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Review

The Great Lakes' most unwanted: Characterizing the impacts of the top ten Great Lakes aquatic invasive species

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ABSTRACT

As of 2023, 188 non-native species have been identified in the Laurentian Great Lakes, with about half being considered benign. Some of these species have been elevated to the status of invasive (i.e. causing extreme negative effects). Here, we identified and quantitatively ranked in order of impact (highest to lowest), the top ten aquatic nonindigenous species (ANS) determined to have the most significant negative environmental and socio-economic effects. To accomplish this, we used an organism impact assessment (OIA) tool developed by the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS). The top ten identified species included: zebra mussel (*Dreissena polymorpha*); quagga mussel (*Dreissena bugensis*); alewife (*Alosa pseudoharengus*); sea lamprey (*Petromyzon marinus*); Japanese stiltgrass (*Microstegium vimineum*); grass carp (*Ctenopharyngodon idella*); water chestnut (*Trapa natans*); common reed (*Phragmites australis australis*); round goby (*Neogobius melanostomus*); and white perch (*Morone americana*). The taxonomic groupings, continent of origin, and vectors of introduction of these top ten invaders do *not* reflect the full diversity of all invasive species in the Great Lakes region. The most common shared negative effects were: direct hazards or threats posed to native species, alteration of predator/prey dynamics, aggressive competition with native species, and costly damage to human recreation, aesthetics, and economic activities. These quantitative rankings of the top ten most harmful ANS can serve as a reference point for researchers, educators and communicators as the Great Lakes continue to be affected by the spread of invasive species and other contemporary and future anthropogenic factors affecting the Great Lakes ecosystem.

1. Introduction

The Laurentian Great Lakes basin contains at least 188 documented aquatic nonindigenous species (ANS), making it one of the most heavily invaded aquatic systems in the world (Sturtevant et al., 2019). While some nonindigenous species are relatively benign or even beneficial, other nonindigenous species are categorized as invasive when they jeopardize environmental, economic, or human health (Executive Order 13112, 1999). Understanding which ANS in the Great Lakes are most harmful is critical to targeting and prioritizing limited management resources and predicting which incoming species may become invasive, which is key to preventing their future spread.

Examining the characteristics of the worst invasive offenders may offer insight into the combination of taxonomic group, life history, and behavioral factors that have made them so successful and so destructive. Biologists and resource managers have spent decades trying to predict "ideal" invader species based on the traits of previously successful introduced species. While certain life histories and behaviors have been associated with increased invasion potential (Kolar and Lodge, 2002; Brown and Therriault, 2022; Gordon et al., 2012; Havel et al., 2015; Petri et al., 2021), factors driving invasiveness across the entire array of taxa are still under debate (Bolius et al., 2020). A vast body of literature on invasive species in the Great Lakes has been produced over the last several decades (Mills et al., 1993; Ricciardi, 2006; Davidson et al.,

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2017; Sturtevant et al., 2019), but to date there have been very few studies that attempt to quantify the impacts of different aquatic invaders in the region relative to one another using the same evaluation method for all species across taxa.

To address this knowledge gap, the GLANSIS program (NOAA, 2024) developed a baseline organism impact assessment (OIA) tool to quantify the potential negative (environmental, ecological, social, and economic) of the 188 nonindigenous species in the Laurentian Great Lakes based on an in-depth review of current scientific and gray literature (Sturtevant et al., 2014). This assessment tool and the database it helps inform, the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS), has provided extensive information about the impacts of Great Lakes aquatic invaders (e.g., Sturtevant et al., 2014; Davidson et al., 2017). However, this paper moves beyond the historic qualitative reporting (high, moderate and low impact) to analyze the semi-quantitative scores in a way that creates quantitative ranking of species within the high impact category. This new quantitative scoring system, better suited to supporting management prioritization, is then demonstrated by identifying and ranking the top ten species determined to have the most significant negative environmental and socio-economic (including both economic and human health impacts) impacts in the Great Lakes basin. Further, we examine the combination and diversity of impacts that make these top invaders uniquely problematic.

In addition to addressing the aforementioned gap in scientific knowledge, highlighting this selection of "most unwanted" species also fulfills an ongoing outreach and communications need among Great Lakes science educators, who often field questions about which invasive species in the region are most damaging and therefore important for the public to learn to identify (Connelly et al., 2016). Ultimately, this study provides a valuable reference for science communicators in the region who need to convey the consequences of ANS to stakeholders.

2. Methods

2.1. Listing criteria

Since 2003, GLANSIS has maintained a curated list of ANS for the Great Lakes. Because the GLANSIS nonindigenous list served as the starting point for our analysis, we briefly summarize GLANSIS listing criteria here:

Geographic criterion: Only species which are found in the Great Lakes basin below the ordinary high-water mark — including connecting channels, wetlands and waters ordinarily attached to the Lakes — are included in the GLANSIS database. Species which have been collected in inland lakes within the Great Lakes basin but not meeting this geographic criterion are not included in the nonindigenous list.

Aquatic criterion: GLANSIS includes only aquatic species. USDA wetland indicator status is used as a guideline for determining whether wetland plants should be included in the list — OBL (obligate wetland), FACW (facultative wetland) and FAC (facultative) plants are included in this list as aquatic; FACU (facultative upland) and UPL (upland) plants are not. GLANSIS currently does not include mammals or birds.

Nonindigenous criterion: The species included in the GLANSIS nonindigenous list are those which are considered nonindigenous within the Great Lakes basin by meeting at least three of the following criteria (based on Ricciardi, 2006):

- the species appeared suddenly and had not been recorded in the basin previously;
- it subsequently spreads within the basin;
- its distribution in the basin is restricted compared with native species;
- its global distribution is anomalously disjunct (meaning it contains widely scattered and isolated populations);
- its global distribution is associated with human vectors of dispersal;
- the basin is isolated from regions possessing the most genetically and morphologically similar species.

Reproduction and overwintering criterion: A nonindigenous species is considered to be in at least the early stages of establishment if it has a reproducing population within the basin and is capable of overwintering, as inferred from multiple discoveries of adult and juvenile life stages over at least two consecutive years. Given that successful establishment may require multiple introductions, species are excluded if their records of discoveries are based on only one or a few non-reproducing individuals whose occurrence may reflect merely transient species or unsuccessful invasions.

GLANSIS and this paper follow the naming conventions established by the Integrated Taxonomic Information System (itis.gov).

2.2. Quantitative impact scoring

To characterize the impacts of the top ten invasive species in the Great Lakes, we generated a ranked list (most negative to least negative impact) of each nonindigenous species. To do this, we re-formulated and implemented a baseline assessment tool to quantify the realized, potential, and unknown impacts of established nonindigenous species in the Great Lakes. This organism impact assessment (OIA) tool was originally developed as a part of the risk assessment that looked at qualitative impacts as published by Sturtevant et al. (2014) and Davidson et al. (2017); however, previous publications focused solely on the qualitative categories of impact level (high, medium, low and unknown impact for environmental and socioeconomic impact), and did not directly use or analyze any of the quantitative scores for individual impact types generated during this process.

Despite previous under-utilization, the quantitative OIA scoring system can be used to assess the magnitude of each species' impact in a standardized manner across all ANS established in the Great Lakes basin. This further allowed a ranking of species more refined than the previous qualitative categories and allowed for a more detailed examination of the individual impact categories across high impact taxa. Given this paper focuses on direct use of the individual quantitative scores, we summarize this scoring system briefly here.

The OIA scores are based on review and synthesis of information from peer-reviewed research publications and gray literature. The original OIA considered two types of ANS impacts: environmental and socio-economic. These were not summed; rather, a 'high impact' in either category was considered sufficient to place the species in the qualitative category 'high impact.' This re-analysis explicitly uses the individual quantitative scores for each of the 6 sub-categories nested within each of those (12 total categories) and examines the sum of scores to create a ranking applicable within the 'high impact' category as well as examines the individual quantitative contributions of each of the 12 impact types to the overall score. *Environmental impacts* were defined as the effects of ANS species on the biotic and/or abiotic components of the ecosystem relative to pre-invasion conditions and were divided into six sub-categories; each posed as a specific question:

1. *Environmental Health*: Does the species pose some hazard or threat to the health of native species?
   a. High (6) Yes, it has resulted in the reduction or extinction of one or more native species populations, affects multiple species, or is a reportable disease
   b. Moderate (1) Yes, but negative consequences have been small (e.g., limited number of infected individuals, limited pathogen transmissibility, mild effects on populations and ecosystems) AND/OR it has significantly affected similar species in past invasions outside of the Great Lakes
2. *Competition*: Does it out-compete native species for resources?

