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Research Article

Distribution of invasive scud, *Apocorophium lacustre* (Vanhoffen, 1911) in the Illinois Waterway, USA: Do habitat and water quality variables influence spatial distribution and relative abundance?

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Abstract

Apocorophium lacustre – a species of benthic amphipod native to American and European estuaries along the North Atlantic Ocean – has rapidly expanded outside of its native range and is now established in the Illinois, Upper Mississippi, and Ohio river systems, USA. *A. lacustre* is considered high risk for colonization and disruption of the Laurentian Great Lakes' benthic communities. To further our understanding of factors influencing *A. lacustre* distribution and its threat to the Great Lakes, zoobenthic and habitat data were collected from colonization samplers (i.e., rock bags) deployed at 370 sites along the Illinois Waterway. *A. lacustre* was found in the lower six pools of the Illinois Waterway and was the most abundant amphipod collected in those pools. Our results parallel other studies in that *A. lacustre* was not observed upstream of Dresden Island Pool, but *A. lacustre* was found ~11 km farther upstream of any previous records. Generalized linear mixed effects modeling indicated that parameters pertaining to food availability, water quality, and impoundment influenced *A. lacustre* abundance. Model averaging identified five statistically significant variables: *A. lacustre* abundance was negatively associated with turbidity, fluorescent dissolved organic matter, and vegetation density and positively associated with temperature and downstream distance (i.e., closer to the next downstream dam). Our findings of what factors influence *A. lacustre* abundance should be of broad interest to risk assessment and invasion forecasting in other regions where *A. lacustre* have been or may be introduced.

Key words: invasive amphipods, invertebrates, Illinois River, large rivers, Mississippi River Basin

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Introduction

Freshwater systems are heavily impacted by invasive species globally (Vitousek et al. 1996; Strayer 2010), which is a consequence of numerous anthropogenic factors. Vessel fouling, the live animal trade, and new artificial waterways are among

the most common vectors and pathways for aquatic invasive species transport (Keller and Lodge 2007; Panov et al. 2009). Invasive species disrupt food webs and extirpate native species, reducing both the ecological and economic productivity of affected systems (Rothlisberger et al. 2012; Gallardo et al. 2016). A prominent example is the invasive zebra *Dreissena polymorpha* (Pallus, 1771) and quagga mussels, *D. rostriformis bugensis* (Deshayes, 1838), which contribute to precipitous declines in phytoplankton populations that – through cascading, bottom-up changes in food web structure – have altered whole lake ecology (Ricciardi et al. 1997; Higgins and Vander Zanden 2010). Another example is the crustacean amphipods *Echinogammarus ischnus* (Stebbing 1899) and *Gammarus tigrinus* (Sexton, 1939) that subsequently displaced native amphipod species in the Laurentian Great Lakes (hereafter Great Lakes) through competition for resources and predation (Grigorovich et al. 2008 and references therein).

Early detection of invasive species – when they are present in low abundance (i.e., introduction phase) – is crucial to facilitate management efforts (i.e., eradication and control) and reduce undesirable ecosystem impacts (Myers et al. 2000; Trebitz et al. 2017). However, extensive sampling is required to detect a rare species that also may have a fragmented spatial distribution within a system (see Harvey et al. 2009; Hoffman et al. 2011). This scenario is further complicated with respect to small invertebrate invaders compared to larger organisms such as fish. Small invertebrates can spread undetected between large geographic barriers because they are readily transported via shipping-related vectors (e.g., ballast water and sediment residue, boat hulls, etc.; Grigorovich et al. 2003; Duggan et al. 2005; Drake and Lodge 2007); although, species introductions from shipping related vectors have decreased significantly following strict ballast water regulation of transoceanic ships by Canada and the United States (Ricciardi and MacIsaac 2022). Additionally, species level identification of small, cryptic invertebrates that can superficially resemble native species requires considerable taxonomic expertise and is labor intensive (Bartsch et al. 1998; Trebitz 2010). Consequently, fewer monitoring surveys and studies focus on invasive invertebrates relative to larger organisms, lowering the probability of both incidental detection and early detection. This results in new observations of invertebrates not occurring until higher densities are present in a system when management options may be limited. Accordingly, the most prevalent aquatic invaders in North America and Europe are invertebrates such as mollusks and crustaceans (Karatayev et al. 2009).

One such small invertebrate, the crustacean amphipod *Apocorophium lacustre* (Vanhoffen, 1911), is another invader whose spread and potential ecological impacts are of increasing concern. *A. lacustre* is a benthic detritus, suspension, and surface-deposit feeding (Llansó and Sillet 2009) amphipod native to both the Atlantic coast of North America (Bousfield 1973) and estuaries of the Baltic and North seas in northern Europe (Faasse and Moorsel 2003; Ezhova and Żmudziński 2005). On both sides of the Atlantic Ocean, *A. lacustre* is known to have a wide tolerance of salinity (Wolf et al. 2009) and electric conductivity (Szöcs et al. 2014) and is commonly found in both minimally saline water and fully fresh water (Shoemaker 1934; LeCroy 2004). The species can exist at hyper densities (>10,000 individuals/m^2; Payne et al. 1989; Krodkiewska et al. 2021) and is found on a variety of substrates including rock, sand, mud, macrophytes, and woody snags (e.g., Payne et al. 1989; Gaston et al. 1998; Faasse and Moorsel 2003; Grigorovich et al. 2008; LeCroy et al. 2009; Krodkiewska et al. 2021).

As a filter-feeding detritivore with a wide geographic range, broad salinity tolerance, and potential to exist at high densities, *A. lacustre* closely matches the profile of other globally successful aquatic invasive species (Karatayev et al. 2009; Bates et

al. 2013). Multiple federal departments in the United States have indicated that *A. lacustre* is a species of particular concern to the Great Lakes. Reports issued by the National Oceanic and Atmospheric Administration have highlighted *A. lacustre* as 1 of 16 species (out of 67) that pose a high risk for introduction and establishment to the Great Lakes (Fusaro et al. 2016; Lower et al. 2019). Similar reports from the U.S. Army Corps of Engineers state that *A. lacustre* is highly likely to be a significant risk to the Great Lakes and Mississippi River watersheds (Veraldi et al. 2011; Grippo et al. 2014). Additionally, results from a recent species distribution modeling study predicted that *A. lacustre* could establish throughout much of the Mississippi River Basin and the Upper Saint Lawrence River Basin, and the authors emphasized that the risk of invasion into the Great Lakes should be seriously considered (Egly et al. 2021a). If established in the Great Lakes, *A. lacustre* is expected to disrupt the benthic communities by overwhelming and outcompeting filter-feeders (Grigorovich et al. 2008), yet to the best of our knowledge, no studies exist on the ecological impacts of *A. lacustre* on the food web and benthic communities in invaded areas (Fusaro et al. 2016).

