics at quadrat and site levels mostly aligned, but models at the site level explained much higher percentages of variation (Table S4).

DISCUSSION

Crayfishes are functionally important organisms in many freshwater ecosystems, but information is often lacking on abiotic factors that regulate their populations. Using a unique, long-term population dataset for 3 crayfish species, we determined that flow and temperature conditions in spring brooding and summer growing periods may explain species-specific effects on annual recruitment dynamics of 3 crayfishes. These species spanned an ecological spectrum ranging from large, fast-growing habitat-type specialists with possible density-dependent recruitment to small-bodied habitat-type generalists with density-independent recruitment. Our findings challenge the widely held belief that ecological characteristics are necessarily similar among closely related lotic crayfish

species (in agreement with Larson et al. 2016, Stites et al. 2017). The focus of our study was *Faxonius* spp., but future research could explore the degree to which species and genera spanning an even broader spectra of life-history strategies respond dissimilarly to flow and temperature.

Crayfish recruitment

Age-0 Golden Crayfish occurred at highest densities at all 4 sites and exhibited a consistently positive spawner–recruit relationship, traits that may help it withstand greater mortality from flood disturbances in suboptimal refuge habitats. Golden Crayfish recruitment was lower in years with more frequent high-flow events in both the spring brooding and summer growing periods. Recruitment strongly increased in years with warmer summer mean daily maximum temperatures. This species' more generalized habitat-selection patterns could result from its small body size and might allow age-0 Golden Crayfish to reduce intra- and inter-specific competition for food and habitat, thereby maintaining a positive spawner–recruit relationship at high densities. For example, Rabeni (1995) found that Golden Crayfish selected vegetated habitats in the absence of interspecific competitors but were excluded from vegetated habitats in the presence of the larger Spothand Crayfish. If larger congeners exclude Golden Crayfish from flow refuge habitats in slower near-shore habitats or under large boulders (Prins 1968, Clark and Kershner 2011), then its small body size could be advantageous for occupying thin laminar flow sublayers found in swifter riffle and run habitats (Maude and Williams 1983, Gore and Bryant 1990, Perry et al. 2013). Within riffles and runs, however, crayfishes are more exposed to swift water velocities, which could explain the higher age-0 mortality linked to high-flow events and highly variable recruitment among years. Later brooding periods by Golden Crayfish (Muck et al. 2002b) could partly compensate for greater exposure to swift water by delaying free-living life stages until summer when flows are typically lower.

In contrast, the more specialized habitat-selection patterns, larger body size, and slightly negative density dependence at high Ozark Crayfish densities may help explain its more stable population sizes through disturbance events. Ozark Crayfish recruitment slightly increased during summers with lower flow minima during drier years. Flinders and Magoulick (2005) found that Ozark Crayfish densities increased with percentages of large substrate. Large cobble and boulder substrate are refugia for macroinvertebrates during elevated flows (Holomuzki and Biggs 2003) and might explain Ozark Crayfish's resistance to frequent high-flow events in spring relative to Golden and Spothand crayfishes. Furthermore, the relatively short, broad chelae of Ozark Crayfish may be useful for anchoring in high flows (Maude and Williams 1983, Clark et al. 2008, Perry et al. 2013).

Finally, Spothand Crayfish were uncommon, large-bodied, and exhibited specialized selection of low-velocity habitat
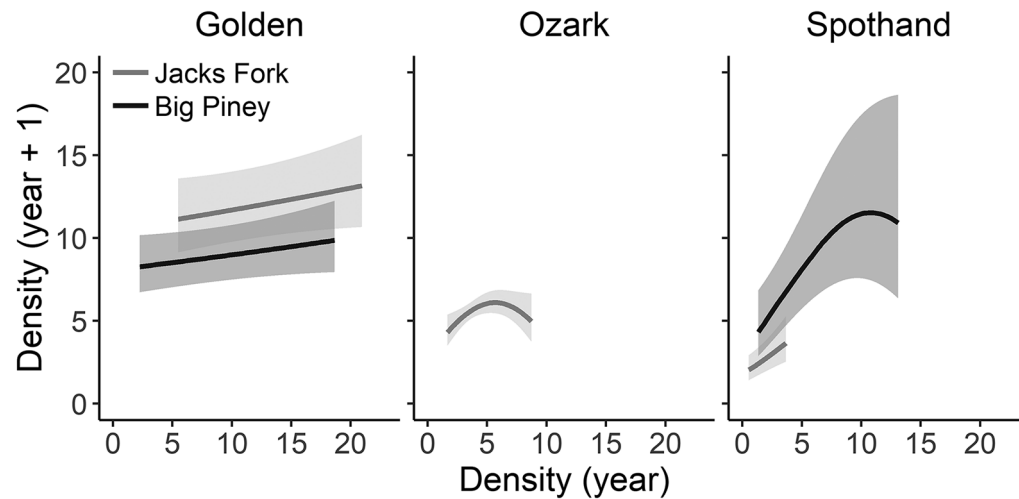
Figure 9. Predicted relationships (±95% CIs) between consecutive years of density of age-0 Golden (*Faxonius luteus* [Creaser, 1933]), Ozark (*Faxonius ozarkae* [Williams, 1952]), and Spothand (*Faxonius punctimanus* [Creaser, 1933]) crayfishes in 1-m² quadrat samples in Big Piney (exempting Ozark Crayfish, 1993–2000) and Jacks Fork (1992–2001) rivers (Missouri, USA). Averages were used as inputs for non-density terms. Predictions span observed ranges of densities within each river.