   a. High (6) Yes, it has resulted in significant adverse effects (e.g., critical reduction, extinction, behavioral changes) on one or more native species populations
   b. Moderate (1) Yes, it has caused some noticeable stress to or decline of at least one native species population
3. *Predator-Prey*: Does it alter predator–prey relationships?
   a. High (6) Yes, it has resulted in significant adverse effects (e.g., added pressure to threatened/endangered species, significant reduction or extinction of any native species populations, creation of a dead end or any other significant alteration in the food web)
   b. Moderate (1) Yes, it has resulted in some noticeable stress to or decline of at least one native species population AND/OR it has resulted in some alteration of the food web structure or processes, the effects of which have not been widespread or severe
4. *Genetics*: Has it affected any native populations genetically?
   a. High (6) Yes, it has caused a loss or alteration of genes which may be irreversible or has led to the decline or extinction of one or more native species
   b. Moderate (1) Yes, some genetic effects have been observed, but consequences have been limited to the individual level AND/OR it has genetically affected the same or similar species in past invasions outside of the Great Lakes
5. *Environmental Water Quality*: Does it negatively affect environmental water quality?
   a. High (6) Yes, it has had a widespread, long-term, or severe negative effect on water quality AND/OR it has resulted in significant negative consequences for at least one native species
   b. Moderate (1) Yes, it has affected water quality to some extent, but the alterations and resulting adverse effects have been mild AND/OR It has significantly affected water quality in past invasions outside of the Great Lakes
6. *Physical Ecosystem*: Does it alter the physical ecosystem in some way?
   a. Yes, it has had a widespread, long term, or severe negative effect on the physical ecosystem AND/OR it has resulted in significant negative consequences for at least one native species

Socio-economic impacts included those that directly affected individual or societal values relative to pre-invasion conditions, and these were divided into an additional six categories:

1. *Human Health*: Does this species pose some hazard or threat to human health?
   a. High (6) Yes, significant effects on human health have already been observed
   b. Moderate (1) Yes, but negative consequences have not been widespread, long lasting, or severe AND/OR It has significantly affected human health in past invasions outside of the Great Lakes
2. *Infrastructure*: Does it cause damage to infrastructure?
   a. High (6) Yes, it is known to cause significant damage
   b. Moderate (1) Yes, but the costs have been small and are largely reparable or preventable AND/OR it has a history of causing significant infrastructural damage in past invasions outside of the Great Lakes
3. *Water Quality for Human Use*: Does it negatively affect water quality for human use?
   a. High (6) Yes, it has significantly affected water quality, and is costly or difficult to reverse
   b. Moderate (1) Yes, but the effects are negligible and/or easily reversed AND/OR it has a history of significantly affecting water quality in past invasions outside of the Great Lakes
4. *Economy*: Does it harm any markets or economic sectors (e.g., commercial fisheries, aquaculture, agriculture)?
   a. High (6) Yes, it has caused significant damage to one or more markets or economic sectors
   b. Moderate (1) Yes, some damage to markets or sectors has been observed, but negative consequences have been small AND/OR it has a history of harming markets or economic sectors in past invasions outside of the Great Lakes
5. *Recreation*: Does it inhibit recreational activities and/or associated tourism (e.g., through frequent water closures, equipment damage, decline of recreational species)?
   a. High (6) Yes, it has caused widespread, frequent, or otherwise expensive inhibition of recreation and tourism
   b. Moderate (1) Yes, but negative consequences have been small
6. *Aesthetics*: Does it diminish the perceived aesthetic or natural value of the areas it inhabits?
   a. High (6) Yes, the species has received significant attention from the media/public, significantly diminished the natural or cultural character of the area, or significantly reduced the area's value for future generations
   b. Moderate (1) Yes, but negative consequences have been small

Each of these sub-categories was associated with a corresponding score that was either '6′ (highly impactful), '1′ (moderately impactful), or '0′ (no known impact) as detailed above. Impacts could also be assessed as 'U' (unknown) if available information was insufficient for proper evaluation. Unknowns were treated as scores of zero computationally, but the total number of unknowns were taken into account when determining the final scores for each impact category. For example, species with an impact score of '1′ and with one or more unknowns or a score of '0′ with two or more unknowns, were categorized overall as 'Unknown' for that impact category and excluded from the analysis. The weighted nature of this scoring system balances diversity of impacts with strength of a single type of impact. With six potential impact sub-categories in each section, a very high impact in a single sub-category is equivalent to moderate impacts in all potential sub-categories. For instance, this scoring system produces the same overall impact score for each sub-category type whether only one sub-category had a high score of 6 ($6 + 0 + 0 + 0 + 0 + 0 = 6$) or each sub-category had a moderate score of 1 ($1 + 1 + 1 + 1 + 1 + 1 = 6$). In this example, both species would be scored as being highly impactful despite having different score distributions across the sub-categories.

Scores for each criterion were then summed, with a higher score indicating greater overall impact. Each category type (environmental or socio-economic) can have a score between 0–36 and an overall (environmental + socio-economic) total score that can range from zero (no impacts) to 72 (highest environmental + socio-economic impacts in all sub-categories). We define species with a score of 2 or more in either the environmental or socio-economic impact categories to be invasive in that they have measurable (moderate) environmental and/or socioeconomic impacts in at least two sub-categories or high impact in at least one category. Thus, we consider a total score of 0 or 1 to indicate that a species is not invasive or its impact is unknown. Here, we only included scores ≥ 2 (invasive) to examine the distribution of negative impact scores. More detailed descriptions of methods and criteria can be found in Sturtevant et al. (2014).

In the 10 + years since this methodology was developed, trained members of the GLANSIS team conducted individual species impact assessments using a standard template and framework based on a comprehensive literature review. All assessments were reviewed by senior members of the team and the GLANSIS program manager for consistency. This full raw data for the assessments is published in the appendices to the NOAA Tech Memo Series (Sturtevant et al., 2014, 2019; Lower et al., 2020; Bartos et al., 2021). The OIA process originally resulted in qualitative category assignments for all 188 Great Lakes nonindigenous species providing the first cross-taxa comparison of Great Lakes nonindigenous species. This reexamination uses the quantitative scores derived from those assessments to directly rank invasive species (the subset scoring ≥ 2) across all taxa, including within the 'high impact' category. Direct use of the quantitative scores provides greater resolution to relative impact than the previously published qualitative data.

2.3. Shared traits and impacts of top invaders

To explore shared traits among the types of organisms found to have the most negative impacts (top ten), we examined how these species compared to all Great Lakes established nonindigenous species in three categories: taxonomic group, continent of origin, and vector of introduction into the Great Lakes. Simple chi-square analysis was used to determine whether the subset (top ten) was representative of the larger dataset or, alternatively, if the top ten exhibited significantly different characteristics relative to the group as a whole. The nonindigenous taxa assessed included fishes, plants, mollusks, crustaceans, insects, annelids, bryozoans, coelenterates, platyhelminthes, algae, protozoa, bacteria and viruses. We focused on a relatively simple comparison of the high-level traits because this information was consistently available for all taxa in the larger group.

3. Results

3.1. Common characteristics of the top ten invaders

Our analysis scored 78 of the 188 species listed in GLANSIS (41 %) as invasive (i.e., having an impact score ≥ 2 for at least one category). The OIA scores fit a truncated Poisson-type distribution (Fig. 1**)**. Of these 78 species, 32 species had moderate impacts with scores from 2 to 5 and 36 species had high impacts with scores from 6 to 18. The remaining 10 species, with scores ≥ 20 made up the upper tail of the distribution, indicating exceptionally strong impacts in multiple categories (Fig. 1).

The top ten species with the greatest environmental and socio-economic impacts (starting with the most negatively impactful overall) were: zebra mussel (*Dreissena polymorpha,* Pallas, 1771); quagga mussel (*Dreissena bugensis,* Andrusov, 1897); alewife (*Alosa pseudoharengus,* Wilson, 1811); sea lamprey (*Petromyzon marinus,* Linnaeus, 1758); Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus); grass carp (*Ctenopharyngodon idella,* Valenciennes in Cuvier and Valenciennes, 1844); water chestnut (*Trapa natans* L.); common reed (*Phragmites australis australis* (Cav.) Trin. ex Steud.); round goby (*Neogobius melanostomus,* Pallas, 1814;); and white perch (*Morone americana,* Gmelin, 1789). Their respective combined environmental and socio-economic impact scores ranged from 22 to 55 (Table 1).

The taxonomic groupings, continent of origin, and vectors of introduction of these top ten invaders (Table 1), do *not* reflect the full diversity of all invasive species (n = 78) in the Great Lakes region (Sturtevant et al., 2014; Sturtevant et al., 2019; Lower et al., 2020; Bartos et al., 2021). Continent of origin was fairly similar between all invasive species and the top ten species in this list, with a majority of species originating from Eurasia ($X^2 = 1.21$, df = 5, p = 0.94; Fig. 2**A**), followed by other parts of North America, then Europe and Asia. The top ten invasive species in this analysis were far less taxonomically diverse than the total collection of invasive Great Lakes species, with only fish (5/10), plants (3/10), and mollusks (2/10) represented in this analysis. Despite not being statistically significant, fishes and mollusks appeared overrepresented and plants underrepresented among the top ten invaders compared to taxonomic distribution of all invasive species ($X^2 = 10.25$, df = 5, p = 0.07; Fig. 2**B**). Ballast water was the main vector of introduction for the top ten invaders, as compared to deliberate release among all invasive species, and travel through canals was significantly overrepresented as a vector of introduction among the top ten list ($X^2 = 21.32$, df = 5, p > 0.01; Fig. 2**C**).

