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Straddling the divide: invasive aquatic species in Illinois and movement between the Great Lakes and Mississippi basins

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Abstract The Laurentian Great Lakes and the Mississippi River are two of the largest freshwater ecosystems in North America, and each contains large numbers of non-native species. In 1900 the Great Lakes and Mississippi were permanently connected with the opening of the Chicago Sanitary and Ship Canal in the US state of Illinois. More recently, movement of trailered boats, bait, and other overland vectors have increased and further enabled movement of non-native aquatic species. To investigate the role of Illinois in continent-wide species spread we assembled a comprehensive database of recorded occurrences of aquatic non-native species in Illinois inland waters. For each species we determined vector, location, current stage in the invasion sequence (introduced or established), and ecological impacts. The arrival of non-native species has accelerated over time. Sixty species are now established, and a further 39 have been recorded. The Great Lakes have been a stronger source of species to Illinois and the Mississippi River basin than the reverse. Over the last two decades the most important vectors delivering non-native aquatic species have been unintentional release and shipping. Through a survey of Illinois aquatic ecologists we found that established species exhibit a continuous range of ecological impacts and that almost a third have high or very high ecological impacts. Local, national, and continental approaches will be required to mitigate the threat of further invasive species spreading into Illinois and between the Great Lakes and Mississippi basins.

Keywords Chicago Sanitary and Ship Canal · Freshwater · Impacts · Policy · Vectors · Nonindigenous

Introduction

Rates of introduction and spread of non-native species continue to increase worldwide, with freshwater ecosystems highly impacted (e.g., Ricciardi 2006; Keller et al. 2009). Human actions have connected aquatic ecosystems directly (e.g., canals; Mills et al. 1993) and indirectly (e.g. international shipping and aquarium trades; Ricciardi 2006; Keller et al. 2011), allowing for unprecedented movement of non-native species across natural barriers. Many of these species become established and a subset causes large ecological and economic impacts.

To become invasive, species must be transported, introduced beyond captivity, establish one or more

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reproducing populations, and then spread and cause harm (Kolar and Lodge 2001). Although many regional studies have determined the suite of non-native species that have been introduced and became established, few have quantitatively assessed which species become invasive. Despite this, it is important for managers and policy-makers to know the number and type of species that are or may become harmful in their region. Such information can be used to prioritize prevention and control strategies and to assess which vectors and taxonomic groups have been responsible for the most harmful species.

The Laurentian Great Lakes and Mississippi River basins are two of the largest freshwater ecosystems in North America and share a long boundary (Fig. 1) across which many non-native species have spread. The Chicago Sanitary and Ship Canal (CSSC) in the state of Illinois is the only connection between these ecosystems that maintains continuous aquatic habitat throughout the year (Jerde et al. 2011). This canal, opened in 1900 to facilitate navigation and disposal of sewage from Chicago (Hill 2000), was originally too polluted to provide viable habitat. Subsequent water quality improvements have enabled several non-native species to spread through it (Hill 2000; Horner et al. 1999), including the zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels which spread from the Great Lakes to the Mississippi and have subsequently moved as far as California (USGS 2014).

The role of the CSSC as a pathway for species range expansion is currently highlighted by the potential for bighead (*Hypophthalmichthys nobilis*) and silver carps (*H. molitrix*; these species are often collectively referred to as Asian carp) to enter the Great Lakes at Lake Michigan. These species have been associated with reduced condition of the native fishes gizzard shad (*Dorosoma cepedianum*) and bigmouth buffalo (*Ictiobus cyprinellus*; Irons et al. 2007), and changes in zooplankton communities (Sass et al. 2014), in the Illinois River. There is concern that similar impacts

