

Aquatic invasion patterns across the North Atlantic

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Abstract

Biological invasions are a major driver of biodiversity loss and socioeconomic burden globally. As invasion rates accelerate worldwide, understanding past invasion dynamics is essential to inform predictions of future invaders and impacts. Owing to a high diversity of pathways and current biosecurity gaps, aquatic systems near urban centres are especially susceptible to alien species establishments. Here, we compiled and compared alien species lists for three different aquatic recipient regions spanning the North Atlantic: Chesapeake Bay, Great Lakes-St. Lawrence River and North and Baltic Seas. Each system is a major trade centre, with a history of invasions, and characterized by a strong natural salinity gradient. Our goal was to compare the alien species across systems, to test for similarities in the taxonomic composition and geographic origin as well as species overlap among the three regions. We selected specific macroinvertebrate, algal and fish taxa for analysis, to control for uneven taxonomic and biogeographic resolution across regions. Cumulatively, we identified 326 individual alien species established in these aquatic systems, with the North and Baltic Seas most invaded overall (163), followed by Great Lakes-St. Lawrence River (84) and Chesapeake Bay (79). Most invasions were from Ponto-Caspian, Eurasian, Northwest Pacific, Northwest Atlantic and North American origins, and mostly comprised Arthropoda, Chordata, Mollusca and Annelida. However, origins and taxonomies differed significantly among destinations, with Ponto-Caspian species particularly successful invaders to the North and Baltic Seas then Great Lakes-St. Lawrence River, but less so to Chesapeake Bay. Nevertheless, approximately eight-tenths of invaders established in only one region, indicating disparate invasion patterns and a high potential for future aliens to accrue from increasingly diverse source pools and pathways. These results support biosecurity strategies that consider a broad range of geographic origins and taxonomic groups to limit the translocation, arrival and spread of alien species worldwide.

KEYWORDS

Baltic Sea, Chesapeake Bay, global shipping, Great Lakes-St. Lawrence River, non-native species, North Sea

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1 | INTRODUCTION

Human-mediated movements of species have significantly altered biogeography, biodiversity and community structure worldwide, as well as caused substantial socioeconomic burdens and losses of ecosystem services (Blackburn et al., 2019; Capinha et al., 2015; Cuthbert, Pattison, et al., 2021; Turbelin et al., 2017). Alien species accumulations have accelerated among many taxonomic groups and locations in recent centuries (Seebens et al., 2017). These anthropogenic introductions have stemmed from increased globalization of trade and transport networks (Bonnamour et al., 2021; Hulme, 2009), greater accessibility of alien species source pools (Seebens et al., 2018), habitat modifications (Pauchard & Alaback, 2004) and climate changes (Hellman et al., 2008). As these processes intensify, rates of invasion are expected to continue in future, with alien species establishment projected to increase by 36% in coming decades worldwide (Seebens et al., 2021). In tandem, biological invasions have accrued massive economic costs across a range of human activity sectors (Haubrock et al., 2021), culminating in a stark economic burden to national economies (Cuthbert, Bartlett, et al., 2021). To aid predictive efforts for future invasions and their impacts, it is essential to understand the past geographic and taxonomic patterning of invasion dynamics.

Historically, alien species have been transported through a range of pathways, both deliberately and accidentally. Accidental introductions have arisen due to commercial trade and travel, such as via ship ballast (Briski et al., 2013), wooden packing materials (Brockhoff & Liebhold, 2017) and soils for horticulture (Hulme et al., 2008). Intentional introductions have arisen due to perceived benefits of alien species associated with past colonialism (Pipek et al., 2020), pet trades (Toomes et al., 2020), religious activities (Wasserman et al., 2019) and classical biological control (Shine et al., 2020), among others. Whilst many species fail to establish following introduction along the stage-based invasion process (Blackburn et al., 2011; Colautti & Maclsaac, 2004), aliens from certain regions might be more likely to succeed than others (Casties et al., 2016; Cuthbert et al., 2020). Centrally, the importance of propagule (i.e. numbers and viability of individuals) and colonization (i.e. numbers of species) pressures for invasion success (Briski et al., 2012; Maclsaac & Johansson, 2017) means population characteristics such as tolerance to diverse environmental conditions and phenotypic plasticity may facilitate the probability of invasion (Lande, 2015). In turn, these traits may be inextricably linked to the environmental origin and taxonomic grouping of species, whereby past environmental heterogeneity could promote traits that enhance invasion success (Reid & Orlova, 2002).