types, which might explain the vulnerability of age-0 individuals during high-current-velocity disturbances. Spothand Crayfish recruitment decreased during years with warmer spring and summer temperatures in BPR, frequent high-flow events, and following high-recruitment years. Morphologically, the large body size and slender chelae of Spothand Crayfish may not be advantageous for anchoring during high-flow events (Maude and Williams 1983, Clark et al. 2008, Perry et al. 2013). Spothand Crayfish occur at higher densities in intermittent streams and may be adapted to stream drying, whereas Ozark Crayfish occur at similar densities in both intermittent and permanent streams (Flinders and Magoulick 2003). Collectively, these findings support Spothand Crayfish's affinity for lower-velocity habitats, including backwaters and aquatic vegetation patches (DiStefano et al. 2003a, Flinders and Magoulick 2005, Magoulick et al. 2017). Lower densities of Spothand Crayfish in the JFR, where the species co-occurs with Ozark Crayfish, may be related to competition between these species for similar, lower-velocity habitats.

Flow-event responses

Our study was among the first to document species-specific crayfish responses to interannual variation in flow (Light 2003, Lynch et al. 2018). Consistent with our predictions, recruitment of Golden and Spothand crayfishes decreased in years with frequent high-flow events, although these decreases could reflect different mechanisms. For example, greater use of riffles and runs likely predisposed Golden Crayfish to direct mortality during high-flow events. In contrast, Spothand Crayfish recruitment could be sensitive to prevalence of water-willow (Brewer et al. 2009), which

is uprooted during extreme high-flow events (Penfound 1940). Furthermore, water-willow is sensitive to desiccation during prolonged low flows, which might explain why Spothand Crayfish was the only species to not have higher recruitment in years with lower summer minima flows. The evolution of diverse responses to environmental variability may temporarily reduce the intensity of competition, thereby permitting coexistence of multiple species. For example, Lynch et al. (2018) found that increasing flood frequency potentially promoted crayfish diversity in Ozark streams. Therefore, diverse portfolios of ecological traits may strengthen the overall crayfish assemblage resilience to increasingly frequent disturbances (Figge 2004).

Our prediction that recruitment in all species would decrease in years with frequent high-flow events was only partially supported because an effect for frequent high-flow events was not included in the best-supported model explaining Ozark Crayfish recruitment dynamics at the quadrat level. However, a negative effect of high-flow events exceeding the 90th percentile during summer was included in the 2nd-ranked model ($w = 0.26$, $\Delta AIC = 0.90$; Table 3) at the quadrat level. Moreover, at the site level, a negative effect for frequent high-flow events during spring brooding was included in the best-supported model. Although measuring recruitment at the quadrat level accounted for timing mismatches between data collection and flow and temperature events, quadrat-level recruitment data have limitations. For example, fine-scale quadrat data are likely sensitive to numerous latent variables and stochasticity manifested as lower explained variation in best-supported models (≤0.20 marginal pR^2) than variation explained at the site scale (marginal pR^2 = 0.47–0.62). Future long-term monitoring designs of

crayfish recruitment might consider standardizing and narrowing the sampling window among years, and sampling for additional years, thereby enabling greater analytical power to examine recruitment dynamics at the site scale. We performed complementary analyses at quadrat and site scales because of limitations with the study design underlying our long-term dataset. Given the support for including terms for high-flow frequency in models aimed at both scales, age-0 Ozark Crayfish recruitment might be negatively affected by high-flow events during summer.

Temperature-maxima responses

Our prediction that recruitment of the 2 larger-bodied crayfishes (Ozark, Spothand) would be higher in warmer, drier summers was inconsistently supported. Of these species, recruitment was higher in summers with lower minimum flows (i.e., drier conditions) only for Ozark Crayfish, and neither species had consistently higher recruitment during warmer summers. In contrast, the smaller-bodied Golden Crayfish had higher recruitment during warmer, drier summers. Warmer, drier summers might enhance age-0 survival of Golden Crayfish by increasing algal mass (an important food source) in shallow, sun-exposed main-channel habitats used more frequently by age-0 Golden Crayfish (Whitledge and Rabeni 1997). Thus, Golden Crayfish in rivers may benefit from future warmer and drier summers. It is unclear whether Golden Crayfish populations that occupy smaller streams than our perennial rivers would also benefit from warmer, drier summers if these conditions result in complete streambed drying. Groundwater influences the distribution and abundance of some crayfish species (Magoulick et al. 2017, Rice 2017) and likely would be influential in smaller streams for buffering against some effects of increasing temperatures and decreasing precipitation on crayfish recruitment in the future.