Since the mid-1900s, *A. lacustre* has rapidly expanded outside of its native range, which is attributed to transport by shipping vessels, where it fouls the hull and colonizes ballast tanks (Gollasch 2002; Llansó and Sillett 2009). *A. lacustre* was documented in estuaries of the Gulf of Mexico in the 1980s (Heard 1982) and in the lower Mississippi River in 1989 (Payne et al. 1989). The species was identified in the Ohio River in 1996, prior to its discovery in other parts of the Upper Mississippi River Watershed (Grigorovich et al. 2008). *A. lacustre* was next found in the Illinois River in 2003 (Benson 2018) before being collected in the Upper Mississippi River in 2005 (Grigorovich et al. 2008). By 2005, *A. lacustre* was reported within 100 river kilometers (rkm) of Lake Michigan in the Dresden Island Pool of the Illinois River (Benson 2018). One potential barrier to entering Lake Michigan and the Great Lakes is the electric dispersal barrier located in the Lockport Pool of Chicago Area Waterway System (CAWS), a portion of the larger Illinois Waterway (IWW) that connects Lake Michigan to the Illinois River (Figure 1). The electric dispersal barrier was designed to prevent interbasin transfer of invasive silver *Hypophthalmichthys molitrix* and bighead carps *Hypophthalmichthys nobilis* and other aquatic invasive species, but a recent laboratory study found that the barrier is likely insufficient for deterring small amphipods, especially if they are attached to vessel hulls or in ballast (Egly et al. 2021b). Fortunately, subsequent sampling efforts targeting the species upstream of the Dresden Island Pool (in the CAWS) have found no evidence that *A. lacustre* has established closer to the Great Lakes (Keller et al. 2017; Egly et al. 2021a). Nonetheless, there remains concern that the spread of *A. lacustre* into Lake Michigan from the IWW is highly likely given that the CAWS provides a direct pathway into the system through the Chicago River, Calumet River, Cal-Sag Channel, the Chicago Sanitary and Ship Canal, and the Des Plaines River – especially considering the opportunity for upstream movement on vessels that move millions of pounds of freight annually between Lake Michigan and the CAWS (Figure 1; Goodman Williams Group 2015).

Despite the growing attention *A. lacustre* has received in the Great Lakes region, there is little data available that describes its distribution, abundance, or behavior throughout the IWW – which connects the Great Lakes and Mississippi River basins. Two previous *A. lacustre* field studies have spatially covered the IWW from the Marseilles Pool upstream through the lower Des Plaines River, the CAWS, and even adjacent Lake Michigan harbors, concluding that *A. lacustre* is not found upstream of the Dresden Island Pool (Figure 1; Keller et al. 2017; Egly et al. 2021a).

These foundational studies on *A. lacustre* in the IWW and nearby Lake Michigan harbors covered a large spatial area but with relatively few sampling sites (70 sites over four years). Egly et al. (2021a) stated that *A. lacustre* presence may have been missed around the known invasion front in Dresden Island Pool (and possibly upstream) due to the possibility of low-density populations that are patchily distributed and that adding more sampling in locations where *A. lacustre* has and has not been found would expand our knowledge of their distribution. Furthermore, there are very few records – none of which are from the past ten years – that describe the distribution or abundance of *A. lacustre* for the lower Illinois River (i.e., Peoria, La Grange, and Alton pools) of the IWW. Lastly, while there is ample evidence that the species is tolerant of a broad range of abiotic conditions and salinity extremes, its relationship to most water quality variables and habitat associations remains unmeasured despite the rapid expansion of *A. lacustre* beyond its native range. Therefore, the objectives of this study were to sample the benthic amphipod community along the length of the IWW to 1) provide comprehensive distributional data for *A. lacustre*, and 2) assess how habitat and water quality variables influence the species' distribution and relative abundance to potentially aid in monitoring for *A. lacustre* in uninvaded areas.

Methods

Study site

As a main tributary to the Mississippi River, the Illinois River forms the basis of the >500-kilometer-long IWW that connects Lake Michigan and the Great Lakes Basin to the Mississippi River Basin (Figure 1). The hydrology of the Illinois River has been heavily modified from its natural state to control flooding and facilitate vessel navigation (Lian et al. 2012). The CAWS, or the upper portion of the waterway, includes the Chicago and Calumet rivers, and the Calumet-Sag Channel, that flow into the Chicago Sanitary and Ship Canal (CSSC) and then into the lower Des Plaines River (Figure 1). The CSSC starts at the Chicago Lock and Dam and flows downstream through the Chicago River and then to the Lockport Lock and Dam. The lower Des Plaines River includes the Brandon Road Pool, and the Illinois River portion of the waterway begins where the Des Plaines and Kankakee rivers join in the Dresden Island Pool (Figure 1). The Illinois River flows through six navigational pools of the IWW (Dresden Island, Marseilles, Starved Rock, Peoria, La Grange, and Alton pools) and into the Mississippi River near Grafton, Illinois (Figure 1). Dresden Island, Marseilles, and Starved Rock pools make up the "upper" Illinois River, while Peoria, La Grange, and Alton pools make up the "lower" Illinois River.

Field sampling

Amphipod, habitat, and water quality data were collected at randomly selected (without replacement) sites along the entire IWW (~566 river kilometers), including Lake Calumet (Figure 1). Given the geographical extent of this study, sampling was completed in two phases. Phase one sampling occurred between August-September 2020 and included all pools from Lockport Pool in downtown Chicago through the Alton Pool near the confluence with the Mississippi River, and phase two sampling occurred between July-August 2021 and included the Cal-Sag Channel, Lake Calumet, and Calumet River. (Figure 1). Random sampling sites were selected from two sampling frames that corresponded to each sampling phase

