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Research Article

An analysis of suspected crayfish invasions in Missouri, U.S.A.: evidence for the prevalence of short-range translocations and support for expanded survey efforts

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Abstract

Reports of alien crayfish invasions are increasingly common and often associated with well-documented ecological effects including native crayfish biodiversity declines. Because most regions in the U.S. and Canada have not been surveyed to detect the presence and gauge the threat status of such invasions, management agencies lack information on the magnitude of problems in their respective jurisdictions. Our objectives were to catalog, confirm and summarize suspected crayfish invasions that were reported in one U.S. state in recent years. Data were also examined for potential spatial patterns, prevalence of certain species as invaders and effects to native crayfishes. We collected reports of crayfish introductions/invasions from 1998–2014, and attempted to confirm them via sampling. We catalogued 34 reports and confirmed 31 as suspected invasions involving 6 invading species. *Procambarus acutus* was easily the most frequent invader, and all invading species were native to at least part of Missouri. Most suspected invasions involved species that were legal for commercial sale in the state, but many also involved non-commercial species that are described as "narrow-range endemics." Invading species were abundant, dominating crayfish communities, at several sites. Native species have apparently declined or been displaced at several locations. Our results suggest the potential for many unreported crayfish invasions in the U.S. and Canada, including those caused by shorter-range (e.g., intrastate) translocations. Ecoregions featuring high crayfish diversity could be threatened with significant declines of native species with narrow ranges. Increased survey efforts in these regions are warranted to estimate threat levels and provide agencies with information to support management actions.

Key words: invasive crayfish, crayfish introductions, *Procambarus acutus*

Introduction

Alien crayfish invasions have adversely affected biodiversity and ecosystem services worldwide (Lodge et al. 2012; Twardochleb et al. 2013). In North America, such invasions have adversely affected plant (Feminella and Resh 1989; Olsen et al. 1991; Lodge et al. 1994) and animal communities (Charlebois and Lamberti 1996; Gamradt et al. 1997; Bobeldyk and Lamberti 2008; Klose and Cooper 2012), altered food webs (McCarthy et al. 2006; Bobeldyk and Lamberti 2010; Nilsson et al. 2012) and ecological function (Charlebois and Lamberti 1996; McCarthy et al. 2006), impacted fisheries (Wilson et al. 2004; Roth et al. 2007) and local economies (Keller et al. 2008), and resulted in a net loss of ecosystem services in receiving systems (Lodge et al. 2012). Crayfishes also carry many parasites and pathogens, but their impact on U.S. and Canadian systems are largely unknown (Longshaw 2011). Conservationists consider alien crayfish invasions to be among the most serious threats to native crayfish diversity in the U.S. and Canada (Lodge et al. 2000; Taylor et al. 2007; DiStefano et al. 2009; Twardochleb and Olden 2013).

Despite the well-documented importance of crayfish to U.S. and Canadian biodiversity (Taylor et al. 2007) and ecosystems (Momot et al. 1978; Momot 1995; Reynolds et al. 2013) most states, provinces or ecoregions have not been systematically surveyed to catalog native crayfish faunas, with a few exceptions (e.g., Pflieger 1996; Taylor and Schuster 2004; Kilian et al. 2010).

Similarly, despite that humans have largely altered the global distribution patterns of crayfishes (Lodge et al. 2012) and the abundance of well-documented ecological problems caused by crayfish invasions, few larger-scale (e.g., regional, statewide) systematic surveys have focused attention on invasive crayfish (e.g., Olden et al. 2006; Larson and Olden 2011). Many such invasions remain undocumented (Lodge et al. 2012), especially in ecoregions or states of high or even moderate crayfish diversity and endemism (e.g., Tennessee, Lower Mississippi, Ohio, Mobile Bay, South Atlantic, Ouachita Highlands, Cumberland, Ozark Highlands, Florida; Abell et al. 2008). Rather, most reports of crayfish invasions are generated 1) from more narrowly-focused stream- or drainage-scale surveys (e.g., Daniels 1980; Martinez 2012; Imhoff et al. 2012), 2) incidentally during ecological studies on smaller geographical scales (e.g., Mueller 2001; Westhoff et al. 2006), or 3) during haphazard or non-systematic collections as reported anecdotally or from museum collections (e.g., Riegel 1959; Bouchard 1977; Crocker 1979), with a few intra-state regional-scale surveys (e.g., Simmons and Fraley 2010; Lieb et al. 2011a; Lieb et al. 2011b). It is important to understand the prevalence of crayfish invasions, particularly in these species rich locations, because native crayfish endemism and narrow natural ranges make these places more prone to suffering species extirpations.

The state of Missouri is somewhat unique in that it developed a statewide crayfish distribution database initially driven by a statewide survey. The survey (Pflieger 1996) included 1,845 collections at 810 sites sampled in the 1970s through early 1990s, catalogued and reported the state's crayfish fauna and determined crayfish species' distributions and general ranges for the 45 U.S. Geological Survey's 8-digit Hydrologic Unit drainages found wholly or partially within the state. The larger statewide database included all of the data generated by Pflieger (1996) but also many more crayfish samples, for a total of 3,055 collections at 1,203 sites (Missouri Department of Conservation [MDC] 2015a) prior to the initiation of data collection for the current study (before 1998). Missouri biologists recognized that the Pflieger (1996) survey was not completely systematic, probably did not detect all species in all drainages, and it did not precede all suspected crayfish invasions. However, when paired with the remainder of the samples in the statewide database it serves Missouri biologists well by providing a reasonably reliable "baseline" database with which to compare subsequent survey and sampling data. Pflieger sampled enough locations in each of the major stream drainages (e.g., Big River drainage = 72 collections at 21 sites, Black River drainage = 81 at 36, Current River drainage = 154 at 55, Eleven Point River drainage = 52 at 17, James River drainage = 56 at 16, St. Francis River drainage = 291 at 110), except the Fabius River drainage (4 at 3), that state biologists feel comfortable that he sufficiently catalogued the native fauna in each. In comparison, there are probably only two other U.S. states or Canadian provinces which have comparable baseline databases (Kentucky [Taylor and Schuster 2004], Maryland [Kilian et al. 2010]) that were developed significantly later. Pflieger (1996) noted a few apparent or suspected crayfish invasions based upon disjointed or illogical distribution patterns. However, in 1998, we began receiving occasional reports of possible crayfish introductions or invasions from MDC field staff, biologists from other natural resources agencies, universities or the general public. We made efforts to investigate and confirm or refute such reports. As the number of reports increased, we proposed to MDC to conduct a statewide survey for alien crayfish introductions and invasions, but that proposal was rejected. Alternatively, we continued and increased our efforts to investigate all reports of alien crayfish in Missouri.

Our primary objective was to catalog, summarize and report one U.S. state's alien crayfish potential introductions and invasions that have been reported and investigated over a 17-year period (1998–2014). Further, we wished to examine these data associated with likely introductions and invasions for 1) obvious patterns in terms of spatial occurrence that could provide our state with information on the severity of the problem and causative pathways or sources, and 2) potential obvious ecological effects to receiving systems in the form of changes to native crayfish communities. We hoped that this effort might elucidate management options for our state and other jurisdictions, particularly those with significant native crayfish diversity and/or endemism.

