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Review Article

An evaluation of research on crayfish invasion pathways in the Great Lakes region

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Abstract

Invasive crayfish species have become a significant ecological concern in the Laurentian Great Lakes Basin, adversely affecting native biodiversity and ecosystem functions. This review synthesizes 24 years of peer-reviewed literature to elucidate crayfish invasion pathways in the Great Lakes. Over this period, the literature has highlighted natural dispersal and bait release as dominant invasion pathways for crayfish in this region, accounting for over half of reported cases. Emerging pathways, including the retail trade and accidental releases, underscore the evolving nature of invasion pathways. Research efforts have concentrated geographically in Wisconsin, Michigan, and Illinois, with limited studies addressing other Great Lakes states, revealing significant gaps to understand the full scope of invasion pathways. This review identified rusty crayfish (*Faxonius rusticus*) and red swamp crayfish (*Procambarus clarkii*) as the focus of much of this work while other species were not as prevalent in introduction pathways research. While historical studies have provided foundational insights, reliance on historical pathways data has limited our understanding of newer mechanisms, such as aquarium trade releases and species misidentifications in retail markets. To address these challenges, we recommend broadening the research focus of future work to encompass underrepresented regions and species, enhancing collaborative efforts among stakeholders, and improving regulatory oversight of retail trade practices. Public engagement is a critical component for mitigating the impacts of invasive crayfish through responsible consumerism and pet ownership practices. This comprehensive synthesis aims to inform future research efforts, policy development and surveillance initiatives, foster coordinated responses to invasive species threats, and contribute to the preservation of the Great Lakes Basin's ecological integrity.

Key words: aquatic invasive species, introductions, non-indigenous species, management, retail trade

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Introduction

Biologists are increasingly aware of the negative ecosystem consequences initiated by the introduction of non-native and non-indigenous species. Protecting global biodiversity will require increased effort to manage these species (Albert et al. 2021). The translocation and introduction of an array of taxa are among the principal challenges facing global biodiversity and ecosystem management in the modern age, along with historic challenges such as a changing climate, increasing extinctions, and habitat loss (Ripple et al. 2017). The ecosystem consequences of non-native species introductions are heavily studied, although difficult to predict (Zalba and Ziller 2007; Freeman et al. 2010; Doherty et al. 2015; Ballari et al. 2016). When non-native species produce negative effects after introduction (thus termed "invasive species"), subsequent management interventions and mitigations are often extremely costly (Lodge et al. 2016). A previous review of aquatic invasive species' economic impacts since the 1960s conservatively attributed $345 billion in costs to the global production of goods, services, and natural resource management to date (Cuthbert et al. 2021). History demonstrates that managing or removing established invasive populations is often extremely difficult or impossible when compared to preventing their introduction to begin with (Zalba and Ziller 2007; Cole et al. 2016; Prior et al. 2018).

Concern regarding aquatic invasive species (AIS) is especially high for inland freshwaters. These ecosystems have high isolation relative to terrestrial systems, preserve high biodiversity, and provide critical services that typically lie at the center of ever-evolving local, regional, national, and international priorities (Rehage et al. 2005; Balian et al. 2008; Hoff et al. 2021). Significant knowledge gaps regarding invasive species threats including emerging invasion pathways, how to best engage managers, and biases in research and monitoring for freshwater ecosystems make it difficult to guide impactful management (Dudgeon et al. 2006; Strayer and Dudgeon 2010; Thomaz et al. 2015; Reid et al. 2019). The interconnected, dendritic, and climatically buffered nature of freshwater systems makes them naturally susceptible to invasion (Moyle and Light 1996; Ricciardi et al. 2021). Human degradation of physical barriers and rapid transport through anthropogenic means (either assisted or accidental) allows freshwater introduced species to rapidly expand the areas they impact (McKinney 2002; Vörösmarty et al. 2013; Reid et al. 2019). Understanding the introduction pathways for AIS and appropriate management actions are among the top invasive species research priorities in the 21st century (Pyšek et al. 2020).

For invasive species to establish successfully in novel environments, there must be both a means of introduction and a suitable environment in which the species can survive and reproduce (Sakai et al. 2001). Introduction can occur through assisted movement, accidental transport, or by self-dispersal following an introduction into nearby habitats (Hulme et al. 2008; Pyšek et al. 2020). When these factors coincide they form invasion pathways, and the study and prioritization of invasion pathways has become the cornerstone of modern invasive species management (Hulme et al. 2008; Blackburn et al. 2011; Padayachee et al. 2017; Lieurance et al. 2023). Although a plethora of invasion pathways are reported in the literature, most AIS invasion pathways can be grouped under six general categories, including unaided, release, escape, stowaway (unintentional transiting of a species), contaminations (i.e., pathogens), and corridors (modification or connection of previously disjoint ecosystems) (Hulme 2015). Invasion pathway assessments attempt to identify and understand how frequently invasive species traverse or are found within one or more of these pathways.