The most common shared impacts of these ten species involve direct harm to native species through predation or amplification of environmental contaminants, alteration of predator/prey dynamics among native species, aggressive competition with native species for food and habitat, and behaviors that result in costly damage to recreation, aesthetics, and economic activities (Table 2).

3.2. Environmental impact results

The top ten highest-impact invasive species (upper tail of the distribution) were examined in depth to determine both impacts they held in common and to determine whether this subset could adequately exemplify the full range of impacts seen in Great Lakes aquatic invasive species.

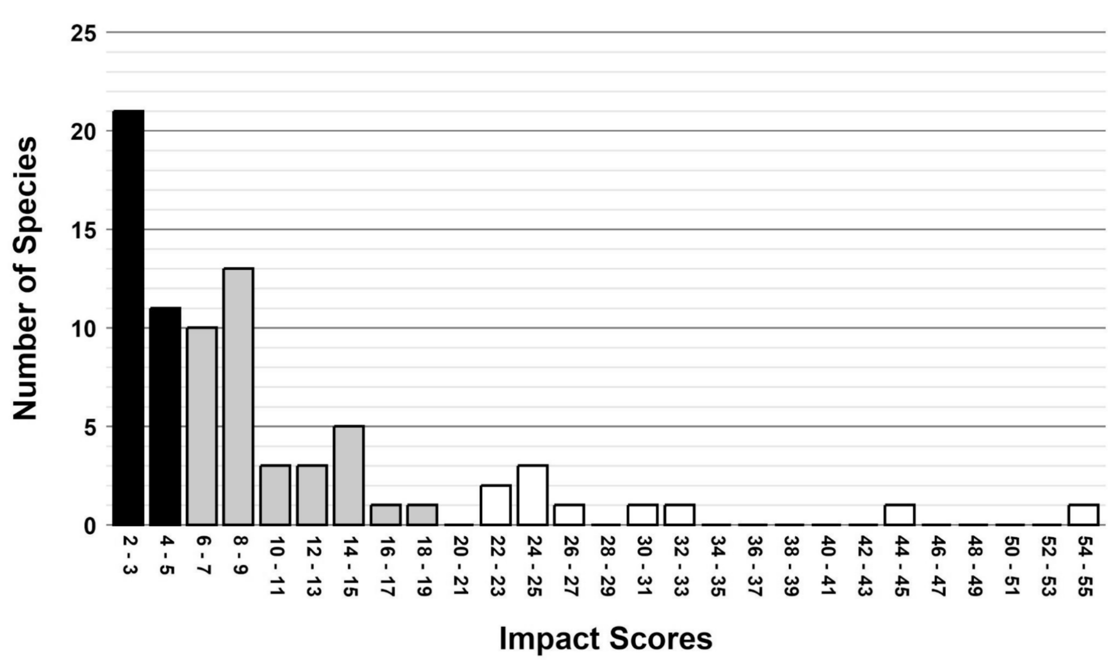

Fig. 1. Distribution of impact scores from organism risk assessments (OIA) across the 78 species with scores ≥ 2. OIAs considered six sub-categories of environmental and socio-economic impacts. The final impact scores were determined by summing the subcategory scores, with a higher score indicating greater overall impact. Species with a score of 2 or more in either category were considered invasive. Of these 78 species, 32 species had moderate impacts with scores from 2 to 5 (black bars), 36 species had high impacts with scores from 6 to 18 (gray bars), and the remaining 10 species, with scores ≥ 20 (white bars), had exceptionally strong impacts in multiple categories.

Table 1
Taxonomic group, continent of origin, and vector of introduction for the ten highest scoring established aquatic nonindigenous species.

Species	Total Impact Score	Taxonomic Group	Continent of origin	Vector of introduction
Zebra mussel (*Dreissena polymorpha*)	**55**	Mollusk	Eurasia	Ballast water
Quagga mussel (*Dreissena bugensis*)	**45**	Mollusk	Eurasia	Ballast water
Alewife (*Alosa pseudoharengus*)	**32**	Fish	North America	Migrated through canal
Sea lamprey (*Petromyzon marinus*)	**30**	Fish	North America	Migrated through canal
Japanese stiltgrass (*Microstegium vimineum*)	**26**	Plant	Eurasia	Introduced with shipment packing material
Grass carp (*Ctenopharyngodon idella*)	**25**	Fish	Asia	Imported for aquaculture
Water chestnut (*Trapa natans*)	**25**	Plant	Eurasia	Intentional introduction
common reed (*Phragmites australis australis*)	**23**	Plant	Europe	Introduced with shipment packing material and solid ballast
Round goby (*Neogobius melanostomus*)	**22**	Fish	Eurasia	Ballast water
White perch (*Morone americana*)	**22**	Fish	North America	Migrated through canal

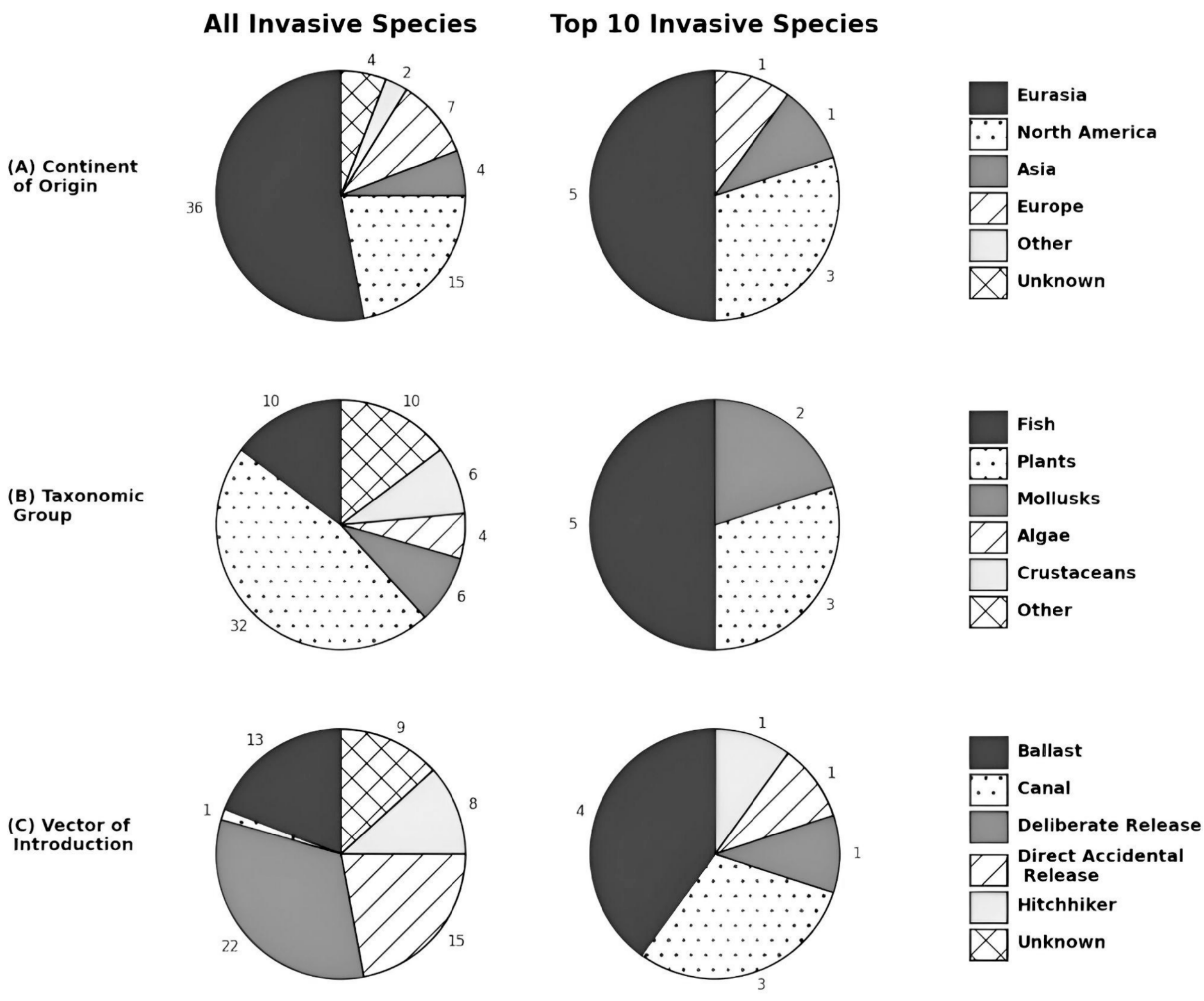

Fig. 2. Comparison of characteristics between all Great Lakes invasive species (n = 89) and top ten invaders: (A) Continent of origin, where continents with values < 2 % (Australasia, Africa, Central America, and South America) were pooled into a single "Other" category; (B) Taxonomic group; and (C) Vector of introduction.