Methods

For the purposes of this paper we followed definitions presented by Occhipinti-Ambrogi and Galil (2004) and defined an "alien" as a crayfish species "occurring outside of its known or consensual range (as documented in scientific publications)", and defined an "invasive" as an alien species that has established and expanded

in its new location (what some might term "established"; Williamson and Fitter 1996). Our definition of "invasive" did not necessarily require documentation of ecological harm, although we could argue that most if not all of what we termed suspected invasions have caused or are "likely to cause environmental harm" as stated in the U.S. National Invasive Species Council (2008) definition.

We began collecting crayfish introduction/ invasion reports in 1998 when a distribution survey for two imperiled native crayfish species inadvertently detected evidence of an alien *Orconectes hylas* ((Faxon, 1890), common name = Woodland Crayfish) invasion with suspected multiple introduction locations (Riggert et al. 1999). Exceptions to this beginning time frame were three invasions (beginning in 1984) reported by Pflieger (1996) in his initial statewide survey of Missouri crayfishes. Reports not generated by the authors typically came by telephone or e-mail to the MDC Resource Science Center (Columbia, Missouri). They were generated from multiple sources with varying levels of perceived credibility, including other MDC systematic crayfish distribution surveys, biological field sampling, graduate students and naturalists from other agencies and universities, MDC field management biologists and a photographer, and private citizens.

Crayfish introduction/invasion reports were usually accompanied by either photographs or preserved specimens of the suspected introduced crayfish species. We attempted to identify photographed specimens or preserved female specimens (with varied success) to species. Male specimens were identified to species using dichotomous keys (Hobbs Jr. 1972; Pflieger 1996). All identified specimens were delivered to the Illinois Natural History Survey Crustacean Collection (Champaign, Illinois) for verification by Dr. C. A. Taylor, and subsequent deposition in that institution's museum. This is also where all voucher specimens from the Pflieger (1996) survey are stored.

When we identified crayfishes that had never previously been known from specific water bodies or drainages that had been repeatedly sampled (Pfleiger 1996; Missouri Department of Conservation 2015a) we were alerted to the possibility of an alien crayfish introduction. In those instances and also when no specimens were provided to us by reporters, we visited reported sites and made a reasonable sampling effort to 1) confirm the presence of a suspected alien crayfish species, 2) determine whether the suspected alien species was abundant, and 3) determine the status of presumed native crayfish species at the site (i.e., presence, relative abundance). Most (about 68%) of the sites for the 34 reported introductions/invasions (Table 1, Appendix 1) were visited a year or more after the initial report was filed, so that the confirmation of continued presence of a suspected alien species suggested that the species had become established (see Appendix 1). At the remaining sites (29%) where confirmation visits took place less than one year after the initial report was filed, either the abundance of the suspected alien species was so high or the fact that it was collected at multiple reaches along the stream (or multiple locations along a lentic water body) led us to a conclusion that it had become established. There was only one report that we did not investigate via a sampling visit because it was filed by a biologist from another state agency who was experienced in crayfish sampling and identification (i.e., a credible source), and voucher specimens were provided to us.

Reported introduction/invasion sites consisted of various types of water bodies (e.g., streams, rivers, large reservoirs, small ponds, wetlands, sloughs/ditches) but most were wadeable streams or small rivers. Crayfish sampling was qualitative, and the method varied depending upon the water body type. Kick seines were used in wadeable streams and rivers, sometimes supplemented with hand capture. We typically obtained 15 – 20 seine hauls, and depending upon crew size, seining required about 1–2 hours (about 2–4 person/hours). We used primarily traps baited with canned, liver-flavored dog food (Litvan et al. 2010) in lentic waters and larger rivers, sometimes supplemented with seining. Trapping effort ranged from 30 – 160 trap nights (trap night = one trap set for one night). Captured crayfish were identified to species and sex. We also recorded detailed information about the sampling sites and obtained GPS coordinates. We determined that a suspected alien crayfish invasion had occurred if the alien species was abundant enough to convince us that we had not simply captured a few individuals that had been recently directly introduced (multiple specimens collected in several seine hauls or multiple traps or constituting a large portion of the crayfish community), especially relative to abundance of other species collected.

Reported introductions/invasions and results of visits to those sites were recorded in a series of internal Agency reports (available upon request from primary author) if they were not already

Table 1. Reported Missouri alien crayfish introductions/invasions 1984 – 2014. "Water body" column notes; CA = state conservation area, NWR = National Wildlife Refuge. [a]"Alien species" column represents the alien species confirmed to be present at each site. Reporter affiliations (MDC = Missouri Department of Conservation, MDNRB = Missouri Department of Natural Resources stream biomonitoring biologists, MDNRN = Missouri Department of Natural Resources Naturalist, USNPS = U. S. National Park Service aquatic biologist, GS = Graduate students working in cooperation with MDC, MSU = Missouri State University biology professor, UA = University of Arkansas biology professor, PC = Private citizen). "Community status" column represents the status of the crayfish community at each site after the introduction/invasion. Supporting data and detailed explanations found in Appendix 1.

Water body	[a]Alien species	Initial report date	Reporter affiliation	[b]Community status
1. Stouts Creek	HY	1984	MDC (Pflieger[c])	ND, AD
2. St. Francis River	HA	1987	MDC (Pflieger[c])	AN, AA
3. Cedar Creek	VI	1992	MDC (Pflieger[c])	AN, AA
4. Carver Creek	HY	1998	MDC (Riggert, DiStefano)	ND, AD
5. Big Creek	HY	1998	MDC (Riggert, DiStefano)	ND, AD
6. Spring River and tributaries	NEC	1998	UA/MDC (Magoulick, DiStefano)	ND, AD
7. South Fork Spring River	AC	2001	UA (Magoulick)	ND
8. Marble/Orr Hollow Creek	HY	2001	MDC (DiStefano)	ND, AD
9. Fassnight Creek	LU	2002	MDC (Westhoff, Guyot, DiStefano)	AN, AA
10. James River	LU	2002	MDC (Westhoff, Guyot, DiStefano)	AN
11. South Creek	LU	2003	MDC (Westhoff, Guyot, DiStefano)	AN, AD
12. Lake Springfield (James River)	AC	2003	MSU (B. Greene)	AN, AA
13. Four Rivers CA Wetlands	AC	2004	MDC (DiStefano)	AN, AA
14. Squaw Creek NWR Wetlands	AC	2006	MDC (Paothong [staff photographer])	A, AA
15. North Fork Spring River	AC	2007	MDNRB (C. Wakefield)	AN, AA
16. Little Tebo Creek	NE	2007	GS (S. Jones)	N
17. South Grand River	AC	2007	PC and GS (S. Jones)	AN, A, AA
18. Truman Reservoir	AC	2007	GS (S. Jones)	AN, AA
19. Upper St. Francis River	AC	2007	MDNRN (M. Cravens)	N
20. St. Francis River	HA	2007	GS (J. Westhoff)	AN, AA
21. Logan Creek	HA	2008	GS (J. Westhoff)	AN, AA
22. Big Lake Creek	HY	2008	MDC/GS (DiStefano, J. Westhoff)	AN, AA
23. Table Rock Reservoir	CL	2009	GS (T. Black)	N
24. Blind Pony Hatchery/Salt Pond Creek	AC	2009	MDC (Hatchery staff)	AN, AA
25. Joliff Spring Branch	NEN	2010	MDC (Imhoff, Moore, DiStefano)	AN, AD
26. Big Spring Sloughs (Current River)	AC	2011	PC (D. Swofford)	AN, AD
27. Miller Lake (Brushy Creek)	AC	2011	PC (D. Swofford)	AN
28. Current River and tributaries	VI	2011	NPS (M. Gossett)	AN, AD
29. Barber Lake (Schell-Osage wetland)	AC	2013	MDC (F. Nelson)	A, AA
30. Bridge Creek	AC	2013	GS (B. Engelbert) and MDC	AN, AA
31. Middle Fabius River	AC	2013	GS (B. Engelbert) and MDC	AN, AA
32. North River	AC	2013	GS (B. Engelbert) and MDC	AN, AA
33. Higgins Ditch	AC	2013	GS (B. Engelbert)	AN
34. Prairie Fork	AC	2014	MDC (C. Ames)	AN, AD, A

