DISTRIBUTION AND ONGOING THREAT OF INVASIVE SCUD (APOCOROPHIUM LACUSTRE) TO THE ILLINOIS RIVER AND LAURENTIAN GREAT LAKES

BY

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THESIS

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ABSTRACT

Apocorophium lacustre is a species of benthic amphipod native to both American and European estuaries along the North Atlantic Ocean, which has rapidly expanded outside of its native range and is now established in the Illinois, Upper Mississippi, and Ohio Rivers. *A. lacustre* has previously been detected in the Illinois River within 100 river km of Lake Michigan and is considered high risk for colonization and disruption of the Great Lakes' benthic communities. In order to further our understanding of factors influencing *A. lacustre* distribution and the threat it poses to the Great Lakes, I deployed rock bag colonization samplers and collected zoobenthic and habitat data at 263 sites distributed across the eight navigational pools of the Illinois River. *A. lacustre* was identified in all pools up to and including the Dresden Island Pool - the species was not observed any closer to the Great Lakes than previously documented. *A. lacustre* were by far the most abundant benthic amphipod collected in pools where the species was present, representing >79% on average of benthic amphipods collected at sites downstream of the Dresden Island Lock & Dam (which represents the leading edge of its invasion). I analyzed abundance and habitat data using two generalized linear mixed effects model (GLMM) and AICc approaches: predicting *A. lacustre* abundance using a negative binomial GLMM and predicting the proportion of *A. lacustre* amongst all benthic amphipods using a binomial GLMM. I identified several variables that are useful predictors of *A. lacustre*'s raw and proportional abundance: dissolved organic matter had a strong negative effect and distance downstream within each river pool (e.g., closer to the next downstream dam) had a strong positive effect in both analyses. The latter result suggests that *A. lacustre* invasion is at least partially facilitated by impoundments on the Illinois River, which create areas of low water velocity, higher salinity, and disrupted biological communities. My results indicate that *A.*

lacustre may struggle to find suitable habitat in the canals of the Upper Illinois River Waterway, but they may be successful in Lake Michigan if introduced.

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LITERATURE REVIEW

Apocorophium lacustre (Vanhöffen, 1911) is a species of benthic, euryhaline amphipod (a scud) native to estuaries of the North Atlantic Ocean. This species of scud was originally assigned to the genus *Corophium* prior to the creation of the *Apocorophium* genus in 1997 (Bousfield & Hoover 1997). All literature published prior to that year, and some documents published since, refer to *A. lacustre* as *Corophium lacustre*. I will only refer to the species here as *A. lacustre*, regardless of the taxonomy used in a referenced text. This species has a wide native range and an expanding invasive range as it continues to move and establish further upstream in river systems within North America and Europe. *A. lacustre*'s expansion since the mid-1900's has attracted increasing attention from ecological researchers and conservation departments (e.g., United States Fish and Wildlife Service, United States Army Corps of Engineers). Despite this growing attention, relatively little specific ecological knowledge or data is available for the species. The purpose of this literature review is to consolidate all available information pertaining to *A. lacustre* and to highlight knowledge gaps in the literature.

Apocorophium lacustre has been anatomically described in several places (e.g., Shoemaker 1947; LeCroy 2004), dating as far back as 1934 (Shoemaker 1934). Relatively early reports of the species noted that it resides on both sides of the Atlantic Ocean, including Germany, Finland, the Netherlands, France, England, and the United States (Crawford 1937). In Europe, the species is currently established in Polish and Russian estuaries along the Baltic Sea (Ezhova & Żmudziński 2005; Jażdżewski et al. 2005); the Polish Oder and Klodnica Rivers (Krodkiewska et al. 2021); the German Werra River (Szöcs et al. 2014); and Belgian, Dutch, and German estuaries along the North Sea (Ysebaert et al. 2000; Faasse & Moorsel 2003; Noordhius et al. 2009; Wolf et al. 2009). *A. lacustre* is considered invasive upriver in Europe (Szöcs et al.

2014; Krodkiewska et al. 2021). In North America, the species' native range is generally agreed to be the Atlantic Coast between the Bay of Fundy, Newfoundland and the Atlantic estuaries of Northern Florida (e.g., Bousfield 1973). Within that range, the species has been documented in the Potomac River (Shoemaker 1934); the Chesapeake Bay and its tributaries (Crawford 1937; Jordan & Sutton 1984; Janiak et al. 2016); the coastal waters and estuaries of the Carolinas (Crawford 1937; Calder et al. 1977; Power et al. 2006); St. Catherine's Island, Georgia (Prezant et al. 2002); the St. Johns River estuary in Florida (Mason 1998; Evans et al. 2004); and the Indian River Lagoon and estuary in Florida (Nelson et al. 1982; Mook 1983; Nelson 1995).

A. lacustre was introduced to the Gulf of Mexico (Bousfield 1973; Power et al. 2006; Grigorovich et al. 2008) and is invasive within the Mississippi River System (Grigorovich et al. 2008; Benson 2018). The literature provides evidence of the scud in the Perdido Key of Northwestern Florida (Rkocinski et al. 1996), coastal tributaries in Mississippi and Louisiana (LeCroy 2004), and estuaries in Texas (Llansó & Sillet 2009). *A. lacustre* has been documented in the Lower Mississippi River near Vicksburg, Mississippi (Way et al. 1995; LeCroy 2004) and in Southeastern Arkansas (Payne et al. 1989). The species was identified in the Ohio River in 1996, prior to discovery in other parts of the Upper Mississippi River Watershed (Grigorovich et al. 2008). U.S. Geological survey records indicate that *A. lacustre* was next identified in the Illinois River in 2003 (Benson 2018) before quickly being identified in the nearby Missouri and Upper Mississippi Rivers around 2005 (Grigorovich et al. 2008). *A. lacustre* was reported within 100 km of Lake Michigan by 2005 in the Dresden Island Pool of the Upper Illinois River (Grigorovich et al. 2008; Benson 2018). Subsequent sampling efforts targeting the species upstream of the Dresden Island Pool have found no evidence that the species has established closer to the Great Lakes (Keller et al. 2017; Egly et al. 2021a).

Several sampling methods have captured *A. lacustre* in previous studies. Hester-Dendy samplers have been used most commonly (Power et al. 2006; Grigorovich et al. 2008; Keller et al. 2017; Egly et al. 2021a). Hester-Dendy's are a form of colonization sampler comprised of a multiple masonite plates spaced across a steel rod, which are deployed at a sample site for a few weeks before collection and processing. Rock bags, another form of colonization sampler, are being tested as an alternative to Hester-Dendys (Egly et al. 2021a). Rock bag samplers are simply nylon mesh bags with a reinforced bottom, partially filled with rocks. Outside of colonization samplers, *A. lacustre* has been collected using kick or dip nets in shallow water (Grigorovich et al. 2008; Noordhuis et al. 2009) and by scrubbing or scraping snags, artificial surfaces, and boat hulls (Mook 1983; Power et al. 2006; Grigorovich et al. 2008; Llansó & Sillet 2009). The scud can also be found on large stones removed from waterways (Payne et al. 1989; Noordhuis et al. 2009) and in sediment samples or cores (Rokocinski et al. 1996; Power et al. 2006).

A. lacustre appear capable of colonizing all varieties of substrate (Nelson 1995), though the species may be more successful on either very hard or very soft substrates based on the literature. Earlier documents described *A. lacustre* as preferring hard and artificial substrates (Shoemaker 1934; Payne et al. 1989) and the scud have repeatedly been found on hard substrate, both natural (Faasse & Moorsel 2003; Noordhuis et al. 2009) and artificial (Payne et al. 1989; Grigorovich et al. 2008). An experimental study using hard, artificial substrate installations found that *A. lacustre* was most abundant on textured surfaces, presumably because they provide refuge from river's flow (Way et al. 1995). However, this species is also commonly found on silty substrates (LeCroy et al. 2009) and has been positively correlated with substrate silt percentage (Krodkiewska et al. 2021).

The genera *Corophium* and *Apocorophium* contain several species of tube-building, filter-feeding, benthic amphipods, including *A. lacustre*. The tubes, assembled using bits of algae or detritus, may serve multiple functions and it is unclear which are important for *A. lacustre*. For example, there is no consensus for whether tubes decrease susceptibility to predation for their builders; one study provided evidence that a similar species (*Apocorophium acutum*) is less susceptible to predation by other amphipods when able to build tubes (Armsby & Tisch 2006), while another found no evidence that *A. lacustre* avoided predation by marine flatworms with their tubes (Janiak et al. 2006). However, there is agreement that the tubes are used for feeding behaviors, which vary between taxa (Dixon & Moore 1997). *A. lacustre* is considered to be a filter-feeder that may consume both suspended particles and deposited biomass (Ysebaert et al. 2000). One study measured *A. lacustre*'s filter mesh size, indicating the smallest particle size they can consume, and found a size range between 1.8 and 5 μm (Borza et al. 2021). *Apocorophium* and *Corophium* species, though not *A. lacustre* specifically, were found to consume exclusively detritus and no algae in a gut content analysis (Guerra-Garcia et al. 2014).

A. lacustre is able to occupy a large range of habitats because it can tolerate a wide range of water conditions. The species is generally considered to be brackish or salinity tolerant (Ysebaert et al. 2000; Evans et al. 2004). Early descriptions acknowledged that the species occupies both saline and borderline freshwater (Shoemaker 1934), including waters with salinity ranging from 0.17 to 20.61 ppt (Crawford 1937). A more recent study verified that *A. lacustre* live and reproduce in salinities up to approximately 30 ppt (Wolf et al. 2009). Similarly, the scud was found to be more dominant over native species in areas of the Werra River, Germany where conductivity was high (>4000 μS/cm; Szöcs et al. 2014). The species is also tolerant of polluted surface water (Evans et al. 2004) and sediments (Rakocinski et al. 2000). Additionally, *A. lacustre* is assumed to be somewhat tolerant of hypoxic conditions, including low levels of dissolved oxygen (Mason 1998). Explicit thresholds or tolerance ranges for *A. lacustre* are absent in the literature for most abiotic and water chemistry variables. More explicit, laboratory-based testing is required to understand the species' full range of tolerances to dissolved oxygen, heavy metal concentrations, water temperature, and other potential environmental factors.