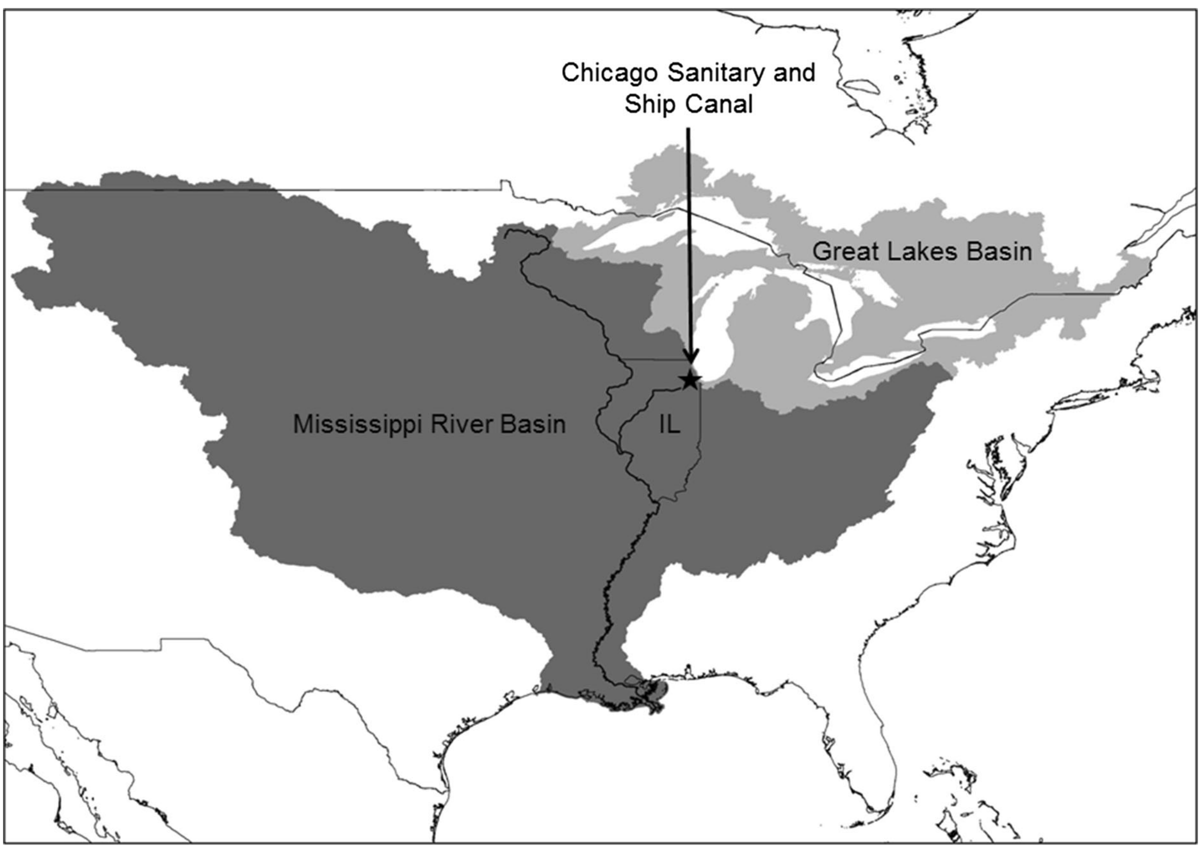

Fig. 1 Map of the Great Lakes and Mississippi River basins, showing the artificial canal connection (Chicago Sanitary and Ship Canal) running through Illinois (IL) that has connected them since 1900

and others will occur if they reach the Great Lakes (Zhang et al. 2016). Additional non-native species have been identified as posing a high risk of transfer from the Great Lakes through the CSSC to the Mississippi River, including fishes, macrophytes, and crustaceans (USACE 2014). Likewise, species in the Mississippi River basin, including the small amphipod crustacean scud (*Apocorophium lacustre*), pose a risk of spread to the Great Lakes (USACE 2014). Management activities to prevent species spread through the CSSC are focused on intensive fish sampling and the operation of electric barriers designed to repel fish (USACE 2014). A possible future option that would address a wider range of taxa is a permanent hydrologic barrier in the CSSC (USACE 2014).

There are several other vectors by which non-native organisms can cross the boundary between the Great Lakes and Mississippi River basins, including 18 sites with intermittent aquatic connections (USACE 2014), overland movement of recreational boats, and the transport of bait, aquarium, and watergarden organisms. These other vectors are widely dispersed across the boundary between the two basins.

Although there is potential for non-native species spread along the full boundary between the Mississippi and Great Lakes basins there are several reasons that the risk of spread is particularly high in Illinois. Most obvious is the presence of the CSSC. Additionally, the boundary between the basins is very close to, and for much of Illinois at, the shore of Lake Michigan. This coincides with the high population density of the Chicago region where there is intense vector activity for recreational boat movements, and the import, sale, and transport of live aquatic organisms. These vectors regularly cross the basin boundary creating a high potential for species movement. Finally, Illinois has a network of lakes and rivers throughout which many non-native species have become established. Each of these waterbodies can then serve as a source for spread into other lakes and rivers, and ultimately to other basins and US states.

Despite the importance of Illinois to continent-wide aquatic invasions there has not previously been a single dataset describing the species established there, how they arrived, and the extent of their impacts. To address this lack of knowledge we assembled a database of known records of aquatic non-native species in the state. We determined which records represent established populations and which represent introductions that failed to establish. To determine which species are invasive we conducted a survey of Illinois aquatic ecologists to gather opinions of the ecological impacts caused by each established species. We analyzed data about the year of first record for each species, determined the most likely vector that delivered it to Illinois, and, where possible, determined whether the species entered Illinois from the Great Lakes or the Mississippi River basin.

Methods

Database development

We defined Illinois to include all inland waters of the state, including those parts of the rivers (Mississippi, Ohio, and Wabash) that form its border. The Illinois portion of Lake Michigan was not included because it is ecologically part of the larger Laurentian Great Lakes ecosystem.