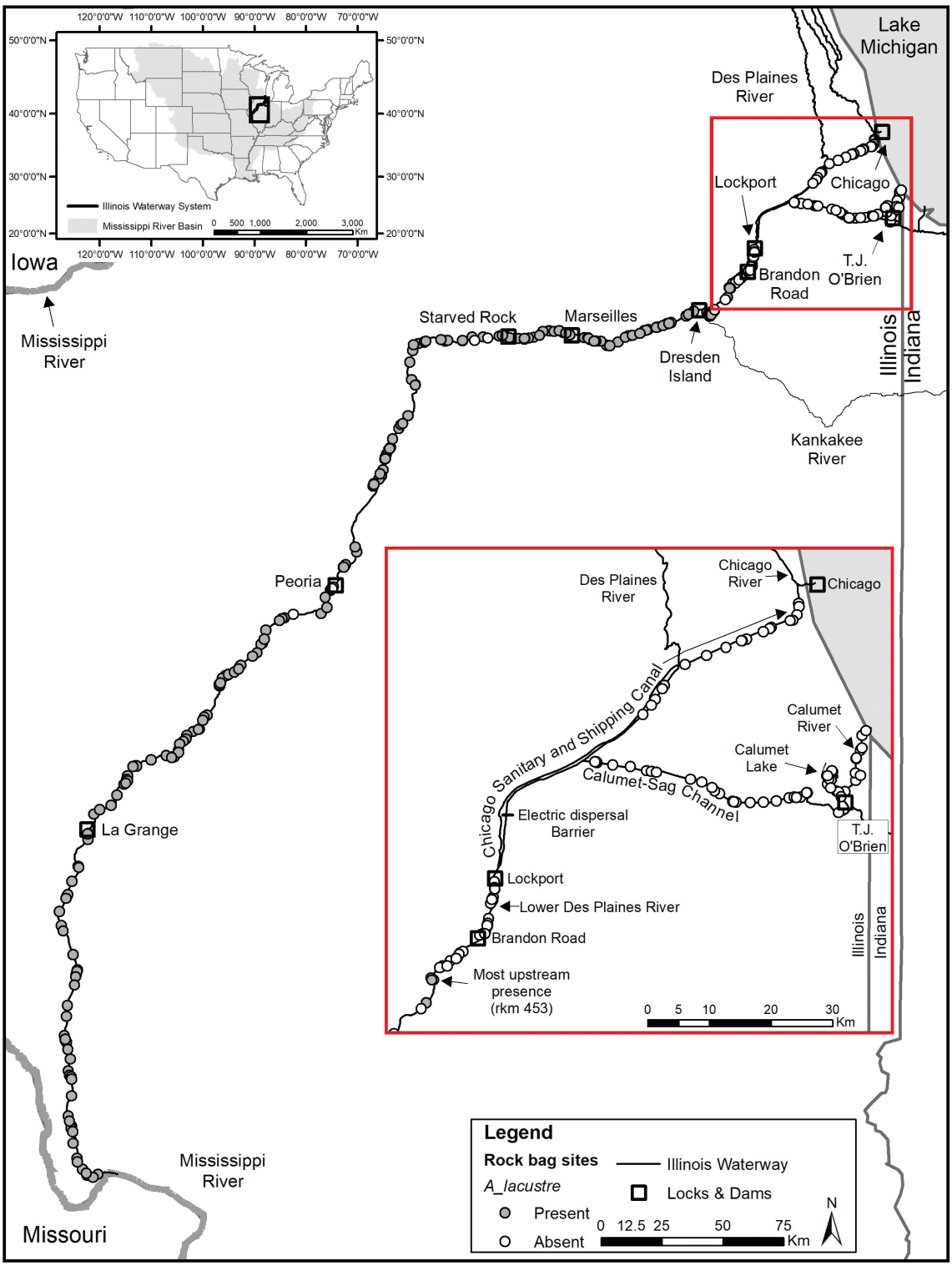

Figure 1. Study area and sampling distribution map showing benthic amphipod rock bag sampling effort in 2020–2021 across the Illinois Waterway. Black squares represent the dams at the downstream end of the pools/reaches of the Illinois Waterway. The Alton Pool ends at the confluence of the Illinois and Mississippi rivers and does not have a dam. The inset map provides a detailed look of the waterbodies comprising the Chicago Area Waterway System and lower Des Plaines River, including the current invasion front of *Apocorophium lacustre* based on this study.

(other than the portion of Lockport Pool upstream of the electric dispersal barrier to the Chicago Lock and Dam). Phase one sites were selected from an existing sampling frame developed by the Upper Mississippi River Restoration, Long-Term Resource Monitoring element for sampling the fish community of all pools of

the Illinois Waterway from Alton Pool to Lockport Pool (below the electric dispersal barrier). Phase two sites were selected from a sampling frame developed by generating sites at 100 m intervals along each section (e.g., Cal-Sag Channel, Calumet River, etc.). Due to Lake Calumet being a lake and not a river, sites were generated from straight lines positioned along the main body and each arm of the lake. To ensure spatial balance among sampling effort within each pool/section, all randomly selected sites were stratified by the upper and lower portions. Our target sampling effort was ~1 rock bag per 2.5 km (or 0.4 rock bags per rkm) for the larger pools of the waterway (i.e., Peoria, La Grange, and Alton pools), but a minimum of 24 rocks bags were deployed in shorter pools/reaches. Note that only 14 rock bags were deployed in Calumet Lake, but this exceeded our target level of sampling effort (Table 2). Also, we only sampled a portion of Lockport Pool (30.6 of 59.6 total rkm) due to safety concerns with sampling near the electric dispersal barrier and limited boat ramp access (Table 2). The higher number of rock bags per pool in the upper portion of the waterway boosted sampling density in areas where an *A. lacustre* population, if present, may be at low density, and allowed for more meaningful comparisons among pools.

Amphipods were collected using a colonization gear known as mesh rock bag samplers (hereafter rock bags; Equinox Limited, Williamsport, Pennsylvania), which have previously been used as an alternative to Hester-Dendy colonization samplers to capture amphipods in the IWW (Egly et al. 2021a). A rock bag consisted of a nylon mesh bag (length = 25.4 cm; width = 17.8 cm) reinforced with 500 µm plastic Nitex® mesh along the bottom 1/3 of the bag to retain small macroinvertebrates upon retrieval. Each rock bag contained a similar amount of Vigoro Decorative Rocks (between 2.5 and 7.6 cm in length), and rock bags were sealed with zip ties to enclose the mesh around the rocks. Rock bags were deployed for ~31 days to allow colonization by aquatic macroinvertebrates. To maintain consistency in the amount of rock within each rock bag, a 1 L, wide mouth bottle was filled with randomly selected rocks to a line that denoted 0.8 L. This amount of rock was based on past sampling results indicating the community of benthic macroinvertebrates was no different when using the amount of rock that filled bottles to 0.8 L or to 1 L (Brandon Harris, unpublished data). Rock bags were typically deployed by attaching them to bamboo stakes or permanent structures on shore using nylon rope except that rock bags in Lake Calumet were attached to small buoys; small concrete anchors were tied ~60 cm below the rock bags to limit their movement. When feasible, rock bags were deployed at a minimum water depth of 0.5 m to avoid air exposure caused by fluctuating river water depth, but this was not possible at every site. Rock bags were retrieved and placed in plastic bags or large plastic containers (filled with river water) in the field and then stored on wet ice until processed. Each sample was processed within 24–48 hours of collection by thoroughly flushing all material in the rock bag and their storage containers through a 500-micron sieve. All sieved contents were preserved in 95% ethanol and then all amphipods were separated from other material under a dissecting scope. Only *A. lacustre* (≥2 mm) and *Hyalella azteca* (Saussure, 1858; typically ≥1 mm) amphipods were identified to species because they are distinct from other gammarid amphipod species in the region, which can be extremely difficult and time consuming to identify to species. However, all other intact amphipods ≥2 mm long were identified to genus and enumerated. Unidentifiable individuals, either below the size thresholds or not intact, were not counted or included in analyses. Post-retrieval, the minimum depth of each site was calculated based on pool-level change in river gauge depth from the nearest stream gage (U.S. Geological Survey 2020). During phase one sampling in 2020, sites that experienced <12 cm

of water depth were excluded from analyses because we assumed those rock bags may have been exposed to air for part of the deployment period. No minimum depth experienced during deployment was considered during phase two sampling because the average depth where rock bags were deployed was deep (min = 0.5 m; mean = 2.1 m ± 2.3 SD) relative to phase one sampling.

The IWW is a large complex river that spans >500 kilometers and has varying levels of water pollution and habitat characteristics as you move from highly urbanized areas near Lake Michigan downstream to the confluence with the Mississippi River (Delong 2005; Battaglin et al. 2020). Given the few specific examples of water quality and/or habitat variables preferred by *A. lacustre*, our intent was to assess water quality and habitat variables that broadly described the lotic environment but that also were known to be important to the distribution and/or abundance of amphipods. A list of suitable variables was compiled by cross-referencing published literature for eight amphipod species present in several large rivers near the IWW (see Grigorovich et al. 2008 for list of river and species). We identified turbidity, water discharge, substrate, conductivity, salinity, water depth, dissolved oxygen, aquatic vegetation, and structure (e.g., large woody debris) as potentially important variables to amphipods (Bousfield 1958; Rees 1972; Grigorovich et al. 2008; Krodkiewska et al. 2021; Benson et al. 2023; Fusaro et al. 2023; Kipp and Hopper 2023; Kipp et al. 2023). We included the distance (in rkm) of a site from the next upstream dam (herein 'downstream distance') as a variable in this study given the hydrologic and ecological trends caused by impoundment (Baxter 1977; Schmutz and Moog 2018), and because it was hypothesized that a lack of navigational pools (i.e., lentic habitat) and associated characteristics may explain why several amphipod species were not present in the Missouri River, USA (Grigorovich et al. 2008). Lastly, fluorescent dissolved organic matter (fDOM) was included as a proxy for dissolved organic carbon (food availability) and dissolved organic matter (water quality; see Fellman et al. 2010, and references therein; Snyder et al. 2018).