Multiple reports issued by federal departments in the United States have indicated that *A. lacustre* is a species of concern to the Great Lakes. A report issued by the National Oceanic Atmospheric Administration in 2016 highlights *A. lacustre* as one of 16 species (out of 67) that pose a high risk for introduction and establishment to the Great Lakes (Fusaro et al. 2016). A 2019 update to that report provided additional evidence that the species is also likely to negatively impact the ecosystem function (Lower et al. 2019). Similar reports from the U.S. Army Corps of Engineers agree that *A. lacustre* are highly likely to pose a significant risk to the Great Lakes and Mississippi River Watersheds (Veraldi et al. 2011; Grippo et al. 2014).
A laboratory study found that the electric dispersal barrier in the Chicago Sanitary and Shipping Canal (installed to prevent upstream or downstream movement of aquatic invasive species) is likely insufficient for deterring small amphipods, especially when aided by boats (Egly et al. 2021b), which bolsters concerns about upstream movement. All of the governmental reports justify their conclusion from two main ideas: *A. lacustre* colonizes at extremely high densities that can overwhelm other benthic macroinvertebrates and it has ample opportunity to be transported into the Great Lakes because it uses boats as a vector mechanism.

Several articles and reports have listed specific colonization densities for *A. lacustre*. The species has been detected at low densities in some estuaries: mean of 15 indv./m^2 in North Sea estuaries along the Belgian coast (Ysebart et al. 2000) and 3-41 indv./m^2 in Atlantic estuaries in

South Carolina (Calder et al. 1977). *A. lacustre* density has been reported at higher levels in several rivers: up to approximately 500 indv./m^2 in the Lower Mississippi River (Way et al. 1995) and up to 456 indv./m^2 in the Upper Mississippi River Basin (Grigorovich et al. 2008). The species' density has occasionally been reported to be extremely high in river systems: >10,000 indv./m^2 in the Lower Mississippi River (Payne et al. 1989) and up to 82,000 indv./m^2 in the Oder River of Poland (Krodkiewska et al. 2021). Additionally, Power et al. (2006) *A. lacustre* are known to outcompete or 'smother' mussels and other benthic filter-feeders. There does seem to be ample evidence that *A. lacustre* can colonize at problematic densities, though it is unclear how common this is, or which types of habitat conditions enable that level of dominance.

A. lacustre is widely described as fouling vessels as a means of vectorization, but there is very little published data documenting this phenomenon. In this review, I found two studies documenting *A. lacustre* on vessel hulls or in ballast tanks. The first collected the scud in ballast sediments and around boat hulls (Gollasch 2002); *A. lacustre* was described as mobile in the boat hull samples, indicating they may not have colonized the surface of the hull. The second study found the species in vessel hull scrape samples both before and after anti-fouling cleaning protocols (Llansó & Sillet 2009). Both of these studies examined large, transoceanic vessels: the former study collected samples from shipping vessels, research ships, and cruise liners entering German ports (Gollasch 2002), while the latter examined three oceanic naval vessels at port in a Texan estuary (Llansó & Sillet 2009). One other set of studies were occasionally cited as evidence of *A. lacustre*'s fouling behavior in the Indian River of Florida (e.g., Mook 1980; Mook 1983), but these articles examined stationary artificial substrate as opposed to vessels. Consequently, none of the mentioned studies provide direct evidence that the species is vectored by vessels. Shipping and commercial traffic on major tributaries of the Mississippi River is largely conducted using simple, flat-bottomed barges that are propelled by towboats. These systems likely provide significantly less suitable surface for colonization compared to transoceanic vessels because they lack ballast tanks and are smaller and less structurally complex. I have not found empirical evidence that *A. lacustre* is using vessels to travel upstream into freshwater systems, but this hypothesis is still the best explanation for how the scud have traveled upstream because they are poor swimmers (Grigorovich et al. 2008; Janiak et al. 2016). A targeted sampling effort of vessel hulls on the Mississippi, Illinois, or Ohio Rivers is needed to confirm whether *A. lacustre* are using boats as a vector method in their invasive range.

The key takeaways from this literature review are: (1) the global distribution of *A. lacustre* is well documented on a regional level and there are numerous dated reports and records that track the species' invasion history; (2) *A. lacustre* have been detected using several common sampling methods for benthic macroinvertebrates, including simple kick or dip net samples and colonization samplers; (3) There is ample data to indicate that the species is tolerant of a broad range of abiotic conditions, salinity extremes, and poor water quality, but its relationship to most water chemistry variables is unmeasured; (4) There are virtually no studies describing the ecology or behavior of *A. lacustre* and it is unclear how readily it extirpates other species as an invader; finally, (5) the literature contains some data to support the hypothesis that *A. lacustre* is transported by vessels, but none documenting this phenomenon in freshwater systems. In order to improve risk forecasting and management of the Great Lakes watershed, future research should aim to observe how *A. lacustre* interacts with benthic communities in its invasive range, measure the species' specific abiotic tolerances, and verify how the species is transported in freshwater systems.

INTRODUCTION

Freshwater systems are heavily invaded 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 for aquatic invaders (Keller & 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). Filter-feeding invertebrates are among the most prevalent aquatic invaders and can cause dramatic changes to ecosystems (Karatayev et al. 2009). For example, dreissenid mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensi*) contribute to precipitous declines in phytoplankton availability once established, causing cascading, bottom-up changes in food web structure (Ricciardi et al. 1997; Higgins & Vander Zanden 2010).

The Laurentian Great Lakes are an important natural resource to surrounding communities, providing recreational, economic, and climate regulatory services (Krantzberg & De Boer 2008; Allan et al. 2015). The Chicago Area Waterway System (CAWS) and the Illinois River connect the Great Lakes to the broader Mississippi River Watershed through a series of natural streams and artificial canals. This river system drains Lake Michigan, the Metropolitan Water Reclamation District of Greater Chicago, and large swathes of agricultural land downstream of the city. The hydrology of the Illinois River has been heavily modified from its natural state to control flooding and facilitate shipping vessel navigation (Lian et al. 2012). It now consists of a dredged main channel that is maintained for large vessels and several lock and dam systems that separate the river into eight pools.

Human activities have made both the Great Lakes and Upper Mississippi River basins vulnerable to a growing number of invasive species over the past century (Ricciardi 2006;

McClelland et al. 2012; Jacobs & Keller 2017). Alien species are contributing to the decline of native communities in the Great Lakes through predation and disease transmission, among other effects (Mandrake & Cudmore 2010). In the Illinois River, invasive species have been implicated in shifting plankton and fish communities (Sass et al. 2014; Solomon et al. 2016). The Great Lakes have a higher number of invaders than the Illinois River, but the two systems are connected and newly established alien species in either system are considered an imminent threat to the other. An electric barrier was installed in the Upper Illinois River to prevent the downstream dispersal of round goby (*Neogobius melanostomus*) from Lake Michigan (Parker et al. 2016). Electric dispersal barriers can be effective at deterring or preventing the spread of invasive fish (Parker et al. 2016; Jones et al. 2021), but laboratory studies have shown they are likely to be insufficient for controlling small invertebrates (Egly et al. 2021b).

Apocorophium lacustre (Vanhöffen, 1911) is a species of marine, benthic amphipod native to both the Atlantic coast of North America (Bousfield 1973), as well as to estuaries of the Baltic and North Seas (Faasse & Moorsel 2003; Ezhova & Żmudziński 2005). On both sides of the Atlantic Ocean, *A. lacustre* is known to have a wide salinity tolerance (Wolf et al. 2009) and is commonly found in both minimally saline water and fully fresh water (Shoemaker 1934; LeCroy 2004). It also has a high tolerance for pollution (Evans et al. 2004) and electric conductivity (Szöcs et al. 2014). The species is assumed to be tolerant of hypoxic conditions (Mason 1998), including low levels of dissolved oxygen (Llansó & Sillett 2009). *A. lacustre* is most commonly sampled on coarse or artificial substrates (Payne et al. 1989; Faasse & Moorsel 2003), though it also frequently found on silty substrates (LeCroy et al. 2009; Krodkiewska et al. 2021). It has been found to colonize in densities exceeding 10,000 individuals/m^2 (Payne et al.

1989; Krodkiewska et al. 2021). This species is a detritivorous filter-feeder that consumes both suspended and sedimented particles (Ysebaert et al. 2000; Llansó & Sillet 2009).

Since the mid 1900's *A. lacustre* has rapidly expanded outside of its native range. It was documented in estuaries of the Gulf of Mexico by the 1980's (Heard 1982) and in the Lower Mississippi River by 1989 (Payne et al. 1989). It was first reported in the Lower Ohio River in 1996 and then the Lower Illinois and Upper Mississippi Rivers in 2003 (Grigorovich et al. 2008). By 2005, the species was detected as far upstream in the Illinois River as the Dresden Island Pool (Benson 2018), which is approximately 92 river kilometers (rkm) from Lake Michigan. Recent studies targeting the species have not found *A. lacustre* further upstream than the Dresden Island Pool (Keller et al. 2017; Egly et al. 2021a).

As a filter-feeding detritivore with a wide geographic range, high tolerance for pollution, and high population density, *A. lacustre* closely matches the profile of other globally successful aquatic invasive species (Karateyev et al. 2009; Bates et al. 2013). Consequently, the species is among the taxa with the greatest threat to the Laurentian Great Lakes (Veraldi et al. 2011; Grippo et al. 2014; Fusaro et al. 2016). It is likely to be introduced to the Great Lakes due to its close proximity and direct pathway into the system. The rapid invasion of *A. lacustre* is attributed to transport by shipping vessels, where it fouls the hull and colonizes ballast tanks (Gollasch 2002; Llansó & Sillett 2009). Millions of tons of freight pass between Lake Michigan and the Chicago Area Waterway System annually, providing ample opportunity for further movement upstream (Goodman Williams Group 2015). If established, *A. lacustre* are expected to disrupt the benthic communities of the Great Lakes by overwhelming and outcompeting native filter-feeders (Grigorovich et al. 2008).

Despite the growing attention *A. lacustre* has received in the Great Lakes region, there is little data available that describes their distribution, abundance, or behavior in the Illinois River. The U.S. Geological Survey has only seven presence-only occurrence records for this species in the Illinois River (Benson 2018). Several recent sampling efforts have targeted *A. lacustre* in the Illinois River upstream of Dresden Island, with a handful of sites in the Marseilles and Starved Rock Pools (Keller et al. 2017; Egly et al. 2021a). There are very few records - none of which are from the past ten years - that describe *A. lacustre*'s distribution or abundance for the rest of river (e.g., the Peoria, La Grange, and Alton Pools).

The objectives of this study are to provide updated occurrence data for *A. lacustre* in the Illinois River Waterway System and assess how habitat variables influence the species' distribution and abundance. I sampled benthic amphipods at sites along the entire length of the Illinois River Waterway System while measuring site-level water chemistry, substrate type, depth, and non-target amphipod abundance. I investigated several hypotheses to identify which factors drive variance in *A. lacustre*'s distribution and relative abundance in the Illinois River using generalized linear models (GLMs) and an Akaike's Information Criterion model-averaging approach. In this paper I document the relationship between *A. lacustre* and habitat covariates and present my best hypothesis for factors driving the species' distribution in Illinois. In doing so, I will provide the most comprehensive and up-to-date description of *A. lacustre*'s distribution in the Illinois River Waterway system. My work can be used to update risk assessment and guide future research that aims to understand *A. lacustre*'s habitat requirements or chemical tolerances.