Aquatic ecosystems are particularly vulnerable to invasions and their impacts (Darwall et al., 2018), with detection rates of aquatic invasions rising rapidly in recent decades and showing little sign of saturation (Bailey et al., 2020). In recent centuries, distinct aquatic biogeographic regions have been principally connected via global shipping networks (Kaluza et al., 2010), but shipping intensities vary markedly along different routes. In particular, regions such as Northern Europe (Northeast Atlantic) and Northwest Atlantic have

been found to exhibit among the highest invasion risks associated with shipping intensity worldwide (Seebens et al., 2013). Similarly, over time the taxonomic composition of aliens and their pathways (i.e. the processes that facilitate introduction) may shift with changing trade patterns and regulations (Ellis et al., 2013; Ricciardi, 2006). This may contribute to asynchronous invasion dynamics spatiotemporally. For example, changes from solid ballast to ballast water systems caused reduced translocations of terrestrial plants, but increased aquatic animal invasions in the Great Lakes (Ricciardi, 2006).

However, considerations for factors other than shipping intensity and trade patterns are needed to robustly predict invasions. Recent work has proposed that aquatic taxa from certain geographical origins are better able to invade than others, with invasion rates exceeding expectations based simply on propagule supply or shipping intensity (Casties et al., 2016). Ponto-Caspian taxa from the Black, Caspian and Azov Seas have been identified as alien species with such a propensity to invade northern Europe and the Great Lakes-St. Lawrence River in North America (Leppäkoski et al., 2002; Ricciardi & Maclsaac, 2000). Similarly, studies have highlighted the disproportionate contributions from the Ponto-Caspian region globally when considering invasion dynamics of key taxonomic groups, such as gammarid crustaceans (Cuthbert et al., 2020). The evolution of tolerance to harsh salinity-temperature heterogeneities may predispose Ponto-Caspian species to invade wide-ranging aquatic conditions worldwide (Paiva et al., 2018; Pauli et al., 2018). However, tests of generalities in invasion dynamics according to species origin lack examination across a broad range of recipient regions, hampering effective management actions and predictive power.

Here, we examined trends in invasion dynamics in three major aquatic regions with very high shipping intensity across the North Atlantic Ocean (Kaluza et al., 2010): Chesapeake Bay, Great Lakes-St. Lawrence River and North and Baltic Seas. Shipping has historically been a pervasive pathway for the introduction of alien species among these regions, and the composition of aliens introduced reflects distinct phases associated with the nature of ships' ballast (Ricciardi, 2006). Following the opening of the St. Lawrence Seaway in 1959, increasing introductions occurred to the Laurentian Great Lakes of phytoplankton and zooplankton species, or taxa with planktonic life stages. Historically, release of Baltic Sea ballast was pronounced and largely unilateral to the Great Lakes due to the transport of wheat to the USSR (Kelly et al., 2009). More recently, high rates of Ponto-Caspian invasion across Europe have facilitated 'stepping stone' invasions to North America since the 1980s, owing to canalization that aided European dispersal (Ricciardi, 2006). However, recent improvements to ballast management systems have reduced numbers of species invading to the Great Lakes substantially (Sturtevant et al., 2019). Whereas Chesapeake Bay has only received relatively recent connection to the Great Lakes via canals, major ports such as Baltimore and Norfolk have among the highest ship arrival numbers in the United States, and particularly from Europe, resulting concurrently in a high rate of invasion (Fofonoff et al., 2013; Seebens et al., 2013).

