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ORIGINAL PAPER

Changes in the distribution of Michigan crayfishes and the influence of invasive rusty crayfish (*Faxonius rusticus*) on native crayfish substrate associations

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Abstract Invasive crayfishes have a strong negative effect on multiple trophic levels, including other crayfishes. However, documentation of the spread of non-native crayfish species and their impact on native crayfishes could be improved, particularly over large spatial scales in stream ecosystems. We collected crayfish and quantified habitat at 461 stream sites throughout Michigan in 2014–2016 and compared our collections to a historical account of crayfish collections published in 1975. Our objectives were to: (1) quantify the change in non-native rusty crayfish (*Faxonius rusticus*) and native species distributions from 1975 to 2014–2016; (2) quantify how rusty crayfish affect the habitat associations of native species in Michigan streams; and (3) determine the effectiveness of dipnets, our primary sampling method. We found all species in more watersheds compared to 1975, likely due in part to increased sampling. However, we found rusty crayfish in 22 more HUC-8 watersheds than in 1975, a larger increase than all other species. Habitat associations of native species also shift in the presence of rusty crayfish. In instances where native species co-occurred with rusty crayfish, most obligate aquatic native species were found in less-preferred habitat such as sand or macrophytes compared to cobble substrate when the species is in isolation. Our results indicate a broad range expansion by rusty crayfish over the last 40 years, suggesting that surveys of crayfish diversity and habitat occupancy should be more routine to inform management of native crayfish species.

Keywords Rusty crayfish · Orconectes · Range expansion · Crayfish · Substrate associations

Introduction

Invasions of non-native species represent one of the most important issues facing native species biodiversity and ecosystem sustainability. Aquatic ecosystems are particularly vulnerable to effects of invasions, and those systems that are prone to habitat modification or disturbance are likely to be most susceptible to introductions of non-native species (Lozon and MacIsaac 1997; Moyle and Light 1996). For the past few decades, scientists have debated the relative roles

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of non-native species and habitat modification as engines of global change (Didham et al. 2005, 2007). While some consensus has emerged that both play important roles, synergies between non-native species introductions and habitat modification represent a potent driver of ecosystem change. Crayfish invasions represent such a nexus. The ability of crayfish to manipulate ecosystems has led them to be labeled 'ecosystem engineers' (Carreira et al. 2014; Hobbs et al. 1989; Lodge and Lorman 1987; Momot 1995; Momot et al. 1978). Further, the burrowing and foraging behavior of many crayfish species can alter both the abiotic and biotic habitat available for native species through hydrologic alterations and macrophyte habitat destruction, respectively (Faller et al. 2016; Wilson et al. 2004).

Crayfish invasions are often followed by extensive ecosystem disruption at a number of trophic levels, from primary producers such as periphyton and macrophytes, to top predators such as fishes (Carreira et al. 2014; Ilheu et al. 2007; Kershner and Lodge 1995; Lodge and Lorman 1987; Roth et al. 2006, 2007; Wilson et al. 2004). Thus, there is considerable interest in the distribution of crayfishes, particularly related to non-native species. The spread of some crayfish species over broad spatial and temporal scales and their effects in the ecosystem are well-documented, particularly for *Procambarus clarkii* in Europe (e.g. Gherardi 2006), but the spread of most species has gone undocumented, at least over longer temporal scales (but see Olden et al. 2006; Taylor and Redmer 1996).

Crayfishes can be a dominant component of freshwater ecosystems, but many species are imperiled (Charlebois and Lamberti 1996; Huner and Lundquist 1995; Lodge et al. 1994; Nystrom et al. 2006). In some aquatic ecosystems, crayfishes account for more biomass than all other macroinvertebrates combined (Rabeni 1992). Crayfishes demonstrate a broad spectrum of life history strategies, such as terrestrial burrowing, that allow them to persist in a wide variety of habitats, including lakes, streams, wetlands, caves, and agricultural fields. These unique life histories have allowed species to coexist by occupying distinct ecological niches depending on seasonal water cycles or habitat heterogeneity (Hobbs 1942, 1981; Welch and Eversole 2006). Nonetheless, crayfishes remain one of the most imperiled taxa in North America. As of the mid-late 1990s, fewer than 50% of crayfish species populations were classified as stable (Taylor et al. 1996; Wilcove et al. 1998). These estimates are likely conservative, as the most recent comprehensive assessment is nearly 20 years old. Further, many species lack adequate information on current distributions, habitat requirements, and threats to conservation that could help prioritize conservation efforts. Substantial attention has been devoted to determining causes of species replacements in crayfish communities related to differential susceptibility to predators (DiDonato and Lodge 1993; Mather and Stein 1993a; Roth and Kitchell 2005), hybridization with native species (Perry et al. 2001a, b), and morphological or behavioral differences among species (Bergman and Moore 2003a; Garvey and Stein 1993; Garvey et al. 1994; Gherardi and Daniels 2004; Pintor and Sih 2009), but less attention has been devoted to changes in crayfish habitat selection following an invasion. Habitat selection associations of native species often change in response to introductions of non-native species (Kiesecker and Blaustein 1998; Losos et al. 1993; Trammell and Butler 1995), and previous studies document that habitat is an important determinant of predation risk in crayfish (DiDonato and Lodge 1993; Saiki and Tash 1979), and other species in aquatic and terrestrial ecosystems (Creel et al. 2005; Hrabik et al. 2014; Valeix et al. 2009; Werner et al. 1983). Studies of crayfish species distributions teamed with habitat surveys through time could inform our understanding of how invasions affect native species, but many locales lack recent data on crayfish distributions (or in-stream habitat) to perform such analyses.

A lack of recent crayfish distribution data is a significant concern in many locations. Many states do not have updated crayfish distribution data, despite findings that indicate that invasive crayfishes are one of the most common threats to native crayfishes(Lodge et al. 1998, 2000). For instance, Wisconsin and Illinois are the only states in the entire Great Lakes Basin that have statewide crayfish surveys in the last 20 years (Olden et al. 2006; Taylor and Redmer 1996). In the state of Michigan, addressing threats to native crayfish posed by invasive species is a management priority. However, the last published comprehensive survey of crayfishes in Michigan was from Creaser (1931), whom provided maps of crayfish collections for individual species. However, these maps lack sufficient resolution to declare which drainages some collections belong. In contrast, Lippson (1975) provides enough detail from their crayfish collections throughout Michigan from the 1960s to provide us with an opportunity to quantify changes in crayfish distributions from a more recent time, albeit from more than 40 years ago. Further, research on changes in native species behavior as it pertains to habitat selection is relatively rare, particularly for non-native crayfish impacts on other crayfish species with a few exceptions (Bergman and Moore 2003a; Jansen et al. 2009; Mather and Stein 1993b). Herein, we document changes in the range of one non-native crayfish species (*Faxonius rusticus*) across the State of Michigan, and quantify how habitat selection of native crayfish species differs in streams where rusty crayfish are present compared to where they are absent.

Eight crayfish species are considered native in Michigan. Three are primarily found in permanent open water habitats such as streams and lakes (*Cambarus robustus, Faxonius propinquus,* and *Faxonius virilis*). Three use subterranean burrows (*Cambarus diogenes, Cambarus polychromatus,* and *Creaserinus fodiens*) and are rarely observed in open water as adults, except in spring and early summer when they release their young. Two are facultative burrowers, depending on conditions such as precipitation and water levels in adjacent water bodies (*Faxonius immunis,* and *Procambarus acutus*) (Hobbs and Jass 1988; Lippson 1975; Thoma et al. 2005).

