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ORIGINAL PAPER

Preemptive legislation inhibits the anthropogenic spread of an aquatic invasive species, the rusty crayfish (*Orconectes rusticus*)

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Abstract The enactment of legal policies is often recommended to prevent anthropogenic introductions of invasive species. In this paper, we evaluated the effectiveness of proactive state legislative policies in deterring colonization by rusty crayfish (*Orconectes rusticus*) and the expected spread into previously uninvaded states using network-based spatial analysis. We found that the presence of regulations was positively associated with the presence of rusty crayfish ($p = 0.027$), but often regulations were put into effect subsequent to the invasion. Regulations that did not explicitly prohibit transport, applied to specific drainages, or prohibited only rusty crayfish were not effective. However, preemptive legislation was effective in reducing the likelihood of invasion, if regulations prohibited the transport of all live crayfish species between water bodies, as only 1 state which passed such legislation prior to invasion by rusty crayfish was subsequently colonized ($S = 12$, $p = 0.031$). Five states are likely to be invaded by rusty crayfish via range expansion across interstate drainages, and dispersal rates suggest that all of these states could be colonized within 10 years. While it is unlikely that regulations will prevent dispersal-based invasion across state lines through shared drainages, preemptive legislation can significantly reduce anthropogenic spread of aquatic invasive species between drainages and effectively retard the expansion of rusty crayfish. Our results suggest that the most effective form of legislation is one that does not require individuals to identify species, thus we recommend states enact policies that explicitly prohibit the transport of all live crayfish between water bodies.

Keywords Anthropogenic dispersal · Dispersal rate · Invasive species · Network-based spatial analysis

Introduction

Anthropogenic introductions of non-native species, especially those used as live bait, such as crayfish have led to the establishment of invasive populations, which negatively impact existing communities. For example, the introduction of *Procambarus clarkii* has contributed to habitat degradation and biodiversity loss in the northeast United States (Antonelli et al. 1999) and in 25 European countries (Gherardi 2006). Legislative policies have been enacted to prevent anthropogenic introductions of exotic species; however policy enactment is still lacking for many invasive species (Fowler et al. 2007). The development of legal policies is an attractive management strategy as the cost associated with development and passage of such regulations is comparatively less expensive than having to react to, and manage, invasions after they occur (Keller et al.

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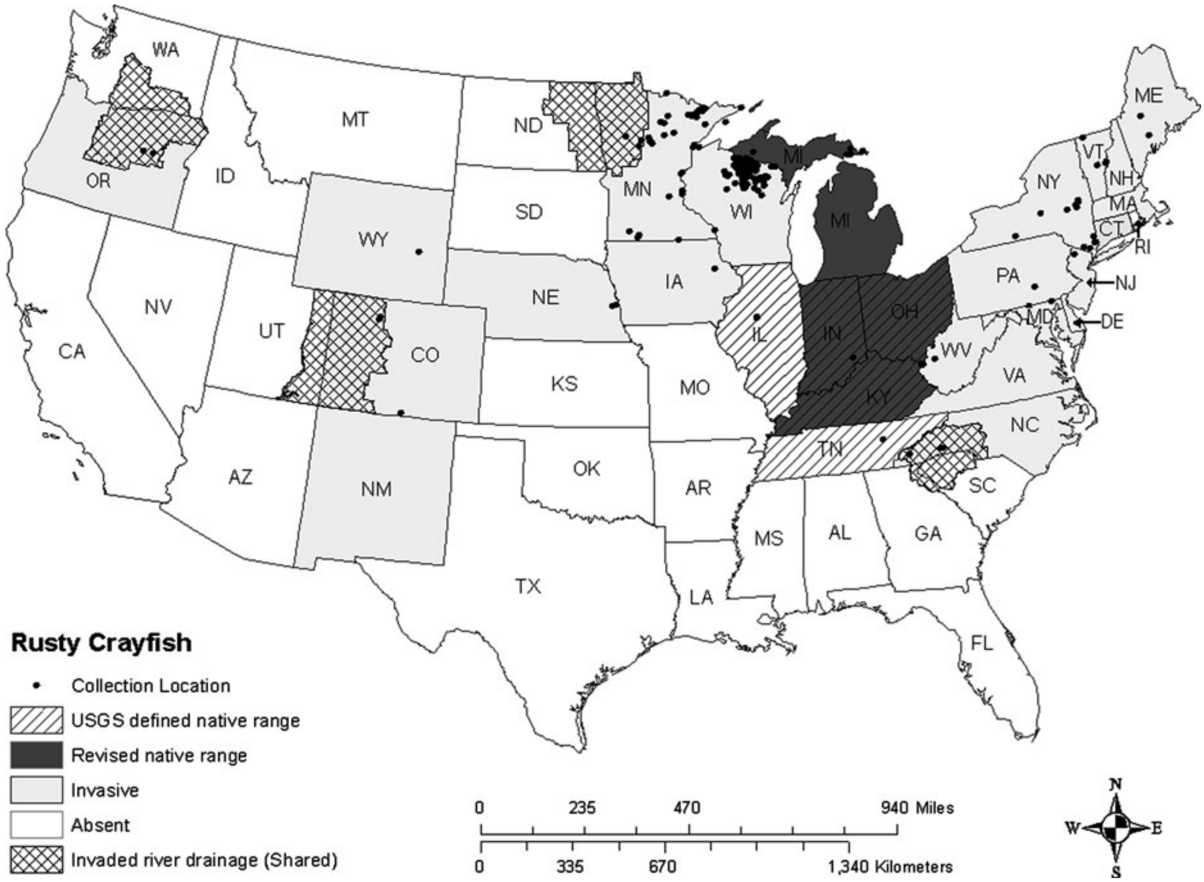