These three systems have received high research effort compared to other regions, enabling sufficient data quality for analyses with a relatively high quantity of reported alien species. Salinity regime is a primary mediator of aquatic invasions (Cuthbert et al., 2020; Ojaveer et al., 2010; Paiva et al., 2018), and each of these aquatic regions is also characterized by a marked natural salinity gradient ranging from the ocean to freshwater (Figure 1) that could permit invasions by taxa with varying salinity tolerances. By compiling comprehensive lists of known established alien species in each of these regions, alongside their geographic origins and taxonomic groupings, we tested for similarities in taxonomic composition and source of alien species. Owing to the previously reported importance of the Ponto-Caspian region for invasions to the Great Lakes-St. Lawrence River and North and Baltic Seas (Casties et al., 2016), we expected a similar and strong contribution of this region for invasions in Chesapeake Bay. However, we expected a dissimilar taxonomic composition of invaders in Chesapeake Bay and the Great Lakes-St. Lawrence River given contrasting salinity patterns, despite their proximal placement in the Northwest Atlantic and a high capacity for secondary, 'stepping stone' invasions. Furthermore, we tested for species that have a simultaneous occurrence (i.e. overlap) in multiple regions, and in doing so, examined whether the majority of invasions to these regions are from unique species, or whether alien species co-occur among destinations. The former would suggest that, hitherto, invasions follow a seeming independent pattern at the species level, whilst the latter would indicate that invasions are dominated by a select group of recurrently successful taxa. Overall, these findings help to characterize dominant donor regions and taxonomic groupings for aquatic alien taxa, informing future predictions and management strategies that seek to limit translocations and introductions via early-stage invasion management (Leung et al., 2002).

2 | MATERIALS AND METHODS

2.1 | Alien species lists

Lists of aquatic alien species were compiled for three aquatic regions in two continents (North America and Europe) with substantial natural salinity gradients: (i) Chesapeake Bay; (ii) Great Lakes-St. Lawrence River; and (iii) North and Baltic Seas (see Cuthbert, Kotronaki, et al., 2021; Figure 1). We selected these systems because they (i) are well-studied invasion hotspots with sufficient data for comparison; (ii) exhibited historic trade connectivity in recent centuries; and (iii) represent the geographic scale over which their data have been aggregated in previous studies (Casties et al., 2016; Fofonoff et al., 2020). For each system, we synthesized available data (as below), and corrected any errors discovered (i.e. homogenizing taxonomic names, refining geographic origins and removing species which were not evidently established), based on current information available in 2021. Furthermore, owing to differences in how aquatic habitats and taxa were defined among lists, we standardized the taxa included in our analyses, focusing on larger taxa that are more easily detected and recognized. Specifically, we opted to remove flowering plants, insects and mammals, as often their habitats are located away from bays, and the boundaries for each system were not consistently defined among databases. We also removed phytoplankton as they are often cryptogenic, as well as microorganisms. We acknowledge that this caused conservative estimation of alien species numbers, but permitted comparability among regions.

Species lists for Chesapeake Bay were initially obtained from the National Exotic Marine and Estuarine Species Information System (NEMESIS; Fofonoff et al., 2020). This database is the most comprehensive account of alien species in Chesapeake Bay and the adjacent Atlantic water and coastal bays. The coverage area also includes