One non-native species of crayfish, the rusty crayfish (*F. rusticus*), has been reported in Michigan for over 130 years with major range expansion occurring during the twentieth century (Creaser 1931; Faxon 1884; Lippson 1975). The initial *F. rusticus* range expansion into the Great Lakes basin is attributed to shipping canals connecting the Ohio River and Maumee River watersheds in Ohio, and subsequent spread in the region is believed to be primarily a result of bait bucket release by anglers or intentional release by lake managers seeking to manage macrophyte communities (Creaser 1931; Olden et al. 2006). *F. rusticus* lives primarily in streams and lakes and is observed to negatively affect populations of native stream and lake dwelling crayfish, including the northern crayfish (*F. virilis*) and northern clearwater crayfish (*F. propinquus*) (Garvey et al. 2003). Negative effects of rusty crayfish are numerous: a variety of studies have demonstrated that they outcompete native species for food and shelter, exhibit less susceptibility to native predators, and hybridize with native *F. propinquus* (Capelli and Munjal 1980, 1982; Hill et al. 1993; Perry et al. 2001b, 2002; Roth and Kitchell 2005). *F. rusticus* can also affect native fish assemblages through egg predation and by altering habitat through extensive macrophyte destruction, thereby disrupting native food webs (Capelli and Munjal 1982; Dorn and Mittelbach 1999; Kreps et al. 2016; Lodge et al. 1998; Morse et al. 2013; Roth et al. 2007).

One of the mechanisms by which *F. rusticus* is believed to negatively affect native species is through displacement from preferred habitats. Habitat associations of crayfish communities have received very little attention, except perhaps in northern Wisconsin lakes subject to rusty crayfish invasions (DiDonato and Lodge 1993; Garvey et al. 2003). Crayfish habitat associations in lotic ecosystems, to our knowledge, have yet to be studied although some information does exist at coarse spatial scales (Burskey and Simon 2010).

The quantity of streams and rivers in Michigan provides an opportunity to evaluate crayfish habitat associations both with and without rusty crayfish present. Further, the past distributional data reported by Lippson (1975) offers an opportunity to quantify how crayfish communities in Michigan have changed through time and across space. This study seeks to (a) update our current understanding of the status and range of stream-dwelling crayfish within Michigan's upper and lower Peninsula, (b) identify habitat associations of crayfish species with and without invasive rusty crayfish, (c) document changes in the range of crayfish species compared to historical data with an emphasis on non-native rusty crayfish, and (d) evaluate the effectiveness of our sampling method. With respect to (b), we hypothesize that native species will associate with less-desirable habitat in the presence of rusty crayfish at a given site. For (c), we hypothesize that rusty crayfish have expanded their range in Michigan over the last 40 years, but native species have contracted their range owing to negative interactions with rusty crayfish. We also provide an analysis of detectability given the uncertainty regarding our specific capture method (dipnets), and to provide insight into the repeatability of this survey. Information derived from this study will highlight large-scale trends in crayfish communities, and could assist in prioritization of habitats for native crayfish conservation as well as locations to focus prevention efforts for rusty crayfish. This study also adds to the growing body of literature regarding indirect effects of invasions as related to how non-native species affect the habitat selection of native species.

Methods

Crayfish collection

Although crayfishes occupy two general habitat types—open water habitats and burrows (Hobbs et al. 1989)—this survey was limited to open water habitats of streams. We used the Michigan Department of Natural Resources (MDNR) Stream Status and Trends Program (SSTP) (Seelbach et al. 1997; Wills et al. 2006) to determine stream sampling sites. Stream segments were selected by stratifying the SSTP database by management unit and major watershed. We selected at random 20% of available stream segments for collection from each watershed stratum to evenly distribute sampling effort across watersheds. Stream segments are inter-confluence stream reaches, defined by tributary confluences or dams. The watershed stratum as defined in the SSTP database were individual streams and their tributaries directly connected to a Great Lake (Wills et al. 2006). All data were collected in summer of 2014–2016. We sampled 69 segments in 2014, 277 segments in 2015, and 133 segments in 2016, for a total of 479 segments and 958 sites (two sites per segment) over the 3-year period of the study.

Technicians worked in pairs to sample stream segments at each site, and generally attempted to access streams from a road crossing, with one individual working upstream and the other downstream of the crossing. Technicians worked to catch as many crayfish as possible in a 20-min period. We sampled crayfish with dip nets, using standard protocols for crayfish collection (Olden et al. 2006). We selected dip nets because it allowed us to implement a consistent sampling technique across all streams regardless of substrate type. This included netting individuals off substrate, lifting rocks or larger substrate with the foot or hand, and using hands and twigs to probe crayfish out of root structures or undercut banks. Collected crayfish were temporarily retained for identification and measuring until dip netting was completed at a site.

Once sampling at a site was complete, we recorded GPS coordinates at the center of each sampling unit. After exiting the stream each crayfish was identified by species. Once crayfish data were recorded, all rusty crayfish were euthanized whereas native crayfish were returned to the stream.

C. diogenes and *C. polychromatus* were combined for all analyses due to their low catch rates and difficulty in distinguishing young individuals. Because both species were formerly part of a species complex (Thoma et al. 2005), data for the two were likely combined during Lippson's survey and will be referred to as the '*diogenes* complex' in this paper (Lippson 1975; Thoma et al. 2005).

Habitat sampling

Substrate characteristics were identified using a visual assessment of upstream and downstream sampling areas. Substrate categories were based on a modified Wentworth scale and included clay (< 1/256 mm), silt (> 1/256 mm, < 1/16 mm), sand (> 1/16 mm, < 4 mm), pebble (> 4 mm, < 64 mm), cobble (> 64 mm, < 256 mm), boulder (> 256 mm), woody material (roots, tree limbs, etc.), detritus, and living macrophytes (Wentworth 1922). Substrate was classified based on amount present in each sampling area using a scale of 0%, 1–24%, 25–49%, 50–74%, and 75–100%.

Data and Statistical Analysis

Detectability

We used occupancy analysis (e.g. Mackenzie et al. 2006) to analyze detect/non-detect data from our survey of sites. These models provide probabilities associated with detecting an individual species in either the same location through time (temporal detectability) or at proximal sites within the same stream segment (spatial detectability). Temporal detectability models were fit to pooled data of both technicians from 22 stream segments that were visited in 2014 and again in 2015. This model tested whether a species would be detected at a location on every occasion that it was sampled. Spatial detectability was modeled by comparing samples from the same stream segment, i.e., one sample from upstream compared to the other from downstream of the road crossing. This model tested whether crayfish assemblages were uniform throughout a stream segment. Samples conducted on the same segment but at different times were treated as their own unique sampling event, allowing a sample size of 479 comparisons for the spatial model.

For this analysis, we made several assumptions consistent with previous applications (e.g. Mackenzie et al. 2006). Foremost, we treated each observer as an independent survey visit, and assumed that if the selected crayfish species was present within one observer's section, it was present at the other. Put another way, we assumed that the occupancy status (i.e., present or absent) applied to both sub-sites sampled. This assumption is critical for the occupancy analysis and implies that if one searcher detects a crayfish species at a site, and the other observer does not, this is due to a non-detection, thus allowing the analysis to provide estimates of detection probability. Two other assumptions were that crayfish did not move into or out of a site within the time to survey a site (i.e., the sites are closed during the time of the survey), and that crayfish were identified accurately (i.e., no false positives).