Fig. 1 Distribution of rusty crayfish (*Orconectes rusticus*) within the contiguous United States by state. The United States Geological Survey (USGS) defines the native range of rusty crayfish to be IN, IL, KY, OH, and TN (*diagonal lines*); however, state and university crayfish researchers argue that the native range should be revised to IN, MI, OH, and KY (*dark gray*). Rusty crayfish are considered non-native in all remaining states; both invaded (*light gray*) and not invaded states (*white*). Four invaded river drainages are shared with five uninvaded states (*cross-hatching*). River distances from known collection points (*black dots*) to uninvaded state lines (*black lines*) along with known dispersal rates were used to estimate the time of rusty crayfish arrival into a previously uninvaded state through dispersal-based range expansion of antropogenically-introduced populations

2008). Enactment of legislative policies also improves our ability to standardize policies across ecologically relevant units and increase public awareness regarding the risks associated with anthropogenic introductions of exotic species. Unfortunately, as with any management strategy, there are limitations to legal policies. The timing of policy enactment is critical in regards to effectiveness, as policies that are enacted reactively are less effective than proactive policies (Peters and Lodge 2009). The degree of effectiveness is also dependent on cooperation across political boundaries because range expansion of invasive species is constrained by ecological boundaries rather than political boundaries. Furthermore, legislative policies may be more effective for species inhabiting terrestrial ecosystems than aquatic ecosystems, as species tend to spread more quickly in aquatic environments (Kinlan and Hastings 2005). Thus, proactive policy enactment is even more critical for exotic aquatic species.

One aquatic species that has been introduced outside of its native range and is now considered invasive throughout most of the United States is the rusty crayfish (*Orconectes rusticus*). Since the late 1960s, the distribution of rusty crayfish has rapidly spread beyond the Ohio River Basin (Fig. 1), displacing native crayfish species (Taylor and Redmer 1996) through hybridization (Perry et al. 2001b) and resource competition (Hill and Lodge 1999). The invasive ability of the rusty crayfish stems from their high genetic diversity (Yue et al. 2010), high abundance (Jansen et al. 2009), high dispersal rate (Wilson et al. 2004), and their role as habitat and resource generalists (Freeman et al. 2010). In addition to the displacement of native crayfish species, rusty crayfish prey on fish eggs (Horns and Magnuson 1981) and contribute more strongly to the decline of game fish than native crayfish species due to their high abundance, large chelae, and aggressive nature (Roth and Kitchell 2005).