METHODS

Distribution Assessment

I collected invertebrate samples in the Illinois River across all of its eight pools between August and September 2020, from the Lockport pool in downtown Chicago through the Alton pool near the confluence with the Mississippi River (Figure 1). I randomly selected sample sites within each pool from sites sampled by the Upper Midwest Environmental Science Center's Long-Term Resource Monitoring (LTRM) program, a long running USGS program, administered in part by the Illinois Natural History Survey. Potential LTRM sites in each pool were split into an upstream and downstream half prior to selection. My target sampling effort was approximately 2 samples for every 3 rkm, but I targeted no fewer than 24 sites per pool. The high site minimum per pool boosted sampling density in the short upstream pools where an *A. lacustre* population, if present, may be at low density. I did not sample any backwaters or side channels, only main channel border habitats.

I used rock bag samplers (Figure 2), a form of colonization sampler, to collect benthic organisms at my selected sampling locations. This gear was tested in recent sampling efforts as an alternative to Hester-Dendy samplers (Egly et al. 2021a). A rock bag sampler consists of a nylon mesh bag, which is reinforced with 500 μm plastic mesh on its bottom third and filled with approximately 0.8 L of river rocks (between 2.5 and 8 cm in length). The bags are sealed with zip ties and tethered to either stakes or permanent structures on shore using nylon rope. Small concrete anchors were tied below the rock bags, separated by approximately 600 cm of rope, to limit drift. I sought to deploy rock bags at a minimum depth of 0.5 m to avoid air exposure caused by river depth changes, but this was not possible at every site. After retrieval, each site's minimum depth was calculated based on pool-level change in river gauge depth (USGS 2020). I excluded sites that experienced <12 cm of water, assuming that they would have been exposed to air for part of the deployment period.

Habitat variables, depth, and water chemistry data were recorded in situ. I adapted the categorical habitat data collection procedures for vegetation density, substrate, and structure presence from the LTRM protocol (Ratcliff et al. 2014). 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) within approximately a 20 m radius of the site. I did not differentiate between emergent and submersed vegetation during this survey effort. Substrate was classified using LTRM 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 approximately 20 m of the site. Depth (cm) was recorded at the location of the rock bag using a meter stick. Water chemistry data was recorded using a multi-meter (YSI EXO2 Sonde); the multi-meter was deployed from the stern of the boat (closer to the center of the channel) to avoid turbidity changes caused by the action of the propeller. I collected temperature (°C), salinity (ppt), dissolved organic matter (fDOM; ppb), dissolved oxygen (DO; mg/L), and turbidity (FNU) using the multi-meter. I used a site's distance (rkm) from the next upstream dam (herein 'downstream distance') when evaluating the distribution of *A. lacustre*. Variations in abundance across downstream distance may be indicative of responses to hydrologic and ecological trends in the river caused by impoundment (Baxter 1977; Schmutz & Moog 2018). I also downloaded pool-level river discharge (ft^3/sec) data collected via USGS river gauges from the same time period that the samplers were deployed (USGS 2020).

Rock bags were left in the river for 31 (±1) days. After retrieval, all sampler contents captured by a 500-micron sieve were stored in a 90% ethanol solution. All intact amphipods ≥2 mm long were identified to genus and counted; *A. lacustre* and *Hyallela 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). Unidentifiable individuals, either below the size thresholds or not intact, were not counted or included in the analysis.

Abundance Analysis

In order to examine which factors influence *A. lacustre* distribution in the Illinois River, I elected to model the species' abundance using a generalized linear model approach. I decided to use a negative binomial (NB) distribution because when compared to a Poisson distribution, which is commonly used for modeling count data, the NB distribution more closely matches the distribution of *A. lacustre* abundance. My *A. lacustre* count data has substantial zero-counts and a high maximum (max = 3887). When compared to a simulated Poisson distribution with the same mean (λ = 190.8) my data is heavily right skewed. I was able to more closely match my *A. lacustre* count data using a NB simulation with the probability (p) = 0.00425; this distribution is right skewed with a long tail, which the Poisson distribution lacks. Aside from the unusual distribution, this dataset also contains inherent spatial collinearity due to the natural gradient of the river and its linear structure. I felt it was necessary to account for this spatial nonindependence in the model structure to avoid violating the independent sampling assumption of a GLM. It is both difficult and data-intensive to build a NB generalized linear model with explicit spatial covariance matrices using publicly available tools for R (v4.0.2; R Core Team

2020). The best way I could achieve a similar effect was to apply a mixed effect structure using the *lme4* package (Bates et al. 2015), including river pool as a random effect. By including this random effect, the model accounts for differences in the *A. lacustre* population between the spatially explicit pools. All models presented in this analysis include river pool as a random effect. Data from the Brandon Road and Lockport pools were excluded from this analysis because they were found to be chemically distinct from the rest of the river.

I generated 11 candidate models by grouping independent variables into themes (Table 1). All numerical covariates were z-score standardized prior to analysis in order to facilitate comparison between covariate effects. I chose to explore as much of my collected data as possible because there is no census in the literature for which variables are important. I did seek to validate the findings of Krodkiewska et al. (2021), which reported a correlation between *A. lacustre* abundance, depth, substrate silt percentage, and current velocity in the Oder River of Poland. All models were assessed for predictor collinearity using variance inflation factor (VIF); variables were rejected if their VIF $\geq$ 4. A null model, which contained only the random effect of river pool, was included in order to contextualize the fit of my best performing models. All models were assessed using a corrected Akaike's Information Criterion (AICc; Akaike 1974; Sugiura 1978; Hurvich & Tsai 1991) with the *AICcmodavg* R package (v2.3-1; Mazerolle 2020). All fixed effects were evaluated using an AICc-weighted model averaging approach (Buckland et al. 1997; Anderson & Burnham 2002) using the same package; parameters were considered to be significant if their model-averaged, log-scale 95% confidence intervals did not include zero.

Proportional Composition Analysis

In order to explore how variation in habitat parameters affects the abundance of *A. lacustre* relative to other benthic amphipods, I used a binomial generalized linear model approach. The binomial distribution, and the multinomial extension, describe random processes with discrete outcomes via probability. Previous studies have used multinomial regression to investigate distribution trends in community-scale analysis by assigning probabilities to observed, discrete biological groups (e.g., Qian et al. 2012; Snedden & Steyer 2013; Lima et al. 2017; Venjakob et al. 2016). I employed this technique using the simpler binomial distribution (i.e., modeling one probability instead of multiple) to assess the proportional composition of the benthic amphipod community in my samples. The response variable in this analysis was a matrix that contained two columns per site: the abundance of *A. lacustre* and the abundance of all other amphipods. Each row of the matrix was interpreted by the model as a set of *n* Bernoulli trials, where *n* is the total number of amphipods at the site, *A. lacustre* individuals are Bernoulli successes, and all other amphipods are Bernoulli failures. The models use the success/failure matrix to model the probability that a detected amphipod is *A. lacustre* and assess how covariates affect that probability. I interpret the model effects in this analysis as changes in the proportional abundance of *A. lacustre* relative to other benthic amphipods.

I developed binomial models as generalized linear mixed-effects models using the *lme4* R package (Bates et al. 2015). All binomial models include river pool as a random effect in order to account for spatial nonindependence. Similar to the abundance analysis, I created 10 candidate models by grouping independent variables into themes (Table 2). This model set is similar to that used in the previous analysis; except I could not use the abundance of other amphipod species as a covariate. I incorporated the results of the abundance analysis into this procedure by including one model that used my best predictors of *A. lacustre* abundance as covariates. All candidate models were assessed for predictor collinearity using VIF and variables were rejected if their VIF ≥ 4. A null model was also included in this analysis to contextualize the fit of the best performing models. I used the same AIC procedure to analyze the binomial models as I did the abundance analysis: models were ranked by AICc and AICc-weighted, model-averaged parameters estimates were generated using the *AICcmodavg* R package (v2.3-1; Mazzerolle 2020). Parameters were considered to be significant if their model-averaged log-scale, 95% confidence intervals did not include zero.

RESULTS

Distribution Assessment

During the summer of 2020, I set 316 sites along the Illinois River Waterway System and successfully recovered sampling gear from 271 sites. After excluding eight samples that may have been exposed to air due to low river levels, I obtained samples from 263 sites (Table 3). My recovery rate varied from pool to pool (minimum = 64%, mean = 83%), but I recovered 16 rock bags in Starved Rock Pool, which had the lowest recovery rate.

A. lacustre was present in the lower 6 pools of the Illinois River (Alton, La Grange, Peoria, Starved Rock, Marseilles, and Dresden Island), which is no nearer to the Great Lakes than previously reported (Table 4). The percentage of sites occupied by the species exceeded 94.9% downstream of Dresden Island Pool, but only 47.8% of sites in the Dresden Island Pool were occupied. *A. lacustre* was most abundant in the La Grange Pool (mean = 431, sd = 649), but its proportional abundance was highest in the Starved Rock Pool (mean = 91.0%, sd = 25.5%). *A. lacustre* remains abundant upstream throughout the middle reaches of the Illinois River (e.g., the Starved Rock and Marseilles Pools), but there is a sharp decline in abundance above the Dresden Island Lock & Dam (Figure 3). Only 75 individuals were counted in the Dresden Island Pool (mean abundance = 3.3, sd = 7.7) and none were found upstream of the Brandon Road Lock & Dam.

A. lacustre abundance tended to be higher moving downstream within each pool (Figure 4). Correlation between *A. lacustre* abundance and distance to the next upstream dam was positive with moderate strength when considering all pools containing the species (Alton to Dresden Island Pools; Table 5). When looking at each pool individually, only the Starved Rock pool did not have a positive correlation between downstream distance and *A. lacustre* abundance (r = -0.40), but it also has the smallest sample size (n = 16). Correlation was strongest in the Dresden Island pool (r = 0.52) and weakest in the Alton pool (r = 0.18), but the Alton pool is not dammed before merging with the Mississippi River, leading to a distinct hydrographic profile.

Abundance Analysis

AICc analysis indicates that the food availability and water chemistry models were the best predictors of *A. lacustre* abundance (Table 2). The food resource model fit best, substantially outperforming the null model (ΔAICc = 39.5). The model containing chemical variables fit only marginally worse than the top model (ΔAICc = 3.3), but this model shares two variables with the food resources model – turbidity and dissolved organic matter. The two models that include downstream distance also performed substantially better than the null model (ΔAICc = approx. 6.7), suggesting that the ecological gradient between dams may be important for explaining observed patterns in *A. lacustre* abundance.