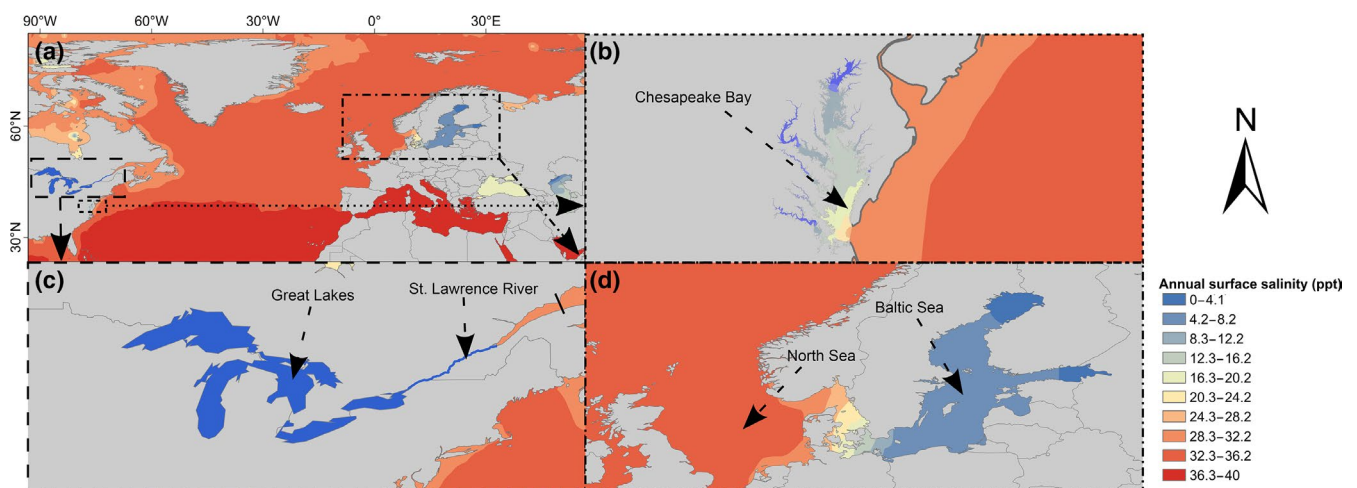


FIGURE 1 Salinity of Chesapeake Bay, Great Lakes-St. Lawrence River, North Atlantic Ocean, North, Baltic, Mediterranean, Black, Azov and Caspian Seas, constructed using average annual salinity data with a $1^\circ \times 1^\circ$ spatial resolution from the World Ocean Atlas database (Antonov et al., 2006; Casties et al., 2016) and Wei (2019) (a). Close-up maps of Chesapeake Bay (b), the Great Lakes-St. Lawrence River (c) and the North and Baltic Seas (d) are shown. Note that although the salinity of the Great Lakes is shown in the range from 0.0 to 4.1 (i.e. dark blue), the salinity of the Great Lakes is under 0.5 ppt (i.e. freshwater). The solid line on (c) demarks the Gulf of St. Lawrence

the tributaries of the bay up to the head of tidewater, as well as tidal wetlands up to the monthly mean high tide line (0–32 ppt). The Great Lakes-St. Lawrence River and North and Baltic Seas lists were compiled as per Casties et al. (2016). For the Great Lakes-St. Lawrence River region, species lists were initially generated following de Lafontaine and Costan (2002), Ricciardi (2006) and the Great Lakes Aquatic Nonindigenous Information System database (GLANSIS, 2014). The region included the Great Lakes basin, as well as any normally attached channels and wetlands (0–32 ppt). The St. Lawrence River was included until the Gulf of St. Lawrence, but the gulf itself was excluded (GLANSIS, 2014; Ricciardi, 2006). For the North and Baltic Seas, the list of alien species was initially compiled using AquaNIS data, the information system on aquatic nonindigenous and cryptogenic species (AquaNIS, 2015; Bij de Vaate et al., 2002; Gollasch et al., 2009; Reise et al., 1999). The region comprised the entire North and Baltic Seas (0–40 ppt), demarcated by a line between Dover, England and the Belgian border, and a line between the Shetland Islands and Norway (AquaNIS, 2015; Casties et al., 2016).

2.2 | Geographic origins

To examine whether aliens from a particular origin region or taxonomic group were contributed more than others, we compiled geographic origin information and taxonomic grouping (kingdom, phylum and class) for each listed alien species. For Chesapeake Bay, alien origins were determined from the NEMESIS database (Fofonoff et al., 2020), whereas origin information for the Great Lakes-St. Lawrence River and North and Baltic Seas was taken from GLANSIS (2014) and AquaNIS (2015) respectively. Where information for species origins was absent, a general internet search was conducted using a search engine.

Each alien species was assigned an origin based on one or more of the following regions (Casties et al., 2016): Northeast Atlantic, Northwest Atlantic, Southeast Atlantic, Southwest Atlantic, Northeast Pacific, Northwest Pacific, Southeast Pacific, Southwest Pacific, North Sea, Baltic Sea, the Great Lakes-St. Lawrence River region, Mediterranean Sea, Eurasia (inland freshwaters except Yangtze River), Mississippi River, Yangtze River, Arctic, Australia (inland freshwaters), New Zealand (inland freshwaters), Indo-Pacific (Indian Ocean and the archipelago of Indonesia, Malaysia and Philippines), Africa (inland freshwaters), North America (inland freshwaters except the Laurentian Great Lakes, St. Lawrence and Mississippi Rivers), South America (inland freshwaters), Ponto-Caspian region and unknown region. Where a species invading a given region was native to several origins, the contribution from that species was divided by the number of origins (i.e. ratio of 1 over the number of origins). For example, a species with two origins was assigned a value of 0.5 per origin. This ensured that each species' contribution was balanced among regions, however, we did not divide species contributions among recipient regions (i.e. if the same species invaded multiple regions), as they represent independent invasion events.