[a]Species codes: AC = *Procambarus acutus*, CL = *Procambarus clarkii*, HA = *Orconectes harrisoni*, HY = *Orconectes hylas*, LU = *Orconectes luteus*, NE = *Orconectes neglectus*, NEN = *Orconectes neglectus neglectus*, NEC = *Orconectes neglectus chaenodactylus*, VI = *Orconectes virilis*.

[b]Community status codes based on confirmation sampling results when available: N = only native species detected (alien introduction unconfirmed), A = Only the alien species was detected, AN = Alien and native species, ND = Alien and native species, but at least one native species that was previously detected (Pflieger 1996; Missouri Department of Conservation 2015a) not detected after substantial sampling, AA = Alien species abundant, AD = Alien species abundant and the dominant species in the community).

[c]Pflieger reports contained in Pflieger (1996).

included in larger reports (i.e., if the suspected introduction/invasion was detected during and included in systematic surveys or studies). All crayfish species (native and alien) occurrence and locality data were stored in the Missouri Statewide Crayfish Database (MDC 2015a). We were unable to statistically analyze for possible patterns concerning the individual invasive species we detected and their spatial distributions because the catalogued suspected invasions were generated from varied sources and in a non-systematic manner. Thus, we attempted to discern and report any obvious patterns in a descriptive manner.

Ultimately we relied upon the crayfish community data existing for sites, streams and drainages contained in the Missouri Statewide Crayfish Database (Pflieger 1996; Missouri Department of Conservation 2015a) as our "baseline" against which we compared results of our confirmation

sampling. In many instances this database did not contain previously-collected samples from the exact sites where we investigated reported introductions/invasions, but typically contained previous samples from the same streams or adjacent streams and also samples from many streams within the same 8-digit Hydrologic Unit drainage. Collection and identification of a crayfish species that had never previously been collected from a drainage (or from the same lentic water body) typically resulted in our determination of a suspected alien species. We recognized the possibility that the statewide database might have missed the presence of some species in some locations. Therefore we have used the term "suspected invasion", which is abbreviated to "invasion" hereafter in this report.

Results

Catalogued invasions

We received and catalogued reports of potential crayfish introductions/invasions at 34 locations in Missouri as of autumn 2014, and confirmed 31 total introductions/invasions (Table 1). We felt confident in classifying at least 30 of those as "invasions". We were unable to determine whether the alien *Procambarus acutus* ((Girard, 1852), White River Crawfish) had become an established invader at one location because only one specimen was collected at the site in Higgins Ditch reported in 2013 by Engelbert, but an MDC crew was present during that collection. Nevertheless, we hereafter refer to all 31 confirmed introductions/ invasions as "invasions."

Thirty-one reports and 28 of the confirmed invasions were reported in the 16 years since we began cataloging reports for an average of nearly two confirmed invasions per year. About 39% of confirmed invasions were reported by individuals from agencies or institutions other than MDC (Missouri's fish and wildlife agency), or from private citizens.

We confirmed one *Procambarus* and five *Orconectes* species as invaders (Table 1); all six were species that are native to some portion of Missouri. One additional native species (*Procambarus clarkii* (Girard, 1852), Red Swamp Crawfish) was reported (T. Black, North Carolina Wildlife Resources Commission, pers. comm.) as introduced in one location, a specimen was provided and the taxonomic identification confirmed. However, multiple confirmation samplings failed to detect any other individuals of that species. *Procambarus acutus* was the most frequent invading species we detected, constituting 52% (16 of 31) of the invasions, followed by *O. hylas* (16%), *Orconectes harrisoni* ((Faxon, 1884), Belted Crayfish, 10%), *Orconectes luteus* ((Creaser, 1933), Golden Crayfish, 10%), *Orconectes neglectus* ((Faxon, 1885), Ringed Crayfish [two subspecies] 6%) and *Orconectes virilis* ((Hagen, 1870), Virile Crayfish, 6%).

Spatial and species patterns

Missouri's confirmed crayfish invasions occurred over much of the state, but all within the Prairie and Ozark Aquatic Faunal Regions (Figure 1; Pflieger 1996; Pflieger 1997). It was difficult to delineate spatial patterns because the report data were not generated from a randomized nor spatially-systematic design. For example, there were nine invasions confirmed in the St. Francis River drainage in southeastern Missouri (Table 1, Sites 1, 2, 4, 5, 8, 19, 20, 21, 22), but detection of seven of these can be attributed to two drainage-wide crayfish surveys conducted there (Riggert et al. 1999; Westhoff 2011). All invasions featured crayfish species that were native to some part of Missouri (but had been assumed translocated beyond their historic native ranges in the state), rather than from species that were alien to the state or the continent.

Most crayfish invasions (23 of 31) occurred in lotic systems, whereas three occurred in impounded lakes or reservoirs, four in wetlands and sloughs, and one invasion occurred at a state fish hatchery (hatchery ponds) and its associated source stream. The Prairie Fork invasion (Site 34) involved both a stream and a pond, but discussions with the landowner indicated that the pond had been stocked with the alien crayfish species.