The following occupancy model allowed us to obtain estimates of site occupancy as well as detection probability (Mackenzie et al. 2006):

$$L(\psi,p) = \left(\psi^{n.}\Pi p_t^{n_t}(1-p_t)^{n.-n_t}\right) \times \left(\psi\Pi(1-p_t) + (1-\psi)\right)^{N-n.} \tag{1}$$

where t is the number of searchers at a site, N is the total number of sites surveyed, and n is the number of sites where at least one detection occurred, ψ is the probability of occupancy, p is the detection probability for a single searcher, and n_t is the number of detections on tth survey. We implemented this occupancy model and obtained estimates via the unmarked package in R (R Development Core Team 2018).

Estimates of detection probability from this model are for a single searcher; we estimated detectability for two searchers using the following equation:

$$p_\mathrm{d} = 1 - (1 - p_\mathrm{s})^2 \tag{2}$$

where p_d is the probability of detection with two searchers and p_s is the probability of detection for a single searcher determined from the occupancy analysis.

Crayfish ranges

Crayfish presence/absence data were compared to Lippson's 1975 dissertation (Lippson 1975) to determine any changes in the range of crayfishes in Michigan. Lippson (1975) presented their data in terms of successful captures for each species found at their sampling locations. We assumed all species captured at a given site were reported, thus all non-reported species were absent. We also compared changes in the co-occurrence of obligate aquatic species (*C. robustus*, *F. propinquus*, *F. virilis*), as a result of increased *F. rusticus* ranges from previous reports. Lippson's (1975) collections are reported at the county, township, range, and section level. We converted the centroid of these locations to GPS coordinates, and then sorted collections by United States Geological Survey (USGS) 8-digit Hydrologic Unit Code (HUC) watersheds and MDNR Fisheries Management Units (FMU) (Michigan Department of Natural Resources 2001; U.S. Department of Agriculture Service Center Agencies—National Geospatial Management Center 2013). In this way, we were able to assign each of Lippson's sampling locations to an 8-digit HUC watershed, for comparison to our survey data. Range maps were constructed using shapefiles published by USDA/NRCS—National Geospatial Management Center and the MDNR in ArcGIS version 10.1 (ESRI 2011; Michigan Department of Natural Resources 2001; U.S. Department of Agriculture Service Center Agencies—National Geospatial Management Center 2013).

Habitat associations

We used model selection to identify significant habitat predictors of presence or absence for all crayfish species. We input habitat predictors into a generalized linear model (GLM) using the logit function, and used backward selection using the step AIC function of the MASS package in R version 3.0.2 (R Development Core Team 2018), to identify significant predictors. We repeated this process for each species using the substrate classifications from the modified Wentworth scale as covariates. Species were coded as 1 (present) or 0 (absent). Habitat covariates were also coded as 0–4, corresponding to modified Wentworth scale abundance classifications. We used a logit link function to fit the GLM. This allowed us to determine if the presence of a crayfish species was positively or negatively associated with individual substrate classes. Log odds ratio output from GLMs permitted us to identify the direction and magnitude of effect, as any log odds value below 0 indicated lower than a 50% chance of finding a crayfish associated with a given habitat, and values further away from 0 indicating larger effects. Log odds ratios quantify the ratio of collecting a species to not collecting the species. Thus, if the presence of a given habitat increases the odds of collecting the species, the ratio will increase, and the log odds ratio will be greater than 0. To quantify changes in substrate associations based on the presence or absence of *F. rusticus,* we ran separate analyses for each native species after dividing samples into those where *F. rusticus* was present and those where *F. rusticus* was absent. We used a significance level of $\alpha = 0.05$ for all tests.

Results

Detectability

The detectability of crayfish was high for obligate stream species both through time and within individual segments. No obligate stream species had less than a 60% probability of detection and most had detectabilities over 80% (Table 1). The primary and secondary burrowing species showed lower detection probabilities, and temporal models for *C. fodiens* and *P. acutus* could not be run due to lack of data, despite having moderate spatial detectability (46% and 67%, respectively).

Crayfish ranges

During May–September of 2014–2016, crayfish species presence and absence was assessed at 461 of the > 2000 unique stream segments in Michigan (Fig. 1). Overall, all of Michigan's native crayfish species were detected in more watersheds during this survey than in 1975 (Table 2). For *F. rusticus*, there is evidence for a substantial range expansion. We found *F. rusticus* in 20% of samples and in 34 of 55 HUC 8 watersheds. By comparison, *F. rusticus* were documented in only 12 HUC 8 watersheds in 1975 (Lippson 1975) (Table 2; Fig. 2). Every watershed that contained *F. rusticus* in 1975 also contained *F. rusticus* in this study (Fig. 2).

Native species ranges appear to have shifted since 1975. Although we sampled more watersheds than Lippson (1975), shifts in the overall range of some native species is apparent, as well as changes in

Table 1 Detectability of crayfish species during 2014–2015 stream surveys over time and space

Species	Spatial detectability		Temporal detectability	
	Ψ	P	Ψ	P
C. diogenes	0.289	0.222	0.182	0.500
C. robustus	0.132	0.607	0.142	0.800
C. fodiens	0.040	0.462	–	–
F. immunis	0.121	0.533	0.182	0.500
F. propinquus	0.548	0.826	0.683	0.966
F. rusticus	0.283	0.852	0.230	0.889
F. virilis	0.354	0.609	0.371	0.857
P. acutus	0.013	0.667	–	–
	n = 350		n = 22	

ψ being occupancy and P being probability of detection

Fig. 1 Stream segments sampled from 2014 to 2016. Each dot represents one paired sample

Table 2 Crayfish occurrence by HUC8 watershed (n = 55)

Species	1975	2016
C. diogenes	8	23
C. robustus	12	17
C. fodiens	3	9
F. immunis	10	18
F. propinquus	45	48
F. rusticus	12	34
F. virilis	33	43
P. acutus	0	3

A comparison of occurrences reported in a 1975 survey and findings during 2014–2016 field sampling. Specific watersheds occurrences are located in the "Appendix"

occurrence within some watersheds (Table 2). The most widely distributed native species in our survey was *F. propinquus*, which we found in 48 of 55 HUC-8 watersheds and 42% of samples. We found *F. propinquus* in three more watersheds than Lippson (1975), but in a lower percent of samples (42 vs. 72%) (Fig. 3, top). When we only consider sites where crayfish were collected, we found *F. propinquus* in 58% of samples, which still represents a 14% decrease from Lippson (1975). The second most common native species found in this survey was *F. virilis*, found in 43 watersheds and 20% of all samples, and 27% of samples that contained crayfish. This represents a substantial increase in occurrence compared to Lippson (1975), who only found *F. virilis* in 33 watersheds, but an identical percent of samples (27%) (Fig. 3, middle). *C. robustus* was found in 17 watersheds, and 5.8% of all samples and 8% of samples that contained crayfish, making it the least common obligate aquatic crayfish species in Michigan (Fig. 3, bottom). We found *C. robustus* in five more watersheds compared to Lippson (1975), who found this species in 6.4% of samples. We found *F. immunis* in 18 watersheds and 4.9% of all samples, and 6.8% of samples containing crayfish. Lippson (1975) found *F. immunis* in eight fewer watersheds, but a similar percent of samples (5.5%) (Fig. 4, top). *P. acutus* was found in three watersheds and < 1% of samples, making it the least common crayfish in Michigan, limited to a few southern watersheds (Fig. 4, bottom). Lippson (1975) did not find *P. acutus* in any samples. The *diogenes* complex was found in 23 watersheds and 5.4% of all samples, and 7.4% of samples containing crayfish. Lippson (1975) only found *C. diogenes* in 3.4% of samples, and in 15 fewer watersheds than the present study (Fig. 5, top). *C. fodiens* was found in nine watersheds and 1.3% of all samples, and in 1.8% of samples containing crayfish. *C. fodiens* was also rare in Lippson (1975), and was only found in 1.5% of samples, although we found this species in six more watersheds (Fig. 5, bottom).