Nevertheless, we acknowledge that not all origin regions contribute equally to invasion events given differences in vectors and timings. For most invasions, however, the relative importance of each origin is not documented, and therefore, the simple ratio methodology was employed here. We assigned taxonomic information for each species using several sources [e.g. Barcode of Life Database (BOLD), European Nature Information System (EUNIS), World Register of Marine Species (WORMS) and Global Biodiversity Information Facility (GBIF)].

2.3 | Formal analyses

Compositions of alien species were examined and compared among the three recipient regions according to geographic origins and taxonomic groupings. Separate pairwise Chi-square tests were used to test the null hypotheses that invasions to each aquatic system were proportionally from the same groups of species origins and phyla. That is, we compared numbers of alien species to each of the three regions pairwise according to the top five most common species origins (two recipient regions \times six origin groups, per pair). Similarly, we repeated these tests to compare the top five phyla compositions among recipient regions. Furthermore, we examined similarities in invasion patterns among systems by determining individual species that invaded more than one region, with respect to their geographic origin and taxonomic grouping.

3 | RESULTS

3.1 | Alien origin regions and phyla

Considering the taxonomic groups that have been relatively well investigated to date and after our aforementioned filters, Chesapeake Bay has been invaded by 79 species, compared to 84 in the Great Lakes-St. Lawrence River and 163 in the North and Baltic Seas. The composition of the top six origin regions differed significantly in Chesapeake Bay compared to both the Great Lakes-St. Lawrence River and North and Baltic Seas (2×6 contingency tables: Great Lakes-St. Lawrence River, $\chi^2 = 27.11$, $df = 5$, $p < .001$; North and Baltic Seas, $\chi^2 = 28.78$, $df = 5$, $p < .001$; Figure 2). Great Lakes-St. Lawrence River and North and Baltic Seas alien origins were also significantly different in composition ($\chi^2 = 69.55$, $df = 5$, $p < .001$).

Invasions from the Ponto-Caspian region were most common overall (Figure 2), but were disproportionately frequent to the North and Baltic Seas (21%), followed by the Great Lakes-St. Lawrence River (17%) and then Chesapeake Bay (8%). Conversely, invasions from Eurasian freshwaters were disproportionately frequent to Chesapeake Bay (12%) and especially the Great Lakes-St. Lawrence River (36%), but only 5% of aliens to the North and Baltic Seas were from Eurasian freshwaters (Figure 2). The other common origins of Chesapeake Bay aliens included North American freshwaters (15%), Northwest Pacific (15%), Mississippi River (10%) and Indo-Pacific