Habitat variables, depth, and water quality data were recorded when rock bags were deployed at each site during phase one sampling; only water depth and temperature were recorded during phase two sampling. We followed the categorical habitat data collection procedures for aquatic submergent and/or emergent vegetation density, substrate, and structure presence from the Long-Term Resource Monitoring Program protocol (Ratcliff et al. 2014) except that we reduced the observational area around the site from 100 m to 20 m radius given the sessile nature of amphipods (relative to fish). Vegetation density was recorded as a categorical variable with three levels: no aquatic vegetation, sparse aquatic vegetation (< 50% coverage), or dense aquatic vegetation (> 50% coverage). Substrate was classified using Long-Term Resource Monitoring element categories: mostly silt, mix of silt/clay/sand, mostly sand, or gravel/rock/hard clay. A site was recorded as containing structure if woody debris, artificial substrate, or revetments were observed within the site. Water depth (cm) was recorded at the location of the rock bag using a meter stick or a depth sounder in deeper water. Water quality data were recorded using a multi-parameter YSI EXO2 water quality sonde; the sonde was deployed immediately upon reaching a site to avoid sediment plumes caused by the boat or when people deployed rock bags. Temperature (°C), salinity (ppt), dissolved organic matter (fDOM; ppb), dissolved oxygen (DO; mg/L), and turbidity (FNU) were collected using the sonde. Downstream distance (rkm) of a site (relative to an upstream dam) was determined using ArcGIS Desktop (version 10.8.1; ESRI 2020). Mean pool-level river discharge (ft^3/sec) data were compiled via pool specific river gauges from the same time period that the samplers were deployed (U.S. Geological Survey 2020).

Abundance analysis

A generalized linear modeling approach was used to examine factors related to *A. lacustre* abundance (number of *A. lacustre* per rock bag) at a site. A negative binomial (NB) distribution was used because it more closely matched (NB simulation with a probability [*p*] = 0.00425) the distribution of *A. lacustre* abundance compared to the more commonly used Poisson distribution for modeling count data. Our *A. lacustre* data had substantial zero-counts and a high maximum (max = 3887). When compared to a simulated Poisson distribution with the same mean (l = 190.8) our data was heavily right skewed, which is captured by the NB distribution. There also was inherent spatial collinearity due to the natural gradient of the river and its linear structure. A mixed effect structure was added to account for spatial nonindependence, including navigational pool/sampling reach as a random effect in our NB models to avoid violating the independent sampling assumption of generalized linear models. By including this random effect, the model accounted for differences in the *A. lacustre* population between the spatially explicit pools. Data from Brandon Road and Lockport pools and the Calumet-Sag Channel, Lake Calumet, and Calumet River were excluded from this analysis because *A. lacustre* did not occupy these areas based on our sampling. Eleven candidate models were generated by grouping independent variables into themes related to Food Resources, Water Quality, Impoundment, Downstream Distance, Structure, Estuarine characteristics, Physical Parameters, Interspecific Competition, Structure, and variables from a previous study by Krodkiewska et al. (2021; Table 1). There is no consensus in the literature for which variables may affect the distribution of *A. lacustre* other than the findings of Krodkiewska et al. (2021) from the native range of *A. lacustre* in the Upper Oden River Catchment, Poland; the authors reported a correlation between *A. lacustre* abundance, depth, substrate silt percentage, and current velocity (only depth and velocity were statistically significant). For this reason, we chose to broadly explore our data but also sought to confirm the findings of Krodkiewska et al. (2021).

The generalized linear mixed-effects model was developed using the *lme4* package in R v4.0.2 (Bates et al. 2015; R Core Team 2020). All numerical covariates were z-score standardized prior to analysis, and all models were assessed for predictor collinearity using variance inflation factor. Menard (2001) suggested that a variance inflation factor >5 was a cause of concern and values >10 indicated severe predictor collinearity, so we rejected any variable if the associated variance inflation factor was >5. A corrected Akaike's Information Criterion (AICc; Akaike 1974; Sugiura 1978; Hurvich and Tsai 1991) was used to assess all models, and all fixed effects were evaluated using an AICc natural model averaging approach (Buckland et al. 1997; Anderson and Burnham 2002) using the AICcmodavg R package (v2.3-1; Mazerolle 2020). The natural model averaging method averages the parameter estimates of each variable only over the models where the variable is present (Symonds and Moussalli 2011). Parameters were considered statistically significant (at $\alpha = 0.05$) when their model-averaged, log-scale 95% confidence intervals did not include zero. Values of the standardized β coefficient were reported to determine magnitude of effect. A positive β-value indicated that a high exposure level of a predictor variable increases the response variable (i.e., *A. lacustre* relative abundance), whereas a negative β-value indicated that a high exposure level of a predictor variable decreases the response variable. Specifically, the β-value refers to how many standard deviations the response variable will change per one standard deviation increase in the predictor variable. The β-value also was used as an estimate of the effect size, with β-values between 0.10–0.29 considered a small effect

Table 1. Model descriptions, K number of parameters, and AICc results for models used in analysis of *Apocorophium lacustre* abundance data. The model was a negative binomial generalized linear models with mixed effects structure. Each Model Theme included one Random Effect – river pool (Pool) – that was included to account for spatial nonindependence of samples. The response variable for the model was site-level *A. lacustre* abundance. Fixed Effects groups were assessed for multicollinearity using Variance Inflation Factor (VIF): no model included any variable with VIF ≥5. All numeric variables were standardized with a z-score prior to use in analyses.

Model Theme	Fixed Effects	Random Effect	K	AICc	ΔAICc
Food Resources	fDOM, Misc. Amphipod Abundance, Turbidity, Vegetation Density	Pool	7	2550.1	0.0
Water Quality	DO, fDOM, Turbidity, Salinity	Pool	7	2553.4	3.3
Impoundment	Depth, DO, Downstream Distance, Silt Substrate, Vegetation Density	Pool	8	2556.7	6.6
Downstream Distance	Downstream Distance	Pool	4	2556.9	6.8
Structure	Hard Substrate, Structure Presence, Vegetation Density	Pool	6	2589.1	39.0
Estuarine Characteristics	DO, Salinity	Pool	5	2589.3	39.2
Physical Parameters	All Substrate Types, Depth, River Discharge, Structure Presence, Temperature, Vegetation Density	Pool	11	2589.4	39.3
Null Model	None	Pool	3	2589.6	39.5
Interspecific Competition	Misc. Amphipod Abundance	Pool	4	2590.8	40.7
Krodkiewska et al. 2021	Depth, River Discharge, Silt Substrate	Pool	6	2592.7	42.6
Substrate Type	All Substrate Types, Structure Presence	Pool	7	2594.6	44.5

size, 0.30–0.49 a medium effect size, and ≥0.5 a large effect size (Cohen 1988). In this way, we were able to use statistical inference to make dichotomous decisions about a variable's statistical effect on *A. lacustre* abundance, etc., which can be used by researchers when building models to predict high probability areas to search for *A. lacustre*. Furthermore, applying qualitative effect size categories to β-values allowed us to determine the magnitude (i.e., biological effect) of the statistical effect on *A. lacustre* abundance, etc.