3.2.1. Environmental health

This impact category describes the negative effects that a nonindigenous species may have on the health of native species, including whether it is a parasite, a pathogen, or a vector for either, whether it is poisonous, or whether it magnifies environmental contaminants. Nine out of the top ten species (90 %) were found to pose some hazard or threat to the health of native species. Four species (zebra mussel, alewife, sea lamprey, Japanese stiltgrass) received an environmental health impact score of 6 (highest impact), meaning that their establishment has resulted in the reduction or extinction of one or more native populations, or has affected multiple species. Five species (quagga mussel, round goby, grass carp, common reed and water chestnut) were identified as having moderate negative impacts on the health of native species. Only white perch had negligible impacts on environmental health.

The sea lamprey, a parasitic fish, is one of the species most infamous for its environmental health impacts in the Great Lakes: it attacks and feeds on other fishes, which often results in the death of the prey (Phillips et al., 1982). Fish not killed outright by the loss of blood and bodily fluids often fall victim to secondary infections, and the mortality rate of fish preyed upon by sea lampreys is around 40–60 %, but it was likely higher in the past (Hanson and Swink, 1989; Madenjian et al., 2008).

Alewives, meanwhile, pose a danger as a prey species: their bodies contain an elevated level of thiaminase, an enzyme that can degrade thiamine in species that eat them (Tillitt et al., 2005). Alewife have been shown to cause thiamine deficiency and, consequently, early mortality syndrome (EMS) in populations of alewife predators. EMS and its adverse effects on recruitment and fish populations are well-documented for coho salmon *Oncorhynchus kisutch* (Walbaum, 1792), lake trout *Salvelinus namaycush* (Walbaum 1792), and Atlantic salmon *Salmo salar* (Linnaeus, 1758), among other fishes (Fitzsimons et al., 1999; Ketola et al., 2000; Brown et al., 2005; Madenjian et al., 2008). On a spawning reef in Lake Ontario, 50–75 % of newly hatched lake trout fry were estimated to suffer from EMS from 1992 to 1999 (Mills et al., 2005).

Japanese stiltgrass is a reservoir for pathogens such as *Bipolaris* sp. (leaf blight disease) and has prompted pathogen emergence and amplification which resulted in spillover to native species (Flory et al., 2011; Kleczewski et al., 2012; Stricker et al., 2016). Japanese stiltgrass has also exhibited allelopathic effects that prevent seed germination on species such as common radish (*Raphanus sativus*) in experimental settings, but its effects on native plant germination rate are uncertain (Pisula and Meiners, 2010; Cipollini and Greenawalt Bohrer, 2016). The common reed also utilizes allelopathy in the form of gallic acid, which is degraded by ultraviolet light to produce mesoxalic acid, effectively hitting susceptible plants and seedlings with two harmful toxins that allow the reeds to form monocultures (Rudrappa, 2009). Water chestnut is also capable of an allelopathic response that inhibits the growth of phytoplankton (Lui et al., 2010).

Zebra mussels and quagga mussels bio-magnify pollutants such as polychlorinated biphenyls (PCBs) as well as natural toxins such as botulinum by concentrating harmful chemicals in their pseudofeces and accumulating them in their tissues, which can be transferred to other trophic levels (Bruner et al., 1994; Snyder et al., 1997). Zebra mussels (6 high impact) are scored in our system as more severe than quagga mussels (1 moderate impact) for this subcategory because of their habitat preferences: zebra mussels are commonly found in nearshore, shallow waters and are thus more likely to be consumed by bird predators than are quagga mussels, which have larger populations offshore. As a result, zebra mussels as a whole have greater exposure to nearshore contaminated sites and have more opportunities to deliver these contaminants up the food chain. By preying on zebra and quagga mussels, round goby facilitates the passage of these pollutants and toxins up the food chain (Hogan et al., 2007, Morrison et al., 2000, Ng et al., 2008). The round goby may also especially be a vector for biomagnification of botulinum toxin, as changes in round goby behavior associated with botulism infection makes it a preferred prey item for birds (Corkum et al., 2004). The increased transfer of benthic biomolecules to aquatic birds, along with other factors, has been implicated in the increase in botulism-related avian mortality (Lafrancois et al., 2011; Hebert et al., 2014).

Grass carp carry several parasites and diseases known to be transmissible to native fishes. Grass carp imported from China are believed to be the source of the introduction of the Asian tapeworm (*Bothriocephalus opsarichthydis)* (Hoffman and Schubert, 1984; Ganzhorn et al., 1992).

3.2.2. Predator-prey

The predator–prey impact category refers to whether a nonindigenous species has harmful effects on native food-web dynamics. All species (100%) were found to alter predator–prey relationships, indicating that effects such as the reduction of native species populations or changes in the food-web dynamics were commonly detected.

Sea lamprey, alewife, white perch, grass carp, and round goby scored as having high impact because their successful establishment has led to significant adverse effects to the predator–prey relationships of native species. Sea lamprey, in combination with other factors such as overfishing, led to the decline of several native species of large predatory fish, allowing prey fish populations to grow unchecked (Madenjian et al., 2008). Alewife populations exploded after the loss of predator fishes, resulting in additional changes to fish species composition in the lakes (Smith and Tibbles, 1980). Large populations of alewife led to a further decline in native fish populations due to predation on native fish larvae (Mason, 1996). White perch and round goby also consume the eggs of native fishes. White perch prey on the eggs of walleye *Sander vitrues* (Mitchill, 1818) and white bass *Morone chrysops* (Rafinesque, 1820), which has led to a large decline in recruitment (Madenjian et al., 2000, Schaeffer and Margraf, 1987). Native fish populations have declined in areas where round goby has become abundant (Crossman et al., 1992) and round goby has been documented to consume eggs of numerous fish species (Chotkowski and Marsden, 1999). Round goby also has been documented to negatively impact invertebrates (Krakowiak and Pennuto, 2008; Kipp et al., 2012). Round goby serve as a 'sink' for glochidia of native unionids rather than a suitable host (Tremblay et al., 2016).

Due to their voracious consumption of plant matter, grass carp alter entire aquatic ecosystems in ways that directly impact predator–prey dynamics: removal of vegetation can have negative effects on native fish, such as elimination of food sources and shelter from predators (Taylor et al., 1984). While vegetation removal by grass carp leads to better growth of rainbow trout (*Oncorhynchus mykiss*) due to increases in phytoplankton and zooplankton production, it also led to higher predation on rainbow trout by cormorants (*Phalacrocorax auritus*) due to lack of cover, as well as leading to extensive changes in diet, densities, and growth of native fishes (Hubert, 1994). Although grass carp are often used to control selected aquatic plants, these fish sometimes feed on preferred rather than on target plant species, and when stocked at high densities, grass carp can eliminate all vegetation in even large aquatic systems (Taylor et al., 1984).

Zebra mussels and quagga mussels also have high impacts on predator–prey relationships. Declines in *Diporeia* spp., a benthic invertebrate, have been highly correlated with both zebra mussels and quagga mussels (Fahnenstiel et al., 2010; Nalepa et al., 2006), although the exact mechanisms responsible have yet to be determined (Madenjian et al., 2015). *Diporeia* is an important prey item linking the benthos to higher trophic levels, and studies have suggested that the shift from *Diporeia* to zebra and quagga mussels transformed the benthic community into an energy sink that may no longer support the upper food web (Nalepa et al., 2009). It is also thought that quagga mussels likely decrease food availability for zooplankton through their rapid filtration of phytoplankton, further altering the food web (Vanderploeg et al., 2012; Vanderploeg et al., 2015).

The common reed has a high impact on predator–prey relationships in areas it infests: it is a less-desirable prey item for the snail *Littoraria irrorata*, which shifted its diet to the smooth cordgrass *Spartina alterniflora* (Kicklighter et al., 2018). This plant increased dabbling duck food energy availability by increasing the consumable seed energy even though it reduced consumable invertebrate energy (Van Neste et al., 2020). *Phragmites australis*-dominated lentic and lotic ecosystems species composition were impacted by increased alien species richness: lentic ecosystems saw increased taxonomic, phylogenetic, and functional diversity, lotic ecosystems saw decreased taxonomic and functional diversity, and both saw increases in all three categories with increases in relative abundance of alien species (Warren et al., 2001).