Our goal was to gather all records for aquatic non-native species that have been sampled in Illinois through the end of 2012, where each 'record' is a non-native species sampled at a specified time and place. An end date of 2012 was used to account for the time it can take data to be made available after it is gathered. In our case, we needed to be sure that data collectors had a chance to publish their work before it was included in our dataset. Data collection began in 2013 and ended in 2015. To locate data, we contacted experts at relevant institutions (e.g., museums, Departments of Natural Resources). From these sources we were able to directly gather data and frequently receive recommendations for additional sources. We also gathered data from aggregate sources, such as the US Geological Survey's Nonindigenous Aquatic Species database (nas.er.usgs.gov) and the Early Detection & Distribution Mapping System (www.eddmaps.org). We searched for records until all leads had been exhausted. Species were classified as introduced if they were non-native and recorded at least once beyond direct human cultivation. Species were classified as established if at least one reproducing population has been reported.

Non-native animals were straightforward to define as aquatic. For plants, we used the USDA PLANTS definition of *obligate wetland*, which is that the species occurs (under natural conditions) in wetlands with a 99% probability (USDA NRCS 2013). Parts of Illinois fall into four USDA wetland regions, and any species defined as *obligate wetland* within at least one was included (Lichvar 2012). The only exception was common reed (*Phragmites australis*) which is classified as *facultative wetland* but was included because of its large impacts in Illinois wetlands (Chambers et al. 1999; Meyerson et al. 2000). Plant nativity to Illinois was determined primarily from the USDA PLANTS database (USDA 2013) and the Biota of North America Project (BONAP; Kartesz 2013). When these sources disagreed we considered local expert opinion, Swink and Wilhelm (1994), and other relevant literature.

For each record we gathered the location and date of sampling, status of the population (i.e., established or not), and the name of the person conducting the sampling. When location data were not given as latitude and longitude coordinates we used descriptions of sampling sites to determine coordinates. When this was not possible the record's location was designated at the county level. The dataset was cleaned to remove duplicate records.

Analysis of introduction and establishment records

The number of new species discovered was summed for each 10 year period between 1873 (the year of first discovery of a non-native species) and 2012. Linear regression on this time series was used to determine if rate of discovery has changed over time.

For species not native to any part of North America we determined the most likely vector that delivered it to the continent. Following Ricciardi (2006), these vectors were shipping (including ballast water, solid ballast, and hull fouling), deliberate release through production or stocking efforts, unintentional release (including ornamental and aquaculture escape, and bait bucket release), aquarium release, and unknown. Species that are hybrids between non-native and native North American species or between two non-native species were excluded from the vector analysis because their geographic origin is uncertain. Sources were Mills et al. (1993), Les and Mehrhoff (1999), Saltonstall (2002), Ricciardi (2006), Jakubowski et al. (2012), US Geological Survey (2014), Efloras (2013), Ramey (2014), Burk (1877), Missouri Botanical Garden (2013), and NatureGate (2014).

We assessed a species as entering Illinois through the Great Lakes if it was discovered in the Great Lakes, and not in the Mississippi River basin, prior to its discovery in Illinois. The reverse rule was used to assess a species as entering through the Mississippi River basin. Resources were Ricciardi (2006), US Geological Survey Nonindigenous Aquatic Species factsheets (2014; USGS NAS), Mills et al. (1993), Les and Mehrhoff (1999), Grigorovich et al. (2008), and Sheen et al. (2009).

Impacts of established species

We searched for written reports of non-native species impacts in Illinois but found that few species have been adequately studied. Despite this, established species are observed regularly in the field by trained ecologists. To leverage these observations we adapted a survey used by Howeth et al. (2016). We identified Illinois experts, invited them to participate, and asked them to score species on a four point scale of ecological impacts. Impact categories were: (1) None to Low: *Non-native species has little to no discernible impact on existing biota*; (2) Moderate: *Non-native species causes discernible decline in the abundance of existing biota in most locations;* (3) High: *Non-native species causes discernible decline in the abundance of existing biota and becomes a dominant component of the food web*; and (4) Very High: *Non-native species causes discernible decline in the abundance of existing biota, with local extirpation of species likely. Food webs are highly altered and ecosystem-level consequences apparent*. Experts checked 'Unknown' when they were unfamiliar with the impacts of a species. Twenty-six surveys were distributed and all were returned (respondents listed in Table 1, Online Resource 1). Scores for each species were averaged for analysis, and based on the scoring system we defined the following impact ranges: average score ≥ 3.5 = *Very High*; 2.5–3.49 = *High*; 1.5–2.49 = *Moderate*; <1.5 = *Low*.

Results

Sampling records

Data for aquatic non-native species were collected from 12 sources within and outside of Illinois (Table 2 in Online Resource 1). The USGS NAS program provided roughly half of the species records (49.4%), followed by the Illinois Natural History Survey (17.0%), and the Illinois Department of Natural Resources (13.8%). Records of species *absence* were not used for analysis because they were infrequently encountered and could not be inferred.