Most (61%) invasions involved one of the four crayfish species that have historically been legal for commercial sale in Missouri, including fishing bait (*P. acutus*, *O. virilis*, *O. immunis* ((Hagen, 1870), Calico Crayfish), *P. clarkii*; Missouri Department of Conservation 2015b). However, the remaining (39%) invasions involved species that have never been permitted for commercial sale and have not been observed in the bait industry (DiStefano et al. 2009). The non-bait species that have been involved in several of the invasions (29% of total invasions) could be classified as narrow-range endemics (*O. harrisoni*, *O. hylas*, *O. luteus* and *O. neglectus chaenodactylus* (Williams, 1952)). Also, each of these invasions occurred in a drainage adjacent to a drainage within the endemic

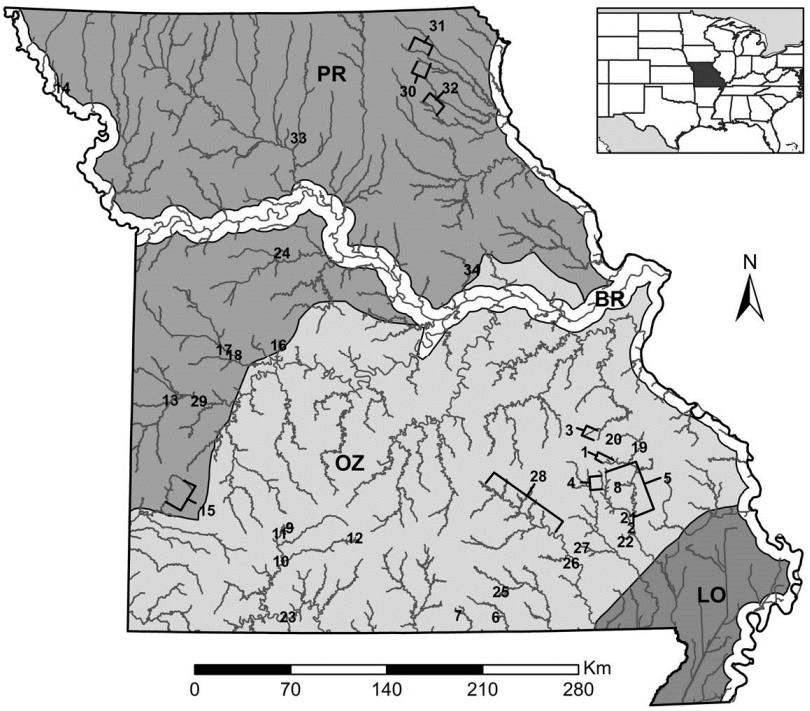

Figure 1. Map of state of Missouri (USA) illustrating numbered locations for 34 reported alien crayfish invasions. All 4th order and larger streams are shown as well as some smaller-order streams at reported invasion sites. Numbers in Figures 1 through 7 correspond to reported invasions (31 confirmed and 3 unconfirmed) identified in Table 1, and are located on UTM coordinates provided in Appendix 1. Several numbered locations represent substantial stream reaches illustrated by an attached bracket (e.g., invasion 28). The state's four recognized Faunal Regions (Pflieger 1996; Pflieger 1997) are also indicated; Prairie (PR), Ozark (OZ), Lowland (LO) and Big River (BR).

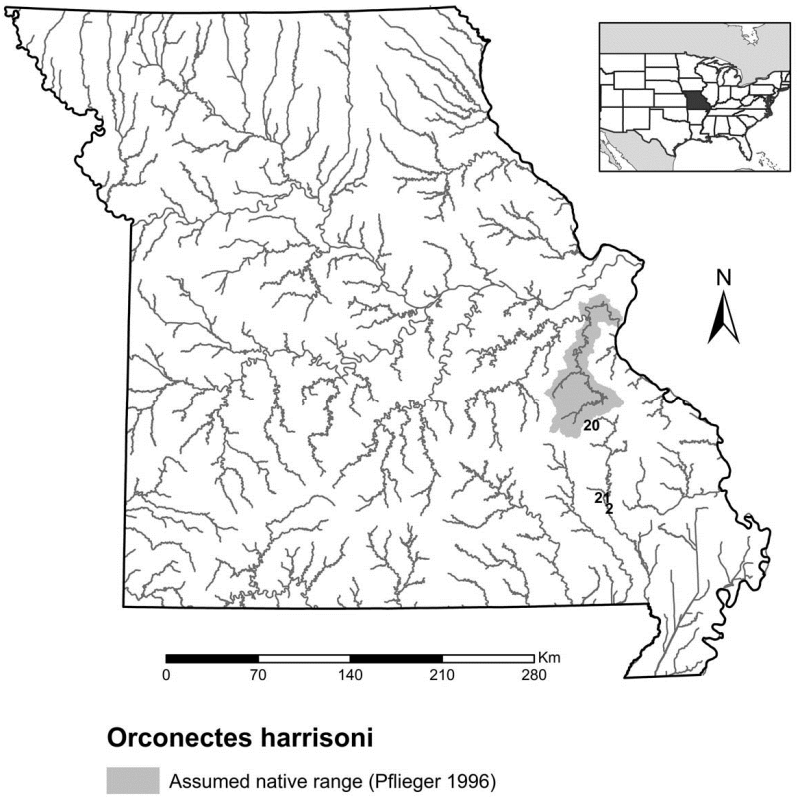

Figure 2. Map of Missouri illustrating numbered locations for confirmed alien *Orconectes harrisoni* invasions. Numbers correspond to invasions identified in Table 1, and are located on UTM coordinates provided in Appendix 1.

species' native range, and 10 of these 12 invasions were located within 30 km of the invading species' native range (Figures 2, 3, 4, 5).

All eight of the confirmed invasions that occurred in lentic water bodies featured *P. acutus* as the invader. *Procambarus acutus* also was the species detected in all of the invasions in the northern half, and in most invasions in the western portion of the state, often far from its native Missouri range (Figure 6) in the Lowland and Big River ecoregions (Figure 1). More than one half of the 16 *P. acutus* invasions were located 160 kms or more outside of their native range and six of those were 300 km or more removed.

The largest confirmed contiguous invasion was located in the U.S. National Park Service's (USNPS) Ozark National Scenic Riverways' Current River (Site 28, *O. virilis*, Figure 7). Recent confirmation sampling by the authors and USNPS staff indicated that this invasion has expanded to at least 67 km of the Current River and also into some tributaries in that reach. *Orconectes hylas* have invaded a large portion of the St. Francis River drainage (Sites 1, 4, 5, 8, and 22; Figure 3). This species has demonstrated substantial range expansion in the drainage, but multiple survey/sampling efforts and population genetic analysis strongly suggest that multiple introductions were involved (Fetzner and DiStefano 2008; DiStefano and Westhoff 2011).

Ecological observations

Crayfish communities at confirmed invaded sites were typically composed of both alien and native species (Table 1). However, the invading species was determined to be abundant and/or dominant (>50% of samples) at 87% (27 of 31) of those sites (all invasions except for Sites 7, 10, 27 and 33; Table 1), and constituted >50% of the community in substantial stream reaches (≥100 m) for at least 9 of 31 (29%) of the invasions. We noted six invasions where at least one native species that had previously been collected at that site or in an adjacent reach of that stream was not detected during confirmation sampling of substantial stream reaches; although sampling for one of these six invasions (*P. acutus* in North Fork Spring River, Site 15) failed to collect enough total crayfish to provide a representative sample. We documented three additional invasions where only the alien species was detected; again, confirmation sampling for one of these invasions (*P. acutus* in Truman Reservoir, Site 18) was not necessarily representative of the entire crayfish community. These observations suggest apparent species displacements associated with at least 7 of 31 (23%) invasions. Three of the species that were displaced are classified as "imperiled" (Missouri Natural Heritage Program 2015); *Orconectes eupunctus* ((Williams, 1952), Coldwater Crayfish), *Orconectes quadruncus* ((Creaser, 1933), St. Francis River Crayfish), *Orconectes peruncus* ((Creaser, 1931), Big Creek Crayfish). These three species are also under consideration by the U. S. Fish and Wildlife Service to determine if they warrant federal listing as "threatened" or "endangered" species.