The goal is to prevent invasions, efficiently use surveillance resources, and inform management and monitoring actions, for example ballast water management regulations (O'Malia et al. 2018; Lieurance et al. 2023). Pathway identification is crucial to manage the risk posed by AIS due to the cryptic nature of invasions in aquatic systems (Muralidharan 2017; Morais and Reichard 2018; Lázaro-Lobo and Ervin 2021; Britton et al. 2023). Once a new invasion is identified, managers should use pathway identification to prevent future introductions alongside management of the novel AIS population (Packer et al. 2017). Many of the challenges of AIS can be mitigated by identifying and managing invasion pathways (Hulme et al. 2008; Hulme 2015; Packer et al. 2017).

The Laurentian Great Lakes Basin (GLB) is among the most invaded aquatic systems in the world and is a prime example of the difficulty associated with large-scale freshwater invasive species management (Lodge et al. 2012, 2016; Sturtevant et al. 2019). Shipping ballast water release was among the first invasion pathways identified and regionally managed. However, over 180 species are now established in the GLB and new invasion pathways continue to emerge (Escobar et al. 2018; Tucker et al. 2020). The spatial and economic scale of the GLB, encompassing 8 US states and 1 Canadian province (2 when including Quebec with the St. Lawrence River), also poses significant hurdles to unified efforts across jurisdictions to prioritize and monitor specific invasion pathways and meet divergent socio-political interests (Pagnucco et al. 2015). Advanced social-scientific communication and understanding must exist to address AIS challenges in the GLB (Folke et al. 2005; Brossard et al. 2005).

Crayfish (superfamilies: Astacoidea and Parastacoidea) have received increasing attention for invasive species management throughout the GLB (and globally) due to their high prevalence in the retail and wholesale trade (Lodge et al. 2012; Oficialdegui et al. 2019). The concern stems from their well-documented impacts on aquatic ecosystems, including aggression toward native crayfish species, high reproductive output, polytrophism, and habitat modification through burrowing (Gherardi 2007, 2011; Freeman et al. 2010). North American crayfish are also susceptible to - and can therefore spread - pathogens to other crustacean species (Stentiford et al. 2010; Stratton et al. 2023). The best known of these pathogens is the crayfish plague (*Aphanomyces astaci*), which is highly virulent to crayfish outside of North America but has limited impacts on North American species (Oidtmann et al. 2002; Kozubíková et al. 2009). Over 50 crayfish species and subspecies, both native and non-native, occur across the eight GLB states, but only 20 species of crayfish are documented within the GLB itself (Peters et al. 2014; O'Shaughnessey et al. 2021; Davidson et al. 2021). Several species are considered invasive, including the rusty crayfish (*Faxonius rusticus*, native to the neighboring Ohio River Basin)(Girard, 1852) and red swamp crayfish (*Procambarus clarkii*, native to the southern United States) (Girard, 1852). Other species, although native within the GLB, have been noted as invasive in other states that surround the GLB, such as Northern/virile crayfish (*Faxonius virilis*) (Hagen, 1870), Northern clearwater crayfish (*Faxonius propinquus*)(Girard, 1852), and the obscure crayfish (*Faxonius obscurus*) (Hagen, 1870). These and other crayfish are of management concern across the basin due to their existing or potential impacts, their increasing prevalence in the aquarium trade, and their ability to readily establish new populations upon release (Andriantsoa et al. 2020; Kouba et al. 2021; Olden and Carvalho 2024). This includes species such as the marbled crayfish (*Procambarus virginalis*) and redclaw crayfish(*Cherax quadricarinatus*) with demonstrated impacts in other locations (Davidson et al. 2021). Preventing the introduction of these species of concern through pathway management and early detection rapid response actions can mitigate the threat of these species to freshwater ecosystems.

Invasive crayfish are widely recognized as highly impactful invaders for native species and ecosystem function, yet few efforts exist to coordinate policy and management strategies to address crayfish introductions across the GLB (Lodge et al. 2012, 2016; Hoff et al. 2021). For example, one of the most well-known and cited pathways is the release of crayfish by anglers, also known as "bait bucket introductions" (Lodge et al. 2012, 2016; Hoff et al. 2021). This has resulted in efforts to inform the public that they should not release crayfish used as live bait. However, while this messaging and educational campaign is important to pursue, the idea and precedent generally rely on studies published in the 1980s (Capelli and Magnuson 1983; Ludwig Jr. and Leitch 1996). More invasion pathways are now recognized than in the past (Hulme 2015; O'Malia et al. 2018; Lieurance et al. 2023), and there is a need to update and examine our understanding of crayfish invasion pathways in the GLB to address the growing number of pathways available for crayfish to reach and move within the basin.