The suspected primary cause of rusty crayfish introduction is the transfer of live crayfish, for use as bait, between water bodies by anglers (Lodge et al. 2000; DiStefano et al. 2009). Repeated human introductions over time could exacerbate the rate of spread and increase the difficulty of controlling this invasive species. Several studies have recommended the enactment of proactive regulations to stop anthropogenic introductions (Puth and Allen 2005; Taylor et al. 2007; DiStefano et al. 2009), but the intention of our study was to quantitatively evaluate the effectiveness of regulations to determine if regulation enactment is an effective strategy to control invasive species. While previous studies have evaluated legislative policies in specific regions within the United States (DiStefano et al. 2009; Peters and Lodge 2009), our review is a nationwide evaluation of the effectiveness of state legislative policies in deterring invasion by rusty crayfish. The three objectives of this study were to test for an association between regulations and rusty crayfish, evaluate the effectiveness of regulations, and estimate rusty crayfish arrival time in states sharing a drainage with a previously invaded state.

Methods

Data collection

We obtained copies of fishing regulations from all states within the contiguous United States (US), through fishing regulation booklets and administrative codes. Fishing regulation booklets are published annually or biannually and summarize fishing regulations, including newly enacted policies relevant to anglers and the general public; the administrative codes include formal details and histories associated with each regulation and are available through each state's government website. We requested past and present fishing regulations from each state and obtained at least the current (2010–2011) regulations from all states within the contiguous US. We used each state's administrative code to obtain the date of enactment and follow changes made to each regulation. We defined the presence of a regulation to prevent anthropogenic introductions of rusty crayfish based on the following criteria; (1) policy explicitly prohibits transport of all live crayfish between bodies of water or (2) policy specifically prohibits the transport of rusty crayfish. For example, regulations were considered absent if only the purchase or sale of crayfish was prohibited, but transport was permitted. Regulations were considered present if transport of live crayfish was prohibited, but the transport of dead crayfish was permitted.

Rusty crayfish collection locations throughout the contiguous US were obtained from the United States Geological Survey (USGS; http://nas.er.usgs.gov:80/queries/collectioninfo.aspx?SpeciesID=214; last date accessed 11/30/2011), which incorporated all published or reported collection locations from 1961 through 2011. We supplemented USGS collection data with data obtained from personal communications with crayfish researchers and employees from the various natural resource departments in each state, some of whom had not reported their collections to the USGS. Each USGS specimen has a corresponding specimen number, which is associated with a state, county, river or lake name, drainage name, and hydrological unit code (HUC) number. The scale at which drainages are defined corresponds to the number of units in the hydrological unit code, where more digits represent a finer scale. For example, a HUC 8 is an 8-digit hydrological unit code, which partitions a HUC 4 drainage into finer categories. The maximum number of HUC digits, or the finest scale at which a drainage can be defined is HUC 12. However, we used a broader scale HUC (HUC 8) to define a single drainage in our study as some collection locations only provided an 8 digit HUC.

We also conducted a literature search to estimate the dispersal rate of rusty crayfish using Web of Science and Google Scholar with the search terms "crayfish dispersal" and "dispersal rate of crayfish". Should regulations be effective in preventing anthropogenic introductions of rusty crayfish among drainages, proactive measures should be taken in currently uninvaded states. However, regulations cannot