Although we found all crayfish species in more watersheds compared to Lippson (1975), we could not detect all species in locations where they were found historically. In terms of facultative burrowing crayfish, we were unable to detect the *diogenes* complex in one watershed that it was reported in 1975, *C. fodiens* was

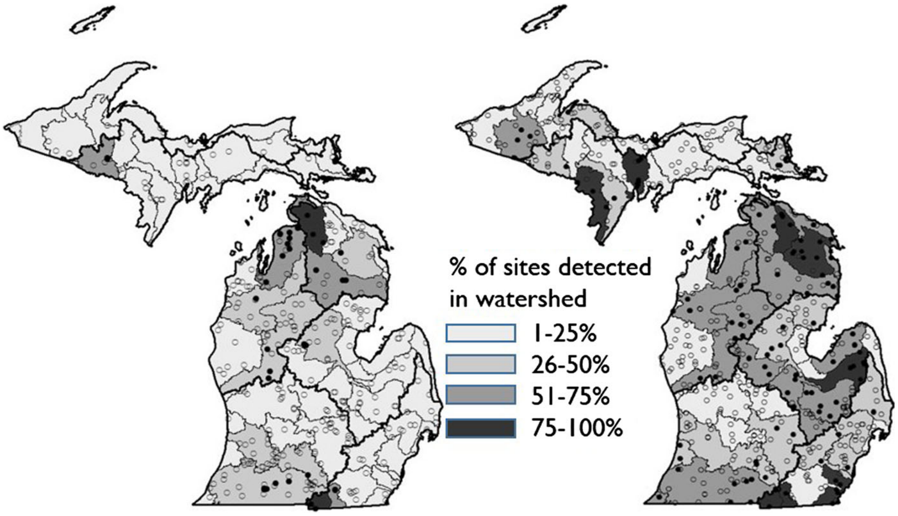
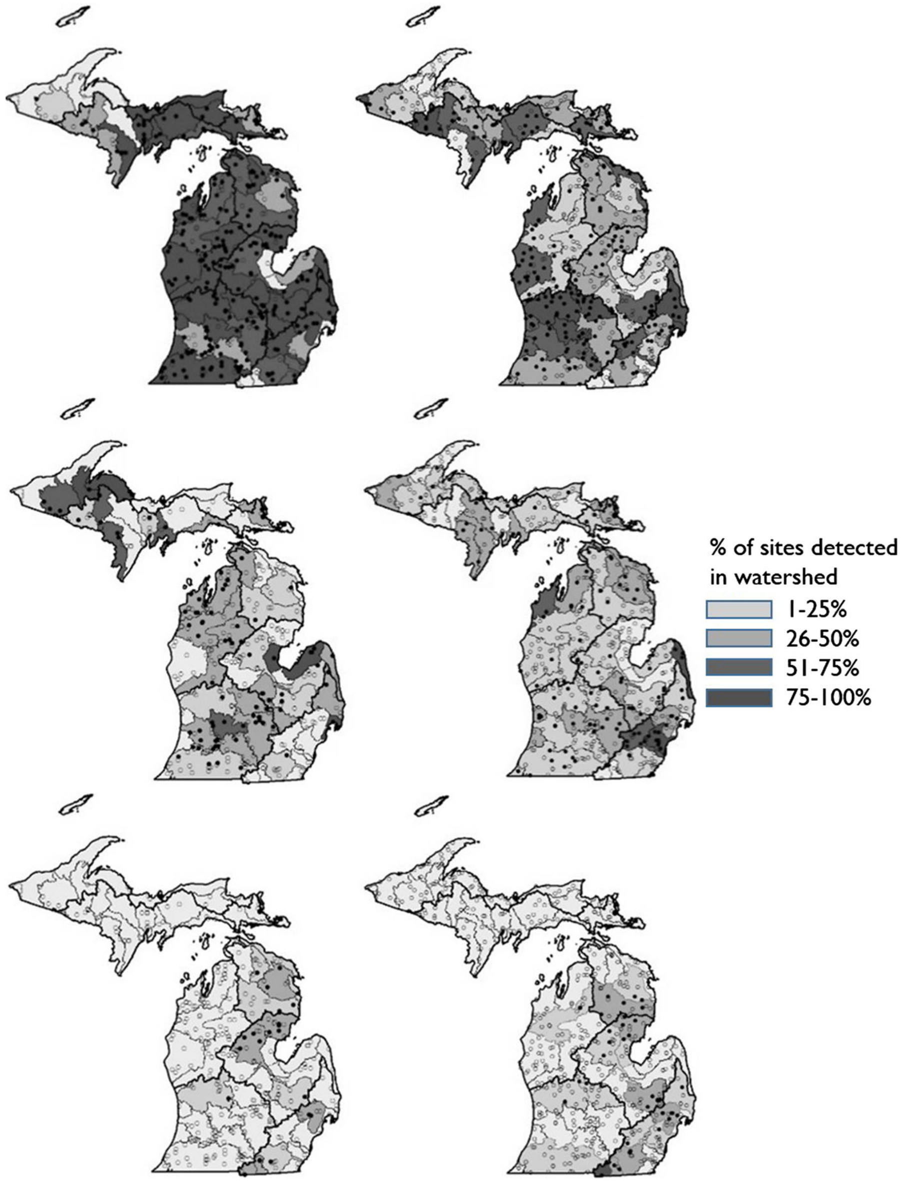


Fig. 2 Distribution of rusty crayfish in 1975 (L) and 2014–2016 (R). Closed circles indicate where *F. rusticus* was found, open circles denote locations where *F. rusticus* was not detected

Fig. 3 Distribution maps of obligate aquatic species, *F. propinquus* (top), *F. virilis* (middle), and *C. robustus* (bottom) from Lippson (1975) (left) and 2014–2016 (right). Closed circles indicate where specimens were found, open circles denote locations where specimens were not detected



not detected in one watershed it was detected in 1975, and *F. immunis* was not detected in four watersheds where it was detected in 1975. For the obligate stream species, we did not detect *C. robustus* in two watersheds that Lippson (1975) did, *F. propinquus* was not detected in three watersheds it was formerly detected in 1975, and *F. virilis* was not detected in six watersheds that it was detected in 1975.