This review synthesizes invasive crayfish literature from the past 24 years to develop a basin-wide perspective on the major crayfish invasion pathways. We believe this review is necessary to update taxonomic changes to species names (including new species descriptions, e.g., *P. virginalis*) (Lyko 2017), and to include new pathways for invasion; for example, new techniques in ornamental species breeding that have complicated the ability of scientists, managers, and the general public to recognize invasive crayfishes (Olden and Carvalho 2024). This increase in the online trade of crayfish, especially ornamental varieties, is likely to contribute to release and escape pathways, further stressing existing regulatory frameworks (Cohen et al. 2013; Patoka et al. 2015; Olden and Carvalho 2024). Changes in climate, land use, and sociopolitical influence on management and research priorities around the GLB constrain institutional capacities to monitor and respond to the introduction of invasive crayfish, which makes the identification of active invasion pathways an important endeavor to increase the efficiency of surveillance efforts. Management agencies require the most up-to-date information to inform local and regional surveillance efforts and the general public.

This review aims to address four questions related to crayfish invasion pathways in the Great Lakes Basin. First, how much work examining or reporting invasion pathways has been published, who is publishing this work, and where has it been produced within the last twenty-four years? Second, what main pathways are identified by authors, and what new pathways have been uncovered? Third, what crayfish species are found in these pathways? Finally, are there insights from this body of research that can inform researchers and managers engaged in invasion pathway management around the GLB?

Methods

Literature search

We conducted an exhaustive search of the published literature to address our questions. This search aimed to determine the scope of published literature between 2000 and 2024 concerning the number of published articles identifying a crayfish invasion pathway in the Great Lakes Basin. This time period was chosen due to the expanding usage of the internet following the new millennium and to provide insight into modern crayfish invasion pathways in the GLB. The search was conducted principally in Web of Science using a brute force approach that sought to use multiple combinations of keywords and replications of the search with quotations around certain keywords. The full list of keywords and combinations we used (along with search results) is provided in Suppl. material 1: table S1. We focused our efforts strictly on the peer-reviewed literature. Our decision to focus on peer-reviewed literature uses a reliable and indexed source of material that facilitated the collation of information of crayfish invasive pathways in this system.

To summarize our search procedure, we performed keyword queries for research papers on crayfish invasion pathways reported A) generally for the entire GLB and B) for individual states and provinces within the GLB (Ontario, Minnesota, Wisconsin, Michigan, Illinois, Indiana, Ohio, Pennsylvania, and New York). We also included the terms "non-indigenous" and "invasive species" to pull more papers that could report relevant information about crayfish but might not be the main topic of the paper. We further included three crayfish species in our searches (common name and species names) -- red swamp crayfish (*Procambarus clarkii*), marbled crayfish (*Procambarus virginalis*), and rusty crayfish (*Faxonius rusticus*) as these three species are of general management interest across the basin. In total, our search included up to 9 unique search terms and 92 total search combinations of these terms, including repeat searches where we modified specific keywords using quotation marks. We then identified the relevant literature for our review based on several decision criteria that filtered for papers pertinent to our study's questions. These criteria include whether the geographic scope of the paper fell within the GLB, if the paper identified/attributed any crayfish invasion pathways in the article, and if the paper was published during the period 2000–2024. These criteria allowed us to identify the recent history of identified crayfish invasion routes in the GLB and identify trends regarding the location of work, species of interest, history of work, and pathways used by crayfish to enter the Great Lakes Basin. We then categorized each article's invasion pathway(s) into one of the 6 general (Hulme) pathways (Release, Escape, Contaminant, Stowaway, Corridor, and Unaided). Finally, the specific pathway, if discussed, such as aquarium release or bait release, was recorded as a subcategorization of the general invasion pathway.

Results and discussion

Our literature search yielded a total of 4671 returns, from which we identified 47 articles that met our inclusion criteria, representing approximately 1% of all returned papers. Most papers we excluded reported on general invasive species topics, pathways for other invasive taxa (e.g., fish), or crayfish topics that otherwise failed to meet our criteria. All selected articles identified, indicated, or otherwise concluded on the presence of an invasion pathway through which an invasive crayfish reached or can reach GLB waterbodies (whether directly through the study's design, risk assessment, or by citing other studies; see Suppl. material 1: table S2).