The annual number of records of established species has increased since the 1870s, with a particular jump during the 1990s and a peak in 2000 (Fig. 1, Online Resource 1). Recent years have included those with the greatest number of records (Fig. 2). The maximum number of established species recorded in a year was 34 in 2008. When the annual number of sampling records for aquatic non-native species, a proxy for sampling effort, is plotted against the number of established species discovered in each year, a logarithmic curve is seen (Fig. 2) which becomes increasingly horizontal at about 30 species sampled per year. This indicates that current sampling methods are capable of finding roughly this number of species and that increased effort using the same methods may not find additional species. Roughly 20 established species are consistently sampled annually and these comprise plants (n = 10), fishes (n = 7), two mollusks, and the rusty crayfish (*Orconectes rusticus*). These species have each been sampled 149 or more times (Table 3, Online Resource 1). In contrast, 21 established species have been sampled on fewer than 20 occasions and during a maximum of 14 years. These species are composed of plants (n = 12), fishes (n = 3), mollusks (n = 3), crustaceans (n = 2), and a freshwater hydroid (*Cordylophora caspia*). The hydroid, a copepod (*Eurytemora affinis*), and a snail (*Bithynia tentaculata*), have been sampled just once each (Table 3, Online Resource 1). Given that absence records are not available it is possible that some species previously recorded as established are now extirpated but not recorded as such in our dataset.

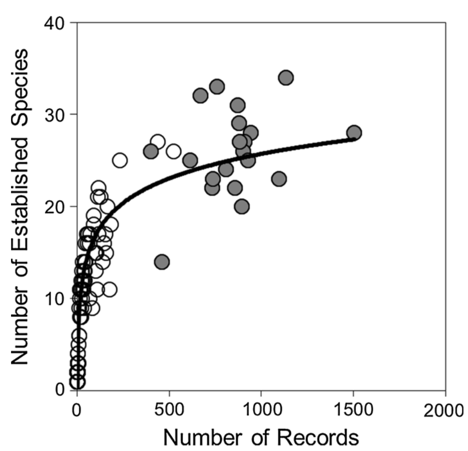

Fig. 2 Number of established non-native species recorded versus total number of non-native species records in Illinois for each year between 1873 and 2012. Line fitted by logarithmic regression: $y = 4.52\ln(x) - 1.5882$ ($r^2 = 0.91$). Shaded circles are the most recent 20 years of sampling records (i.e., 1992–2012)

Introduced species

A total of 99 aquatic non-native species were recorded from Illinois waters, represented by 22,275 records (Tables 3, 4, Online Resource 1). Thirty-nine species (265 total records) have failed to establish (Table 4, Online Resource 1), with the earliest of these being American shad (*Alosa sapidissima*), first sampled in 1873. Species that failed to establish have generally been sampled infrequently, were intentionally stocked, and/or are from climatically different regions. For example, red-bellied pacu (*Piaractus brachypomus*), a tropical fish popular in the aquarium trade, has been recorded on four occasions without becoming established.

The number of introduced species discovered per decade increased from 1873 through 2012 (Fig. 3; linear regression, n = 14 decades, $r^2 = 0.601$, $p = 0.001$). A second-order polynomial ($y = 0.004x^2 - 13.79x + 12{,}795$, $r^2 = 0.989$) better fits the data of cumulative number of species over time than a linear line ($r^2 = 0.946$; Fig. 3). This confirms the regression result that the cumulative number of introduced species has increased at an accelerating rate. Average rate of discovery over the full period was 0.71 species per year or one new species every 17 months. Over the last 30 years (1982–2012), the rate was 1.33 species per year or one new species every 9 months.

Established species

Sixty non-native species have become established in Illinois, represented by 22,010 records. The earliest recorded establisher was watercress (*Nasturtium officinale*) in 1877. Since then, species from five phyla have become established (Table 1).

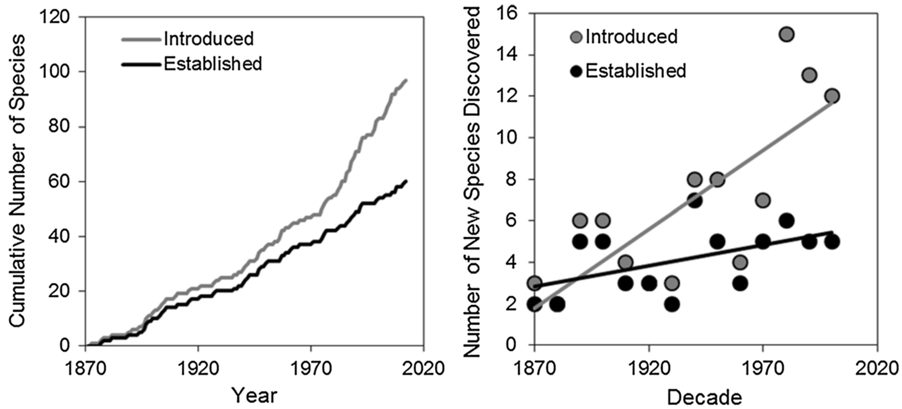

Fig. 3 **a** Cumulative number of introduced and established species discovered in Illinois inland waters from 1873 through 2012 and **b** number of new introduced (*gray points*) and established (*black points*) species discovered in each decade. Line fitted by linear regression for introduced ($y = 0.076x - 140.43$, $r^2 = 0.601$, $p = 0.001$), and established ($y = 0.0202x - 34.982$, $r^2 = 0.276$, $p = 0.054$) species