Table 1 Dispersal rates of crayfish species in either a lake or river system

Crayfish species	Water body type	Flow direction	Dispersal rate (km/year)	References
Orconectes rusticus	Lake		0.68	Wilson et al. (2004)
Orconectes rusticus	Lake		0.7	Perry et al. (2001a)
Pacifastacus leniusculus	River	Downstream	18.0–24.4	Hudina et al. (2009)
Orconectes limosus	River	Upstream	2.5	Hudina et al. (2009)
Pacifastacus leniusculus	River	Downstream	2.8	Bernardo et al. (2011)
Procambarus clarkii	River	Not specified	2.0	Bernardo et al. (2011)

prevent movement of crayfish through shared stream connections between states. In the case where populations are established in interstate drainages we determined which states are likely to be invaded through dispersal-based range expansion and when the invasion is expected to occur. Few estimates of rusty crayfish dispersal rates are available in the literature and all reflect dispersal within lake systems (Perry et al. 2001a; Wilson et al. 2004). However, rusty crayfish are more likely to invade new states through stream systems, thus we have included dispersal rates of other crayfish species through stream systems (Table 1). Dispersal rates varied between upstream and downstream movement, so we used a conservative (slowest rate) and an aggressive (fastest rate) estimate of crayfish dispersal capabilities (0.68 and 24.4 km/year, respectively) to incorporate the variation in crayfish dispersal rate present in the literature.

Data analysis

Our first objective was to test for an association between regulations and rusty crayfish. States where rusty crayfish are considered native and states outside of the contiguous US (Alaska and Hawaii) were excluded from this analysis. Due to the discrepancy between the native range proposed by the USGS (Ohio, OH, Kentucky, KY, Indiana, IN, Tennessee, TN, and Illinois, IL) and the range accepted by researchers of invasive crayfish (Taylor 2000; DiStefano et al. 2009; Peters and Lodge 2009) (OH, KY, IN, and Michigan, MI) we conducted two analyses, one for each native range (USGS native range and revised native range). Each state was placed into one of four categories, (1) both regulations and rusty crayfish are present, (2) regulations are present and rusty crayfish are absent, (3) regulations are absent and rusty crayfish are present, and (4) both regulations and rusty crayfish are absent. If regulations were present prior to invasion by rusty crayfish states were placed in the first category, but if regulations were passed subsequent to rusty crayfish presence states were placed into the third category. We used a Fisher's exact test in program R to test for a significant association between regulations and rusty crayfish.

Our second objective was to evaluate the effectiveness of regulations against the spread of rusty crayfish. Wisconsin was the first state to enact regulations against the use of live crayfish bait in 1983; however, rusty crayfish were discovered prior to policy enactment, thus the first proactive regulation was not enacted until 1986 by Utah. At the time of the initial enactment of the first proactive state regulation, rusty crayfish had not invaded 35 of the 43 contiguous and non-native states, which reflects both of the proposed native ranges. Between 1986 and 2011, 13 states were invaded, yielding a 37.1 % (13 of 35 states) invasion probability. We used a binomial test in R to determine if the number of states with proactive regulations and were subsequently invaded was less than expected, based on the invasion probability of 37.1 %.

Our third objective was to estimate the time required for rusty crayfish to invade states sharing a drainage with a previously invaded state. A drainage was identified based on its unique HUC 8 number as defined by the USGS and a drainage was classified as invaded if at least one rusty crayfish collection point was located within the drainage. Shared invaded drainages were identified by overlaying the three data layers, state boundaries, drainage boundaries, and USGS rusty crayfish collection locations in ArcMap 10 (ESRI, Redlands, CA). After states at risk for dispersal-based invasion across state borders were identified, ArcGIS Network Analyst was used to conduct a network-based spatial analysis, which calculated the river distance between the known collection point in the previously invaded state and the uninvaded state border. The river distances were divided by the conservative and aggressive dispersal rates of crayfish obtained from the literature to estimate the amount of time required for rusty crayfish to arrive into the previously uninvaded state. The date associated with the rusty crayfish collection point was used to estimate when rusty crayfish would arrive in the uninvaded state.

Results

Since the first documented discovery of rusty crayfish outside of their native range in 1967, rusty crayfish have invaded approximately 50 % of states in the contiguous US, depending on the native range used (21 out of 43 states based on the USGS native range and 22 out of 44 states based on the revised native range; Fig. 1). Despite the rapid range expansion of rusty crayfish and their known detrimental effects on ecological communities, approximately 37 % of states in the contiguous US, where rusty crayfish are considered non-native, still have not enacted regulations (16 out of 43 based on the USGS native range and 16 out of 44 based on the revised native range; Fig. 2).