Our comprehensive search strategy, employing 92 search terms, effectively captured the relevant publications for this review. As our search progressed, subsequent terms failed to uncover additional literature beyond what had already been identified by prior searches, indicating the thoroughness and exhaustiveness of our approach and the redundancy of search terms used. We generally observed that invasive crayfish reports increased over time, but few articles specifically identify the invasion pathway through which species reach the study location. This observation makes sense because freshwater invasions often go undetected for long periods before discovery, at which point managers' rapid response protocols will relegate the need to identify the probable pathways in lieu of containment measures to mitigate negative impacts (Muralidharan 2017; Morais and Reichard 2018; Lázaro-Lobo and Ervin 2021; Britton et al. 2023). In other words, it is difficult for managers to justify spending time and limited resources investigating how exactly the crayfish came into the system in the first place. Identifying the pathway used for any introduction is difficult to determine with certainty and this difficulty increases the longer an invasion goes undiscovered. Consequently, the majority of the published work we examined originated from academic laboratories or arose from collaborations between non-management and management entities (e.g., academic laboratories or non-governmental organization collaborating with a state's Department of Natural Resources).

Publications on crayfish invasion pathways in the Great Lakes Basin

From 2000 to 2024, our investigation revealed an average of ~2 articles per year that addressed crayfish invasion pathways in the GLB, indicating a modest output of papers that identified crayfish invasion pathways. Notably, during the first half of this period, we found an average of 0.91 articles per year that identified the invasion pathway used by crayfish to reach a location. In contrast, we observed an increase in the latter half of the period to 2.5 articles per year that identified the invasion pathway. This is an almost threefold rise in the rate of publications that identify the crayfish invasion pathway in their study. This increased trend in annual publications highlights the importance of research on crayfish invasion pathways. The majority of articles identified a single invasion pathway used by crayfish.

The spatial distribution of research papers on crayfish pathways encompassed several geographic foci (Fig. 1). Wisconsin, Michigan, and Illinois emerged as the primary research locales for recent literature on crayfish invasion pathways, accounting for 57% of regionally focused articles. Of the thirteen articles published in Wisconsin eight were released between 2001 and 2007 while in Michigan eight of the eleven articles have been published since 2017. The increase on crayfish invasion pathway research in Michigan occurred following the confirmation of red swamp crayfish within the state (Sard et al. 2023). The remaining 45% of papers identified invasion pathways in Canada, Indiana, New York, Ohio, and Pennsylvania. Only one state in the GLB, Minnesota, had no papers that identified crayfish invasion pathways specifically in that state. Seven papers on crayfish invasion pathways focused on the GLB region, with one additional nationwide analysis that included the GLB. This distribution highlights the geographic focus of existing research and underscores the importance of expanding the range of locations where we examine crayfish invasion pathways. We noticed that certain researchers and their lab groups (i.e. David M. Lodge – 7 publications) are well represented among the studies that identify crayfish invasion pathways, resulting in the high concentrations of papers on a subset of the states within the GLB (see Suppl. material 1: table S2).

Existing and emerging pathways

Non-native crayfish are introduced through a variety of invasion pathways. When we assessed the specific crayfish invasion pathways found in the GLB, the most common were natural dispersal (26%) and bait release (34%) (Fig. 2). Over fifty percent of all pathways identified in the literature were from these two categories. Escape from the retail trade was the third most common specific pathway found in the GLB (11%). The remaining specific pathways identified in the literature comprised less than 30% of crayfish invasion pathways. We found several relevant trends when assessing the first and second half of the review period. We noticed that from 2000 to 2012 over 70% of pathways identified were from either natural dispersal or bait release, while these two pathways comprised only 50% of specific pathways from 2013 to 2024 (Fig. 2). This 20% decrease suggests an increase in new pathways, awareness of previously unrecognized or underestimated pathways, and/or a decreased reliance on