The co-occurrence between obligate aquatic species and *F. rusticus* did not substantially change from Lippson (1975), except for the reduced occurrence of *F. propinquus* in areas occupied by *F. rusticus* (Table 3). We found *F. propinquus* co-occurring with *F. rusticus* in 23% of samples, which represents a substantial decrease from Lippson (1975) who found *F. propinquus* in 43% of samples that contained *F. rusticus*. In contrast *F. virilis* was found in 16% of samples that contained *F. rusticus* in 1975, and 15% of samples in 2014–2016. *C. robustus* was found in 8% of samples that contained *F. rusticus* in 1975 and 10% of samples in 2014–2016. We also found similar co-occurrences of *C. robustus* with other species across studies. *F. propinquus* was present in 62% of *C. robustus* samples in both 1975 and 2014–2016. *F.*

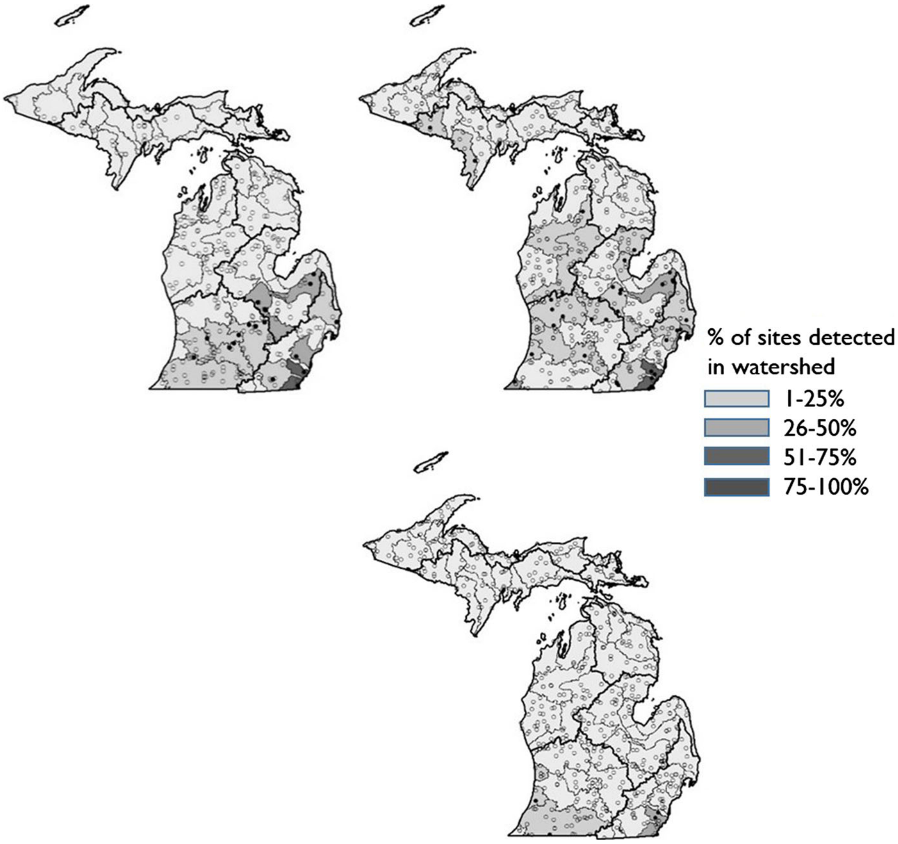


Fig. 4 Distribution map of facultative burrowing species *F. immunis* (top) and *P. acutus* (bottom). Data for *F. immunis* is present from Lippson (1975) (left) and 2014–2016 (right), whereas no *P. acutus* were found in Lippson (1975). Closed circles indicate where specimens were found, open circles denote locations where specimens were not detected

rusticus was in 12% of *C. robustus* samples in 1975, and 16% of samples in 2014–2016. *F. virilis* was in 12% of *C. robustus* samples in 1975, and 18% of samples in 2014–2016. At sites where *F. propinquus* was found, it co-occurred with *F. rusticus* in 6% of samples in 1975 and 9% in 2014–2016. *F. virilis* occurred in 20% of samples in both 1975 and 2014–2016. *C. robustus* occurred in 6% of samples in 1975, and 9% of samples in 2014–2016.

Habitat Associations

Model selection results for the substrate covariates and their effect on species presence were successfully calculated for all species except for *P. acutus* due to small sample size (Table 4). The best model for the burrowing species *C. fodiens* only contained detritus, but this species was strongly positively associated with this substrate (log odds ratio = 0.75, $z = 3.83$, $p < 0.0001$; Table 4). The *C. diogenes* complex was also positively associated with detritus (log odds ratio = 0.46, z = 3.56, $p = 0.0004$), but the best model for this species also contained boulder although this variable was not significant (log odds ratio = − 1.06, z = − 1.263, $p > 0.1$). *F. immunis*, which is known to burrow but is more often found in slow waters with live vegetation, was found to be positively associated with silt (log odds ratio = 0.33, z = 3.47, $p < 0.001$) and live vegetation (log odds ratio = 0.28, z = 2.29, $p = 0.02$), which agrees with the life history of this species (Lippson 1975; Tack 1939; Taylor et al. 2015).

Substrate associations of obligate stream dwelling species also agreed with literature descriptions of their life history, for the most part. Model selection for *C. robustus* indicated positive associations for silt, sand, pebble, cobble, boulder, and wood (all $p < 0.02$ except for boulder which was not significant) (Table 4) *F. propinquus* demonstrated strong positive associations with cobble, pebble, and sand (all $p < 0.001$), and *F. virilis* with live vegetation (log odds ratio = 0.30, z = 4.332, $p < 0.001$), detritus (log odds ratio = 0.23, z = 2.23, $p = 0.026$), and silt (log odds ratio = 0.13, z = 2.28, $p = 0.023$), which agrees with descriptions of their life history (Hobbs and Jass

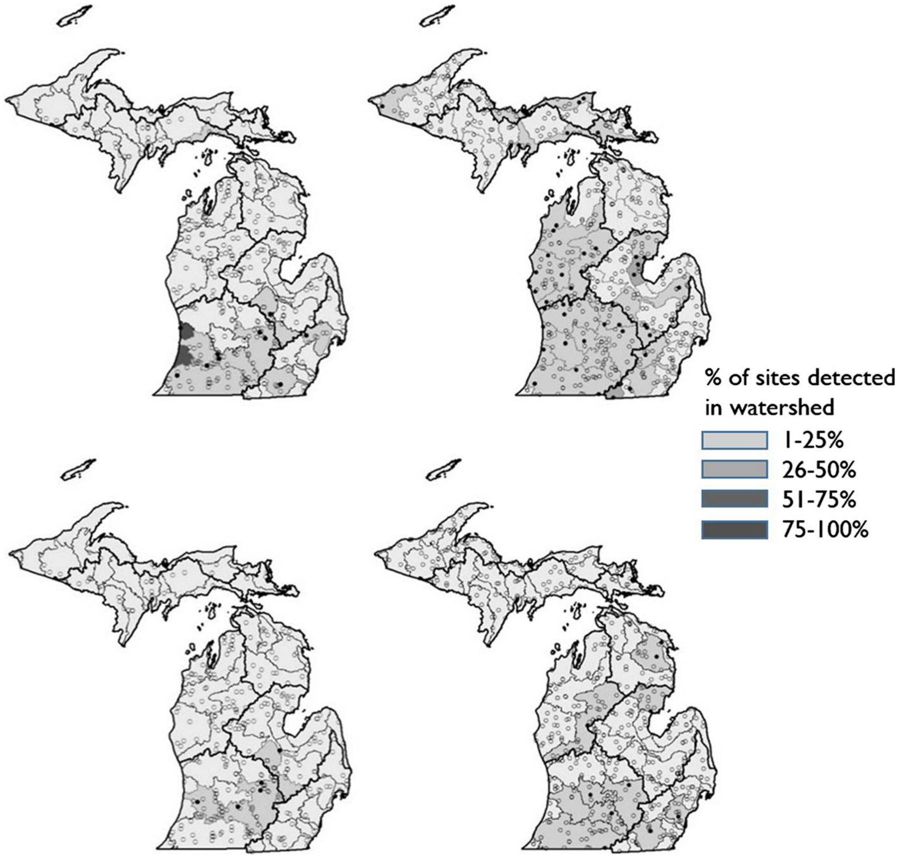


Fig. 5 Distribution maps of obligate burrowing species, *C. diogenes* (top) and *C. fodiens* (bottom) from Lippson (1975) (left) and 2014–2016 (right). Closed circles indicate where specimens were found, open circles denote locations where specimens were not detected