Table 1 Number of established aquatic non-native species in Illinois in taxonomic divisions

Phylum or division	Number of species
Crustaceans	4
Fishes	16
Hydroid	1
Mollusks (bivalves and gastropods)	6
Vascular plants	33
Total	60

A linear regression over time with number of established species discovered in each decade showed a positive but non-significant trend (Fig. 3; $n = 14$, $r^2 = 0.276$, $p = 0.054$). The trendline of year with cumulative number of established species is well fit by a linear line (Fig. 3; $y = 0.429x - 806.37$, $r^2 = 0.991$), indicating a relatively constant rate of discovery of new established species. This rate overall (from 1873 through 2012) was 0.43 per year, equivalent to one new species every 28 months. Over the last 30 years the rate was 0.57 species per year or one new species every 21.2 months.

Established species that are not native to North America ($n = 43$) were delivered to the continent through a range of vectors (Fig. 4a). Prior to 1990 deliberate releases (e.g., fish stocking), and unintentional releases (e.g., movement of vascular plants through the solid ballast of ships) were most important (Fig. 4b, c). More recently (1990 onwards), unintentional release and shipping have been the dominant vectors, with shipping transporting species from three different phyla (Fig. 4b, c). The highest number of new established fishes was discovered between 1960 and 1989; three of these as a result of deliberate release through stocking (Fig. 4b, c).

Twenty-eight species were established in the Great Lakes basin, but not the Mississippi River basin, prior to their discovery in Illinois. Six species were established in the Mississippi River basin prior to discovery in Illinois. Of these six species, three (bighead carp, grass carp [*Ctenopharyngodon idella*], water flea [*Daphnia lumholtzi*]) have been recorded in the Great Lakes basin, and silver carp eDNA has been detected in Lake Michigan (Jerde et al. 2011). Twenty species entered Illinois from unknown sources. Six taxa are hybrids and were removed from the analysis of species spread.

Ecological impacts

Two established species (the plant *Crypsis schoenoides* and the hydroid *Cordylophora caspia*) were not assessed for ecological impacts because we were unable to find experts familiar with them. All other species received two or more rankings, with the maximum being 13 for curly pondweed (*Potamogeton crispus*) and purple loosestrife (*Lythrum salicaria*; Table 5, Online Resource 1).

Established species were rated as having a range of ecological impacts (Fig. 5; Table 5, Online Resource 1).

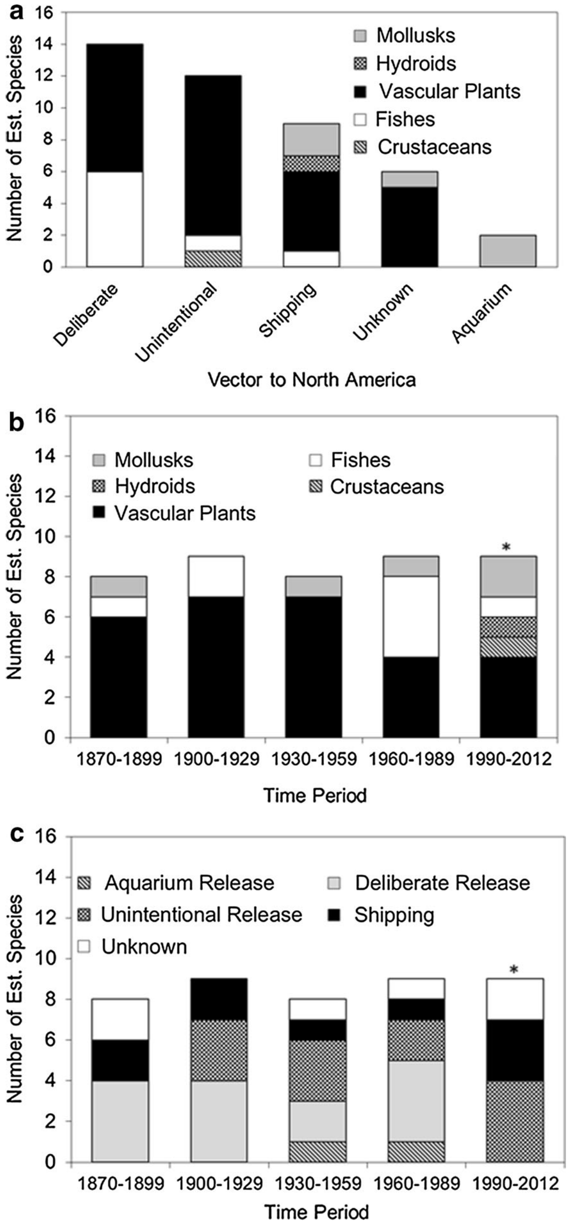

Fig. 4 Number of species non-native to North America and initial vector to North American freshwaters. **a** Initial vectors of established species in inland Illinois waters non-native to North American freshwaters from 1870 to 2012. **b** Number of established species in inland Illinois waters discovered by 30 year time periods from 1870 to 2012 (*indicates bar spans 22 years). **c** Vectors of established species in Illinois inland waters non-native to North American freshwaters discovered by 30 year time period from 1870 to 2012