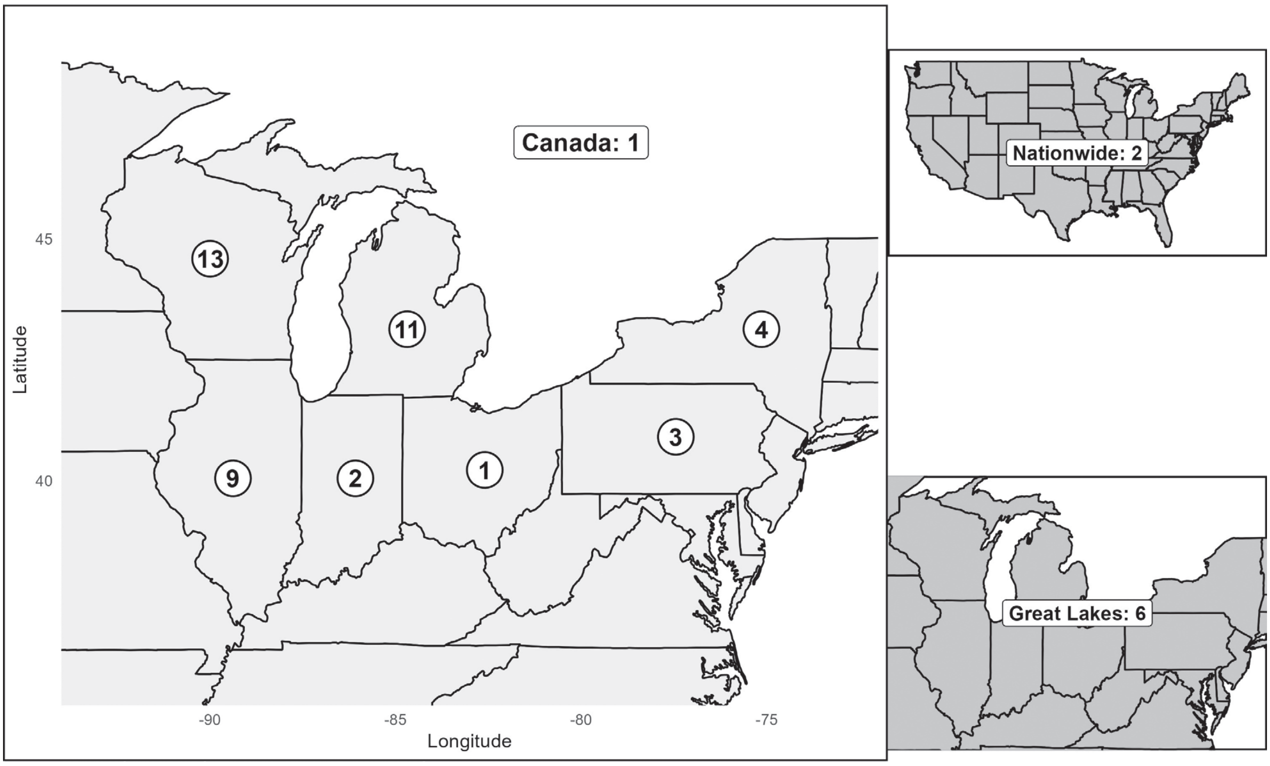

Figure 1. Map showing the number of articles published by region in the North American Great Lakes Basin. Each paper was counted once for the broadest scale it assessed. Geographical concentrations of authors repeatedly publishing on crayfish invasion pathways were found in Illinois, Michigan, and Wisconsin.

historical literature to identify invasion pathways for crayfish in the GLB. We observed four times more publications identifying the retail trade in the latter half of the assessment period. We also identified ten new pathways in the literature from 2013–2024 that did not appear in previous years. Only one specific pathway category, general release, was not reported from 2013–2024. The loss of this invasion pathway could be due to the increased specificity with which authors identified invasion paths and explained the increase in the number of described pathways found in the invasive crayfish literature for the GLB from 2013–2024.

The majority of crayfish invasions in the GLB occurred via release or unaided dispersal when using the general invasion pathway categorizations from Hulme et al. (2015). 42% of all the invasions across the study period occurred via the release pathway, which suggests an important role of people in the establishment of invasive crayfish populations. A caveat is that many invasions that were reported occurring via release are potentially confounded by the citation of previous work. In other words, many papers attributed a release as the invasion pathway without independent verification of this pathway as the source of an invasive population (Bobeldyk and Lamberti 2008, 2010; Szela and Perry 2013; Arcella et al. 2014; Glon et al. 2017). Unaided dispersal was the second most common general pathway found in the literature and comprised 36% of the total pathways identified. The interconnected nature of waterways in the Great Lakes Basin could explain the prevalence of unaided dispersal following establishment in this system (Bouvier et al. 2009; Milt et al. 2018; Morreale et al. 2023). Escapes made up ~15% of the remaining general invasion pathways, while stowaway and corridor introductions comprise less than 7% of the reported general invasion pathways. Stowaway was the only reported general pathway to appear only prior to 2012. Every other reported general pathway category was represented throughout the review period.