Discussion

Prevalence of crayfish invasions

The importance of documenting crayfish invasions is underscored by the growing body of literature concerning them and their many adverse ecological effects throughout the world (e.g., Lodge et al. 2000; Larson and Olden 2011; Lodge et al. 2012; Gherardi 2013; Twardochleb et al. 2013). Native crayfish biodiversity is particularly threatened by such invasions in the U.S. and Canada (Taylor et al. 2007; Phillips et al. 2009; Hamr 2010). However, little work has been conducted in these countries to determine the prevalence of crayfish invasions in regions featuring high native crayfish diversity and endemism.

We confirmed 31 crayfish invasions in Missouri, which is likely a conservative number for several reasons. We conducted neither a systematic survey nor a directed search. Although recent comprehensive crayfish surveys have been reported from several Missouri drainages (e.g., Riggert et al. 1999; Westhoff et al. 2006; Engelbert 2013), there are many drainages in the state where comprehensive surveys have never been conducted.

Additionally, three pre-1998 collection locations for *O. virilis* and two locations for *P. acutus* noted by Pflieger (1996) were thought to have resulted from introductions (Pflieger 1996; W. L. Pfleiger, MDC, personal communication), however, we counted none of these as invasions.

We also discounted two reported possible invasions (Sites 19, 23) from credible sources because we could not confirm them through our sampling.

Our results suggest the potential for a large number of existing but unreported crayfish invasions in other geographic areas (ecoregions, states, provinces, etc.) of the U.S. and Canada where surveys have not been conducted. This appears

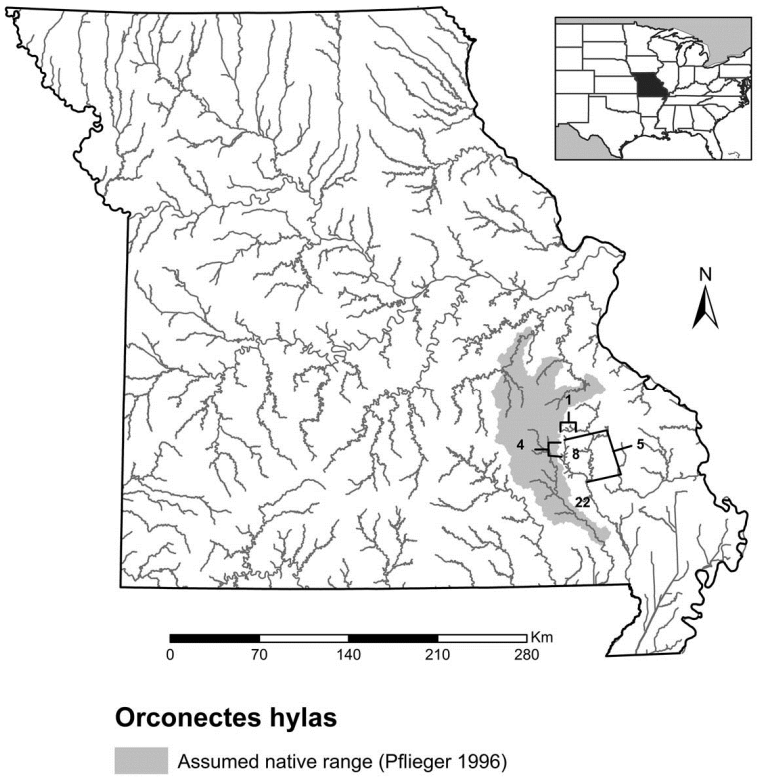

Figure 3. Map of Missouri illustrating numbered locations for confirmed alien *Orconectes hylas* invasions. Numbers correspond to invasions identified in Table 1, and are located on UTM coordinates provided in Appendix 1. Three numbered locations (1, 4, 5) represent substantial stream reaches illustrated by an attached bracket.

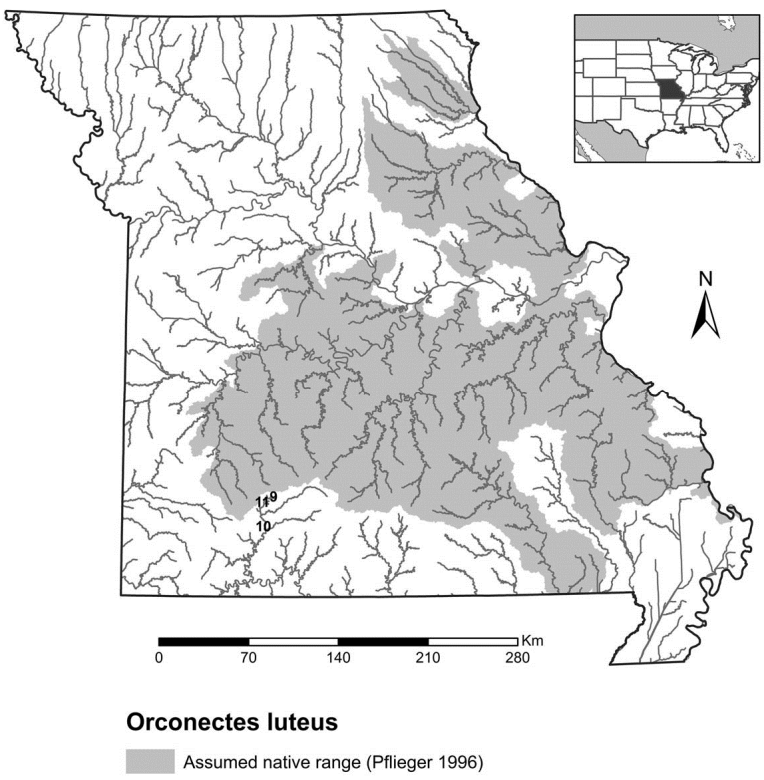

Figure 4. Map of Missouri illustrating numbered locations for confirmed alien *Orconectes luteus* invasions. Numbers correspond to invasions identified in Table 1, and are located on UTM coordinates provided in Appendix 1.