Model-averaging the coefficients from this set of models yielded five significantly non-zero effects (Table 6). Parameters associated with food availability, including fDOM (β = -1.35), vegetation density (β = -1.00), and turbidity (β = -0.46), all had negative log-scale effects on *A. lacustre* abundance. Temperature (β= 0.26) and downstream distance (β = 0.66) had positive log-scale effects on *A. lacustre* abundance.

Proportional Composition Analysis

I found that one of my candidate models dramatically outperformed all of the other options (Table 3): the model containing variables affected by impoundment was the best fitting model for predicting the proportion of *A. lacustre* relative to other amphipod taxa (AICc = 9413).

All other models had ΔAICc > 300, strongly suggesting that impoundment related factors are most important. However, most of the other models outperformed the null model by a similarly dramatic AICc difference ($\Delta AICc_{NULL} = 1235$).

A majority of the covariates included in this analysis had significantly non-zero effects on *A. lacustre* probability after AICc-weighted model averaging (Table 7). Only river discharge, structure presence, depth, hard substrate, and mixed substrate lacked significant effects. Salinity ($\beta = -0.57$), sand substrate ($\beta = -0.51$), dissolved organic matter ($\beta = -0.43$), turbidity ($\beta = -0.06$), and temperature ($\beta = -0.04$) all had negative log-scale effects on the proportion of *A. lacustre*. Dissolved oxygen ($\beta = 0.35$), dam distance ($\beta = 0.36$), and silt substrate ($\beta = 0.46$) all had positive log-scale effects on the proportion of *A. lacustre*.

DISCUSSION

This study is the most comprehensive effort yet to understand how *A. lacustre* interact with benthic habitat and communities, producing several key findings. First, my sampling efforts indicate that *A. lacustre* still have not established any further upstream than the Dresden Island Pool, while confirming that the species is abundant and dominant in the lower pools of the Illinois River. Additionally, I found that *A. lacustre* abundance is correlated with distance downstream within each pool and tended to be greatest just upstream of dams. My abundance analysis showed that several variables have an effect on *A. lacustre* abundance, including parameters pertaining to food availability, water chemistry, and impoundment. Finally, composition analysis revealed numerous factors that influence the likelihood of *A. lacustre*'s dominance over other benthic amphipod taxa. I hope that these findings will be used to refine risk assessment and invasion forecasting for this species within the Great Lakes watershed and in other regions where *A. lacustre* have been introduced.

My pool-level distribution data is consistent with USGS records and recent sampling efforts. I identified *A. lacustre* in the lower six pools of the Illinois River: the Alton, La Grange, Peoria, Starved Rock, Marseilles, and Dresden Island Pools. These pools collectively represent approximately 85% of the river distance between the Mississippi River and Lake Michigan, with only approximately 70 rkm between the Brandon Road Lock & Dam and the lake. My data corroborates USGS records (Benson 2018) that showed *A. lacustre* is present throughout the river up to Dresden Island. Despite the species' swift invasion history and documented upstream progression, I did not expect to find it any closer to Lake Michigan in this study. Keller and colleagues have repeatedly, through targeted benthic surveys, found no evidence that *A. lacustre* has invaded further up the Illinois River or into the Calumet, Chicago, Des Plaines, or Kankakee

Rivers (Keller et al. 2017; Egly et al. 2021a). My study area overlapped with those previous efforts, but with higher sample effort, and I also found no individuals upstream of the Dresden Island Pool. Keller and colleagues sampled 15 sites in the Dresden Island Pool, 12 sites in the Brandon Road Pool, and fewer than 10 sites in the Lockport pool over three years (Keller et al. 2017; Egly et al. 2021a). I sampled 23 sites in the Dresden Island Pool, 21 in the Brandon Road Pool, and 19 sites in the Lockport Pool simultaneously and found no evidence of *A. lacustre* outside of their known range.

While examining the intra-pool distribution of *A. lacustre*, I found that the species' abundance was higher further downstream within most pools (only Starved Rock pool did not follow this trend). This pattern is likely the result of broad changes that occur in the hydrology and ecology of impounded rivers. The areas upstream of a dam will experience decreased water velocity, increased sediment deposition, flooding, and lake-like stratification caused by the combination of increased depth and low water velocity (Baxter 1977; Schmutz & Moog 2018). These habitat changes likely make impoundments more hospitable to *A. lacustre* by increasing their similarity to deltas and estuaries, which also have low water velocity, high silt deposition, and lower oxygen levels when compared with lower-order streams (Summers 2001). Reservoirs and impoundments are also thought to aid upstream invasion of brackish organisms by containing water that is slightly more saline compared to surrounding water bodies (Lee & Bell 1999; Havel et al. 2009). 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 & Rundle 2002; Johnson et al. 2008). Impoundments may also experience higher invasion propagule pressure from upstream invasion sites (Allen & Ramcharan 2001) and recreational usage (Havel & Stelzleni-Schwent

2000). The distribution of *A. lacustre* in my data shows that the species has benefitted from this combination of factors that make impoundments more vulnerable to invasion and more hospitable to brackish creatures.

I was able to address multiple hypotheses simultaneously about what factors influence *A. lacustre*'s abundance and distribution because of my robust sampling effort. While analyzing this dataset, I found that a handful of variables were useful predictors of *A. lacustre* abundance in the bottom 6 pools of the Illinois River: dissolved organic matter, vegetation density, turbidity, water temperature, and downstream distance. There are virtually no published data or hypotheses that quantify *A. lacustre*'s relation to habitat characteristics for me to compare with my results. However, the species is described as tolerant of wide ranges of salinity, dissolved oxygen, and substrate types (e.g., Mason 1998; LeCroy et al. 2009; Wolf et al. 2009). My results support these descriptions as I found no significant relationship between *A. lacustre* abundance and salinity, dissolved oxygen, or any of the substrate types I documented (silt, silt/clay/sand mix, sand, gravel/rock/hard clay, or submerged structures). The species has also been described as pollution tolerant (Evans et al. 2004), but I was not able to locate water pollution data in areas of the river occupied by *A. lacustre* to assess this claim. The Metropolitan Water Reclamation District of Greater Chicago publishes robust water quality datasets, but they only extend as far downstream as the Brandon Road Pool (MWRDGC 2018).

The upstream extent of the *A. lacustre* invasion in the Illinois River is effectively identical to the well-studied leading edge of the silver and bighead carp (*Hypophthalmichthys molitrix* and *H. nobilis*) invasion (ACRCC 2021). Neither the scud or carp have been detected further upstream than the Dresden Island Pool in over 10 years, indicating that there are one or more conditions acting as a barrier (e.g., Blackburn et al. 2011) to further spread. Barriers may result from the physical characteristics of the habitat (Rahel & Olden 2008) or biological interactions (Davis et al. 2000; Shea & Chesson 2002). Recent research investigating the physiology of invasive carp at the leading edge of their invasion has determined that toxic pollutants are the most probable barrier to the carp's expansion, as opposed to limited food availability or a physical impasse (Jeffrey et al. 2019; Curtis-Quick et al. 2021). The Upper Illinois River experiences numerous pollution inputs including water treatment effluent (Peverly et al. 2015); pharmaceuticals and household chemicals (Groschen et al. 2004); and road salt runoff (Kelly et al. 2010). Additional laboratory-based studies would be helpful for verifying that water chemistry is the primary barrier for *A. lacustre* and for identifying which substances, if any, act as a chemical barrier to the species.

I chose to conduct the proportional composition analysis to contextualize the results of the abundance analysis and provide evidence to support or reject the assumption that *A. lacustre* displace other benthic species. The abundance analysis provided no information about how *A. lacustre*'s abundance increases relative to other species – it is unclear if predictors of *A. lacustre* abundance are distinct from predictors of amphipod abundance in general. My composition analysis implicated several habitat variables as factors that increase *A. lacustre*'s proportional abundance. Similar to the prior analysis, I found that variables related to impoundment were among the most important; distance downstream, dissolved oxygen, and silt substrate presence all had significant, positive relations to *A. lacustre*'s proportional abundance. The species has previously been described as preferring hard or artificial substrate (Shoemaker 1934; Payne et al. 1989), but I found no evidence to support this; my results showed *A. lacustre* abundance and proportion had no relationship to hard or artificial substrate. Instead, my results provide strong evidence that *A. lacustre* is more successful on silt substrate, corroborating some of the results of a recent paper that correlated *A. lacustre* abundance with substrate silt percentage, depth, and water velocity (Krodkiewska et al. 2021). However, I did not find a relationship between *A. lacustre* and depth in any of my analyses. River discharge, my equivalent to water velocity, had strong negative effects in both the abundance and composition analyses, but I could not draw conclusions on the effect size because of substantial uncertainty. The high uncertainty for river discharge effects were likely caused by the use of low-resolution, pool-level discharge data, which is all I had access to for this study.

Underlying my interpretation of these results is the assumption that the success of *A. lacustre* in a patch of habitat comes at the expense of competing taxa (i.e., the competitive exclusion principle; Hardin 1960). This assumption is bolstered by my data, which showed that *A. lacustre* comprised, on average, >79% of benthic amphipods collected at sites downstream of the Dresden Island Lock & Dam. The Lockport and Brandon Road Pools also had similar mean amphipod abundances ($\bar{x} = 201$ and $\bar{x} = 60.2$, respectively) when compared to the closest downstream pools, Dresden Island and Marseilles ($\bar{x} = 94.3$ and $\bar{x} = 259$, respectively), indicating that *A. lacustre* may be replacing other amphipods. One common benthic amphipod species in the Illinois River, *Hyallela azteca*, has a flexible diet and can exploit deposits of algae, leaf litter, or other detritus (Hargrave 1970). This diet plasticity likely limits competitive pressure between *H. azteca* and *A. lacustre* for food resources, suggesting that interspecific habitat competition may be more important. *H. azteca* have previously been associated with soft, silty substrate (Hargrave 1970), suggesting that their preferred habitat may overlap significantly with *A. lacustre*, which was more dominant on silt substrates in my proportional composition analysis. Habitat-dependent competitive exclusion has been documented in benthic amphipods in the Great Lakes (González & Burkart 2004), but may not have been captured in this sampling effort;

I only sampled sites on the main channel of the river, but native species could be more abundant in side channels or areas that were too shallow or heavily vegetated to sample.