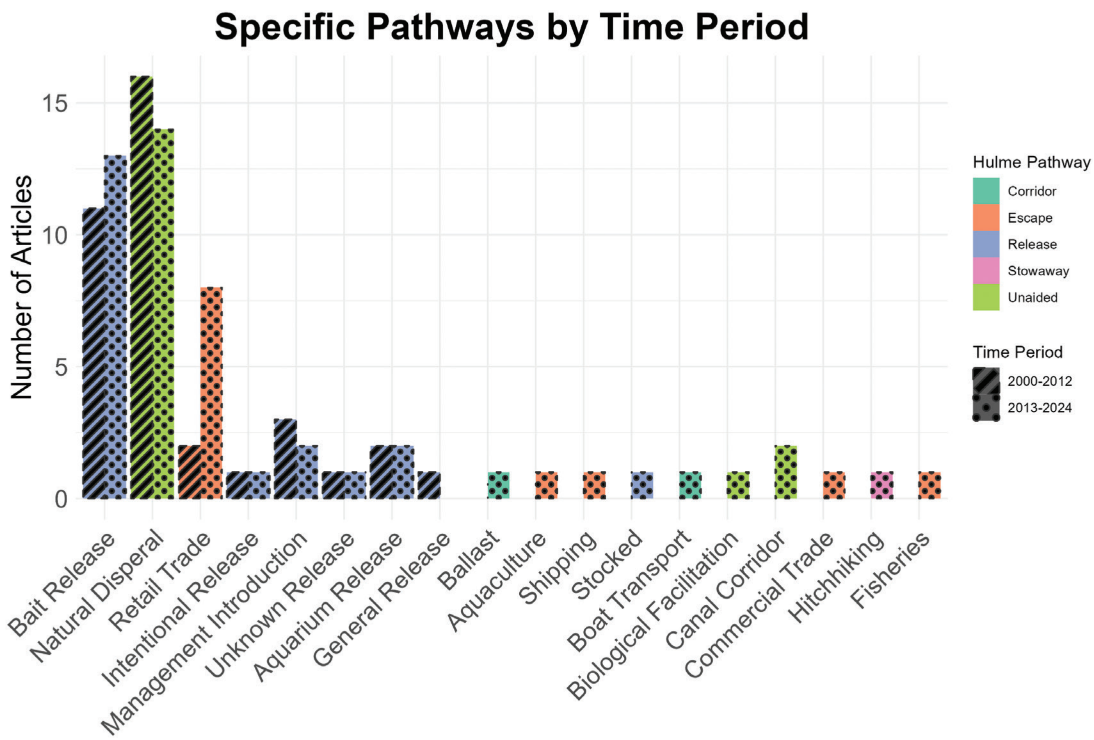

Figure 2. Histogram of the specific and general (Hulme 2015) invasion pathways identified for crayfish in the Great Lakes Basin. Published work was grouped from 2000–2012 and 2013–2024. The Hulme pathway is indicated by the color of the bar and the time period is indicated by the pattern.

Crayfish species and invasion pathways

We found invasion pathways explicitly linked to 13 crayfish species (Suppl. material 1: fig. S1) spanning three crayfish families (Astacidae, Cambaridae, and Parastacidae) (Crandall and Buhay 2008). The Cambaridae and Astacidae comprise Holarctic species in Europe and Western Asia (Astacidae) and the United States (Cambaridae and Astacidae), while the Parastacidae are strictly Neotropical and Australasian. The reported species included species native to the United States that are expanding their range through natural dispersal, and those introduced through accidental or intentional translocations, primarily from the Australasian and Eastern European biogeographic regions (Gherardi 2007, 2011).

Astacidae crayfish

Two Astacid crayfish were reported in the literature, one native to Eastern Europe and the other native to the Western United States (Crandall and Buhay 2008). The narrow-clawed crayfish (*Pontastacus leptodactylus*) (Eschscholtz, 1823) is native to Eurasia, with a broad range extending from eastern Europe through the Russian Urals with a southern range margin extending into Turkey (Davidson et al. 2021). Only a single study reported this crayfish occurring within the geographic scope covered in this review. In contrast, the other Astacid crayfish reported was the signal crayfish (*Pacifastacus leniusculus*) (Dana, 1852), native to the Upper Pacific coast of the United States (Larson and Olden 2011). This species is a well-documented invasive species in Europe, owing to intentional stocking to supplement fisheries harvests (Henttonen and Huner 1999; Bohman et al. 2006; Jussila et al. 2015). The species has proven to be an aggressive species to native European crayfish as well as a major carrier of crayfish plague (*Aphanomyces astaci*), to which European species are highly susceptible (Bubb et al. 2004; Bohman et al. 2006; Ruokonen et al. 2018). In the United States, *P. leniusculus* is predominantly restricted to the Pacific coastal states as the Rocky Mountains and the Great Basin are significant biogeographic barriers to their natural dispersal (Larson and Olden 2011). Our review found only a single publication identifying an invasion pathway for Astacid crayfish as part of an analysis on improving surveillance for the Great Lakes (Davidson et al. 2021). No Astacid crayfish are confirmed to be established in the GLB.