Six plant species and one mollusk species (11.67% of all established species) received an average impact rank of *Very High* while eleven species (18.33%; plants, fishes, mollusks, and crustaceans) were ranked as having *High* impacts (Table 2). Twenty species (33.33%; plants, fishes, and crustaceans) were ranked as having *Moderate* impacts, and the remaining twenty species (33.33%; plants, fishes, and mollusks) were ranked as having *Low* impacts (full data in Table 5, Online Resource 1). Standard Deviation of rankings ranged from 0 to 1.4 (Fig. 5; Table 5, Online Resource 1), reflecting that experts were uniform in their assessments of some species and divergent for others. Goldfish (*Carassius auratus*), for example, received 11 rankings, all of which were *None to Low* or *Moderate*. In contrast, parrot feather watermilfoil (*Myriophyllum aquaticum*) received nine rankings, consisting of five *None to Low*, one *Moderate*, and three *High*.

The average impact scores for species non-native to the United States were not significantly related to the vector that delivered them to North America (ANOVA, $p = 0.932$, $F = 0.071$, $df = 2$). There was also no significant relationship between year of first discovery in Illinois and average impact when the 58 assessed established species were considered (Linear regression, $r^2 = 0.048$, $p = 0.099$), or when vascular plants ($r^2 = 0.044$, $p = 0.247$) or fishes ($r^2 = 0.002$, $p = 0.871$) were analyzed separately. Average impact increased with total number of records for vascular plant species only (linear regression, $r^2 = 0.265$, $p = 0.003$) but not for fishes ($r^2 = 0.231$, $p = 0.060$) or all species combined ($r^2 = 0.056$, $p = 0.073$). Average impact increased with the number of Illinois counties in which the species was sampled when all species were considered ($n = 58, r^2 = 0.180, p = 0.001$), as well as when only vascular plants ($n = 32$, $r^2 = 0.245$, $p = 0.004$) or fishes ($n = 16, r^2 = 0.479, p = 0.003$) were included. A Bonferroni correction to account for the ten statistical tests here gives a p value for significance of 0.005 and does not change the significance of any tests.

Discussion

Illinois waterways provide the only continuous aquatic habitat connecting the Great Lakes and the Mississippi River basins, two of the most ecologically and economically valuable freshwater ecosystems in North America. Within Illinois the Great Lakes

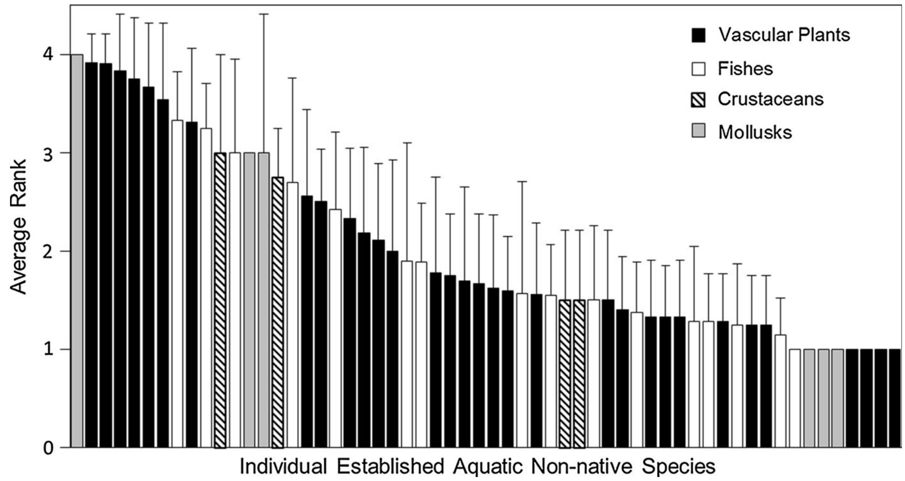

Fig. 5 Average impacts of Illinois established species. Experts ranked ecological impacts of established species from one (low) to four (high; see text and Table 5, Online Resource 1 for full scale and definitions). *Error bars* indicate one standard deviation. Average ranks were defined as follows: ≥3.5 = *Very High*; 2.5–3.49 = *High*; 1.5–2.49 = *Moderate*; <1.5 = *Low*