My findings have two major implications for risk assessment of *A. lacustre* establishing further upstream or into Lake Michigan. First, the species may struggle to establish in the remaining upstream areas of the Illinois River Waterway due to their hard, artificial substrate. My results suggest that *A. lacustre* is most successful in impounded areas just upstream of dams with silted substrates. There are few natural river reaches upstream of Dresden Island Pool, only 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 may also be unsuitable for the species due to high pollution levels or differences in water chemistry. However, the second implication is that *A. lacustre* may find ample suitable habitat in Lake Michigan if introduced. I found that the species is dominant in the most lake-like portions of each pool, preferring slow-flowing waters. 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 Illinois River Waterway. But invasive dreissenid mussels have bioengineered the Great Lakes benthos to be more suitable for benthic, filter-feeding amphipods similar to the scud (Ricciardi et al. 1997), providing further reason to suspect that *A. lacustre* would be successful in the Great Lakes.

I conducted this study to provide the most up-to-date assessment of *A. lacustre* in the Illinois River Waterway and a comprehensive dataset documenting its relationship to habitat characteristics. While there are numerous biological threats to the Great Lakes system, this species has been repeatedly identified as a concern for future management, despite limited data. This study provides insights into the mechanisms underlying *A. lacustre*'s distribution and provides the most robust dataset available for further risk assessment analyses. Despite this new information, there are still lingering questions about why the species has not established further upstream and whether it would be successful in the Great Lakes. I hope that researchers will leverage these results by developing studies to identify *A. lacustre*'s interactions with benthic communities and its tolerance for the abiotic conditions of Lake Michigan.

TABLES

Table 1: Model description and AICc results for models used in analysis of *Apocorophium lacustre* abundance data. All models are negative binomial generalized linear models with mixed effects structure; all models include one random effect, river pool (Pool), that was included to account for spatial nonindependence of samples. The response variable in all models was site-level *A. lacustre* abundance. Fixed effect groups were assessed for multicollinearity using Variance Inflation Factor (VIF): no model included any variable with VIF ≥ 4. All numeric variables were standardized with a z-score prior to use in analysis.

Model Theme	Fixed Effects	Random Effect	K	AICc	ΔAICc
Food Resources	fDOM, Misc. Amphipod Abundance, Turbidity, Vegetation Density	Pool	7	2550.1	0
Water Chemistry	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

Table 2: Model description and AICc results for models used in analysis of benthic amphipod community composition. The response variable in this analysis was a matrix containing two columns per site: the abundance of *Apocorophium lacustre* and the abundance of all other amphipods. All models are binomial generalized linear models with a mixed effects structure; all models include one random effect, river pool (Pool), that was included to account for spatial nonindependence of samples. Fixed effect groups were assessed for multicollinearity using Variance Inflation Factor (VIF): no model included any variable with VIF ≥ 4. All numeric variables were standardized with a z-score prior to use in analysis.

Model Theme	Fixed Effects	Random Effect	K	AICc	ΔAICc
Impoundment	DO, Downstream Distance, fDOM, Silt Substrate, Vegetation Density	Pool	7	9413.1	0
Water Chemistry	DO, fDOM, Salinity, Turbidity	Pool	6	9745.3	332
Best Abundance Predictors	Downstream Distance, fDOM, River Discharge, Temperature, Turbidity, Vegetation Density	Pool	8	9806.7	394
Estuarine Characteristics	DO, Salinity, Turbidity	Pool	5	9917.8	505
Physical Parameters	All Substrate Types, Depth, River Discharge, Structure Presence, Temperature, Vegetation Density	Pool	10	100007	594
Food Resources	fDOM, Turbidity, Vegetation Density	Pool	5	10054	641
Downstream Distance	Downstream Distance	Pool	3	10100	687
Substrate Type	All Substrate Types, Structure Presence	Pool	6	10118	705
Structure	Misc. Amphipod Abundance	Pool	5	10609	1196
Null Model	*None*	Pool	2	10649	1235

Table 3: Summary of biological sampling effort on the Illinois River Waterway System during August and September of 2020. Sample locations were randomly selected within each pool from existing sites targeted by the Upper Midwest Environmental Science Center's Long-Term Resource Monitoring program. Target sample density was approximately 2 samplers per 3 river kilometers (mean = 0.66 samplers/km). At each site I set a rock bag sampler to collect benthic invertebrates, documented basic habitat data (e.g., water depth, substrate class, aquatic vegetation density), and recorded a suite of water chemistry variables using a multi-meter (YSI EXO2 Sonde). Rock bags were left in the river for 31 (± 1) days until retrieval. Sites were excluded if the sampler experienced <12 cm of water, based on USGS river gauge data, during deployment.

Pool	Pool length (river km)	Sites set	Recovered sites (excluded)	Recovery rate (%)	Recovered sample density (#/rkm)
Lockport	59.6	24	19 (1)	79.2	0.32
Brandon Road	8.0	24	21	87.5	2.65
Dresden Island	24.1	24	23	95.8	0.95
Marseilles	41.8	32	31	96.9	0.74
Starved Rock	22.5	25	16	64.0	0.71
Peoria	119	50	50	100	0.42
La Grange	123.9	87	60 (7)	69.0	0.48
Alton	122.3	50	43	86.0	0.35
Total	518.2	316	263 (8)	83.2	0.51

Table 4: Pool-level data describing *Apocorophium lacustre* distribution in the Illinois River Waterway System based on my 2020 benthic invertebrate survey. Parenthetical values are standard deviations of mean estimates. Invertebrates were collected with rock bag samplers. All intact amphipods ≥2 mm long were identified to genus and counted; *A. lacustre* and *Hyallela azteca* were identified to species. *H. azteca* are distinct from other species in the region and were identified and counted regardless of size as long as key features were visible (typically ≥1 mm). Mean amphipod abundance includes all taxa. *A. lacustre* proportion is the percent of identified amphipods in a sample that are that species.

Pool	Samples	Occupied sites (%)	Mean amphipod abundance (#)	Mean *A. lacustre* abundance (#)	Mean *A. lacustre* proportion per site (%)
Lockport	19	0	201 (343)	0	0
Brandon Road	21	0	60.2 (39.5)	0	0
Dresden Island	23	47.8	94.3 (52)	3.3 (7.7)	4.7 (10)
Marseilles	31	100	259 (172)	218 (180)	79.6 (25.5)
Starved Rock	16	100	194 (198)	182 (195)	91.0 (14.2)
Peoria	50	95.2	98.7 (96.3)	76.1 (85.1)	73.8 (26.4)
La Grange	60	94.9	470 (660)	431 (649)	78.5 (26.3)
Alton	43	97.7	292 (207)	240 (199)	75.5 (24.6)
Pools with A. lacustre	216	91.7	270 (395)	226 (389)	70.1 (33.3)
All Pools	263	77.3	247 (378)	192 (367)	59.0 (39.9)

Table 5: Pearson correlation coefficients (*r*) between the *Apocorophium lacustre* abundance and downstream distance within each pool where the species was detected during 2020 benthic surveys across the Illinois River Waterway System. Downstream distance reflects the distance from a sample to the next upstream dam in rkm. *n* is the number of samples captured in each pool. The Combined values is based on all of the pools that contained *A. lacustre*.

Pool	Alton	La Grange	Peoria	Starved Rock	Marseille	Dresden Island	*Combined*
r	0.18	0.48	0.40	-0.40	0.220	0.52	0.34
n	43	60	50	16	31	23	216

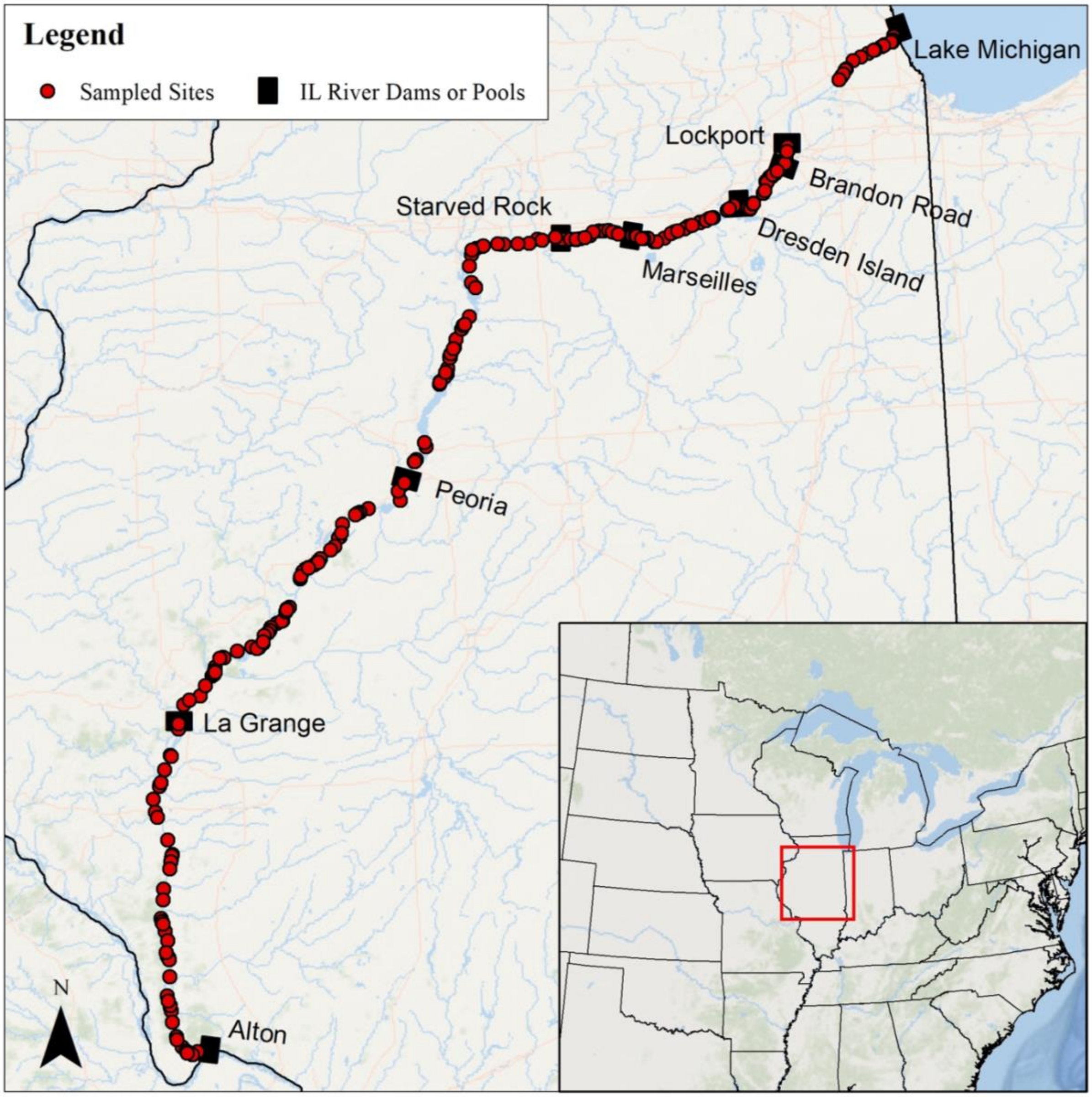
Table 6: Results of AICc model averaging procedure on fixed effect parameters included in negative binomial mixed effects models predicting *Apocorophium lacustre* abundance. Stars (**) indicate parameter effects that are considered to be significant based on the 95% confidence intervals. Confidence intervals are also presented on the log-scale.