At the time of our analysis in 2011, we found a significant positive relationship between the presence of regulations and the presence of rusty crayfish using both proposed native ranges. Excluding states where rusty crayfish are considered native by the USGS and the non-contiguous states, 4 states had proactive regulations and rusty crayfish, 12 states had proactive regulations and no rusty crayfish, 17 states had no regulations or reactive regulations and rusty crayfish, and 10 states had neither regulations nor rusty crayfish ($p = 0.027$, Fisher's exact test). Excluding states where rusty crayfish are considered native by crayfish experts and the non-contiguous states, 4 states had proactive regulations and rusty crayfish, 12 states had proactive regulations and no rusty crayfish, 18 states had no regulations or reactive regulations and rusty crayfish, and 10 states had neither regulations nor rusty crayfish ($p = 0.027$, Fisher's exact test).

In our analysis of the impact of proactive regulations on the likelihood of invasion, we found that the number of invaded states was not significantly lower than expected using either proposed native ranges ($S = 16$, $p = 0.233$, Binomial test). Following the enactment of the first proactive regulation in 1986, 16 states had proactive regulations; however, 4 states were invaded, which was not significantly lower than the expected number of state invasions of 5.94 (5.94 of 16 states or 37.1 %). However, when the presence of regulations was redefined to exclude state regulations that required species identification knowledge, the number of invaded states was significantly lower than expected using both proposed native ranges (USGS native range, $S = 12, p = 0.031$, Binomial test; Revised native range, $S = 13$, $p = 0.021$, Binomial test).

Three states with proactive legislation (North Dakota, ND, Utah, UT, and Washington, WA) and two states without legislation (South Carolina, SC and Georgia, GA) would likely be invaded by rusty crayfish, regardless of regulations, due to range expansion through shared stream connections (Fig. 1). Of these five states, three states may have already been invaded based on our estimated arrival times. South Carolina would likely be invaded between 2001 and 2078 through a shared drainage with North Carolina, Georgia would likely be invaded between 2003 and 2077 also through a shared drainage with North Carolina, and North Dakota between 1995 and 2160 through a shared drainage with Minnesota. Two states with shared drainages likely remain uninvaded, even if rusty crayfish continuously move at the maximum dispersal rate; Utah is expected to be invaded between 2021 and 2424 and Washington is expected to be invaded between 2017 and 2438 through a shared drainage with Oregon.

Discussion

Our results show that proactive regulations successfully impeded the spread of rusty crayfish at the national level. This is especially relevant based on the mechanisms of rusty crayfish spread and the consequences of establishment (Lodge et al. 2000; Taylor et al. 2007; DiStefano et al. 2009). However, our results have two caveats, legislation is only effective if transport of all crayfish is prohibited and it only reflects the prevention of anthropogenic introductions rather than dispersal-based range expansion through shared