Parastacidae crayfish

Two species of crayfish from Parastacidae were reported to have a potential invasion pathway in the literature reviewed. These two species, *Cherax tenuimanus* (Smith, 1912) and *Cherax destructor* (Clark, 1936) were explicitly mentioned in a single publication examining the assessment of regulations for AIS and surveillance of AIS in the GLB (Davidson et al. 2021). Parastacid crayfish are found only in the Southern hemisphere; these species originated in Australia (Furse 2014). These species of Parastacid crayfish are of interest in the pet and aquarium trade, providing opportunities for their intentional or accidental release in new environments (Horwitz 1990; Chucholl 2013). To prevent the introduction of Parastacid crayfish into the GLB, it will be essential to assess the policies and surveillance of the retail and private trade of live crayfish while educating the public about the dangers of AIS (Lodge et al. 2016; Hoff et al. 2021). No Parastacid crayfish were reported to be established in the GLB.

Cambaridae crayfish

Thirteen species of Cambaridae crayfish were identified in the literature review. The preponderance of these species' invasion paths was focused on *Faxonius rusticus*, the rusty crayfish. Rusty crayfish are native to the Ohio River Basin in the United States and have long been a species of concern in the GLB (Wilson 1994; Kuhlmann and Hazelton 2007; Bobeldyk and Lamberti 2010; Olden et al. 2011; Tobler and Morehouse 2013). This species helped give rise to the concept of the "bait-bucket introduction," and these historical studies of crayfish invasion pathways are still commonly cited as the pathway for rusty crayfish invasion (Capelli and Magnuson 1983; Hobbs et al. 1989; Ludwig Jr. and Leitch 1996). Most research identifying rusty crayfish invasion pathways has come from a relatively small group of authors. The other Cambarid species that has received the most attention is *Procambarus clarkii*, the red swamp crayfish. Red swamp crayfish is a global invader that has historically been introduced as a food source in the aquaculture industry and today are often transported in the retail, aquarium, and scientific trade (Harper et al. 2002; Oficialdegui et al. 2020). Native to the Southern United States and Northern Mexico, red swamp crayfish have a variety of ecological impacts in invaded ecosystems (Gherardi 2006; Oficialdegui et al. 2020). The other remaining Cambarid species are understudied in comparison to rusty and red swamp crayfish (most being reported in at least one publication), with these species' invasion pathways being identified in broad threat analyses or reviews in the GLB (Lieb et al. 2011; Peters et al. 2014; Davidson et al. 2021). If crayfish invasions into the GLB continue, further examination of these other Cambarid species will be vital. They may utilize different pathways to expand their ranges in the GLB from the more frequently studied rusty and red swamp crayfish.

New information and opportunities for invasion pathway management in the Great Lake Basin

After reviewing published research over the past 24 years, there is substantial evidence that release and natural dispersal are the principal crayfish invasion pathways currently active within the GLB. Furthermore, the literature concludes that these two pathways are coupled: where release happens, dispersal to surrounding systems inevitably follows (Byron and Wilson 2001; Aquiloni et al. 2005; Gherardi 2006; Sard et al. 2023). The coupling of these pathways creates challenges for researchers and managers who seek to reduce the subsequent adverse effects of the invasion. Focusing efforts to constrain the release pathway would require a combined approach of public engagement and legislative enforcement to encourage awareness and proactive engagement (Seekamp et al. 2016). Inspection authorities could also develop training and workshops for agents and commercial owners to increase compliance and self-reporting (Oele et al. 2015). However, efforts to constrain natural dispersal are challenging to implement. Complete eradication of established invasive crayfish populations may be an impractical goal; instead, early detection and rapid response should be prioritized to prevent the establishment of new populations. One example of a successful early detection and rapid response to a crayfish invasion occurred in Eastern Wisconsin where an invasive population was successfully eradicated. This case study highlights the importance of early detection and rapid response and the difficulty in eradicating crayfish populations.

Another novel takeaway is that there is some consistency in the rate of work being published that explores crayfish invasion pathways throughout the GLB. However, given the bulk of research output was centered on three states and only a few species, researchers across the GLB currently have a relatively narrow lens for gauging active crayfish invasion pathways within the region. On the one hand, this could be interpreted as a positive sign that introductions do not occur at a rapid rate and that current management measures intended to prevent introductions (through release prohibitions, outreach programs, or regulations) effectively limit introduction rates. On the other hand, this narrow focus highlights the need for broader investigations that account for lesser-studied pathways, species, and geographic regions to ensure management strategies remain robust to potential future introductions.