Parameter	Log-Scale Effect	95% Confidence Interval	
		Lower	Upper
fDOM**	-1.35	-1.74	-0.95
Vegetation Density**	-1.00	-1.83	-0.17
River Discharge	-0.85	-1.96	0.27
Turbidity**	-0.46	-0.77	-0.15
Mixed Substrate	-0.33	-1.00	0.33
Salinity	-0.20	-0.58	0.19
Depth	-0.12	-0.35	0.10
DO	-0.11	-0.44	0.21
Hard Substrate	-0.07	-0.59	0.44
Silt Substrate	0.02	-0.42	0.46
Sand Substrate	0.07	-0.50	0.64
Misc. Amphipod Abundance	0.08	-0.12	0.28
Structure Presence	0.15	-0.34	0.64
Temperature**	0.26	0.01	0.52
Downstream Distance**	0.66	0.45	0.88

Table 7: Results of AICc model averaging procedure on fixed effect parameters included in binomial mixed effects models predicting benthic amphipod community composition. Stars (**) indicate parameters that are considered to be significant based on the 95% confidence intervals. Confidence intervals are also presented on the log-scale. Effects are interpreted as changes in the likelihood of an individual benthic amphipod at a site being *Apocorophium lacustre* and therefore do not reflect changes in raw *A. lacustre* abundance.

Parameter	Log-Scale Effect	95% Confidence Interval	
		Lower	Upper
River Discharge	-0.93	-1.95	0.09
Salinity**	-0.57	-0.64	-0.51
Sand Substrate**	-0.51	-0.60	-0.42
fDOM**	-0.43	-0.50	-0.35
Structure Presence	-0.06	-0.14	0.02
Turbidity**	-0.06	-0.11	-0.0004
Temperature**	-0.04	-0.09	-0.002
Depth	0.04	-0.01	0.09
Hard Substrate	0.06	-0.02	0.14
Mixed Substrate	0.09	-0.04	0.22
DO**	0.35	0.29	0.40
Downstream Distance**	0.36	0.32	0.40
Silt Substrate**	0.46	0.40	0.53

FIGURES



Service Layer Credits: Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure 1: Study system and sampling distribution map documenting 2020 benthic invertebrate sampling effort across the Illinois River Waterway System. Sample sites were randomly taken from existing Upper Midwest Environmental Science Center's Long-Term Resource Monitoring sites. Black rectangles represent the dams at the downstream end of the eight pools of the Illinois River, which provide the names of those pools. The Alton pool ends at the confluence of the Illinois and Mississippi Rivers and does not have a dam.

Figure 2: An example of a rock bag sampler prior to deployment on the Illinois River. The rock bag (left) contains approximately 0.8 L of rocks and is separated from the concrete anchor (right) by approximately 600 cm of rope. This configuration was deployed at each site and tethered to a stake or permanent structure on shore.

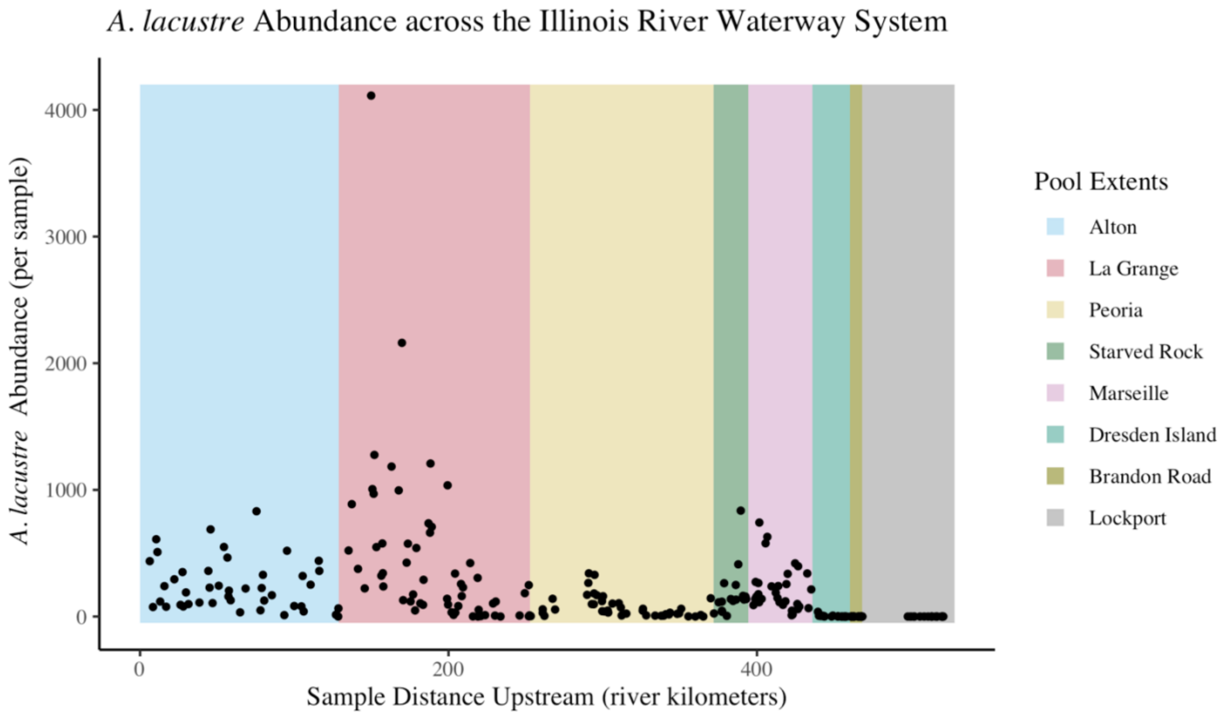


Figure 3: *Apocorophium lacustre* abundance in samples collected during 2020 benthic invertebrate survey across the Illinois River Waterway System (n = 263). Invertebrates were collected with rock bag samplers at sites utilized by the Upper Midwest Environmental Science Center's Long-Term Resource Monitoring program. The x-axis indicates the samples location along the length of the waterway, where x = 0 represents the confluence of the Illinois and Mississippi Rivers and x = 528 represents the Chicago Lock where Lake Michigan drains into the Chicago River.

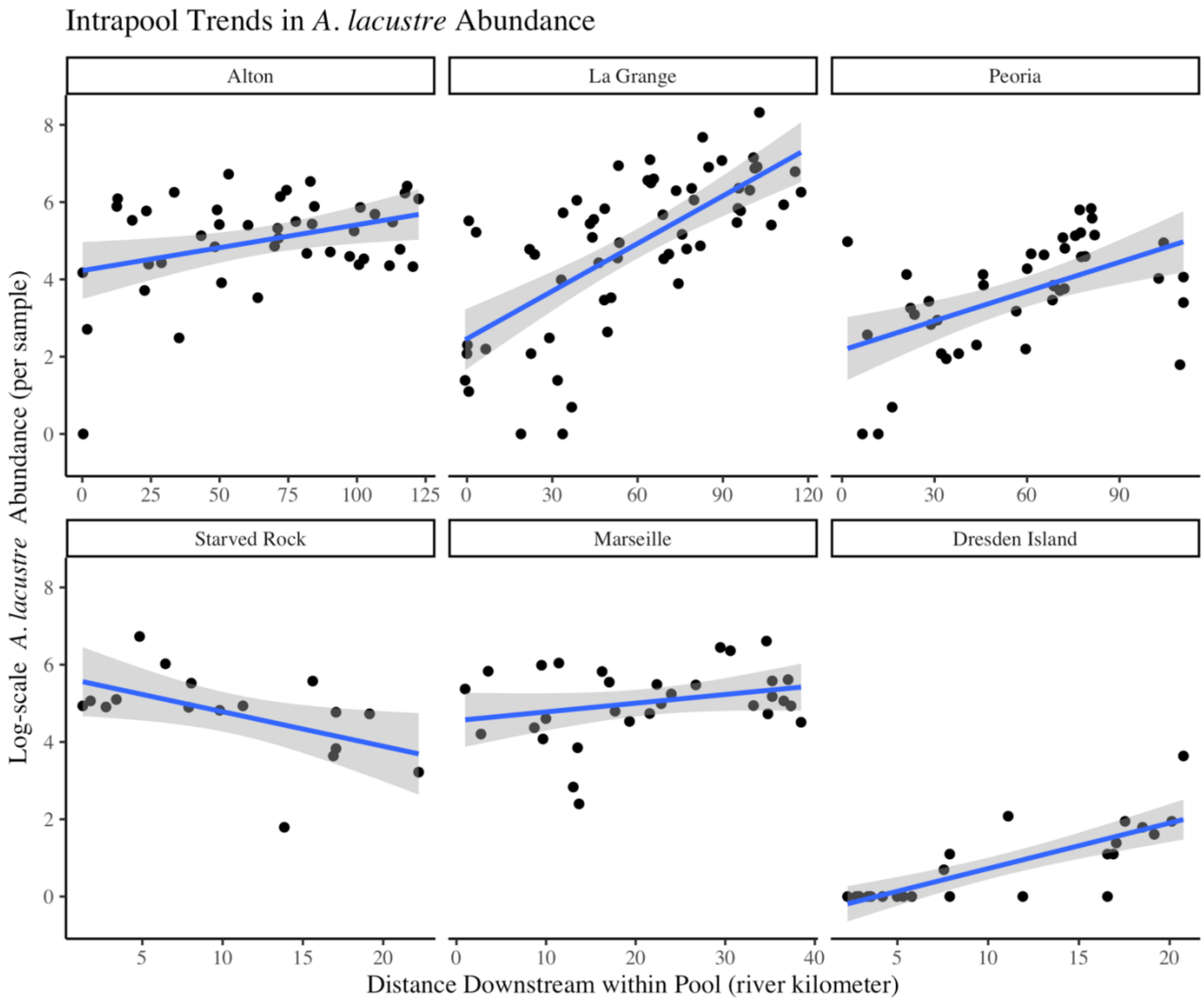


Figure 4: Trends in *Apocorophium lacustre* abundance within all pools where I detected individuals during 2020 benthic surveys across the Illinois River Waterway System. The y-axis represents *A. lacustre* abundance per sample on the log-scale - calculated with natural log of abundance + 1. The x-axis represents the distance downstream (rkm) within each pool – higher values are closer to the next downstream dam, except in the Alton Pool which ends with the confluence of the Illinois and Mississippi Rivers.