Results

Distribution assessment

During 2020 and 2021, rock bags were deployed for 33 days (± 3 days) at a total of 370 sites along the IWW (Figure 1). Rock bags were successfully recovered from 316 of 370 sites; eight sites were then removed because they met criteria indicating they may have been exposed to air due to a drop in water levels (Table 2; Figure 1). The mean depth across sites was 1.2 m (range: 0.4–9.2 m). The overall recovery rate was high (85.4%) but varied among pools/reaches, with the lowest recovery rate occurring in Starved Rock Pool (17/25 or 68.0%) and highest in the Cal-Sag Channel/Calumet River (39/40 or 97.5%; Table 2). *A. lacustre* was captured at 64.3% of all sites (198 of 308 sites) across the waterway (Suppl. material 1, Table 2). *A. lacustre* was not collected upstream of Dresden Island Pool, which is consistent with previous sampling (Egly et al. 2021a; Table 2, Figures 1, 2). However, we did collect *A. lacustre* ~11 rkm upstream (at rkm 453) of the previously known invasion front in Dresden Island Pool (Figure 1). Overall, *A. lacustre* was captured in the lower six pools of the Illinois Waterway (Alton, La Grange, Peoria, Starved Rock, Marseilles, and Dresden Island; Table 2, Figure 1). Where present, the percentage of sites where *A. lacustre* was captured was lowest in Dresden Island Pool (47.8%) and highest in Marseilles and Starved Rock pools (100.0%; Table 2). *A. lacustre* was abundant in all pools of the lower Illinois River and Starved Rock and Marseilles pools of the upper

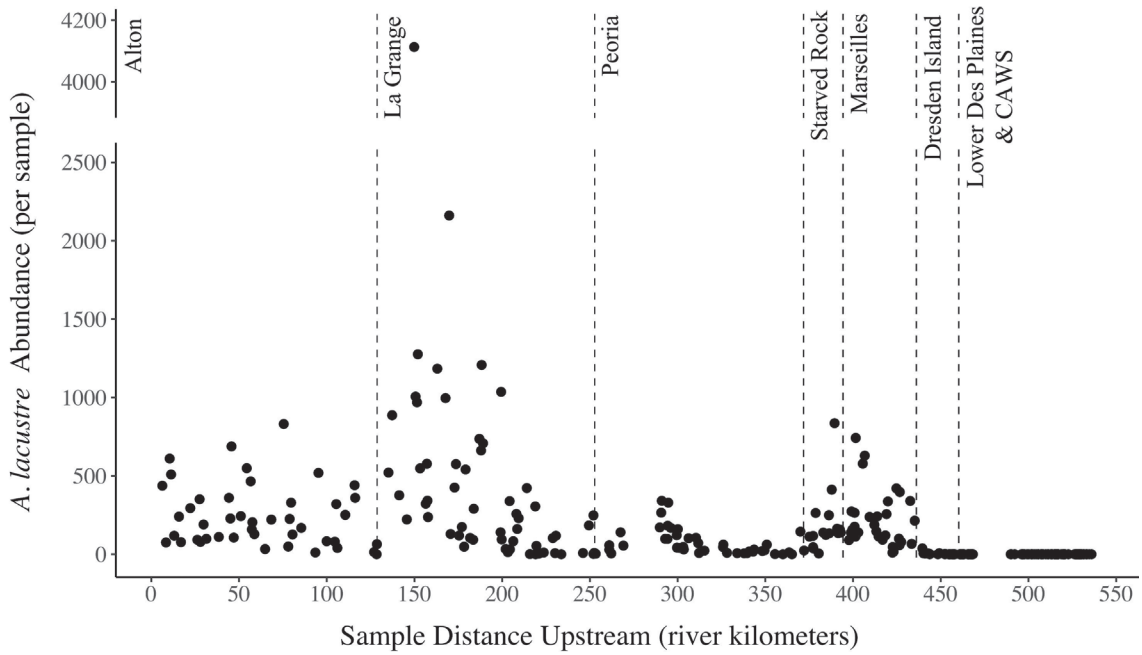

Figure 2. *Apocorophium lacustre* abundance in rock bag samples collected during 2020–2021 benthic amphipod survey across the Illinois Waterway (n = 308). The x-axis indicates a sample's location in river kilometers along the length of the Illinois Waterway. See Figure 1 for a detailed description of the Illinois Waterway but note that river kilometers are identical for portions of the Chicago Sanitary and Ship Canal and the Calumet-Sag Channel/Calumet River. The value x = 0 represents the confluence of the Illinois and Mississippi rivers; x = 526 in the Sanitary and Ship Canal represents the Chicago Lock and Dam where Lake Michigan drains into the Chicago River, and x = 536 is where Lake Michigan drains into the Calumet River (located south of the Chicago River).

Illinois River. *A. lacustre* was not abundant in Dresden Island Pool (the most upstream pool of in the upper Illinois River), where we saw a 66-fold decrease in mean *A. lacustre* abundance (only 75 total *A. lacustre* individuals in samples) relative to the adjacent Marseilles Pool (Table 2; Figure 2).

Percent of sites occupied by *A. lacustre*, mean amphipod and *A. lacustre* (where present) abundance (mean number of individuals per rock bag across all sites within a pool), and proportion of *A. lacustre* (relative to all amphipod taxa) varied considerably across pools/reaches of the IWW but generally increased from upstream to downstream (Table 2). Pool-specific mean amphipod abundance across sites was lower in the upper portion of the waterway (i.e., CAWS and upper Illinois River) and higher in the lower portion of the waterway, but Lockport (mean = 201.1 ± 342.8 SD) and Peoria pools (mean = 98.7 ± 96.3 SD) were exceptions to this pattern (Table 2). Where present, mean *A. lacustre* abundance was quite variable, with Dresden Island Pool having the lowest mean abundance (mean = 3.3 ± 7.7 SD) and La Grange Pool having the highest (mean = 431.3 ± 648.8 SD; Table 2). The mean proportion of *A. lacustre* (relative to all amphipod taxa) across sites was lowest for Dresden Island Pool and increased downstream, with pools having proportions that ranged from 73.8–79.6%, except for the Peoria Pool (mean = 91.0% ± 14.2 SD; Table 2).

A. lacustre relative abundance appeared to be higher moving downstream within each pool (Figures 2, 3). There was a statistically significant, positive correlation (medium effect size) between *A. lacustre* abundance and distance to the next upstream dam when considering all pools (i.e., Dresden Island to Alton pool) containing the species ($r[214] = 0.34$, $p < 0.05$). Across pools, only Starved Rock Pool did not have a positive correlation (medium effect size) between *A. lacustre* abundance and downstream distance ($r[15] = -0.40$, $p > 0.5$),

Table 2. Summary of biological sampling effort at randomly selected sites on the Illinois Waterway during 2020–2021. At each site, a rock bag sampler was deployed for 33 (± 3) days to collect amphipods. Not all samplers were recovered (Recovered sites), and some sites were excluded due to water levels dropping to the point where rock bag samplers may have not been fully submerged. All intact amphipods ≥2 mm long were identified to genus and counted; *Apocorophium lacustre* and *Hyalella azteca* were identified to species. *H. azteca* is distinct from other species in the region and was identified and counted regardless of size as long as key features were visible (typically ≥1 mm). Mean amphipod abundance (including all taxa) and mean *Apocorophium lacustre* abundance represented an average across sites, within each specific pool/reach of the waterway. Percent of sites occupied by *A. lacustre* was the number of sites where *A. lacustre* was present divided by the total number of sites within that pool/reach, expressed as a percentage. Mean *A. lacustre* proportion was the number of *A. lacustre* in a sample (i.e., a site) relative to the number of all amphipod taxa within that sample, expressed as a percentage.