Table 2 Established non-native aquatic species in Illinois (n = 18) that have average ecological impact rating of ≥2.5

Type	Scientific name	Common name	Average rank
Mollusk	*Dreissena polymorpha*	Zebra Mussel	4
Vascular Plant	*Phalaris arundinacea*	Reed Canarygrass	3.92
Vascular Plant	*Typha x glauca*	Hybrid Cattail	3.91
Vascular Plant	*Phragmites australis*	Common Reed	3.83
Vascular Plant	*Typha angustifolia*	Narrowleaf Cattail	3.75
Vascular Plant	*Myriophyllum spicatum*	Eurasian Watermilfoil	3.67
Vascular Plant	*Lythrum salicaria*	Purple Loosestrife	3.54
Fish	*Hypophthalmichthys molitrix*	Silver Carp	3.33
Vascular Plant	*Potamogeton crispus*	Curly Pondweed	3.31
Fish	*Hypophthalmichthys nobilis*	Bighead Carp	3.25
Crustacean	*Daphnia lumholtzi*	Water Flea	3
Fish	*Cyprinus carpio*	Common Carp	3
Mollusk	*Cipangopaludina chinensis malleata*	Chinese Mystery Snail	3
Mollusk	*Bithynia tentaculata*	Faucet Snail	3
Crustacean	*Orconectes rusticus*	Rusty Crayfish	2.75
Fish	*Neogobius melanostomus*	Round Goby	2.7
Vascular Plant	*Egeria densa*	Brazilian Waterweed	2.56
Vascular Plant	*Butomus umbellatus*	Flowering Rush	2.5

See text for description of *Average Rank*

borders the Mississippi River basin very close to Lake Michigan (Fig. 1), and non-native species transport as contaminants of recreational boats, bait buckets, and other overland vectors is likely also important. Preventing the arrival and spread of invasive species in these basins is a large priority (Glassner-Shwayder 1999; USACE 2014) with one of the main risks to each being spread through Illinois. Our results show that the rate at which new introductions are discovered in Illinois has significantly increased over time, with the last 30 years having the highest rates ever recorded. The rate at which new established species are discovered has not increased at a significant rate, although the most recent 30 years show higher rates than previous periods.

Almost half (n = 28/60) of all established aquatic species in Illinois were present in the Great Lakes, and six in the Mississippi River, prior to their discovery in Illinois. These results lead us to three conclusions. First, the Great Lakes have been a stronger donor of species to Illinois and the Mississippi River basin than the reverse. This is consistent with the Great Lakes being one of the most heavily invaded freshwater ecosystems on Earth (Ricciardi 2006). It may also be a function of the direction of flow in the Chicago Area Waterway System (CAWS) and Illinois Rivers, which is from the Great Lakes to the Mississippi River. We note, however, that for many species this flow could be overcome by transport on boats as fouling organisms, independent swimming, or anthropogenic transport (e.g., in bait buckets).

Second, once a species becomes established somewhere within the Great Lakes or Mississippi basins there is currently little potential to prevent its spread into Illinois. In turn, Illinois policy-makers and managers may be best able to achieve protection from these species through coordinated efforts with regional and federal agencies, and environmental organizations, to prevent initial introductions to North America. Over the last two decades the most important vectors delivering those species to North America have been unintentional release and shipping. Efforts are underway to better manage shipping at the national level, for example through ballast water management, and there is evidence that this may be reducing the arrival of new species to the Great Lakes (Ruiz and Reid 2007). Species that are unintentionally released can be imported by a range of industries (e.g., the watergarden trade, aquaculture). Controlling these at the regional, national, and continental levels is likely to require increased and more consistent efforts at risk assessment by state and federal agencies, and by academics, to identify high risk species. This should be combined with border protection efforts to ensure that those species are not introduced (Environmental Law Institute 2002).

Third, the substantial subset of established species ($n = 20/60$) that were not established in the Great Lakes or Mississippi prior to Illinois suggests that Illinois is itself a major source of non-native species. The Chicago Region has a large population and high activity for many vectors (e.g., live food, aquarium, watergardening, bait sales) and many species are imported directly (Keller and Lodge 2007). If these are released they can readily spread into both the Great Lakes and the Mississippi River basins. In contrast to the subset of species described above, there may be more potential to reduce introduction of these species through state-based regulations and other activities.

The true number of species introduced to Illinois is likely to be higher than our records suggest because many species have likely not persisted long enough to be recorded (Taylor and Hebert 1993; Ricciardi 2006). Additionally, our results suggest that there may be species established in Illinois that have not yet been found. Although sampling intensity (as judged by the annual number of presence records) has increased over recent years (Fig. 2), it remains uncommon for more than half of all established species to be sampled annually. The most well organized sampling efforts target fishes (Illinois DNR 2015), and we consider it least likely that unrecorded established species come from this taxonomic group. Instead, unsampled species are most likely to be taxa that require high levels of expertise for identification, live in habitats that are difficult to sample, and/or those currently at relatively low densities. When organizing our impact survey we found very few Illinois experts actively studying and sampling freshwater algae, coelenterates, and crustaceans.