Japanese stiltgrass and water chestnut both have moderate impacts on predator–prey dynamics. The reduction in herbaceous plant cover caused by the introduction of Japanese stiltgrass reduces arthropod abundance and richness across multiple trophic levels (Marshall and Buckley, 2009; Simao et al., 2010). These altered trophic interactions between native insect species reduced the abundance of American toad (*Anaxyrus [Bufo] americanus)* in invaded forests (DeVore and Maerz, 2014). Declines in sub-canopy habitat in New Jersey deciduous forests caused by the invasion of Japanese stiltgrass may have resulted in the decline in abundance of some guilds of birds between 1980 and 2005 (Baiser et al., 2008). Meanwhile, water chestnut offers little nutritional value for wildlife (IPANE, 2013, Pennsylvania Sea Grant, 2012; Vermont Department of Environmental Quality, 2012) and exhibits allelopathy that inhibits the growth of phytoplankton (Lui et al., 2010). These two impacts may alter existing predator/prey relationships as native species go elsewhere to search for food.

3.2.3. Competition

This category refers to whether nonindigenous species are able to out-compete native species for resources such as habitat, nutrients, food, and light. Nine out of ten assessed organisms (90 %) were found to exhibit this competitive ability: alewife, white perch, round goby, grass carp, zebra mussel, quagga mussel, Japanese stiltgrass, water chestnut, and common reed. Sea lamprey are not known to significantly compete with native species for resources, as they are parasites and typically are not competitive until hosts become limited.

Three of the fish species (alewife, white perch, and round goby) were scored as high-impact in this category, meaning they caused behavioral changes or the reduction, extirpation, or extinction of one or more native populations. There is also overlap in the diets of alewife, white perch, and round goby; they compete with other native fishes for small macroinvertebrates and zooplankton (Crowder and Binkowski, 1983; French and Jude, 2001; Parrish and Margraf, 1990; Parrish and Margraf, 1994). This can lead to declines or even local extirpation of native fish populations, as well as causing physical and behavioral changes as seen in the bloater *Coregonus hoyi* (Milner, 1874), which evolved shorter gills and shifted to a benthic habitat much earlier in their life history as a result of competition with alewife (Crowder, 1984). Additionally, the round goby is an aggressive and successful competitor for space and utilizes habitats similar to those of logperch *Percina caprodes* (Rafinesque 1818) (Balshine et al., 2005). The round goby also competes for spawning sites with mottled sculpin *Cottus bairdii* (Girard1850) (Janssen and Jude, 2001).

Zebra mussel and quagga mussel also received high impact scores for competing with native organisms for food and habitat resources. Zooplankton abundance dropped 55–71 % following the zebra mussel invasion in Lake Erie, with micro-zooplankton such as nauplii and rotifers most heavily impacted (MacIsaac et al., 1995). Spring phytoplankton biomass and primary production in Lake Michigan decreased 87 % and 70 %, respectively, from 1995 to 1998 to 2007–2008 (Fahnenstiel et al., 2010). Reductions in zooplankton biomass may cause increased competition, decreased biomass, and higher mortality rates of planktivorous fish. Zebra mussels caused declines and local extirpations of native unionid mussels by physically hampering their movements and directly competing with them for food and space (Schloesser et al., 1996). Quagga mussel also negatively impacts native unionids, but to a lesser degree than zebra mussel (Burlakova et al., 2014).

Grass carp may directly influence other animals through competition when plant food is scarce. Grass carp are known to out-compete native species for both food and habitat. Research in small closed systems has demonstrated that due to grass carp's preference for native aquatic plants over watermilfoil (*Myriophyllum* spp.), these fish compete with waterfowl, which feed on these plants as well (McKnight and Hepp, 1995; Pine and Anderson, 1991). Direct competition for plant material may also occur between grass carp and other native fishes that include macrophytes in their diet, such as gizzard shad (*Dorosoma cepedianum*), lake sturgeon (*Acipenser fulvescens*), as well as several species of buffalo (*Ictobius* spp.)(Cudmore and Mandrak, 2004). Grass carp may compete with planktonic and benthic species, including catfishes and hybrid sunfishes for aquatic plants (Shireman and Smith, 1983), especially during grass carp juvenile stages and at lower water temperatures (Fedorenko, 1978). Direct competition for habitat has been found to occur between grass carp and other fish species, particularly bluegill. With their schooling habit, grass carp invade and disturb bluegill spawning areas, greatly reducing bluegill weight and numbers (Forester and Lawrence, 1978).

All aquatic plants included in this analysis had high competitive abilities. Water chestnut is a fast-growing species that forms mats of vegetation that float on the water's surface (IPANE, 2013; Swearingen et al., 2002) and is able to cover the water with up to three layers of leaves (Pemberton, 2002). These dense mats inhibit the growth of native aquatic species and enable water chestnut to outcompete other species for sunlight, nutrients, and space (IN DNR, 2012; OISAP, 2013; Pennsylvania Sea Grant, 2012). Japanese stiltgrass can quickly outcompete or replace existing vegetation, and fill vacant niches. Its fast growth and adaptations to low light allows it to reduce tree and other native plant regeneration through shading of the sub-canopy (Leicht, 2005; Oswalt et al., 2007; Flory, 2010). Notably, suppression of native plants by Japanese stiltgrass can promote secondary invasion of other nonindigenous plants (such as garlic mustard (*Alliaria petiolata)*) (Flory, 2010). Common reed displaces native species including sedges, rushes, and cattails and reduces wildlife habitat diversity, resulting in loss of food and shelter for native wildlife (Avers et al., 2014, Blanke et al., 2019). Reduction and degradation of wetland wildlife habitat is due in part to this plant's dense and prolific growth pattern (Swearingen and Saltonstall, 2010b): the introduced common reed forms impenetrable monocultures and is capable of dominating wetlands with its increased canopy height within a few years (Rudrappa, 2009).

3.2.4. Environmental water quality

This category accounted for increased turbidity, decreased nutrients, oxygen, or other chemical availability, and degradation of the physical ecosystem in some way. It also factored in erosion, siltation, hydrology, macrophyte and phytoplankton communities, and changes to the substrate. Water quality issues affecting human use are detailed separately in the socioeconomic impact section later in this paper.

Four of the top ten invasive species negatively affect water quality —- zebra mussel, quagga mussel, grass carp, and water chestnut. The invasion of zebra and quagga mussels was associated with high impacts, as realized by increased water clarity and a decline in phytoplankton biomass and chlorophyll *a* (Fahnenstiel et al, 1993; Kerfoot et al., 2010). Total phosphorus also declined after the establishment of quagga mussel in Lake Michigan (Mida et al., 2010). The high filtration rates of these mussels allow them to redirect or store nutrients like phosphorus, altering local water chemistry. The establishment of these dreissenid mussel colonies also appears to favor the growth of toxic cyanobacteria (*Microcystis* spp.) by changing the nitrogen:phosphorus ratio (Bykova et al., 2006) and allowing more light to penetrate the water column due to the increased water transparency (Fishman et al., 2010).

Grazing by grass carp has been associated with alterations of water quality. The decay of these large volumes of dead aquatic plants due to grass carp's grazing and waste production elevate nutrient levels in water, induce phytoplankton blooms, reduce water clarity, and decrease oxygen levels (Bain, 1993; Boyd, 1971). A single grass carp can digest only about half of the approximately 45 kg of plant material that it consumes each day. The remaining material is expelled into the water, enriching it and promoting algal blooms (Rose, 1972). These blooms can reduce water clarity and decrease oxygen levels (Bain, 1993).

During the growing season, dense surface mats of water chestnut block the air exchange between the water's surface and the atmosphere (Pennsylvania Sea Grant, 2012). Caraco and Cole (2002) found that beds dominated by water chestnut had dissolved oxygen levels below 2.5 mg/l about 40 % of the time. Low levels of oxygen caused by the presence of this species makes areas with large water chestnut populations unsuitable for fish species and likely affects the redox reactions in bottom sediments (Caraco and Cole, 2002). When water chestnut populations die and sink, the decomposition of this large amount of plant material reduces the dissolved oxygen level even further, and, in extreme cases, can cause fish kills (IN DNR, 2012; OISAP, 2013; Swearingen et al., 2002; Vermont Department of Environmental Quality, 2012).

None of the remaining six species highlighted in this paper were found to negatively affect environmental water quality.

3.2.5. Physical ecosystem

This impact category refers to whether a species negatively changes components of the physical ecosystem by altering hydrology, facilitating erosion or siltation, altering macrophyte or phytoplankton communities, or inducing physical or chemical changes in substrate. Zebra mussel, quagga mussel, Japanese stiltgrass, grass carp, water chestnut, and common reed (60 % of top ten species) were identified as altering the physical ecosystem in some way. White perch, sea lamprey, alewife, and round goby were not found to significantly alter the physical ecosystem.

Zebra mussel and quagga mussel had high impact scores due to their powerful impacts on the physical ecosystems in the Great Lakes basin. Indeed, they are often considered to be "ecosystem engineers" due to their dramatic effects on the physical habitat and by altering resource availability for other species (Hecky et al., 2004). Quagga and zebra mussels are filter-feeders and are able to remove substantial quantities of phytoplankton and suspended particles from the water (Fahnenstiel et al., 2010). The rate of biosedimentation and biodeposits through pseudofeces production is high in both quagga and zebra mussels, and can affect multiple trophic levels via changes in the physical environment (Klerks et al., 1996). This effect may be responsible for the increased water clarity that has been observed since mussel introduction (Klerks et al., 1996). Increased water clarity allows light to penetrate deeper, which may promote larger macrophyte populations, including the nuisance benthic alga, *Cladophora* (Skubinna et al., 1995; Auer et al., 2010).