Pool/Reach	Length (km)	Sites set	Recovered sites (excluded)	Sample density (no./rkm)	Mean amphipod abundance (±SD)	Mean *A. lacustre* abundance (±SD)	Percent of sites occupied by *A. lacustre* (%)	Mean proportion (%) *A. lacustre*/ site (±SD)
Lake Calumet	12.8	14	13	1.02	20.1 (19.0)	0	0.0	0
Cal-Sag Channel/ Calumet River	46.7	40	39	0.84	66.3 (74.8)	0	0.0	0
Lockport	30.6	24	19 (1)	0.62	201.1 (342.8)	0	0.0	0
Brandon Road	8.0	24	21	2.63	60.2 (39.5)	0	0.0	0
Dresden Island	24.1	24	23	0.95	94.3 (52.0)	3.3 (7.7)	47.8	4.7 (10.0)
Marseilles	41.8	32	31	0.74	259.1 (172.0)	218.5 (179.5)	100.0	79.6 (25.5)
Starved Rock	22.5	25	17	0.76	193.7 (198.3)	181.5 (195.2)	100.0	91.0 (14.2)
Peoria	119.0	50	42	0.35	98.7 (96.3)	76.1 (85.1)	95.2	73.8 (26.4)
La Grange	123.9	87	59 (7)	0.48	470.1 (660.1)	431.3 (648.8)	94.9	78.5 (26.3)
Alton	122.3	50	44	0.36	292.0 (206.9)	240.3 (198.6)	97.7	75.5 (24.6)

but this relationship was not statistically significant. Positive correlation of *A. lacustre* abundance with downstream distance was statistically significant with a large effect size in the Dresden Island Pool ($r[21] = 0.52$, $p < 0.05$), followed by a medium effect size for La Grange Pool ($r[57] = 0.48$, $p < 0.05$), and Peoria Pool ($r[40] = 0.40$, $p < 0.05$). Similarly, both Marseilles Pool ($r[29] = 0.22$, $p > 0.05$) and Alton Pool ($r[42] = 0.18$, $p > 0.05$) had positive correlations with downstream distance, but these correlations were not statistically significant and had a small effect size.

Abundance analysis

Food availability and water quality models were the best predictors of *A. lacustre* abundance based on AICc (Table 1). The food resource model fit best, substantially outperforming the null model (ΔAICc = 39.5; Table 1). The model containing water quality variables fit only marginally worse than the top model (ΔAICc = 3.3), but this model shared two variables with the food resources model – turbidity and fDOM (Table 1). The two models that included downstream distance also performed substantially better than the null model (ΔAICc = 6.6–6.8), suggesting that the ecological gradient between dams may be important for explaining observed patterns in *A. lacustre* abundance (Table 1). Model-averaging the coefficients from this set of models yielded five significant non-zero effects (Table 3). Turbidity (b = -0.46), fDOM (b = -1.35), and vegetation density (b = -1.00) all had negative effects on *A. lacustre* abundance (with medium to large effect sizes), while temperature (b= 0.26) and downstream distance (b = 0.66) had positive log-scale effects on *A. lacustre* abundance with small and large effect sizes, respectively (Table 3). Specific conductivity was excluded because its VIF greatly exceeded our threshold of ≥5 and it was correlated with salinity.

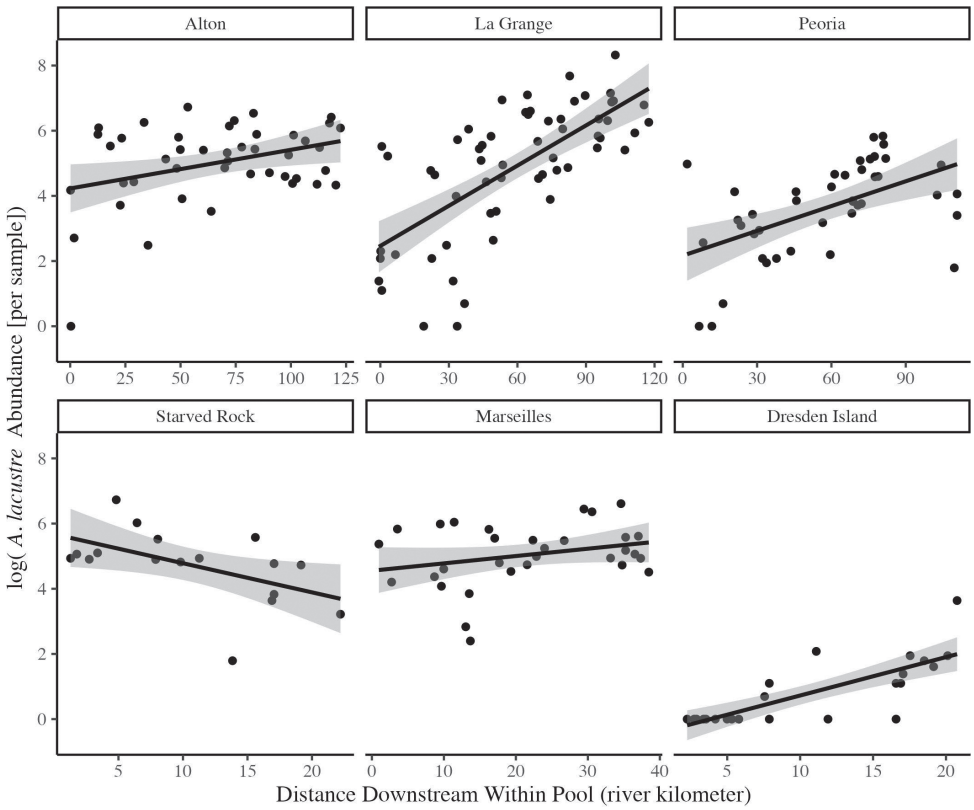

Figure 3. *Apocorophium lacustre* abundance (per sample on the log-scale, calculated with natural log of abundance + 1) at rock bag sites within all pools (where detected) across the Illinois River portion of the Illinois Waterway as a function of distance downstream in river kilometers (higher values are closer to the next downstream dam). Note that the Alton Pool is an exception because it is undammed; the downstream end of the Alton Pool is the confluence of the Illinois and Mississippi rivers whereas the downstream ends of other pools are dammed. Pool specific trendlines represent linear lines of best fit based on associated data points.

Table 3. Results of AICc model averaging procedure on fixed effect parameters included in negative binomial mixed effects models predicting *Apocorophium lacustre* abundance. Asterisks (**) indicate parameter effects that were considered statistically significant when the 95% confidence intervals did not include zero. Confidence intervals are presented on the log-scale. The magnitude of the log scale effects were qualitatively categorized as having no magnitude (<0.10, represented by "–"), small (0.10–0.29), medium (0.30–0.49), or large (≥0.50) based on Cohen (1988). See Methods for a detailed description of each parameter.