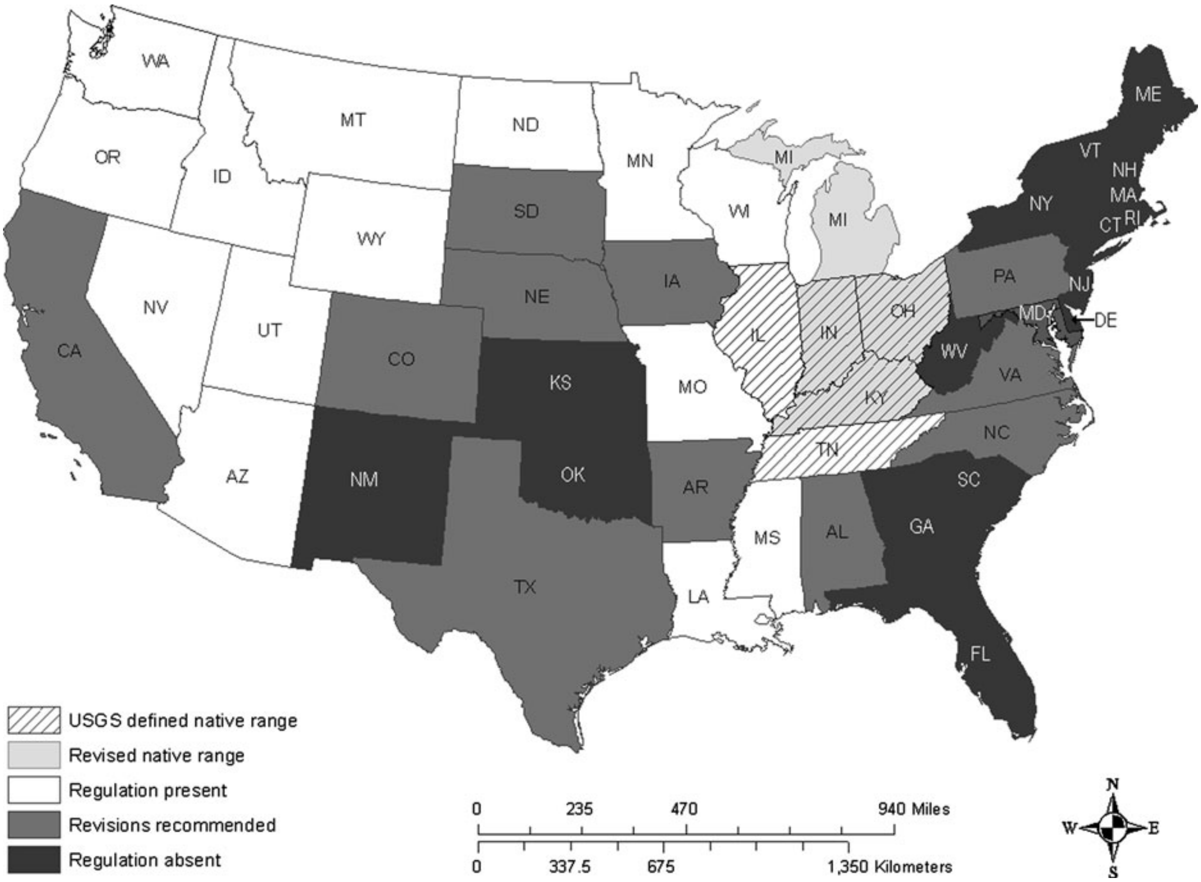

Fig. 2 Presence of regulations to stop anthropogenic introductions of non-native crayfish species by state. States were labeled post hoc as regulation present (*white*) if phrasing clearly prohibits transport of all crayfish species, revisions recommended (*medium gray*) if current phrasing requires species identification knowledge or applies only to a subset of drainages, and regulation absent (*dark gray*) if none exist. The United States Geological Survey (USGS) defines the native range of rusty crayfish (*Orconectes rusticus*) as IN, IL, KY, OH, and TN (*diagonal lines*); however, state and university crayfish researchers argue that the native range should be revised as IN, MI, OH, and KY (*light gray*)

stream connections. Dispersal-based range expansion is likely restricted to within a drainage, given the poor dispersal ability of crayfish across terrestrial habitats (Claussen et al. 2000). Rusty crayfish invasion, via range expansion from an anthropogenic introduction point, threatens five states (GA, ND, SC, UT, and WA) because they share drainages with previously invaded states. While our analyses indicated rusty crayfish arrival as early as 1995, based on a dispersal rate of 24.4 km/year, new research indicates that daily movement of *Orconectes hylas* can be as fast as 0.25 km/day (Westhoff 2011), thus rusty crayfish arrival could be much earlier than predicted. Several of these states have proactive regulations; however, these policies may require more rigorous enforcement, greater public awareness, and improved cooperation within and between states in order to contain the probable invasion to a single drainage. For those states that have yet to implement regulations, our findings strongly support the proactive enactment of regulations to control the spread of rusty crayfish. Alternative to the enactment of regulations, post-invasion strategies, such as trapping adult crayfish and increasing fish predation, can reduce rusty crayfish abundance, but do not completely eradicate rusty crayfish after introduction, although these strategies have only been evaluated in lake systems (Hein et al. 2006). Thus, enactment of proactive regulations banning the transportation of all crayfish currently appears to be the most effective strategy to control the spread of rusty crayfish.