Grass carp's intense removal of vegetation can have negative effects on native fish, such as elimination of food sources, shelter, and spawning substrates (Taylor et al., 1984). Declines have occurred in the diversity and density of organisms that are dependent on structured littoral habitats and food chains based on plant detritus, macrophytes, and attached algae as a consequence of reduced plant surface habitat, increased invertebrate food supplies (i.e. plant detritus), altered substrate conditions, and increased dissolved oxygen conditions (Bain, 1993).

Japanese stiltgrass and common reed were found to have significant impacts on the physical ecosystem, while water chestnut had moderate effects. Alterations to local soil chemistry by Japanese stiltgrass invasion have been shown to favor its growth and spread over native species. *M. vimineum*'s high nitrogen demand promotes the activity of nitrifying cycling bacteria and archaea, leading to increased nitrification rates and transformation of ammonia to nitrate (Lee et al., 2012; Rodrigues et al., 2015; Shannon-Firestone et al., 2015; Rippel et al., 2020). A larger nitrate pool benefited stiltgrass growth and spread, resulting in increased soil pH that further increased nitrification rates (Kourtev et al., 1998, 2002; Ehrenfeld et al., 2001). Carbon-cycling is also impacted by Japanese stiltgrass invasion: its rapid growth and effect on soil microbes accelerated carbon-cycling, resulting in a net loss of soil carbon which may have implications on long term soil fertility (Strickland et al., 2010; Strickland et al., 2011; Craig and Fraterrigo, 2017). Common reed displaces native plants and reduces wildlife habitat diversity, resulting in loss of food and shelter for native wildlife (Avers et al., 2014). Reduction and degradation of wetland wildlife habitat is due in part to *Phragmites*' dense, prolific growth pattern (Swearingen and Saltonstall, 2010). Additionally, *Phragmites* alters wetland hydrology through increased evaporation and trapping of sediments, causing marsh soils to dry out (Avers et al., 2014; Swearingen and Saltonstall, 2010). Large infestations of water chestnut can reduce water flow and even clog waterways (Naylor, 2003, Pennsylvania Sea Grant, 2012), but has fewer overall effects on the physical environment than the other two plant species detailed here.

3.2.6. Genetics

This category refers to whether introduced species are able to affect native species genetically through hybridization, introgression or selective pressure. This was a relatively uncommon impact, with only two of the species (20 %) being found to negatively affect the genome of any native populations. White perch are able to hybridize with native species belonging to the same genus. White perch is known to hybridize with the native white bass (*Morone chrysops*) (Todd, 1986), and hybrids of white perch with *Morone mississippiensis* (Jordan and Eigenmann in Eigenmann, 1887) have also been found in the Illinois River (Irons et al., 2002).

In controlled experiments, the introduced and native lineages of the common reed were found to hybridize, which has the potential to act as a mechanism for further decline of native *Phragmites* in North America where it comes in contact with introduced stands (Meyerson et al., 2010, Williams et al., 2019). It has been posited that low levels of sexual reproduction or differences in phenology were reducing the chances of naturally occurring hybridization between the two *P. australis* lineages (Saltonstall et al., 2010). However, studies show that hybridization does occur in nature, just at seemingly low levels (Saltonstall et al., 2012). Both the native and the introduced lineages regularly sexually reproduce and establish via seed dispersal and have extensive flowering time overlap, which allows for hybridization opportunities (Brisson et al., 2008; Meyerson et al., 2010; Saltonstall et al., 2014, Wu et al., 2015).

No documentation of genetic impact was found for the remaining eight species in this assessment.

3.3. Socioeconomic impact results

3.3.1. Recreation

The recreation category refers to whether a species inhibits recreational activities or tourism through water or beach closures, equipment damage, or harm to species that are important for recreation. Nine out of ten (90 %) species were found to inhibit recreational activities and/or tourism in some capacity. Alewife, zebra mussels, round goby, sea lamprey, and were all ranked as high-impact, meaning that these species have caused severe and widespread, frequent, or otherwise expensive inhibition of recreation and tourism. Grass carp, quagga mussels, water chestnut, common reed, and white perch had moderate negative impacts on recreation. Only Japanese stiltgrass was not found to have notable effects on recreation.

Several of the species in this paper directly harm popular sportfish favored by anglers. The state of Ohio has had to shut down the catch-and-release smallmouth bass *Micropterus dolomieu* (Lacépède 1802) fishery in Lake Erie during May and June in recent years due to high predation rates by round goby on smallmouth bass eggs because even briefly pulling adult bass away from the nests they were guarding allowed gobies to devour almost all their eggs (Steinhart et al., 2004). Round goby are also reported to steal bait off angler lines (Jude, 1993) and high populations of round gobies lead to negative perceptions of fishing quality (Dunning et al., 2006) Sea lamprey has caused declines in native lake trout and walleye populations, and has impacted introduced recreationally and commercially introduced salmon species in the Great Lakes (Scott and Crossman, 1973).

Other species in this category can substantially reduce recreational access and inhibit the use of affected waterways and shorelines. Historically, alewives prevented beach and waterway access; their periodic large-scale die-offs through the 1960 s left the shores of the Great Lakes littered with rotting dead fish and caused beach closures (Becker, 1983; Brown, 1968). Tall, dense stands of the introduced common reed impede shore access, as penetration of a stand of introduced *Phragmites* can not only be difficult but can also result in abrasions from the sharp-edged vegetation (Avers et al., 2014). Recreational value for birdwatchers, walkers, naturalists, boaters, and hunters is further diminished through reduction of native fish and wildlife populations (Olson, 2007). Such use impairment and restricted shoreline view also reduce property values (Avers et al., 2014). Infestations of water chestnut can also limit or even prevent recreational activities such as boating, fishing, and hunting (WI DNR, 2012). These nuts can also wash up and accumulate along the shore; reducing the access to beaches (IN DNR, 2012, OISAP, 2013). In Vermont, many previously fished bays of southern Lake Champlain are now inaccessible, and floating mats of water chestnut can create a hazard for boaters.

Zebra and quagga mussels can impede navigational and recreational boating by increased drag from attached mussels. They can also enter engine cooling systems, where they cause overheating and mechanical damage. There have been instances of navigational buoys sinking under the weight of attached zebra mussels, and dock pilings can likewise deteriorate when they are encrusted with mussels (Griffiths et al., 1991). Vilaplana and Hushak (1994) reported increased maintenance and insurance costs for Lake Erie boat owners due to zebra mussels. Quagga mussels have lower byssal thread production rates, lower attachment strength and a curved ventral edge, all of which prevent them from attaching as effectively as zebra mussels (Mills et al., 1996; Peyer et al., 2009), but this species is successful enough to still have significant impacts on recreation.

Grass carp cause increased turbidity both algal and abiotic, which can moderately affect recreation (Bonar et al., 2002, Lembi et al., 1978, Maceina et al., 1992). While white perch also impacts recreationally important species through competition, egg and larval predation, and possible hybridization, these effects are not documented to be as extreme as the other species, leading to a moderate impact score of 1 (Schaeffer and Margraf, 1987).

3.3.2. *Economy*

The economic impact category refers to harm caused to commercial fisheries, aquaculture, agriculture, and other Great Lakes-based industries. Nine out of ten species (90 %) were found to impact these economic sectors and markets. Zebra mussels, quagga mussels, sea lamprey, and water chestnut were all ranked as high-impact, while alewife, white perch, grass carp, common reed, and Japanese stiltgrass were ranked as moderate-impact, and only round goby was scored as not causing any identifiable damage to economic sectors.

Commercial fisheries have been heavily impacted by many of these top ten invaders since the mid-20th century. The introduction of the sea lamprey caused a collapse in the commercial fisheries in the 1940s and 1950s in many parts of the Great Lakes (Christie, 1974; Courtenay, 1993; Emery, 1985; Lawrie, 1970; Scott and Crossman, 1973; Smith and Tibbles, 1980). Furthermore, the cascading impacts of sea lamprey establishment, beginning with the decline of native commercially fished species, resulted in an explosion of introduced forage fish stocking (Egan, 2018). The alewife has affected commercial fisheries through predation and early mortality syndrome (EMS) (Tillitt et al., 2005). White perch affects commercially important fish species through predation, egg predation, and hybridization (Schaeffer and Margraf, 1987). The collapse of the walleye fishery on the north shore of Lake Ontario coincided with an increase in the white perch population (Schaeffer and Margraf, 1987). While grass carp have not been directly implicated in the collapse of specific fisheries, they can destroy existing food chain relationships and threaten the spawning grounds of commercial fishes (Petr and Mitrofanov, 1998; Chapman et al., 2013; Embke et al., 2016).