What we also noticed from author affiliations was the high frequency of partnerships being leveraged by management and non-management entities to publish these research articles (e.g., the state Department of Natural Resources collaborating with academic laboratories). Such collaborations underscore the importance of integrating management and academic expertise to study crayfish invasions in the GLB effectively. For example, we identified that a current shortcoming of crayfish invasion pathway research in the GLB is an over-reliance on historical citations to identify the invasion pathway without further scrutiny (e.g., Capelli and Magnuson 1983; Ludwig Jr. and Leitch 1996). Alternate plausible invasion pathways can be uncovered through closer examination of newly established populations (e.g., Sard et al. 2023), and this work can further benefit from combining resources through partnerships and collaborations (Capelli and Magnuson 1983; Ludwig Jr. and Leitch 1996; Sard et al. 2023). Our findings, therefore, suggest that cooperative research efforts will be critical to current and future crayfish pathways research and can enhance our ability to communicate more clearly with the public and policymakers concerning where specifically to focus outreach and legislative efforts (Folke et al. 2005; Davidson et al. 2021; Hoff et al. 2021). Future pathways research for crayfish will likely need to rely on existing or more broadly established partnerships to fully assess and quantify pathway risks.

One area that can benefit from well-informed legislative efforts concerns the retail trade (e.g., aquarium shops, biological suppliers, wholesalers, and individual breeders), which could unintentionally (or otherwise) trade species under incorrect species and common names that would easily escape the attention of inspectors (Chucholl 2013; Olden and Carvalho 2024). Strengthening retail trade practice oversight, pet/aquaria ownership responsibility awareness, oversight of restricted species in biological supply for classrooms, and public education on the ecological consequences of introducing non-native species could mitigate this risk. Additionally, more systematic efforts to monitor and audit retail pathways would help detect and address these issues before they result in further introductions (Oficialdegui et al. 2025). Improving the accessibility to pet surrender and rehoming organizations may curtail the number of releases in the increasingly global and online ecosystem where a variety of species are readily available to individuals.

Through this review, we found steady progress in the last 24 years in researching crayfish invasion pathways within the GLB. Our findings add neatly to the global body of work on AIS invasion pathways, but despite this, significant gaps that limit our understanding of their full scope remain. Keller et al. (2011) noted historical knowledge deficiencies in invasion pathways in Europe, although they identified similar (ornamental trade) and different pathways (fisheries stocking) specific to this region . In contrast for South America, Loureiro et al. (2015) and de Oliveira et al. (2023) discussed the importance of the pet retail trade and aquaculture for invasive red swamp crayfish introductions, but little information is available overviewing active crayfish invasion pathways for this extremely biodiverse region of the world. While comprehensive and large-scale studies like ours for crayfish invasion pathways remain sparse, fortunately new research interest is increasing to examine the complexity of invasion pathways across larger and global spatial scales (e.g., Oficialdegui et al. 2019, 2020; Olden and Carvalho 2024). We also note that the available research disproportionately focuses on a narrow range of species and locations, leaving other potential pathways and regions underexplored. A reliance on older studies to identify pathways underscores the need for updated and comprehensive investigations into contemporary pathways, particularly new pathways identified in the second half of the review period. White papers, governmental reports, public websites, online databases (i.e. Great Lakes Aquatic Nonindigenous Species Information System), and theses/dissertations (i.e. gray literature) would likely further inform our regional understanding of crayfish invasion pathways. Strengthening collaborations between management entities, academic researchers, and policymakers to increase attention and efforts address emerging threats like misidentifications in the retail trade, will be critical to prevent future invasions. Existing researchers who are active in this area are valuable resources for managers and policymakers. We would encourage these groups to collaborate with researchers who are active in this space to implement science-based approaches and techniques. By broadening the scope of research and improving public outreach and regulatory frameworks we can more effectively safeguard the GLB's ecosystems against the continued threat of invasive crayfish.

Author contribution

Research conceptualization: WB, RK, PS, BR. Sample design and methodology: WO, WB, RO. Investigation and data collection: WO, WB. Data analysis and interpretation: WO. Ethics approval: NA. Funding provision: WB, BR. Roles/writing: original draft: WO, WB. writing - review & editing: WO, WB, RK, PS, BR.

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Data availability

Data including the manuscript data used for this review and all additional tables and figures are included as online Supplemental material with this manuscript.

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Supplementary material 1

Additional information

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Explanation note: **table S1.** Table of keywords used in searches on Web of Science. **table S2.** Table of papers included in this review that identified a crayfish invasion pathway.

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