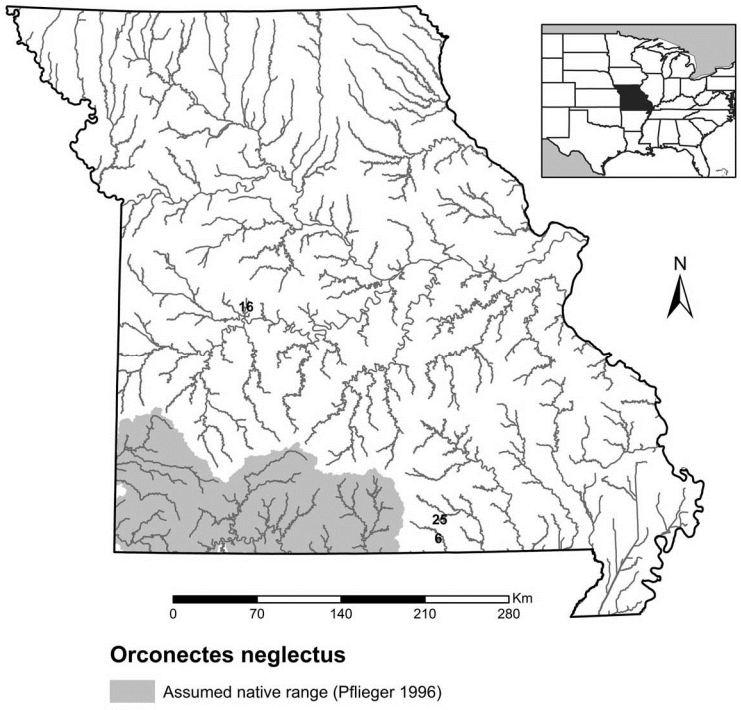

Figure 5. Map of Missouri illustrating numbered locations for confirmed (6, 25) and one unconfirmed (16) alien *Orconectes neglectus* invasions. Numbers correspond to invasions identified in Table 1, and are located on UTM coordinates provided in Appendix 1.

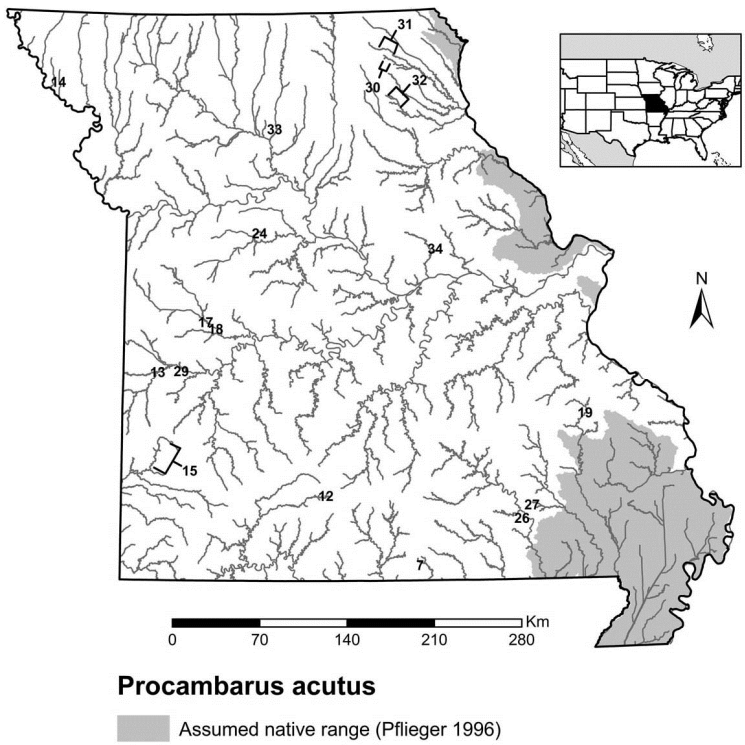

Figure 6. Map of Missouri illustrating numbered locations for confirmed and 1 unconfirmed (19) alien *Procambarus acutus* invasions. Numbers correspond to invasions identified in Table 1, and are located on UTM coordinates provided in Appendix 1. Three numbered locations (15, 30, 31) represent substantial stream reaches illustrated by an attached bracket.

to be supported by more than 2200 locations where alien crayfish have been detected as reported in a U.S. national database (U.S. Geological Survey 2014), for which the majority of reports were generated from sources other than systematic crayfish surveys. All five recent comprehensive crayfish surveys conducted in Missouri (Riggert et al. 1999; Flinders and Magoulick 2005; Westhoff et al. 2006; DiStefano et al. 2008; Engelbert 2013; R. J. DiStefano, MDC, unpublished data) have detected previously undocumented crayfish invasions. Several recent crayfish surveys in other regions of the U.S. have each detected invasions of one or more alien species (Bouchard et al. 2007; Kilian et al. 2010; Simmons and Fraley 2010; Lieb et al. 2011a; Loughman and Simon 2011), although this is not always the case (Ratcliffe and DeVries 2004; Wagner et al. 2010).

North America contains the highest crayfish biodiversity in the world, and most of this biodiversity is associated with the southeastern U.S. and surrounding geography (Taylor 2002) such as the Tennessee, Lower Mississippi, Ohio, Mobile Bay, South Atlantic, Ouachita Highlands, Cumberland, Ozark Highlands, and Florida ecoregions (Abell et al. 2008). These regions also contain an abundance of narrow-range endemic species that are especially susceptible to extirpation from multiple threats including invasive crayfishes (Taylor et al. 2007). We suggest that increased crayfish survey efforts in these regions, including increased attention to lentic and big river systems, are warranted to understand the prevalence of alien crayfish invasions and their threat status to native species and ecosystems on a wider scale.

Spatial and species patterns

We were surprised by the relatively high number of invasions that appeared to involve intrastate versus interstate (or international) translocations. It is conceivable that invasions featuring *P. acutus* or *O. virilis* could have involved long-range interstate translocations (but also these introductions could have just as conceivably originated from within-state populations). However, at least a quarter (and likely many more) of the total invasions almost certainly originated from within-state populations, because they featured Missouri endemic species (Table 1; e.g., *O. harrisoni*, *O. hylas*) and additional invasions featured a species (*O. luteus*) that barely ranges into one border state (Pflieger 1996). This relatively high proportion of intrastate invasions is a contrast to the substantially lower proportion (10%; 221 out of 2256) of intrastate invasions (versus 90% interstate) reported for U.S. states combined in one database (U.S. Geological Survey 2014) but in agreement with invasions in Pennsylvania (Bouchard et al. 2007; Lieb et al. 2011a,b). We are unclear about what may be the cause of this disparity in Missouri and Pennsylvania, but it could be related to increased detection capability arising from the relatively high amount of recent crayfish survey work conducted in both states (Pflieger 1996; Riggert et al. 1999; Flinders and Magoulick 2005; Westhoff et al. 2006; Magoulick and DiStefano 2007; Lieb et al. 2011b; Engelbert 2013; R. J. DiStefano, MDC, unpublished data). Increased survey efforts in other U.S. states and Canadian provinces could similarly detect increased numbers of crayfish invasions that are attributable to more localized translocations.

The majority of crayfish invasions we documented were in lotic systems in the Ozarks ecoregion of southern Missouri (Figure 1), most of which were in wadeable streams (Table 1). This was not necessarily a representative pattern of crayfish invasions in Missouri, but perhaps more a function of the relative amount of biological benthic and crayfish sampling that occurs in that ecoregion and especially in small streams versus larger rivers or lentic systems. We did confirm several invasions in large rivers, impoundments or public lakes.