Parameters	Log-scale effect	Magnitude of Effect	95% Confidence Interval		SE
			Lower	Upper	
fDOM**	-1.35	Large	-1.74	-0.95	0.20
Vegetation Density**	-1.00	Large	-1.83	-0.17	0.42
River Discharge	-0.85	Large	-1.96	0.27	0.57
Turbidity**	-0.46	Medium	-0.77	-0.15	0.16
Mixed Substrate	-0.33	Medium	-1.00	0.33	0.34
Salinity	-0.20	Small	-0.58	0.19	0.20
Depth	-0.12	Small	-0.35	0.10	0.11
DO	-0.11	Small	-0.44	0.21	0.17
Hard Substrate	-0.07	–	-0.59	0.44	0.26
Silt Substrate	0.02	–	-0.42	0.46	0.22
Sand Substrate	0.07	–	-0.50	0.64	0.29
Misc. Amphipod Abundance	0.08	–	-0.12	0.28	0.10
Structure Presence	0.15	Small	-0.34	0.64	0.25
Water Temperature**	0.26	Small	0.01	0.52	0.13
Downstream Distance**	0.66	Large	0.45	0.88	0.11

Discussion

This study represents the first comprehensive and the most intensive effort to date to determine the distribution of *A. lacustre* in the IWW and understand how *A. lacustre* interact with benthic habitat, producing several noteworthy findings. First, our study advanced the known upstream location of *A. lacustre* by ~11 rkm in the IWW, and importantly, our results confirmed previous studies that found *A. lacustre* still has not established farther upstream than the Dresden Island Pool. Second, we determined that *A. lacustre* is abundant from Marseilles Pool downstream to Alton Pool and dominates the amphipod community in those pools. Lastly, we found that several variables are correlated with *A. lacustre* abundance, including parameters pertaining to food availability, water quality, and impoundment. Overall, our findings greatly add to our understanding of what factors influence *A. lacustre* distribution and abundance, which should be useful in future risk assessment and invasion forecasting for this species within the Great Lakes watershed and in other regions where *A. lacustre* have been introduced.

Our pool-level distribution data is consistent with United States Geological Survey records and previous studies. *A. lacustre* was found in the lower six pools of the IWW (Table 2; Figure 2). These pools represent ~85% of the river distance between the Mississippi River and Lake Michigan – with only approximately 70 rkm between the Brandon Road Lock & Dam and Lake Michigan. It is a positive sign that our results show *A. lacustre* has not invaded pools farther upstream of Dresden Island Pool, where sampling has previously occurred (Keller et al. 2017; Benson 2018; Egly et al. 2021a). Our collection of *A. lacustre* in 2020 advanced the known upstream presence of *A. lacustre* in the Dresden Island Pool by ~11 rkm (collected at rkm 452) from the 2019 upstream location found by Egly et al. (2021a; Figure 1). This warrants further monitoring of *A. lacustre* around the current known invasion front to ensure this detection is not continued upstream spread of the species but rather just differences in sampling locations among studies. Our results show that the *A. lacustre* population in this area is low density and may be patchily distributed, which calls for intensive sampling so that movement of the invasion front can be accurately monitored.

The robust sampling effort in this study spanned the entire IWW and permitted us to address multiple hypotheses simultaneously about what factors may influence the abundance and distribution of *A. lacustre*. Our analysis indicated several statistically significant predictors of *A. lacustre* abundance: fDOM, vegetation density, turbidity, water temperature, and downstream distance. To the best of our knowledge, there are virtually no published studies that quantify *A. lacustre* and its relation to water quality and habitat characteristics – especially in their invaded range. Our model indicated that the abundance of *A. lacustre* increased as water temperature and downstream distance (i.e., closer to downstream impounded area of pool) increased, while *A. lacustre* abundance decreased as FDOM, vegetation density, and turbidity increased (Table 3; Figure 3). No statistically significant association between *A. lacustre* abundance and substrate was identified in this study, which is consistent with the species being commonly found on a variety of soft and hard substrates (e.g., Payne et al. 1989; Gaston et al. 1998; Faasse and Moorsel 2003; Grigorovich et al. 2008; LeCroy et al. 2009; Krodkiewska et al. 2021). Interestingly, we did not find any statistically significant relationship with *A. lacustre* abundance and water depth like that of Krodkiewska et al. (2021) in the Upper Oden River Catchment, Poland. We found a strong negative – but not statistically significant – relationship between *A. lacustre* abundance and river discharge (Table 3), which contrasts the findings that *A. lacustre* was mainly associated with

faster river velocities by Krodkiewska et al. (2021). Although interesting, no conclusions should be drawn given that we used discharge as a proxy for site specific water velocity and the relationship was not statistically significant.

We do not entirely understand why *A. lacustre* abundance was negatively associated with turbidity, vegetation density, and fDOM in the IWW, and further research is needed to better understand potential mechanisms (Table 3). Like some amphipod species, *A. lacustre* may just have an aversion to turbidity (Anteau et al. 2011), while other species have been found to be more abundant in the presence of high turbidity for reasons such as decreased predation by visual fish predators (Kotta et al. 2013). Increased turbidity in the Missouri River, USA (relative to the Ohio and Upper Mississippi rivers) was hypothesized as one reason why several amphipod species (including *A. lacustre*) did not establish in the Missouri River (Grigorovich et al. 2008). The mixture of suspended solids that cause water turbidity also can vary widely in composition from inorganic to organic matter and plankton and microorganisms, etc., likely with differing effects. Similar to turbidity, some amphipod species show strong positive associations with aquatic vegetation (Anteau et al. 2011; Larson et al. 2022; Kipp and Hopper 2023) while other species abundance is independent of vegetation. This aversion of *A. lacustre* to vegetated habitats could possibly be due to their tube dwelling behavior and filter-feeding ability (Fusaro et al. 2023) that may decrease overall predation risk, lowering the need to seek refuge and compete for resources in vegetated habitats occupied by other species. fDOM is considered a proxy for dissolved organic carbon concentration (Snyder et al. 2018), and dissolved organic matter plays a critical role in aquatic food webs because it is the source of carbon and nitrogen for heterotrophic organisms (Fellman et al. 2010, and references therein). A negative association with fDOM could be due to higher fDOM indicating more food availability, especially in the lower food web. Increased food availability may support a more species rich invertebrate community – thus increasing biotic resistance to invaders in those environments (Levine and D'Antonio 1999). Conversely, or in parallel, the negative effect of fDOM on *A. lacustre* abundance in this study could indicate some level of pollution sensitivity. fDOM increases as you move upstream in the IWW, and although nuanced, treated wastewater can be an important input to dissolved organic matter in urbanized streams (Meng et al. 2013). Along those lines, treated wastewater and/or industrial discharge comprise approximately 40% of river flow in the Des Plaines River, which drains into the upper Illinois River in Dresden Island Pool (see Panno et al. 2008).