Zebra mussels and quagga mussels have both caused reductions in plankton biomass due to their filter feeding, which has likely caused increased competition, decreased survival and decreased biomass of many planktivorous fish, including some commercially important species (Pothoven and Madenjian, 2008). Furthermore, quagga and zebra mussels colonize reefs used as spawning habitat by fish. Marsden and Chotkowski (2001) demonstrated that the presence of zebra mussels decreased both spawning activity and egg survival for lake trout.

The cost of control can be significant for the invasive plants listed in this assessment. Dense patches of water chestnut can hinder commercial navigation (IN DNR, 2012, IPANE, 2013). The major economic costs associated with water chestnut populations are mechanical or chemical control efforts (Naylor, 2003). The Pennsylvania Department of Conservation and Natural Resources (n.d.) states that this species costs hundreds of thousands of dollars to control. Millions of dollars have been spent on mechanical harvesting and manual removal of water chestnut populations, but these programs have had limited success (Wu and Wu, 2006). Vermont spent almost $500,000 in 2000 to mechanically remove water chestnut (Pennsylvania Sea Grant, 2012), and from 1982 to 2005 various state organizations spent over $5 million to control water chestnut in Lake Champlain (IPANE, 2013). The cost of controlling Japanese stiltgrass and common reed are significant as well, with the common reed additionally reducing property values for landowners by restricting shoreline access and waterfront views.

3.3.3. *Aesthetics*

Aesthetic impacts refer to introduced species having significantly reduced public perceptions of an area's beauty or value, diminished the natural or cultural character of an area, or received significant negative attention from the media and public. Nine out of ten species (90 %) examined were found to diminish the perceived aesthetic or natural value of the areas they inhabit. Alewife, zebra mussels, quagga mussels, round goby, Japanese stiltgrass, and sea lamprey were all ranked as causing high impacts. White perch received a ranking of unknown, as an exhaustive literature search did not yield enough information to provide a ranking to date.

The aesthetic impacts of these invasive species are wide-ranging. Residents and business owners on Lake Ontario have attributed decreases in revenue and property values to excessive blooms of *Cladophora* following the zebra mussel invasion (Limburg et al., 2010). The quagga mussel has the potential to have the same effects. Although increased water clarity provides better views of Great Lakes shipwrecks, biofouling by mussels on shipwrecks may compromise the structural integrity of these underwater cultural artifacts (Binnie et al., 2009).

The periodic large-scale die-offs of alewives in the 1960 s caused Great Lake shorelines to be littered with rotting fish carcasses, which happened so frequently they became known as annual spring and summer events (Brown, 1968). Grass carp can also impact the aesthetics of water bodies by increasing turbidity (Bonar et al., 2002,). It was noted in a large survey-based study that round goby catches led to a public perception of poor fishing quality and to frustration among anglers (Dunning et al., 2006). The sea lamprey is the best-publicized cause of the collapse of fish stocks in the mid-20th century , and anglers are often alarmed and disgusted to find them attached to the sides of sport fish, where their bite marks may leave trophy fish less suitable for mounting.

Japanese stiltgrass and common reed can both block sightlines and reduce the aesthetic value of a landscape for birdwatchers, naturalists, and other recreational users, as well as reducing property values (Avers et al., 2010). The spiny nuts of water chestnut often wash up on beaches, limiting access to – and thus the aesthetic value – of the shoreline (IN DNR, 2012, OISAP, 2013).

3.3.4. *Infrastructure*

The infrastructure impact category refers to a species causing damage to water tanks, pipes, dams, and other industrial or recreational structures. Three organisms (30 %) examined were found to cause some level of harm to infrastructure: both quagga mussels and zebra mussels were ranked as high-impact, as they are notorious for causing significant damage, while common reed was ranked as moderate-impact. Based on the literature review, the other seven species were not found to damage infrastructure.

Both zebra and quagga mussels are strong biofoulers that colonize water pipes, intake structures, and screens to the point of constricting water flow and thereby reducing pumping capabilities for power and water supply plants (Connelly et al., 2007; Griffiths et al., 1991). Zebra mussels have incurred significant costs in the form of maintenance and repair of power plants due to intakes being clogged by masses of the mollusks. Estimates of the cost of repairs due to zebra mussels range from $92,000 per hydroelectric plant to $6.5 billion dollars over a ten-year span (Lovell et al., 2006). Average annual cost per electric facility or water treatment plant for control of zebra mussels was calculated at $30,000 (Connelly et al., 2007). The quagga mussel has the same

Table 2
Environmental and socioeconomic organism impact assessment scores for the ten highest scoring established aquatic nonindigenous species. The organism risk assessments considered environmental and socio-economic impacts, each divided into six sub-categories. Scores ranging from '6' (highly impactful), '1' (moderately impactful), to '0' (no known impact) were assigned to sub-categories, and impacts could be assessed as 'U' (unknown).

Species	Environmental Organism Impacts							Socioeconomic Organism Impacts							
	Environmental Health	Competition	Predator-Prey	Genetics	Environmental Water Quality	Physical Ecosystem	Total Environmental Impact	Human Health	Infrastructure	Water Quality (Human Use)	Economy	Recreation	Aesthetics	Total Socioeconomic Impact	Total Impact
Zebra mussel	6	6	6	0	6	6	**30**	0	6	1	6	6	6	**25**	**55**
Quagga mussel	1	6	6	0	6	6	**25**	0	6	1	6	1	6	**20**	**45**
Alewife	6	6	6	0	0	0	**18**	0	0	1	1	6	6	**14**	**32**
Sea lamprey	6	0	6	0	0	0	**12**	0	0	U	6	6	6	**18**	**30**
Japanese stiltgrass	6	6	1	U	0	6	**19**	0	0	0	1	0	6	**7**	**26**
Grass carp	1	1	6	0	6	6	**20**	1	0	1	1	1	1	**5**	**25**
Water chestnut	1	6	1	0	6	1	**15**	1	0	1	6	1	1	**10**	**25**
Common reed	1	6	6	1	0	6	**20**	1	1	0	1	1	1	**5**	**25**
Round goby	1	6	6	0	0	1	**14**	1	0	0	0	6	1	**8**	**22**
White perch	1	6	6	6	0	0	**19**	1	0	0	1	1	0	**3**	**22**

potential to cause major costs for the hydropower industry (Claudi and Prescott, 2007). While quagga mussels do not have the same attachment efficacy as zebra mussels, they are still capable of fouling hard surfaces (Mills et al., 1996; Peyer et al., 2009).

The Michigan Department of Transportation (MDOT) considers common reed to be a safety hazard, as its height and dense growth may block signs and view of access roads, drives, and curves (B. Batt, MDOT, pers. comm.). During its dormant season, when dry biomass is high, the introduced common reed also creates a potentially serious fire hazard to structures (Avers et al., 2010; Swearingen and Saltonstall, 2010a).

3.3.5. *Water quality for human use*

This impact category refers to water quality issues specifically pertaining to human uses such as drinking water, swimming, or wading. 5 (50 %) species examined were found to have moderately negative effects on water quality in a way that affects human populations, including alewife, quagga mussels, zebra mussels, grass carp, and water chestnut.

The reemergence of the nuisance algal species *Cladophora* in Lakes Erie, Michigan, and Ontario has been largely attributed to the resulting change in nutrient cycling and water clarity since the establishment of zebra mussels (Auer et al.,; Hecky et al., 2004). Similar observed effects between zebra mussel and quagga mussel filtering ability suggest that quagga mussels likely contribute to this impact as well (Nalepa; 2009). In the 1950 s and 1960 s, fish kills of alewives were shown to contribute to oxygen depletion and hypoxia in the water column, and also made beaches and surrounding water completely unsuitable for human recreation after their mass die-offs (Becker; 1983).

Grass carp increase turbidity and may produce algal blooms when introduced to an area, rendering water unsuitable for human use (Bonar et al., 2002). Water chestnut also has a moderate impact on water quality for human use, as it may cause fish kills when its vegetation dies and decomposes, thereby creating a reduction in water oxygenation (IN DNR, 2012; OISAP, 2013; Swearingen et al., 2002; Vermont Department of Environmental Quality, 2012).

Round goby, white perch, common reed, and Japanese stiltgrass were not found to negatively affect water quality as it pertains to human use. There was no information available in the literature to assess sea lamprey impact on water quality for human use, so it was ranked as unknown for this impact.

3.3.6. *Human health*

This impact category refers to organisms that pose some hazard to human health through magnifying toxin levels, being poisonous, or being a virus, bacteria, parasite, or vector of one that can infect humans. 4 (40 %) organisms were found to impact human health: round goby, grass carp, water chestnut, and common reed were ranked as having moderate negative effects that are not widespread or severe within the Great Lakes basin.