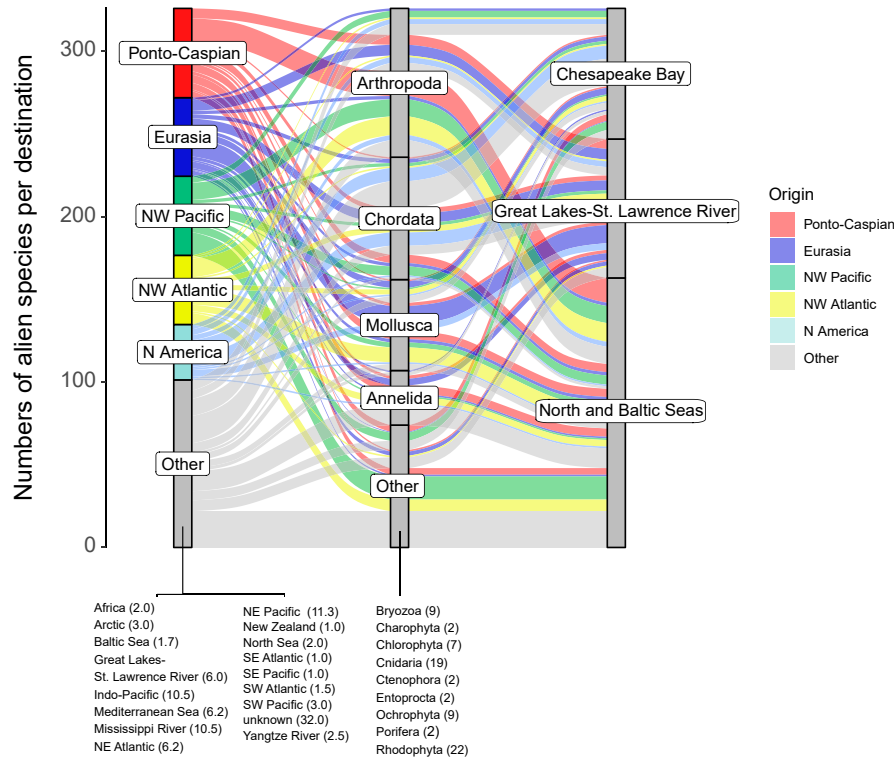


FIGURE 2 Flows of alien species from the commonest origins and phyla to Chesapeake Bay, Great Lakes-St. Lawrence River and North and Baltic Seas destination regions. The thickness of each flow corresponds to the numbers of aliens from each source. The 'Other' categories comprise individual origins or phyla with, respectively, fewer than 15 or 30 reported aliens overall (expanded at bottom of figure). Note that, within regions, if an alien had several origins, the contribution of that species was divided among those origins (i.e. ratio of 1 divided by the origin number). This ensured equal contribution from each taxon. However, if a single species invaded multiple regions, the contribution was not divided among recipient regions as they reflect separate invasion events. The numbers of the y-axis are not cumulative among regions. N, North; NE, Northeast; NW, Northwest; S, South; SE, Southeast; SW, Southwest

(9%). For the Great Lakes-St. Lawrence River, North America also contributed 19% of aliens and Northwest Atlantic (7%). The North and Baltic Seas were also commonly invaded from the Northwest Pacific (21%), Northwest Atlantic (19%) and Northeast Pacific (5%).

Arthropoda was the largest group of aliens overall (predominantly from crustaceans), followed by Chordata, Mollusca and Annelida, as well as nine other phyla (Figure 2). The composition of the five commonest alien phyla did not differ significantly in Chesapeake Bay compared to the Great Lakes-St. Lawrence River (2×5 contingency table: Great Lakes-St. Lawrence River, $\chi^2 = 2.86$, $df = 4$, $p = .58$), but was significantly different to the North and Baltic Seas, $\chi^2 = 36.06$, $df = 4$, $p < .001$). Great Lakes-St. Lawrence River and North and Baltic Seas alien phyla were additionally significantly different in composition ($\chi^2 = 28.99$, $df = 4$, $p < .001$).

Invasions to Chesapeake Bay were predominantly by Chordata, Arthropoda and Mollusca (Table 1; Figure 2). To the Great Lakes-St. Lawrence River, Chordata was again most frequent, followed by Arthropoda and Mollusca. In turn, the North and Baltic Seas were mostly invaded by Arthropoda, Mollusca and Annelida, followed by Rhodophyta, with Chordata less numerous. The full lists of species invading each region are detailed in Cuthbert, Kotronaki, et al. (2021).

Overall, the largest shares of alien Arthropoda were from the Ponto-Caspian (23%), then Northwest Pacific (16%), Northwest Atlantic (15%), Eurasia (11%) and North America (11%). Chordata invaded most commonly from North America (23%), Eurasia (14%) and Northwest Pacific (13%), Mississippi River (12%) and Ponto-Caspian (12%). Mollusca mostly invaded from Eurasia (31%), Northwest Atlantic (22%), Ponto-Caspian (15%) and North America (11%). Annelida invaded from the Ponto-Caspian (21%), Eurasia (18%) and Northwest Atlantic (12%) primarily (Figure 2).