REFERENCES

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723.

Allan, J. D., Smith, S. D., McIntyre, P. B., Joseph, C. A., Dickinson, C. E., Marino, A. L., Biel, R. G., Olson, J. C., Doran, P. J., Rutherford, E. S., Adkins, J. E., & Adeyemo, A. O. (2015). Using cultural ecosystem services to inform restoration priorities in the Laurentian Great Lakes. *Frontiers in Ecology and the Environment*, *13*(8), 418–424.

Allen, Y. C., & Ramcharan, C. W. (2001). Dreissena distribution in commercial waterways of the U.S.: Using failed invasions to identify limiting factors. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(5), 898–907.

Anderson, D. R. & Burnham, K. P. (2002). Avoiding Pitfalls When Using Information-Theoretic Methods. *Journal of Wildlife Management*, *66*(3), 912–918.

Armsby, M., & Tisch, N. (2006). Intraguild predation and cannibalism in a size-structured community of marine amphipods. *Journal of Experimental Marine Biology and Ecology*, *333*, 286–295.

Asian Carp Regional Coordinating Committee (ACRCC). (2021). Asian Carp Action Plan for Fiscal Year 2021.

Bates, A. E., McKelvie, C. M., Sorte, C. J. B., Morley, S. A., Jones, N. A. R., Mondon, J. A., Bird, T. J., & Quinn, G. (2013). Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1772), 20131958.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, *67*(1).

Baxter, R. (1977). Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics*, *8*(1), 255–283.

Benson, A. J. (2018). *Apocorophium lacustre Vanhoffen, 1911*. U.S. Geological Survey, Nonindigenous Aquatic Species Database.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, *26*(7), 333–339.

Borza, P., Arbačiauskas, K., & Zettler, M. L. (2021). Multidimensional niche differentiation might buffer invasion impacts: The case of oligohaline corophiids (Crustacea: Amphipoda) in the Baltic Sea. *Biological Invasions*, *23*(6), 1891–1900.

Bousfield, E. L. (1973). *Shallow-water gammaridean Amphipoda of New England*. Comstock Pub. Associates.

Bousfield, E. L., & Hoover, P. M. (1997). The Amphipod Superfamily Corophiodea on the Pacific Coast of North America. Part V. Family Corophiidae: Corophiinae, New Subfamily. Systematics and Distributional Ecology. *Amphipacifica: Journal of Systematic Biology*, *2*(3), 67–139.

Buckland, S. T., Burnham, K. P., & Augustin, N. H. (1997). Model Selection: An Integral Part of Inference. *Biometrics*, *53*(2), 603–618.

Crawford, G. I. (1937). A Review of the Amphipod Genus Corophium, with Notes on the British Species. *Journal of the Marine Biological Association of the United Kingdom*, *21*(2), 589–630.

Curtis-Quick, J. A., Ulanov, A. V., Li, Z., Bieber, J. F., Tucker-Retter, E. K., & Suski, C. D. (2021). Why the Stall? Using metabolomics to define the lack of upstream movement of invasive bigheaded carp in the Illinois River. *PLOS ONE, 16*(10), e0258150.

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*(3), 528–534.

Dixon, I. M. T., & Moore, P. G. (1997). A comparative study on the tubes and feeding behavior of eight corophioid Amphipoda and their bearing on phylogenetic relationships within the Corophioidea. *Philosophical Transactions: Biological Sciences*, *352*(1349), 93–112.

Egly, R. M., O'Shaughnessey, E. M., & Keller, R. P. (2021a). Updated occurrence data and species distribution modeling of the invasive amphipod Apocorophium lacustre in North America. *Freshwater Science*, *40*(1), 162–174.

Egly, R. M., Polak, R. D., Cook, Z. A., Moy, H. D., Staunton, J. T., & Keller, R. P. (2021b). Development and First Tests of a Lab-Scale Electric Field for Investigating Potential Effects of Electric Barriers on Aquatic Invasive Invertebrates. *Frontiers in Ecology and Evolution*, *9*.

Evans, D. L., Strom, D. G., Higman, J., Hughes, E., Hoover, E. A., & Line, L. M. (2004). *An Evaluation of Benthic Macroinvertebrate Data from 20 Surface Water Sites Within the Lower St. Johns River Basin, 2002—2003* (Special Publication No. SJ2004-SP41). St. Johns River Water Management District.

Ezhova, E., & Żmudziński, L. (2005). Long-term trends in the macrozoobenthos of the Vistula Lagoon, southeastern Baltic Sea. Species composition and biomass distribution. *Bulletin of the Sea Fisheries Institute*, *1*(164), 55–73.

Faasse, M., & van Moorsel, G. (2003). The North-American amphipods, Melita nitida Smith, 1873 and Incisocalliope aestuarius (Watling and Maureer, 1973) (Crustacea: Amphipoda: Gammaridea), introduced to the Western Scheldt estuary (The Netherlands). *Aquatic Ecology*, *37*, 13–22.

Fusaro, A., Baker, E., Conard, W., Davidson, A., Dettloff, K., Li, J., Núñez-Mir, G., Sturtevant, R., & Rutherford, E. (2016). *A Risk Assessment of Potential Great Lakes Aquatic Invaders*. Great Lakes Environmental Research Laboratory.

Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, *22*(1), 151–163.

Gollasch, S. (2002). The Importance of Ship Hull Fouling as a Vector of Species Introductions into the North Sea. *Biofouling*, *18*(2), 105–121.

González, M. J., & Burkart, G. A. (2004). Effects of Food Type, Habitat, and Fish Predation on the Relative Abundance of Two Amphipod Species, Gammarus fasciatus and Echinogammarus ischnus. *Journal of Great Lakes Research*, *30*(1), 100–113.

Goodman Williams Group. (2015). *Industrial Usage of Chicago Area Waterway System* (Draft Phase II). City of Chicago.

Grigorovich, I. A., Angradi, T. R., Emery, E. B., & Wooten, M. S. (2008). Invasion of the Upper Mississippi River system by saltwater amphipods. *Fundamental and Applied Limnology*, *173*(1), 67–77.

Grippo, M., Fox, L., Hayse, J., Hlohowskyj, I., & Allison, T. (2014). *Risk of Adverse Impacts from the Movement through the CAWS and Establishment of Aquatic Nuisance Species in the Great Lakes and Mississippi River Basins*. *Volume II* (Appendix E).

Groschen, G. E., Arnold, T. L., Harris, M. A., Dupré, D. H., Fitzpatrick, F. A., Scudder, B. C., Morrow Jr., W. S., Terrio, P. J., Warner, K. L., & Murphy, E. A. (2004). *Water Quality in the Upper Illinois River Basin, Illinois, Indiana, and Wisconsin, 1999-2001* (Circular Report 1230; p. 42). U.S. Geological Survey.

Guerra-García, J. M., Tierno de Figueroa, J. M., Navarro-Barranco, C., Ros, M., Sánchez-Moyano, J. E., & Moreira, J. (2014). Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. *Journal of Sea Research*, *85*, 508–517.

Hardin, G. (1960). The Competitive Exclusion Principle. *Science*, *131*(3409), 1292–1297.

Hargrave, B. T. (1970). Distribution, Growth, and Seasonal Abundance of Hyalella azteca (Amphipoda) in Relation to Sediment Microflora. *Journal of the Fisheries Research Board of Canada*, *27*(4), 685–699.

Havel, J. E., & Stelzleni-Schwent, J. (2000). Zooplankton community structure: The role of dispersal. *SIL Proceedings, 1922-2010*, *27*(5), 3264–3268.

Havel, J. E., Lee, C. E., & Vander Zanden, M. J. (2009). Do Reservoirs Facilitate Invasions into Landscapes? *BioScience*, *55*, 518–525.

Heard, R. W. (1982). *Guide to Common Tidal Marsh Invertebrates of the Northeastern Gulf of Mexico*. Mississippi-Alabama Sea Grant Consortium.

Higgins, S. N., & Vander Zanden, M. J. (2010). What a difference a species makes: A meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs*, *80*(2), 179–196.

Hurvich, C. M., & Tsai, C.-L. (1991). Bias of the corrected AIC criterion for underfitted regression and time series models. *Biometrika*, *78*(3), 499–509.

Jacobs, A. I., & Keller, R. P. (2017). Straddling the divide: Invasive aquatic species in Illinois and movement between the Great Lakes and Mississippi basins. *Biological Invasions*, *19*(2), 635–646.

Jeffrey, J. D., Jeffries, K. M., & Suski, C. D. (2019). Physiological status of silver carp (Hypophthalmichthys molitrix) in the Illinois River: An assessment of fish at the leading edge of the invasion front. *Comparative Biochemistry and Physiology Part D: Genomics and Proteomics*, *32*, 100614.

Johnson, P. T., Olden, J. D., & Vander Zanden, M. J. (2008). Dam invaders: Impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment*, *6*(7), 357–363.

Jones, P. E., Tummers, J. S., Galib, S. M., Woodford, D. J., Hume, J. B., Silva, L. G. M., Braga, R. R., Garcia de Leaniz, C., Vitule, J. R. S., Herder, J. E., & Lucas, M. C. (2021). The Use of Barriers to Limit the Spread of Aquatic Invasive Animal Species: A Global Review. *Frontiers in Ecology and Evolution*, *9*.

Karatayev, A. Y., Burlakova, L. E., Padilla, D. K., Mastitsky, S. E., & Olenin, S. (2009). Invaders are not a random selection of species. *Biological Invasions*, *11*, 2009–2019.

Keller, R. P., & Lodge, D. M. (2007). Species Invasions from Commerce in Live Aquatic Organisms: Problems and Possible Solutions. *BioScience*, *57*(5), 428–436.

Keller, R. P., Habeeb, G., Henry, T., & Brenner, J. (2017). Non-native amphipod, Apocorophium lacustre (Vanhoffen, 1911), in the Illinois River and Chicago Area Waterway System. *Management of Biological Invasions*, *8*(3), 377–382.

Kelly, W. R., Panno, S. V., Hackley, K. C., Hwang, H.-H., Martinsek, A. T., & Markus, M. (2010). Using chloride and other ions to trace sewage and road salt in the Illinois Waterway. *Applied Geochemistry*, *25*(5), 661–673.

Krantzberg, G., & De Boer, C. (2008). A valuation of ecological services in the Laurentian Great Lakes Basin with an emphasis on Canada. *Journal AWWA*, *100*(6), 100–111.

Krodkiewska, M., Rewicz, T., Cebulska, K., Koczorowska, A., & Konopacka, A. (2021). Distribution pattern of the brackish Apocorophium lacustre (Vanhoffen, 1911) (Amphipoda: Corophiidae) and the structure of the amphipod assemblages in the upper Oder River catchment. *International Review of Hydrobiology*, *106*(3–4), 149–163.