Table 3 Relative co-occurrence (%) of Michigan obligate stream-dwelling crayfish in samples of *C. robustus* (n = 56 for this study), *F. propinquus* (n = 405 for this study), and *F. rusticus* (n = 198 for this study) for years 1975 and 2016 and the amount of change between years

Co-occurring species	Survey species					
	C. robustus		*F. propinquus*		*F. rusticus*	
	1975	2016	1975	2016	1975	2016
C. robustus			6	9	8	10
F. propinquus	62	62			43	23
F. rusticus	12	16	6	9		
F. virilis	12	18	20	20	16	15

It should be noted that the number of samples for 1975 in unknown

1988; Lippson 1975; Taylor et al. 2007, 2015). The best model for invasive *F. rusticus* contained clay, cobble, and boulder (Table 4), although only the latter two were significant (Cobble: log odds ratio = 0.38, z = 6.67, $p \ll 0.001$; Boulder: log odds ratio = 0.35, z = 2.988, $p = 0.002$).

Evidence of the impact of rusty crayfish on native species was supported by an analysis that separated samples where *F. rusticus* co-occurred with native species from those where *F. rusticus* was absent. The analysis indicated shifts in substrate associations for some species when *F. rusticus* was present (Table 5).

Table 4 Summarized generalized linear model results showing the best model from stepwise model selection for crayfish species presence or absence based on habitat

	Log odds (SE)	Log odds (SE)	Log odds (SE)	Log odds (SE)	Log odds (SE)	Log odds (SE)	Log odds (SE)
	C. diogenes	*C. robustus*	*C. fodiens*	*F. immunis*	*F. propinquus*	*F. rusticus*	*F. virilis*
(Intercept)	− 2.99 (0.17)***	− 5.60 (0.77)***	− 4.78 (0.36)***	− 3.58 (0.25)***	− 1.00 (0.13)***	− 1.90 (0.12)***	− 1.80 (0.12)***
Clay						− 0.56 (0.47)	
Silt		0.59 (0.20)**		0.33 (0.10)***			0.13 (0.06)*
Sand		0.42 (0.17)*			0.26 (0.05)***		
Pebble		0.47 (0.18)**			0.21 (0.16)***		
Cobble		0.83 (0.17)***			0.18 (0.05)***	0.38 (0.06)***	
Boulder	− 1.06 (0.84)	0.48 (0.27)				0.35 (0.11)**	
Wood		0.94 (0.29)**					
Detritus	0.46 (0.13)***		0.75 (0.20)***				0.23 (0.10)*
Live veg.				0.28 (0.12)*			0.30 (0.07)***

Potential covariates were clay, silt, sand, pebble, cobble, boulder, wood, detritus, and live vegetation. Asterisks indicate significance at $p < 0.05$(*), < 0.01(**), < 0.001(***)

The best model for *C. robustus* presence in the absence of rusty crayfish contained a variety of substrates (silt, sand, pebble, cobble, boulder, and wood), with the first four of these significant predictors (all $p < 0.02$). However, in the presence of rusty crayfish, *C. robustus* was only positively associated with cobble and wood, with wood being the sole significant predictor (log odds ratio = 1.56, z = 2.86, $p = 0.004$). The best model for *F. immunis* in the absence of *F. rusticus* contained positive associations with clay, silt, sand, detritus, and live vegetation, with silt being the only significant predictor of *F. immunis* presence at a given site (log odds ratio = 0.49, z = 3.048, $p = 0.002$; all others $p > 0.06$) (Table 5). However, when *F. rusticus* was present, vegetation was the only positive association with *F. immunis*, and this variable was not significant (log odds ratio = 0.44, z = 1.66, $p = 0.10$). The best model for *F. immunis* in the presence of *F. rusticus* also contained negative associations with sand, pebble, and cobble, with sand being the only significant variable in the best model (log odds ratio = − 0.54, z = − 2.12, $p = 0.03$; all others $p > 0.06$). *F. propinquus* shifted from a best model with significant, positive associations with cobble, pebble, and sand (cobble: log odds ratio = 0.36, z = 5.8, $p < 0.001$; pebble: log odds ratio = 0.19, z = 2.86, $p = 0.004$; sand: log odds ratio = 0.27, z = 5.26, $p < 0.001$) in the absence of *F. rusticus* to a best model with only one significant positive association, with live vegetation, when *F. rusticus* were present (log odds ratio = 0.48, z = 2.35, $p = 0.02$). Other, non-significant habitat associations of *F. propinquus* include positive associations with clay, pebble, and detritus, and negative associations

Table 5 Comparison of generalized linear model results showing the best model from stepwise model selection for crayfish species presence or absence where habitat predictors of crayfish species presence or absence is influenced by the presence or absence of *F. rusticus*

	F. rusticus present Log odds (SE)	*F. rusticus* absent Log odds (SE)
C. robustus		
(Intercept)	− 4.33 (0.80)***	− 5.33 (0.80)***
Clay		
Silt		0.56 (0.21)**
Sand		0.39 (0.18)*
Pebble		0.42 (0.19)*
Cobble	0.45 (0.27)	0.83 (0.17)***
Boulder		0.51 (0.30)
Wood	1.56 (0.54)**	0.62 (0.37)
Detritus		
Live veg.		
F. immunis		
(Intercept)	− 1.46 (0.61)*	− 4.52 (0.61)***
Clay		0.61 (0.33)
Silt		0.49 (0.16)**
Sand	− 0.54 (0.26)*	0.25 (0.18)
Pebble	− 1.00 (0.53)	
Cobble	− 0.33 (0.21)	
Boulder		
Wood		
Detritus		0.40 (0.22)
Live veg.	0.44 (0.27)	0.30 (0.18)
F. propinquus		
(Intercept)	− 1.78 (0.33)***	− 0.90 (0.14)***
Clay	8.17 (441.3)	
Silt	− 0.40 (0.21)	
Sand		0.27 (0.05)***
Pebble	0.27 (0.16)	0.19 (0.07)**
Cobble		0.36 (0.06)***
Boulder	− 0.55 (0.44)	
Wood		
Detritus	0.52 (0.29)	
Live veg.	0.48 (0.20)*	
F. virilis		
(Intercept)	− 1.96 (0.25)***	− 1.21 (0.14)***
Clay		
Silt		
Sand		− 0.21 (2.75)**
Pebble		
Cobble		
Boulder		
Wood		
Detritus		
Live veg.	0.31 (0.21)	0.21 (0.08)**

with silt and boulder. All these variables were not significant (all $p > 0.05$), although the negative association with silt was marginally significant (log odds ratio = − 0.4, z = − 1.9, $p = 0.06$) (Table 5). *F. virilis* showed relatively little change in the presence of rusty crayfish. Without *F. rusticus*, the best model for *F. virilis* contained a negative association with sand (log odds ratio = − 0.21, z = − 3.22, $p = 0.001$) and a positive association with vegetation (log odds ratio = 0.21, z = 2.75, $p = 0.006$). The best model with *F. rusticus* only contained vegetation, although this predictor was not significant (log odds ratio = 0.31, z = 1.48, $p > 0.1$).