It is also possible that some species have been recorded without the records being published. It is impossible to estimate how many species this may apply to, but we suspect that it is a low number given the attention paid to non-native species and the fact that only three established species in our database have been sampled just once. We also note that as sampling effort has increased over time the likelihood of an established species being discovered has increased. Some species may have been established for many years before discovery, and species introduced recently are more likely to have been discovered even if they did not persist. It is not possible to quantify how changing sampling effort may have affected our results, but we speculate that for fishes and plants, which are relatively well sampled and make up the bulk of known species, it has probably not had a large impact on our results.

A main innovation of our work is the explicit consideration of the ecological impact caused by established species. To overcome the lack of published studies we surveyed experts that have experience with these species in the field. Thirty percent of established species were rated as having *high* or *very high* ecological impacts. Average impact increases with species distribution (measured by the number of counties where the species has been recorded), and the number of times that a species has been sampled. This is logical, given that these metrics point to species being more widespread and at higher densities, each of which are positively related to total impacts (Parker et al. 1999). We note, however, that this may be affected by an artifact of sampling effort in which species perceived to be most harmful are searched for most intensively (Hansen et al. 2013).

Many studies have assessed species as *invasive* only if there are written records of ecological or economic impacts (e.g., Kolar and Lodge 2001). While this approach is useful for some questions, our results show that reducing invasiveness to a binary variable loses a lot of information. The plot of average impacts (see Fig. 5; Table 5, Online Resource 1) displays no clear break where a threshold could unambiguously be applied. This is compounded by the occasionally large standard deviation among expert opinions and emphasizes the somewhat subjective nature of the term *invasive* when used as a binary variable to denote species that do or do not cause harm. This subjectivity extends to species management, where a distinction must be made between established species that will and will not be targeted for control based on their impact levels, and distinctions must also be made based on the potential for harm from species that have not yet arrived. Our results indicate that such distinctions will not always be straightforward.

Policy implications

Local, state, regional, national, and international policies have aimed over recent decades to reduce the rate of species invasion into the Great Lakes and Mississippi River basins. One measure of progress towards this goal is that the arrival into Illinois of intentionally introduced species has slowed, with none recorded since 1986. These species previously arrived most often through fish stocking programs. Despite this, overall rates of discovery of introduced and established species have continued to rise, showing a similar pattern to other ecosystems, including the Great Lakes (Ricciardi 2006) and Great Britain (Keller et al. 2009).

Since 1990, three species from three different phyla that were introduced to the Great Lakes through shipping have spread into Illinois and the Mississippi River basin. This is consistent with previous results showing that the Great Lakes is a starting point for new invasions across the region (Vander Zanden and Olden 2008; Rothlisberger and Lodge 2013). Shipping and other unintentional vectors (e.g. contaminated imports, ornamental and aquaculture escape) are now the most important vectors of aquatic non-native species to North America that become established in Illinois.

Further development of programs at multiple geographical scales, and coordination across jurisdictions, will likely be required to slow rates of species introduction. For example, shipping remains a strong vector and the scale of this industry means that it can be best managed at the international level. The trade in ornamental plants and animals is also important, but the nature of this industry means that at least some level of local and state management will be required. There is a strong need for more advanced and widely applied risk assessment programs and efforts to ensure that high risk species are kept out. These should be implemented at the relevant geographical and taxonomic scales, and the results applied by the jurisdiction(s) that have authority and ability to manage the vectors and species in question.

Recent efforts at the state, regional, and national levels are worth highlighting. In Illinois, the *Be a Hero, Transport Zero* campaign (http://transportzero.org/) aims to educate recreational boaters about the risks from accidental species introduction and spread on boats, and the *Hydrilla Hunt!* campaign (http://www.niipp.net/hydrilla) is aimed at early detection and rapid eradication of the aquatic plant *Hydrilla verticillata* should it be found in the state. Additionally, Illinois recently added 27 species of aquatic plants to the list of non-native species that are banned from sale in the state. This is particularly encouraging because Indiana, a neighboring state, recently banned the sale of the same set of species. These initiatives are in addition to the work being done on the CSSC to implement electric and other barriers that could prevent the spread of non-native species (USACE 2014).

At the regional level, the Great Lakes Water Quality Agreement Annex 6, between Canada and the US, aims to prevent the arrival of new non-native species to the Great Lakes. Finally, at the US national scale, the US Fish and Wildlife Service has recently assessed a large number of aquatic animal species and made the results publicly available (http://www.fws.gov/fisheries/ans/species_erss_reports.html). As described above, it will ultimately take more effort and coordination across jurisdictions to achieve the goals of slowing invasion rates in the Great Lakes and Mississippi River basins. Particular attention will need to be paid to Illinois because of its high vector activity, the proximity of the basin boundary to Lake Michigan, and the CSSC.

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