We have shown that enactment of regulations at the state level is effective at preventing the anthropogenic spread of rusty crayfish, but we believe that state regulations could be more effective if neighboring states mutually agreed upon regulations. DiStefano et al. (2009) mentioned that one of the bait shops sampled in 2004 indicated that they expected a shipment of *O. rusticus* from a wholesaler in Wisconsin, despite regulations prohibiting transport of live rusty crayfish within the state of Wisconsin, regulations do not restrict movement of crayfish out of the state. Although the shipment was never confirmed, the lack of communication and cooperation between states is clear. We encourage all states to prohibit the transport and sale of all live crayfish between water bodies. Not only would prohibiting the transport of all live crayfish stop the anthropogenic spread of rusty crayfish, but it would also act as a preventative measure against the spread of other invasive crayfish species. Another benefit of these regulations is that they do not require anglers or bait shop owners to be competent in distinguishing between native versus invasive crayfish species, knowledge that is lacking among bait shop owners in particular. A survey conducted in Missouri in 2007, indicated that 87 % of the surveyed bait shops admitted that they did not know what species they sold, and 97 % of bait shop managers were unable to name the crayfish species they sold (DiStefano et al. 2009). The inability of bait shops to identify the species they sell likely extends to the anglers that use the live crayfish bait. By enacting regulations that apply to all crayfish species, bait shop owners and anglers do not have to be able to identify the crayfish species they are using. Lastly, regulations banning the transport of all live crayfish would still allow anglers to catch and use crayfish as live bait within the same body of water and allow anglers to transport dead bait; minimizing the necessary alterations in angler behavior, while preventing non-native introductions across drainages.

Our study was the first nationwide evaluation of state regulations in regards to preventing the spread of the invasive rusty crayfish; however, these data are presented with the caveat that collection locations reflect the search and reporting effort made by each state to the USGS, which may vary between states. We attempted to minimize this bias by supplementing USGS data with data obtained from personal communications with natural resource department representatives and crayfish experts from each state. Additionally, our ability to assign an accurate enactment date for state regulations was dependent on the availability of old fishing regulations, documentation of wording changes in the administrative codes, and cooperation of state legislative representatives. Despite these limitations, slight deviations in enactment dates or initial rusty crayfish collection dates are unlikely to change the qualitative results of this study as incorporation of newly acquired data from experts rarely changed the category to which the state was originally assigned. Furthermore, this study focuses on the presence or absence of state regulations in fishing regulation handbooks and the administrative code; however, enforcement and public awareness are also likely important factors in the effectiveness of regulations and should be considered in future research.

In this study, we have provided quantitative evidence that legislative regulations are effective in stopping the spread of an invasive aquatic invertebrate, which we hope will inspire policy makers to instate proactive regulations to stop the anthropogenic spread of rusty crayfish in the US. While we focused on the effectiveness of regulations in preventing the spread of rusty crayfish, proactive regulations are likely to be effective in preventing the spread of other aquatic invasive species, particularly several other crayfish invaders that are having negative effects in the US and Canada. Although the effectiveness of regulations has not been quantified in Europe, a few examples suggest that regulations are an effective management strategy within and between countries as well. Such as in Northern Ireland, where stringent legislation was passed prior to 2003 banning imports of crayfish and as of 2011 still do not have any non-indigenous crayfish species. The majority of eradication and control strategies for invasive species are reactive and often ineffective because they are implemented after non-native species have already begun to spread (Gherardi and Angiolini 2004). While, regulations can be implemented at any time during the invasion process, and may slow down the invasion, our results show that proactive regulations can prevent the initial invasion. The one caveat though, is that the regulations need to be worded broadly enough, such that species identification is not required of the general public. Given this, we recommend that all states enact or revise their current policies to prohibit the transport of all live crayfish species.

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