Discussion

The introduction and subsequent spread of non-native species, and their consequent effects on native fauna, is a central issue in the conservation of biodiversity. Research to inform the management of aquatic invasions needs to combine mechanistic, typically small-scale, studies of invasive species to understand how the invaders cause negative effects on native species, with broad-scale investigations of invasion spread and ecosystem response. The study reported here focuses on this latter component, combining an extensive survey of contemporary crayfish distributions in Michigan with observations of habitat association shifts in native crayfish species in response to the presence of an invader—the rusty crayfish. Our research complements a similarly broad-scale study in crayfish distribution changes in Wisconsin (Olden et al. 2006) and Illinois (Taylor and Redmer 1996) and adds evidence for effects of rusty crayfish on habitat use by native crayfish. Rusty crayfish have been intensively studied, and their impact on native fauna in individual systems has been well-documented, particularly in northern Wisconsin lakes (e.g. Roth et al. 2007; Wilson et al. 2004). There is some prior evidence of the effect of their geographical spread on the distribution of native crayfishes (Olden et al. 2006). Our study adds substantially to this record, and also provides evidence for a potential mechanism for these effects—namely displacement of native crayfishes into less preferred habitats. Broad-scale research of this type provides a valuable foundation for both documenting the extent of an invasion's impact on native ecosystems, and suggesting hypotheses about mechanisms giving rise to the observed patterns that can subsequently become the focus of more mechanistic investigations.

Ranges of Michigan crayfishes

Native crayfish species remain broadly distributed across Michigan, but we found evidence of an ongoing expansion of *F. rusticus* from previous surveys (Creaser 1931; Lippson 1975). The increase in *F. rusticus* range concomitant with a decrease in co-occurrence with *F. propinquus* suggests that *F. rusticus* locally displace *F. propinquus,* consistent with previous literature. *F. rusticus* are known to hybridize with *F. propinquus*, which acts to shift the genetic and phenotypic population toward characteristics exhibited by *F. rusticus* (Capelli and Munjal 1980; Perry et al. 2001b, 2002). Antagonistic interactions between native crayfishes and *F. rusticus* likely exacerbate rusty crayfish invasions (Mather and Stein 1993a, b), and give rise to habitat use shifts, as discussed below. Previous work has shown that *F. rusticus* outcompete both *F. propinquus* and *F. virilis* for habitat, while exhibiting lower susceptibility to native predators (Bergman and Moore 2003a, b; Capelli and Munjal 1982; DiDonato and Lodge 1993; Garvey et al. 2003; Hill and Lodge 1994; Roth and Kitchell 2005). Our findings are consistent with these studies given the shift in *F. propinquus* associations away from preferred cobble and woody debris toward vegetation. The exclusion of *F. propinquus* from preferred habitat could make them more susceptible to predation, or place them in suboptimal habitat for growth. However, more research must be conducted to quantify predation on *Faxonius* crayfishes in stream habitats and the role of predation in species displacement, as previous studies were conducted in lakes (e.g. DiDonato and Lodge 1993; Garvey et al. 2003; Roth and Kitchell 2005).

Differences in watershed-level species presence–absence between our survey and Lippson's earlier survey may have arisen for multiple reasons. First, our sampling effort, at least in terms of the number of sites where crayfish were captured, was substantially greater than Lippson's (694 vs. 326). Second, either survey could have failed to detect a species in a watershed where they were actually present, particularly if the habitat preferred by a species was not observed at the sites where samples were collected, but was in fact present in the watershed. Third, in-stream biochemical and habitat conditions have likely changed in some watersheds over the past 40 years, so that our sampling detected actual changes in species ranges due to habitat change. Finally, as noted above the distributions of some native species may have changed as a consequence of the increased range of *F. rusticus*. The relative importance of these factors in explaining observed changes in native species distributions will require further study.

Habitat associations of Michigan crayfishes

Previous studies indicate that *F. virilis* adults (in isolation) prefer rocky substrates, and macrophyte beds are important nursery habitat for young (Crocker and Barr 1968; France 1985; Momot and Gowing 1983). Although *F. virilis* is often considered a habitat generalist, it is vulnerable to exclusion from preferred habitat types as a result of competition, particularly with congeners *F. propinquus* and *F. rusticus* (Hobbs and Jass 1988; Lippson 1975; Peck 1985; Taylor et al. 2015). In this study, *F. virilis* demonstrated an affinity for cobble and a negative association with sand in the absence of both *F. propinquus* and *F. rusticus*. However, in areas where *F. virilis* co-occur with either *F. propinquus* or *F. rusticus* we observed that *F. virilis* was positively associated with vegetation and silt, and was no longer associated with cobble (Table 6). Further community change could arise if *F. rusticus* has a negative effect on macrophyte beds, thus eliminating the remaining refuge for *F. virilis* and *F. propinquus* (Lodge and Lorman 1987; Roth et al. 2007). Prior to *F. rusticus* invasion, *F. propinquus* and

Table 6 GLM output for substrate co-variate effect on *F. virilis* presence when *F. propinquus* and *F. rusticus* were absent compared to when either *F. propinquus* or *F. rusticus* were present in samples

	FR and FP absent	FR and FP present
(Intercept)	− 1.46 (0.30)***	− 1.89 (0.15)***
Clay		
Silt		0.15 (0.09)*
Sand	− 0.29 (0.11)**	
Pebble		
Cobble	0.31 (0.12)**	
Boulder	− 0.73 (0.45)	
Wood	0.58 (0.31)	
Detritus	0.22 (0.13)	
Live veg.	0.22 (0.11)	0.34 (0.10)***

F. virilis likely lived in preferred habitat in the absence of the other, with *F. virilis* persisting in vegetative habitat when the two co-occurred (Garvey et al. 2003; Hill and Lodge 1994; Peck 1985). This still appears to be the case in many locations. However, when *F. rusticus* excludes *F. propinquus* from cobble, areas where the three species overlap could result in the eventual removal of *F. virilis*.

C. robustus appeared largely unaffected by *F. rusticus* despite preferring large coarse substrates. This finding is consistent with Berrill (1978), suggesting that unknown differences in behavior or ecological roles might allow *C. robustus* to co-occur with *F. rusticus* and other members of *Faxonius* spp. This result is echoed by Reid and Nocera (2015), which indicate that *C. robustus* may occupy a unique niche compared to *Faxonius* species. However, a report by Daniels (1998) suggests that *F. rusticus* might be displacing *C. robustus* in an Ontario watershed. Our data suggests that since 1975 the cohabitation of *C. robustus* and the other obligate aquatic species, including *F. rusticus*, is stable. This further suggests that there are determinants that influence the coexistence between *C. robustus* and *Faxonius* spp. other than substrate. Berrill et al. (1985) indicate that low pH conditions could be favorable to *C. robustus*, but the vast majority of rivers in Michigan have pH levels > 7.0 (https://waterdata.usgs.gov/mi/), which is above the threshold of 5.5 described in Berrill et al. (1985).