LeCroy, S. E. (2004). Families Bateidae, Biancolinidae, Cheluridae, Colomastigidae, Corophiidae, Cyproideidae and Dexaminidae. In *An Illustrated Identification Guide to the Nearshore Marine and Estuarine Gammaridean Amphipoda of Florida* (Vol. 3). Florida Department of Environmental Protection.

LeCroy, S. E., Gasca, R., Winfield, I., Ortiz, M., & Escobar-Briones, E. (2009). Amphipoda (Crustacea) of the Gulf of Mexico. In D. L. Felder & D. K. Camp (Eds.), *Gulf of Mexico-Origins, Waters, and Biota: Vol. Biodiversity* (pp. 941–972). Texas A&M University Press.

Lee, C. E., & Bell, M. A. (1999). Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology & Evolution*, *14*(7), 284–288.

Lian, Y., You, J.-Y., Sparks, R., & Demissie, M. (2012). Impact of Human Activities to Hydrologic Alterations on the Illinois River. *Journal of Hydrologic Engineering*, *17*(4), 537–546.

Lima, A. C., Sayanda, D., Soares, A. M. V. M., Wrona, F. J., & Monaghan, K. A. (2017). Integrating taxonomic and trait analyses to assess the impact of damming on fish communities in a northern cold region river. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(4), 452–463.

Llansó, R. K., & Sillett, K. (2009). *Hull Biofouling of Beaumont Reserve Fleet Vessels Pioneer Contractor, Mount Vernon, and Cape Florida*. Versar, Inc.

Lower, E., Boucher, N., Alsip, P., Davidson, A., & Sturtevant, R. (2019). *2018 Update to "A Risk Assessment of Potential Great Lakes Aquatic Invaders."* Ann Arbor, Michigan.

Malmqvist, B., & Rundle, S. (2002). Threats to the Running Water Ecosystems of the World. *Environmental Conservation*, *29*, 134–153.

Mandrak, N. E., & Cudmore, B. (2010). The fall of Native Fishes and the rise of Non-native Fishes in the Great Lakes Basin. *Aquatic Ecosystem Health & Management*, *13*(3), 255–268.

Mason, W. T. (1998). Macrobenthic Monitoring in the Lower St. Johns River, Florida. *Environmental Monitoring and Assessment*, *50*(2), 101–130.

Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)* (2.3-1) [R package].

McClelland, M. A., Sass, G. G., Cook, T. R., Irons, K. S., Michaels, N. N., O'Hara, T. M., & Smith, C. S. (2012). The Long-Term Illinois River Fish Population Monitoring Program. *Fisheries*, *37*(8), 340–350.

Mook, D. (1980). Seasonal variation in species composition of recently settled fouling communities along an environmental gradient in the Indian River Lagoon, Florida. *Estuarine and Coastal Marine Science*, *11*(5), 573–581.

Mook, D. (1983). Indian River Fouling Organisms, A Review. *Florida Scientist*, *46*(3–4), 162–167.

Metropolitan Water Reclamation District of Greater Chicago (MWRDGC). (2018). *Chicago Area Waterways Water Quality Data*.

Nelson, W. G. (1995). Amphipod Crustaceans of the Indian River Lagoon: Current Status and Threats to Biodiversity. *Bulletin of Marine Science*, *57*(1), 143–152.

Nelson, W. G., Cairns, K. D., & Virnstein, R. W. (1982). Seasonality and Spatial Patterns of Seagrass-Associated Amphipods of the Indian River Lagoon, Florida. *Bulletin of Marine Science*, *32*(1), 121–129.

Noordhuis, R., van Schie, J., & Jaarsma, N. (2009). Colonization patterns and impacts of the invasive amphipods Chelicorophoium curvispinum and Dikerogammarus villosus in the IJsselmeer area, The Netherlands. *Biological Invasions*, *11*, 2067–2084.

Panov, V. E., Alexandrov, B., Arbačiauskas, K., Binimelis, R., Copp, G. H., Grabowski, M., Lucy, F., Leuven, R. S., Nehring, S., Paunović, M., Semenchenko, V., & Son, M. O. (2009). Assessing the risks of aquatic species invasions via european inland waterways: From concepts to environmental indicators. *Integrated Environmental Assessment and Management*, *5*(1), 110–126.

Parker, A. D., Glover, D. C., Finney, S. T., Rogers, P. B., Stewart, J. G., Simmonds, R. L., & Rosenfeld, J. (2016). Fish distribution, abundance, and behavioral interactions within a large electric dispersal barrier designed to prevent Asian carp movement. *Canadian Journal of Fisheries & Aquatic Sciences*, *73*(7), 1060–1071.

Payne, B. S., Bingham, C. R., & Miller, A. C. (1989). *Life History and Production of Dominant Larval Insects on Stone Dikes in the Lower Mississippi River* (No. 18; Lower Mississippi River Environmental Program, p. 46). USAEWES Environmental Laboratory.

Peverly, A. A., O'Sullivan, C., Liu, L.-Y., Venier, M., Martinez, A., Hornbuckle, K. C., & Hites, R. A. (2015). Chicago's Sanitary and Ship Canal sediment: Polycyclic aromatic hydrocarbons, polychlorinated biphenyls, brominated flame retardants, and organophosphate esters. *Chemosphere*, *134*, 380–386.

Power, A., Mitchell, M., Walker, R., Posey, M., Alphin, T., & Belcher, C. (2006). *Baseline Port Surveys for Introduced Marine Molluskan, Crustacean, and Polychaete Species in the South Atlantic Bight* (Project Number R/HAB-15; NOAA National Sea Grant Aquatic Nuisance Species Program).

Prezant, R. S., Toll, R. B., Rollins, H. B., & Chapman, E. J. (2002). Marine Macroinvertebrate Diversity of St. Catherines Island, Georgia. *American Museum Novitates*, *2002*(3367), 1–31.

Qian, S. S., Cuffney, T. F., & McMahon, G. (2012). Multinomial regression for analyzing macroinvertebrate assemblage composition data. *Freshwater Science*, *31*(3), 681–694.

R Core Team. (2020). *R: A language and environment for statistical computing* (4.0.2) [Computer software]. R Foundation for Statistical Computing.

Rahel, F. J., & Olden, J. D. (2008). Assessing the Effects of Climate Change on Aquatic Invasive Species. *Conservation Biology*, *22*(3), 521–533.

Rakocinski, C. F., Brown, S. S., Gaston, G. R., Heard, R. W., Walker, W. W., & Summers, J. K. (2000). Species-abundance-biomass responses by estuarine macrobenthos to sediment chemical contamination. *Journal of Aquatic Ecosystems Stress and Recovery*, *7*, 201–214.

Ratcliff, E. N., Glittinger, E. J., O'Hara, T. M., & Ickes, B. S. (2014). *Long Term Resource Monitoring Program procedures: Fish monitoring* (Federal Government Series No. 2014-P001; p. 98). U.S. Geological Survey.

Ricciardi, A., Whoriskey, F. G., & Rasmussen, J. B. (1997). The role of the zebra mussel (Dreissena polymorpha) in structuring macroinvertebrate communities on hard substrate. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 2596–2608.

Ricciardi, A. (2006). Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions*, *12*(4), 425–433.

Rothlisberger, J. D., Finnoff, D. C., Cooke, R. M., & Lodge, D. M. (2012). Ship-borne Nonindigenous Species Diminish Great Lakes Ecosystem Services. *Ecosystems*, *15*(3), 1–15.

Sass, G. G., Hinz, C., Erickson, A. C., McClelland, N. N., McClelland, M. A., & Epifanio, J. M. (2014). Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research*, *40*(4), 911–921.

Schmutz, S., & Moog, O. (2018). Dams: Ecological Impacts and Management. In J. Sendzimir & J. Huisman (Eds.), *Riverine Ecosystem Management* (Vol. 8, pp. 111–128). Springer.

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, *17*(4), 170–176.

Shoemaker, C. R. (1934). The Amphipod genus Corophium on the east coast of America. *Proceedings of the Biological Society of Washington*, *47*, 23–32.

Shoemaker, C. R. (1947). Further notes on the amphipod genus Corophium from the east coast of America. *Journal of the Washington Academy of Sciences*, *37*(2), 47–63.

Snedden, G. A., & Steyer, G. D. (2013). Predictive occurrence models for coastal wetland plant communities: Delineating hydrologic response surfaces with multinomial logistic regression. *Estuarine, Coastal and Shelf Science*, *118*, 11–23.

Solomon, L. E., Pendleton, R. M., Chick, J. H., & Casper, A. F. (2016). Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. *Biological Invasions*, *18*(10), 2883–2895.

Sugiura, N. (1978). Further analysts of the data by akaike' s information criterion and the finite corrections. *Communications in Statistics - Theory and Methods*, *7*(1), 13–26.

Summers, J. K. (2001). Ecological condition of the estuaries of the Atlantic and Gulf coasts of the United States. *Environmental Toxicology and Chemistry*, *20*(1), 99–106.

Szöcs, E., Coring, E., Bäthe, J., & Schäfer, R. B. (2014). Effects of anthropogenic salinization on biological traits and community composition of stream macroinvertebrates. *Science of the Total Environment*, *468–469*, 943–949.

U.S. Geological Survey (USGS). (2020). *National Water Information System (USGS Water Data for the Nation)*.

Venjakob, C., Klein, A.-M., Ebeling, A., Tscharntke, T., & Scherber, C. (2016). Plant diversity increases spatio-temporal niche complementarity in plant-pollinator interactions. *Ecology and Evolution*, *6*(8), 2249–2261.

Veraldi, F. M., Baerwaldt, K., Herman, B., Herleth-King, S., Shanks, M., Kring, L., & Hannes, A. (2011). *Non-Native Species of Concern and Dispersal Risk for the Great Lakes and Mississippi River Interbasin Study*. U.S. Army Corps of Engineers.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., & Westbrooks, R. (1996). Biological invasions as global environmental change. *American Scientist*, *84*(5), 468.

Way, C. M., Burky, A. J., Bingham, C. R., & Miller, A. C. (1995). Substrate roughness, velocity refuges, and macroinvertebrate abundance on artificial substrates in the lower Mississippi River. *Journal of the North American Benthological Society*, *14*(4), 510–518.

Wolf, B., Kiel, E., Hagge, A., Krieg, H.-J., & Feld, C. K. (2009). Using the salinity preferences of benthic macroinvertebrates to classify running waters in brackish marshes in Germany. *Ecological Indicators*, *9*, 837–847.

Ysebaert, T., De Neve, L., & Meire, P. (2000). The subtidal macrobenthos in the mesohaline part of the Schelde Estuary (Belgium): Influence by man? *Journal of the Marine Biological Association of the UK*, *80*, 587–597.