In Missouri, large rivers, impoundments and public lakes are popular locations for recreational fishing. Water bodies that support such substantial angling activity may also experience higher propagule pressure in the form of alien crayfish bait releases (Drake and Mandrak 2014a, b). The majority of invasions we catalogued including those on large rivers and lentic waterbodies featured crayfish species that have long been approved for commercial sale and were common in Missouri's fishing bait industry (DiStefano et al. 2009). It is likely that at least some of these invasions resulted from "bait bucket introductions" (Litvak and Mandrak 1993; Ludweig and Leitch 1996). The fishing bait industry is often cited as the primary vector for alien and invasive crayfish in North America (Lodge et al. 2000; DiStefano et al. 2009; Kilian et al. 2012). Almost half of U.S. states and Canadian provinces/territories have experienced alien crayfish invasions thought to have resulted from live bait releases (DiStefano et al. 2009; Hamr 2010). Individuals are prohibited from releasing live crayfish to state waters in Missouri (Missouri Department of

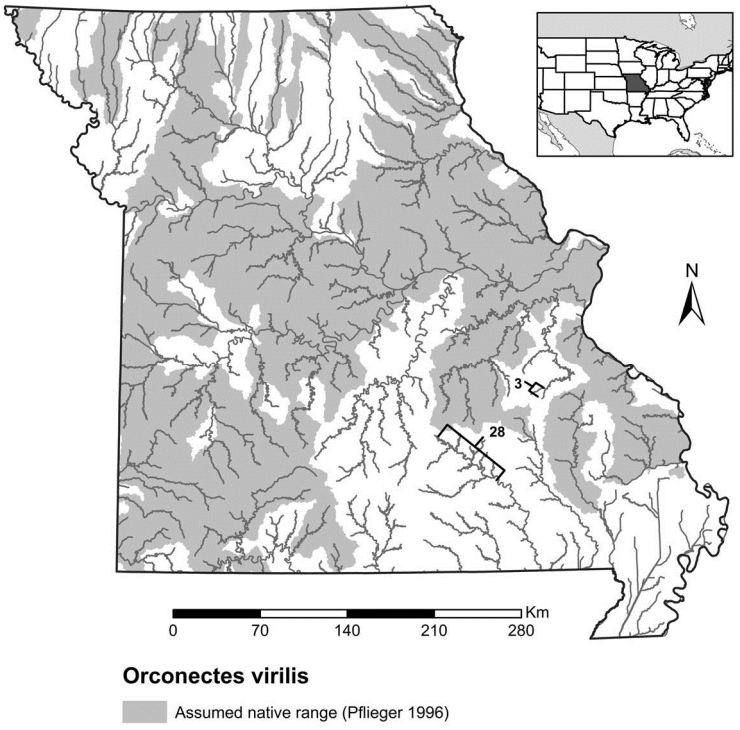

Figure 7. Map of Missouri illustrating numbered locations for confirmed alien *Orconectes virilis* invasions. Numbers correspond to invasions identified in Table 1, are located on UTM coordinates provided in Appendix 1, and represent substantial stream reaches as illustrated by an attached bracket.

Conservation 2015b) and many other states (DiStefano et al. 2009); however as many as 40% of surveyed anglers report releasing live bait in Missouri (Banek and Colatskie 2011); 36% in Wisconsin/Michigan (Kulwicki et al. 2003), 25% in Manitoba (Lindgren 2006), 69% in Maryland (live crayfish bait, Kilian et al. 2012), and 20–40% in Ontario (Litvak and Mandrak 1993; Drake and Mandrak 2014b). Missouri bait shop owners have estimated that about half of the live crayfish they sold were purchased by those who fish with set lines (trot lines, bank poles, limb lines, jug lines; DiStefano and Reitz 2010), and these methods are typically practiced on larger rivers and impoundments in the state.

Procambarus acutus was the most common invasive crayfish we found in Missouri (Table 1). It was also the invader that occupied all of the lentic sites, including all of the sites in northern Missouri, and most of the sites in the western portion of the state, typically far outside (>160 km) of its native range in the state (Figure 6). This species was easily the most frequent and abundant crayfish found in a statewide survey of bait shops, and >96% of the shops selling it were outside of its assumed native range (DiStefano et al. 2009). Interestingly, neither *O. immunis* nor *P. clarkii* were detected in any confirmed invasions, and they were the least commonly sold of the four legal species in Missouri's bait industry (DiStefano et al. 2009). *Procambarus acutus* was not commonly found entering the state in the biological supply trade (DiStefano, MDC, unpublished data) to supply classrooms, which is another documented pathway for alien crayfish invasions (Larson and Olden 2008). MDC staff strongly suspect that the introduction pathway for one of the confirmed *P. acutus* invasions (Blind Pony Fish Hatchery/Salt Pond Creek, Site 24) was via a transfer from the aquaculture industry to the MDC hatchery, contained in a shipment of *Pimephales promelas* ((Rafinesque, 1820), Fathead Minnow).

A *P. acutus* congener, *P. clarkii*, is a well-documented invasive crayfish that has had among the most widespread and significant ecological effects of any invasive crayfish (Gherardi 2006; Twardochleb et al. 2013), including native crayfish declines, on multiple continents including North America (e.g., Lowery and Mendes 1977; Gil-Sánchez and Alba-Tercedor 2002; Rudnick and Resh 2005; Matsuzaki et al. 2009; Klose and Cooper 2012). *Procambarus clarkii* is also known to carry or act as a host for pathogens and

parasites that may affect native crayfish (Holdich 1999; Longshaw 2011). However, we found minimal published accounts of *P. acutus* invasions (mostly in the U.S.: Bouchard 1977; Pickett and Sloan 1985; Hobbs III et al. 1989; Mills et al. 1996; Larson and Olden 2011; Lieb et al. 2011a), although there are a few reports of this species expanding outside of its native range through introductions (Simmons and Fraley 2010; Lieb et al. 2011a; U.S. Geological Survey 2014). The invasion successes of *P. clarkii* have been attributed to several of its biological properties such as rapid growth rate, early maturity and large number of eggs/offspring, (Gherardi 2006). *Procambarus acutus*' invasion capabilities and potential to affect recipient ecosystems is unknown (Twardochleb et al. 2013). This species does not share with *P. clarkii* the ability to breed multiple times per year. However, *P. acutus* is a temperate species possessing several traits that may facilitate its invasive capabilities (i.e., rapid growth rate and large size, early maturity, high fecundity, large chelae), particularly in cooler climates where it can grow faster and larger than *P. clarkii* (Mazlum and Eversole 2005; McClain and Romaire 2007; Larson and Olden 2010). Our data from multiple invasion sites (Table 1; Sites 14, 17, 18, and 29) suggest that *P. acutus* invasions may lead to native crayfish species declines, and that this species is at least capable of causing "moderate" to "major" impacts according to one classification system (Blackburn et al. 2014).