We did not observe any negative effects of *F. rusticus* on native burrowing species. Generally, burrowing species tended to prefer silt or detritus substrates, which *F. rusticus* did not prefer in our study. The lack of influence of *F. rusticus* on the presence of these species is likely due in part to their differing life histories. The ability of burrowing species to occupy temporary water bodies and construct semi-terrestrial burrows likely excludes them from much of the shelter competition faced by obligate aquatic species. However, there is a void in literature relating to the relationships between these species and *F. rusticus*.

Detectability

Exclusively sampling streams likely resulted in the under-reporting of Michigan's burrowing crayfish despite their need to enter water during the spring to release young into the water (Hobbs and Jass 1988; Lippson 1975). Although we observed burrowing species in more watersheds than Lippson (1975), caution should be used when interpreting this result as a range expansion due to our lack of understanding regarding the specific methods used to capture burrowing crayfish in Lippson (1975). Lippson (1975) indicates that he used a variety of methods including dipnets, seines, burrow excavation, and baited traps, but he was unspecific about which method was used to capture individual specimens or species. The current conservation status of burrowing crayfish in Michigan, and in many other locales, is unknown (Taylor et al. 2007). We suggest conducting further surveys aimed at more accurately depicting the range, habitat associations, and status of burrowing species to gain a fuller understanding of burrowing crayfish populations in the state. Surveys could include ephemeral waterbodies, wet meadows, roadside ditches, burrows near streams and ponds, and any other wetlands. Little is known on the status of burrowing species in the state and no extensive work has been done since *C. polychromatus* was described, separating it as a species apart from *C. diogenes* (Thoma et al. 2005). An evaluation of burrowing crayfish is particularly relevant given the recent detection of red swamp crayfish (*P. clarkii*) in multiple locations in Michigan (Smith et al. in press). All discoveries were in the southern portion of the state in lentic waterbodies (lakes or retention ponds) that were not the focus of the study. However, the discovery of this highly invasive species is concerning not only for the conservation of burrowing crayfish, but for all crayfish species and aquatic food webs as a whole.

Overall our methods of dip netting appear to have sufficiently sampled streams for obligate aquatic species of crayfish. Dip netting allowed us to sample all substrate types within flows typical of wading streams. Dip netting also removed the possibility of sample bias related to habitat preferences and sex-specific behavior (Hill and Lodge 1994; Olden et al. 2006; Price and Welch 2009; Smily and Dibble 2000) Passive methods of capture, such as trapping, results in a bias toward males of more aggressive species and might result in different catch rates in different waterbodies based on predator densities (Collins et al. 1983; Dorn et al. 2005). Other studies have stated detection probabilities upwards to 88% for throw traps (Dorn et al. 2005), 68% for electroshocking, 38% for trapping, and dip netting as low as 32% (for one half hour) (Price and Welch 2009). Our detectability model showed that dip netting appeared to be an effective method of detecting crayfish in a stream. For obligate aquatic species, spatial or temporal detectability was never below 60%, which is substantially higher than the other studies.

Conclusion

This study presents evidence that rusty crayfish have continued to expand their distribution in the state Michigan since the last comprehensive survey more than 40 years ago, based on a systematic and representative survey of catchments throughout the state. We also found that habitat selection by the two most widespread native species, *F. propinquus* and *F. virilis*, shifts when the invasive *F. rusticus* is present, suggesting a mechanism for biogeographic effects of this invader on native crayfishes. Our study provides a model for broad-scale investigations of the spread and effects of an aquatic invasive species, and helps to guide more intensive, mechanistic investigations into the causes of invasive species impacts on native species, ideally leading to advice on strategies for mitigating the negative effects of invaders.

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Appendix

See Table 7.

Table 7 Crayfish occurrence by HUC8 watershed (n = 55)

HUC8	Watershed	*L. diogenes*		*C. robustus*		*F. fodiens*		*F. immunis*		*F. propinquus*		*F. rusticus*		*F. virilis*		*P. acutus*	
		1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016
	Sum	8	23	12	17	3	9	10	18	45	48	12	34	33	43	0	3
4080101	Au Gres-Rifle		x	x	x		x		x	x	x		x				
4070007	Au Sable			x	x					x	x	x	x	x	x		
4010302	Bad-Montreal										x						
4060104	Betsie-Platte		x							x	x			x	x		
4020201	Betsy-Chocolay		x							x	x				x		
4080104	Birch-Willow									x	x			x	x		
4070005	Black			x						x	x		x		x		
4050002	Black-Macatawa	x	x						x	x	x		x		x		x
4020101	Black-Presque Isle		x								x				x		
4060105	Boardman-Charlevoix									x	x	x	x	x	x		
4060107	Brevoort-Millecoquins	x	x							x	x			x	x		
4030106	Brule								x	x	x	x	x	x			
4070002	Carp-Pine		x							x	x				x		
4080205	Cass		x					x	x	x			x	x			
4030109	Cedar-Ford									x	x		x		x		
4070004	Cheboygan									x	x	x	x	x	x		
4090003	Clinton	x		x	x				x	x	x		x		x		
4020105	Dead-Kelsey										x		x	x	x		
4090004	Detroit				x		x	x		x	x		x		x		
4030110	Escanaba										x				x		
4030112	Fishdam-Sturgeon		x							x	x			x	x		
4080204	Flint			x	x					x	x		x	x	x		
4090005	Huron		x		x					x	x		x		x		
4050003	Kalamazoo	x	x			x	x	x	x	x	x	x	x	x	x		
4080102	Kawkawlin-Pine		x		x				x		x			x			
4020103	Keweenaw Peninsula																
4090002	Lake St. Clair								x		x			x			
4040001	Little Calumet-Galien								x	x	x		x		x		
4070003	Lone Lake-Ocqueoc			x						x	x		x		x		
4050006	Lower Grand		x	x	x				x	x	x			x	x		

Table 7 continued

HUC8	Watershed	*L. diogenes*		*C. robustus*		*F. fodiens*		*F. immunis*		*F. propinquus*		*F. rusticus*		*F. virilis*		*P. acutus*	
		1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016
4060103	Manistee		x		x				x	x	x	x	x	x	x		
4060106	Manistique									x	x				x		
4050005	Maple		x		x				x	x	x			x	x		
4030108	Menominee								x	x			x	x	x		
4030107	Michigamme									x	x			x			
4060102	Muskegon		x				x		x	x	x	x	x	x	x		
4020102	Ontonagon									x	x		x	x	x		
4100001	Ottawa-Stony							x	x	x			x		x		x
4060101	Pere Marquette-White		x							x	x				x		
4080103	Pigeon-Wiscoggin									x	x		x	x	x		
4080202	Pine									x	x		x		x		
4100002	Raisin	x	x	x	x		x	x	x	x	x			x	x		
4080203	Shiawassee	x	x			x		x	x	x	x		x	x	x		
4090001	St. Clair				x			x	x	x	x		x	x	x		
4050001	St. Joseph 1	x	x		x		x	x		x	x	x	x	x	x		x
4100003	St. Joseph		x	x	x							x	x				
4070001	St. Marys									x	x		x	x	x		
4020104	Sturgeon													x	x		
4030111	Tacoosh-Whitefish									x	x		x	x			
4020202	Tahquamenon									x	x						
4050007	Thornapple		x				x	x		x	x			x	x		
4070006	Thunder Bay			x	x		x			x	x	x	x	x	x		
4100006	Tiffin			x	x							x	x				
4080201	Tittabawassee			x	x					x	x	x	x	x	x		
4050004	Upper Grand	x	x			x	x	x		x	x		x	x	x		

A comparison of occurrences reported in a 1975 survey and findings during 2014–2016 field sampling

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