Downstream distance and water temperature had a significant positive relationship on *A. lacustre* abundance (Table 3). To investigate distance further, we examined the intra-pool distribution of *A. lacustre* and found that the species' abundance was higher farther downstream within a pool (Starved Rock Pool did not follow this trend). This pattern is possibly the result of broad changes that occur in the hydrology and ecology of impounded rivers. The areas upstream of a dam can experience decreased water velocity and increased sediment deposition, flooding, and lake-like stratification caused by the combination of increased depth and low water velocity (Baxter 1977; Schmutz and Moog 2018). These habitat changes likely make impoundments more hospitable to *A. lacustre* by increasing their similarity to deltas and estuaries (i.e., their native habitats; Summers 2001). From a community perspective, dams remove the natural flow and disturbance regimes of rivers, which disrupts the natural structure of the biological communities and makes the system more vulnerable to invasion (Malmqvist and Rundle 2002; Johnson et al. 2008). Impoundments may also experience higher invasion propagule pressure from upstream invasion sites (Allen and Ramcharan 2001) and recreational usage (Havel and Stelzleni-Schwent 2000). The distribution of *A. lacustre* in our data showed

that the species has likely benefitted from this combination of factors that make impoundments more vulnerable to invasion and more hospitable to species adapted to brackish habitats. This finding supports another hypothesis of Grigorovich et al. (2008) that *A. lacustre* may be absent from the Missouri River because it lacks large areas of lentic habitat (i.e., navigational pools) compared to other large rivers within the Mississippi River Basin (e.g., Mississippi River, Ohio River, Illinois River). With respect to temperature, *A. lacustre* is found across a wide range of water temperatures from 1–31 °C (Fusaro et al. 2023). Possibly, this positive association indicates a small preference for warmer water temperatures not previously documented, which would not be surprising given the lack of studies involving *A. lacustre*. However, water temperature was not found to be a predictor of *A. lacustre* abundance in the Upper Oden River catchment in Poland (Krodkiewska et al. 2021).

A. lacustre is known to foul vessel hulls (Gollasch 2002; Llansó and Sillett 2009) and multiple studies have concluded that the most plausible explanation for its rapid, and often discontinuous, expansion in an area was due to transport by ships, with *A. lacustre* attaching to biofilm on hulls (e.g., Krodkiewska et al. 2021) or residing in the interstitial spaces of zebra mussel colonies on hulls (e.g., Grigorovich et al. 2008). *A. lacustre* was not collected during a small pilot study that scraped vessel-hulls on the La Grange Pool of the IWW (see Supplemental Information Section; Suppl. material 2). This is somewhat surprising considering their propensity to foul vessel hulls (Gollasch 2002; Llansó and Sillett 2009) and that La Grange Pool had the highest abundance of *A. lacustre* in our study (55% more *A. lacustre* per sample on average; Table 1). It is possible that a more dedicated and widespread hull scraping effort could find *A. lacustre* fouling vessel hulls in the IWW, so we encourage further research to attempt to confirm the presence of *A. lacustre* on vessel hulls and determine the potential for spread from this vector.

We must acknowledge potential limitations to our study that should be considered when interpreting our conclusions. First, we used a single sampling gear – rock bags – to collect *A. lacustre*. Gear types such as Hester-Dendy samplers, scrapes of large woody debris, Eckman dredges, rock bags, and kick nets (e.g., Grigorovich et al. 2008; Keller et al. 2017; Krodkiewska et al. 2021; Egly et al. 2021a) have been used to collect *A. lacustre* by other studies, including the use of multiple gear types in some studies. It is our opinion that rock bags were the most appropriate sampling gear for collecting *A. lacustre* in the IWW. Rock bags have previously been used to collect *A. lacustre* and similar organisms in the IWW and Lake Michigan (Brandon Harris, unpublished data; Egly et al. 2021a), they are inexpensive, and the resulting samples are relatively easy to process (i.e., limited debris). These gear attributes were important considering our goal was to maintain a high sampling intensity along the length of the IWW. Second, we sampled sites that ranged in water depth from as shallow as 0.4 m to as deep as 9.2 m, but it was only feasible to sample main channel border habitat given the spatial scale of our study and commercial vessel traffic. It is plausible that the amphipod community could differ in the main channel offshore habitat. Third, we do not know the relationship between the abundance and subsequent detection of *A. lacustre* using rock bags or how it may vary across habitats, but our results lend some additional evidence that rock bags may be suitable for collecting *A. lacustre*. For example, below Dresden Island Pool, the pool-specific site presence of *A. lacustre* ranged from 95–100% over a wide range of mean *A. lacustre* catch, including in the Starved Rock Pool where the mean catch of *A. lacustre* was >5 fold less compared to the mean catch in the La Grange Pool (Table 1). Similarly, only 75 *A. lacustre* were collected in Dresden Island Pool, but *A. lacustre* was collected at 48% (11 of 23) of sites (Table 2). Lastly, *A. lacustre* was not found upstream of the Dresden Island Pool

and could have been overlooked in samples – although this is unlikely given the species' visually distinctive characteristics (i.e., large pediform second antennae) among amphipods in the Mississippi River Basin (Keller et al. 2017). Moreover, our results corroborate other studies in the IWW (e.g., Keller et al. 2017; Egly et al. 2021a) that found *A. lacustre* has not invaded upstream of Dresden Island Pool.

Conclusion

A. lacustre has been repeatedly identified as a high-risk species for invading the Great Lakes. This study provided insights into the mechanisms underlying the distribution of *A. lacustre* in the IWW and represents the most robust dataset available for further risk assessment in other systems. While there are numerous biological threats to the Great Lakes, *A. lacustre* has been repeatedly identified as a concern for future management despite limited data. Our findings have two major implications for risk assessment of *A. lacustre* establishing farther upstream or into adjacent Lake Michigan. First, the species may struggle to establish in the remaining upstream areas of the IWW because our results broadly suggest that *A. lacustre* is most successful in impounded areas just upstream of dams. There are few natural river reaches upstream of Dresden Island Pool, mostly a series of deep, hard-walled, artificial canals. These canals do not experience the effects of impoundment and may not provide suitable habitat for *A. lacustre*. Water quality in the upstream pools also may be unsuitable for the species due to high pollution levels or differences in water quality from the rest of the waterway. Second, *A. lacustre* may find ample suitable habitat in Lake Michigan if introduced. We found that the species is dominant in the most lake-like portions of each pool. If introduced to Lake Michigan, competition between *A. lacustre* and other species might be mediated by habitat conditions that are more favorable to locally adapted species than the heavily modified and polluted IWW. However, invasive dreissenid mussels have bioengineered the Great Lakes benthos to be more suitable for amphipods like *A. lacustre* (Ricciardi et al. 1997), providing further reason to suspect that *A. lacustre* would be successful in the Great Lakes. Despite this new information, our work invites further research into why the species has not established farther upstream in the IWW and whether it would be successful in the Great Lakes. We hope that researchers will leverage these results by developing studies to identify interactions of *A. lacustre* with species-level benthic amphipod community data and its tolerance for the abiotic conditions of Lake Michigan.

Author contributions

TH – Investigation and data collection, data analysis and interpretation, roles/writing – original draft, review & editing; BH – Research conceptualization, sample design and methodology, investigation and data collection, roles/writing – review & editing; BS – Research conceptualization, sample design and methodology, investigation and data collection, funding provision, review & editing; RK – Research conceptualization, sample design and methodology, review & editing; JL – Research conceptualization, sample design and methodology, review & editing.

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Ethics and permits

Authors have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects, and that they are willing to share the original data and materials if so requested.

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Supplementary material 1

Geo-referenced species records displayed in Figure 1

Authors: Trent W. Henry, Brandon S. Harris, Bradley Smith, Reuben P. Keller, James T. Lamer
Data type: xlsx

Link: https://doi.org/10.3391/ai.2024.19.2.121730.suppl1

Supplementary material 2

Map showing the location of vessel-hull scraping on the La Grange Pool of the Illinois Waterway, near Havana, Illinois

Authors: Trent W. Henry, Brandon S. Harris, Bradley Smith, Reuben P. Keller, James T. Lamer
Data type: jpg

Link: https://doi.org/10.3391/ai.2024.19.2.121730.suppl2