The general negative relationship we observed between crayfish recruitment and frequent high-flow events aligns with previous research linking high stream flows to increased mortality in crayfish species (Light 2003, Parkyn and Collier 2004). However, these patterns may not have been detected through the use of traditional fecundity-based recruitment indices (e.g., Skurdal et al. 2011). Given that attached age-0 crayfishes during brooding may be displaced during environmental disturbances, our results underscore the importance of survival during brooding and post-brooding periods in determining annual crayfish recruitment. Using fecundity (ova) as an index of recruitment in these species likely would have produced different apparent environmental relationships for some species. For example, the least abundant species in this study (Ozark and Spothand crayfishes) actually produce the most fertilized ova each year (Muck 1997).

Environmental variables, such as temperature and flow, can influence range expansion and competitive abilities of invading crayfishes, which may lead to the exclusion of native species (Flynn and Hobbs 1984, Bubb et al. 2004, Mazlum and Eversole 2005). For example, future populations of the narrowly endemic Spothand Crayfish could be affected by the introduced Virile Crayfish *Faxonius virilis* (Hagen, 1870), which has invaded at least 117 km of the Current River downstream of JFR study sites (DiStefano et al. 2015, Rozansky 2019). Virile and Spothand crayfishes are ecologically (Pflieger 1996), morphologically (Rozansky 2019), and genetically (Crandall and Fitzpatrick 1996, Taylor and Knouft 2006) similar. Virile Crayfish could negatively affect Spothand Crayfish populations through hybridization (Rozansky 2019) or competition for resources. In Ozark rivers high-flow events might temporarily ease competition, thereby allowing less-dominant crayfish species to coexist with more dominant competitors. In contrast, low flows generally favor establishment and spread invaders (Mathers et al. 2020).

Broader implications

Our results compel further research on crayfish responses to environmental variables at the individual, population, and range-wide scales. Advancements in the miniaturization of Passive Integrated Transponder tags would allow researchers to study how individual crayfish of multiple species behaviorally respond to flow and thermal changes in river reaches (Westhoff and Sievert 2013). Some *Faxonius* crayfishes have limited dispersal ability (DiStefano and Westhoff 2011) to find refuge during disturbance events, and better understanding of species- and assemblage-level dispersal patterns would better inform management decision making. Furthermore, knowledge of thermal effects on growth, survival, and habitat selection are lacking for >90% of described species (Westhoff and Rosenberger 2016). Hydrologic and thermal effects on crayfish populations will likely interact with other stressors, such as water chemistry, sediment aggradation, disease, and interactions with invasive species, to affect crayfish population trajectories.

Long-term ecological research has disproportionately influenced environmental policy and management, yet funding for this research has declined (Hughes et al. 2017). In the context of environmental change, long-term studies are important for detecting ecological trends, especially those that are naturally dynamic over shorter time periods. Crayfish conservation in the Ozark Highlands would benefit from long-term datasets from multiple streams across the region to understand how distinct flow regimes in this varied region structure crayfish diversity, distributions, and dynamics (DiStefano et al. 2009, Rice et al. 2018, Chilton et al. 2020).

Our results demonstrated that even closely related species respond differently to variation in stream flow and air temperature. Thus, crayfish responses to climate change could depend on species-level differences in life history, morphology, habitat selection, and competitive abilities. To account for these habitat dynamics, managers may also consider actions to promote sensitive habitats, such as aquatic

vegetation patches, to promote species resilience under the more variable flow regimes predicted under climate change. Increases in temperatures and precipitation will lead to more frequent high-flow events (Pachauri and Meyer 2014) and decreases in baseflow (Ayers et al. 2019), which might affect thermal- and flow-sensitive stream communities. Although disturbances may be important for alleviating competitive pressures among species, increasing frequency of extreme events over longer temporal periods could favor some species over others. Based on our results, it is unclear which species would consistently benefit under predicted future conditions. Golden Crayfish could benefit from warmer spring and summer temperatures and lower summer baseflows but might be adversely affected by more frequent high-flow events. Similarly, benefits of lower summer-flow minima for Ozark Crayfish might be offset by negative effects of warmer summers. In contrast, sensitivity to high-flow events and warmer temperatures may particularly predispose Spothand Crayfish to adverse effects of future climate-associated stream conditions. As conditions within Ozark stream systems change, it is likely the composition of crayfish assemblages will also change. Given the important roles of crayfishes in these systems, changes to their assemblages could reverberate through broader communities encompassing fish, invertebrates, and macrophytes.

Data Availability Statement: Data available from the authors upon reasonable request.

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