Because of its predation on zebra mussels, the round goby is capable of facilitating the bioaccumulation of contaminants up the food chain to piscivores that feed on it, which may eventually be consumed by humans (Hogan et al., 2007; Morrison et al., 2000; Ng et al., 2008). Areas of stagnant water caused by dense stands of water chestnut create breeding grounds for mosquitoes (Naylor, 2003). The hard, spiny seeds of water chestnut, also known as water caltrops, are sharp enough to puncture leather and can cause painful wounds to humans and animals that step on them (Swearingen et al., 2002). Common reed can cause cuts and scrapes from its sharp-edged vegetation when people try to navigate through its stands (Avers et al., 2014; Olson, 2007). Grass carp is a host of the Asian tapeworm (*Bothriocephalus acheilognathi)*, which can infect humans who consume it in undercooked meat (Bain, 1993; Salgado-Maldonado and Pineda-Lopez, 2003).

Based on the literature review, the other six species were not found to cause harm to human health.

4. Discussion

These findings are in agreement with much of the previously published literature on the large-scale impacts of aquatic invasive species in the Great Lakes and beyond. All five of the fish species identified in this top ten list also appear in the top ten highest ranked invasive fish identified by expert questionnaire (Howeth et al., 2016). Both water chestnut and common reed are identified in the US and Canadian Aquatic Weed Risk Assessments (Gordon et al., 2012; Gantz et al., 2014 respectively). Eight of our top species are identified in the USFWS Ecological Risk Screening Summaries (2018), eight by the University of Notre Dame STAIR assessments (Plants = Gantz et al., 2015; Fish = Howeth et al., 2015; Mollusks = Keller et al., 2007) and three by the Canadian Ballast Risk Assessment (Casas-Monroy et al., 2014). The top ten invasive species identified by our quantitative scoring system are also mostly congruent with previously identified lists of worst invaders for the Great Lakes region. Four (sea lamprey, alewife, white perch and zebra mussel) appear on the short list of 'exotic species considered to have substantial impacts' published by Mills et al. (1994). All are currently regulated by at least some of the jurisdictions in the Great Lakes basin. All appear in the shortlists generated by independent state/provincial assessment protocols: Minnesota Invasive Species Advisory Council (2020 – all 10), New York Invasive Species Information (Jordan et al., 2012 – 8), Wisconsin Department of Natural Resources assessments (2020—–7), Ontario Climate Change Research Report (Buckley et al., 2021 – 5). None of these assessments have attempted to create a cross-taxa ranked list applicable to the Great Lakes as a whole, as does our method.

The most frequently occurring impacts of the top ten species are: altering predator/prey dynamics (10/10), hazards or threats to native species (9/10), outcompeting native species (9/10), recreation (9/10), economy (9/10), and aesthetics (9/10). Collectively, the top ten list generated by this analysis encompass the entire range of impact categories, and even within each category, a wide diversity of impact types are represented by this small subset of species. This shows that (a) our method is robust in capturing the full diversity of possible impacts (e.g., not biased in favoring any particular category such as economic impacts) and (b) high impact species are not all impactful in the same way.

Based on this analysis of the top ten species, we could expect the profile of an especially impactful invasive species to be 1) a fish (5 of the 10) 2) from Eurasia (5 of the 10) that 3) is a ballast water invader (3 of the 10). However, this characterization most likely is a mere artifact of the particular pathway (ballast water from Eurasia) that dominated introductions during the period of peak historic introduction rates (1959–2002 at 1.81 species per year; Sturtevant et al. 2019). While fish are arguably 'overrepresented' in this list of most impactful invaders, this is not statistically significant. Furthermore, their life histories (as evidenced by taxonomic diversity) and ecological effects in the Great Lakes differ markedly from one another, and there does not seem to be a specific "profile" of an archetypical invader that can be generated from this analysis. This regional finding for a small subset of highest impact invasives reinforces the more extensive *meta*-analysis conducted by Boltovskoy et al. (2021) which found that non-significant outcomes were more common than significant ones in studies examining the relationships between traits and impacts. The most important commonalities hinge only on the multiple direct threats that these invasive species pose to native species (preying on, outcompeting, and/or disrupting the habitats of natives), and the economic impacts thereof (impeding recreational and commercial activities and requiring costly management efforts).

Havel et al. (2015) highlighted the community-level damage caused by ANS through their tendencies to cause food web alteration and act as ecosystem engineers with broad-scale negative effects that cannot be easily summarized by one or even a handful of impact sub-categories. The high scores reflected in the OIA indicate that each of these species are not simply harmful for one specific reason such as predation or biofouling: instead, they cause system-wide disruptions through negative impacts that may influence and even be amplified by one another. Likewise, the socio-economic damage caused by these top ten invaders was not limited to a handful of separate negative outcomes per species, such as being unsightly or clogging boat propellers, but instead reflect multiple interacting, mutually-reinforcing factors that damage the perceived beauty and recreational value of the Great Lakes and result in significant expenses for both prevention and control.

As Great Lakes environmental managers move to prioritize control efforts, cross-taxa assessments of the relative impact of established nonindigenous species may help to prioritize species for regional-scale control (Steinberg et al., 2007). However, the diversity in the taxa, origin, vectors, and life histories of the top ten most impactful species in the Great Lakes highlights the conspicuous absence of clear-cut characteristics among these top ten invasive species, and emphasizes the difficulty in predicting whether a newly introduced species will actually become invasive in the region. This ambiguity reinforces the critical importance of ongoing early detection and rapid response efforts and constant vigilance in the face of future biological invasions.

Nonetheless, that the primary commonality among the top ten species is found only in their impact suggests that taking a closer look at species' behavior and history of impacts in other locations may be particularly useful in predicting outcomes when they are introduced to the Great Lakes region, and that these factors should therefore be given greater emphasis in risk assessment work, a recommendation also supported by previous research (Havel et al., 2015, Besek, 2019, Stohlgren et al., 2005). While invasion history was included as a factor in our OIA whenever possible, significant gaps remain in the literature, as negative or null study results are rarely published, and relevant studies from around the world that are published in non-English literature may not be accessible to English-speaking researchers (Davidson et al., 2017). As a synthesized review of current scientific literature in the Great Lakes, the rankings of the species listed in this paper may be expected to change over time as new and improved information about each of these top ten invasive species, and the 180 + other ANS currently identified in the Great Lakes region, becomes available.

The strength of our methodology lies in its capacity to create an objective, quantitative ranking of species by impact that works across all taxa. As such, we are hopeful that it will serve as a key piece of information for management prioritization. As a quantitative metric, this impact score can easily be combined with other metrics reflecting distribution, spread, population densities, and availability/cost of management options in devising additional frameworks for management decision making.

In addition to identifying a quantitative ranking of the most severely impactful species for academic researchers and managers based on a synthesis of current literature, we intend our top ten list to also serve as a reference point for science educators and communicators who address Great Lakes invasive species in their programming. Sagrans et al. (2022) wrote that large open-source data sets pose challenges including how to curate the data, and navigating the context and complexities of the data, but that using data sets in the classroom is critical to meaningful, relevant student learning. In a project involving 18 teachers learning to use large data sets in their high school classrooms, many teachers expressed that they "did not have time to find data sets that were just right for their students in terms of size and complexity (Sagrans et al., 2022)". In 2023, the GLANSIS team conducted a series of semi-structured interviews with teachers and other environmental educators who teach about Great Lakes invasive species as part of a user group needs assessment (using the process documented in Lower et al. (2020). One finding was that some teachers felt overwhelmed by the amount of information available about the nearly 200 introduced species within the Great Lakes basin; this ranked list of the top ten most impactful species will thus allow educators to focus on a much smaller subset of organisms across multiple taxa that are both the highest impact and represent the full range of environmental and socioeconomic impact types. While the full taxonomic range is not adequately captured, major taxa familiar to students are well-represented in this subset. With the inclusion of Great Lakes science in the Next Generation Science Standards curriculum (NGSS Lead States, 2013), *meta*-analyses of the most up-to-date ANS research conducted in the region will enable educators to develop more effective lesson plans and outreach material. While the effects of nonindigenous species on native species and environments can be complex, an improved understanding of their myriad impacts will foster more effective conservation, management, and restoration efforts in the Great Lakes.

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Authors' contributions

- EL served as lead author and is responsible for drafting, editing, and reviewing this manuscript, as well as its underlying data analysis and synthesis.
- RS is the GLANSIS project manager, analyzed and synthesized much of the raw data for this project, and provided significant contributions to manuscript editing and feedback.
- JR is a GLANSIS data associate and contributed to the statistical analysis used in this paper.
- SI is a former research assistant with the GLANSIS team and collated the raw data from the GLANSIS database that formed the original outline of this manuscript.
- FM is the GLANSIS project co-PI and provided manuscript editing and feedback.
- ER is a member of the GLANSIS team and provided manuscript editing and feedback.
- DM is a member of the GLANSIS team and provided manuscript editing and feedback.
- AE is the GLANSIS project co-PI and provided manuscript editing and feedback.

Ethics and permits

All research pertaining to this article did not require any research permit(s).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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