It might be considered surprising that we found *O. virilis* to be involved in only two confirmed invasions (Table 1, Sites 3, 28), given that they 1) are the most widespread crayfish species in Missouri (Pflieger 1996, Missouri Department of Conservation 2015a), 2) were the second most common species found in Missouri's bait trade (DiStefano et al. 2009), 3) are a proven invasive species (e.g., Kilian et al. 2010, Larson and Olden 2011; Martinez 2012; Kilian and Ciccotto 2014), and 4) showed high potential for invasiveness relative to most other species in the region (Larson and Olden 2010). However, it has been suggested that this species' wide distribution in the state might represent substantial numbers of unreported invasions that occurred prior to efforts to catalog them (Pflieger 1996; Pfleiger, MDC, personal communication). It is also conceivable that the state's largest invasion featuring *O. virilis* (Figure 7) resulted from multiple introductions along the 67-km invaded reach of Current River, one of the most recreationally popular rivers in Missouri.

In contrast to the *P. acutus* invasions involving relatively long-range transport across several of Missouri's drainage basins (Figure 6), many confirmed invasions featured narrow range endemic *Orconectes* species (including the subspecies *O. n. chaenodactylus*) that appear to have been translocated very short distances (<30 km) from neighboring drainages (Figures 2, 3, 4, 5). These species have never been permitted nor observed in commercial trade in the state (DiStefano et al. 2009), so it is likely that their introductions resulted from pathway(s) other than bait sales. The *Wildlife Code of Missouri* permits individuals possessing a valid fishing license to catch and possess up to 150 live crayfish, and transport them anywhere in the state, including to be used as bait on nearly all water bodies (Missouri Department of Conservation 2015b). This regulation provides a mechanism for wild crayfish capture and transport in Missouri; studies in other U.S. states indicate that crayfish are a moderately popular bait and that many anglers using them prefer to catch their own (Nielsen and Orth 1988; Kilian et al. 2012). Results of a recent Missouri survey (Reitz 2015) indicated that about 27% of the responding anglers who used crayfish bait, obtained their bait from waters other than those where they fished. Thus it is conceivable that these *Orconectes* invasions resulted from bait bucket introductions or other illegal live releases by individuals who legally captured and transported wild crayfish. One recent study concluded that regulations designed to prevent the spread of invasive crayfish are effective only if they include prohibitions on such transport of all crayfish (Dresser and Swanson 2013).

Ecological observations

We documented substantial native crayfish species declines or apparent displacements associated with confirmed invasions, including three species previously classified as "imperiled" (Missouri Natural Heritage Program 2015). Impacts to native species associated with invasions by *O. hylas* and *O. neglectus* could be classified as "major" according to Blackburn et al. (2014). Several of those invasions continue to expand (Magoulick and DiStefano 2007; DiStefano and Westhoff 2011), further threatening those and other crayfish species. The literature contains many reports of similar changes in crayfish communities associated with invasions (e.g., Taylor and Redmer 1996: Olden et al. 2006; Kuhlmann and Hazelton 2007; Jansen

et al. 2009; Loughman et al. 2009: Larson and Olden 2011), but few of these reports originate from regions of high crayfish diversity. Forty-two percent of our confirmed invasions occurred in drainages featuring relatively high levels of native crayfish endemism with at least one crayfish species that occurs in only that or a neighboring drainage (Pflieger 1996), so future threats to the conservation status of other species are likely. We suggest that similar native crayfish declines and displacements have occurred but remain undetected in regions rich in crayfish biodiversity and endemism, such as the southeastern U.S. (Taylor 2002), where few comprehensive surveys have been conducted.

We did not attempt to measure ecological effects beyond those to native crayfishes, but further effects to these invaded systems are likely (Lodge et al. 2012; Twardochleb et al. 2013). Crayfish are among the most disruptive invaders relative to many other aquatic organisms (Karatayev et al. 2009; Strayer 2010; Blackburn et al. 2014), and their invasions are associated with serious effects to habitats and across multiple levels of freshwater food webs, suggesting that they decrease prey and habitat resources for other animals such as insects, snails, fish and amphibians (Lodge et al. 1994; Matsuzaki et al. 2009; Lodge et al. 2012; Twardochleb et al. 2013; Jackson et al. 2014). Invasive *Orconectes* species, such as those found in approximately one half of the invasions we confirmed, are well known for causing major changes in aquatic community structure (Lodge et al. 2012). Furthermore, replacement of native crayfishes by invaders can amount to more than species loss, but rather biotic homogenization, which is known to simplify food webs, and can lead to ecosystems' reduced resilience to environmental disturbance, weakened gene pools and altered genetic selection processes (Olden et al. 2004).

Conclusions

Our effort to catalog, summarize and identify patterns among Missouri's alien crayfish invasions over 17 years revealed a higher number of invasions than we anticipated. During the process we were also surprised to learn that all reported, confirmed invasions featured crayfishes that were native to some part of the state, possibly resulting from intrastate translocations. The most common invader was the most common and abundant species previously found in Missouri's bait industry. However, many invasions also featured species that are not sold commercially and have small natural ranges.

Much public and media discussion concerning invasive species, including crayfish, focuses on long-range transport and introductions of alien species across political boundaries (e.g., trans-continental, or across country, state and provincial borders). This is reflected to some degree in the scientific literature (e.g., Hobbs III et al. 1989; Perrings et al. 2002; U.S. National Invasive Species Council 2008; Lodge et al. 2012; Gherardi 2013). This focus can lead to a misunderstanding of this issue among the general public, stakeholders and even some natural resources management professionals as we observed during a recent process to gather public input concerning proposed regulations to address Missouri's invasive crayfish problems. Many individuals were not aware (and some refused to believe) that crayfish transported short distances from their known range into neighboring drainages could become invasive (e.g., Fennewald 2012; Frazee 2012). Transport and introduction of local aquatic species have produced impacts that are as severe as those resulting from aquatic invaders from around the globe (Goodchild 1999). Our data suggest that these short-range crayfish translocations and subsequent invasions could be more common and perhaps more problematic than long-range translocations in some ecoregions, and that species-diverse regions could be particularly vulnerable.

Prevention is generally regarded as the most effective tool in managing crayfish invasions, but early detection of invasions is also cited as a critical step to provide management agencies time to evaluate and implement management options for conserving native species and ecosystem services (Lodge et al. 2012; Gherardi 2013). In this regard, Missouri has benefitted from a statewide crayfish conservation and management program that has focused initially on a series of comprehensive crayfish surveys and accompanying public outreach and education. These efforts were directly responsible for detection of the vast majority of alien crayfish invasions in the state. Data from these surveys have provided managers with sufficient support to propose and pass regulations concerning sale and purchase of live crayfish that are aimed at prevention of further invasions (Missouri Department of Conservation 2015b). We suggest that increased survey efforts in other U.S. states and Canadian provinces, particularly in regions of high crayfish diversity, will lead to increased detection and provide opportunity for more effective management.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Missouri Suspected Alien Crayfish Invasions as of July 2014.

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2015/Supplements/MBI_2015_DiStefano_etal_Supplement.xls