3.2 | Regional similarities in invading species

Of the 274 unique species which invaded Chesapeake Bay, Great Lakes-St. Lawrence River and North and Baltic Seas, only 46 species established in more than one region: six species invaded all three regions and 40 invaded two regions [i.e. 274 (unique species) + 40 (double events) + 12 (triple events) = 326 total invasion events, at least]. Accordingly, the majority of invasions occurred by individual species and were regionally unique introductions (83%; 228/274). Of the six species in all three regions, half were of Ponto-Caspian origin (common carp *Cyprinus carpio*, zebra mussel *Dreissena*

TABLE 1 Percentage taxonomic compositions of invasions in Chesapeake Bay, Great Lakes-St. Lawrence River and North and Baltic Seas, illustrating contributions among phyla and classes therein

Invaded region	Phylum (%)	Class (%)
Chesapeake Bay	Chordata (39%)	Actinopterygii (81%)
	Arthropoda (20%)	Malacostraca (75%)
	Mollusca (18%)	Gastropoda (64%) Bivalvia (36%)
Great Lakes-St. Lawrence River	Chordata (33%)	Actinopterygii (100%)
	Arthropoda (26%)	Maxillopoda (46%) Branchiopoda (27%)
	Mollusca (20%)	Bivalvia (53%) Gastropoda (47%)
North and Baltic Seas	Arthropoda (32%)	Malacostraca (69%) Maxillopoda (23%)
	Mollusca (15%)	Gastropoda (50%) Bivalvia (50%)
	Annelida (15%)	Polychaeta (67%) Clitellata (33%)
	Rhodophyta (11%)	Florideophyceae (100%)

Note: Total contributions up to at least 70% are shown within each respective taxonomic level.

polymorpha and hydrozoan *Cordylophora caspia*), and the other half were Eurasian origin (Asian clam *Corbicula fluminea*, Chinese mystery snail *Cipangopaludina chinensis* and tubificid worm *Branchiura sowerbyi*; Figure 3).

Of the 40 species which jointly invaded two regions, the largest share occurred between Chesapeake Bay and North and Baltic Seas ($n = 18$), with the remainder evenly split between Chesapeake Bay and Great Lakes-St. Lawrence River ($n = 11$), as well as Great Lakes-St. Lawrence River and North and Baltic Seas ($n = 11$). However, the regions of origin therein differed markedly among shared species invasions (Figure 3a). Eurasian species dominated those that invaded both Chesapeake Bay and Great Lakes-St. Lawrence River (55%) followed by North America (32%). Joint aliens to Chesapeake Bay and the North and Baltic Seas were more diverse among origins, but the Northwest Pacific was most common (56%) followed by the Ponto-Caspian (11%). Contrastingly, Ponto-Caspian species very commonly invaded the Great Lakes-St. Lawrence River and the North and Baltic Sea jointly (55%), followed by North American freshwaters (18%; Figure 3a).

For phyla, joint invasions to both Chesapeake Bay and Great Lakes-St. Lawrence River were dominated by Arthropoda (36%: 50% malacostracans Malacostraca, 25% maxillopods Maxillopoda, 25% branchiopods Branchiopoda), Chordata (27%: 100% ray-finned fishes Actinopterygii) and Mollusca (27%: 100% gastropods Gastropoda). Invasions shared between Chesapeake Bay and the North and Baltic

Seas were from more diverse phyla, with the biggest share from Arthropoda (28%: 100% malacostracans Malacostraca), Cnidaria (17%: 67% Hydrozoa, 33% Anthozoa), Chordata (11%: 100% ascidians Ascidiacea), Mollusca (11%: 100% bivalves Bivalvia) and Annelida (11%: 100% bristle worms Polychaeta). In turn, joint invasions to the Great Lakes-St. Lawrence River and North and Baltic Seas were dominated by Arthropoda (46%: 60% malacostracans Malacostraca, 20% branchiopods Branchiopoda, 20% maxillopods Maxillopoda) and Chordata (27%: 100% ray-finned fishes Actinopterygii).

4 | DISCUSSION

This study identified differences in invasion dynamics among three interconnected aquatic systems in the North Atlantic that have a natural salinity gradient. Invasions have originated from a broad range of geographic origins and taxonomic groups. We found that invasions to Chesapeake Bay were dominated by taxa of North American, Northwest Pacific and Eurasian origins, Great Lakes-St. Lawrence River by Eurasian, North American and Ponto-Caspian taxa and North and Baltic Seas invaders predominated from the Ponto-Caspian, Northwest Atlantic and Northwest Pacific. Strikingly, whilst Ponto-Caspian species were highly prevalent invaders in the North and Baltic Seas and Great Lakes-St. Lawrence River, comparatively fewer species of Ponto-Caspian origin invaded

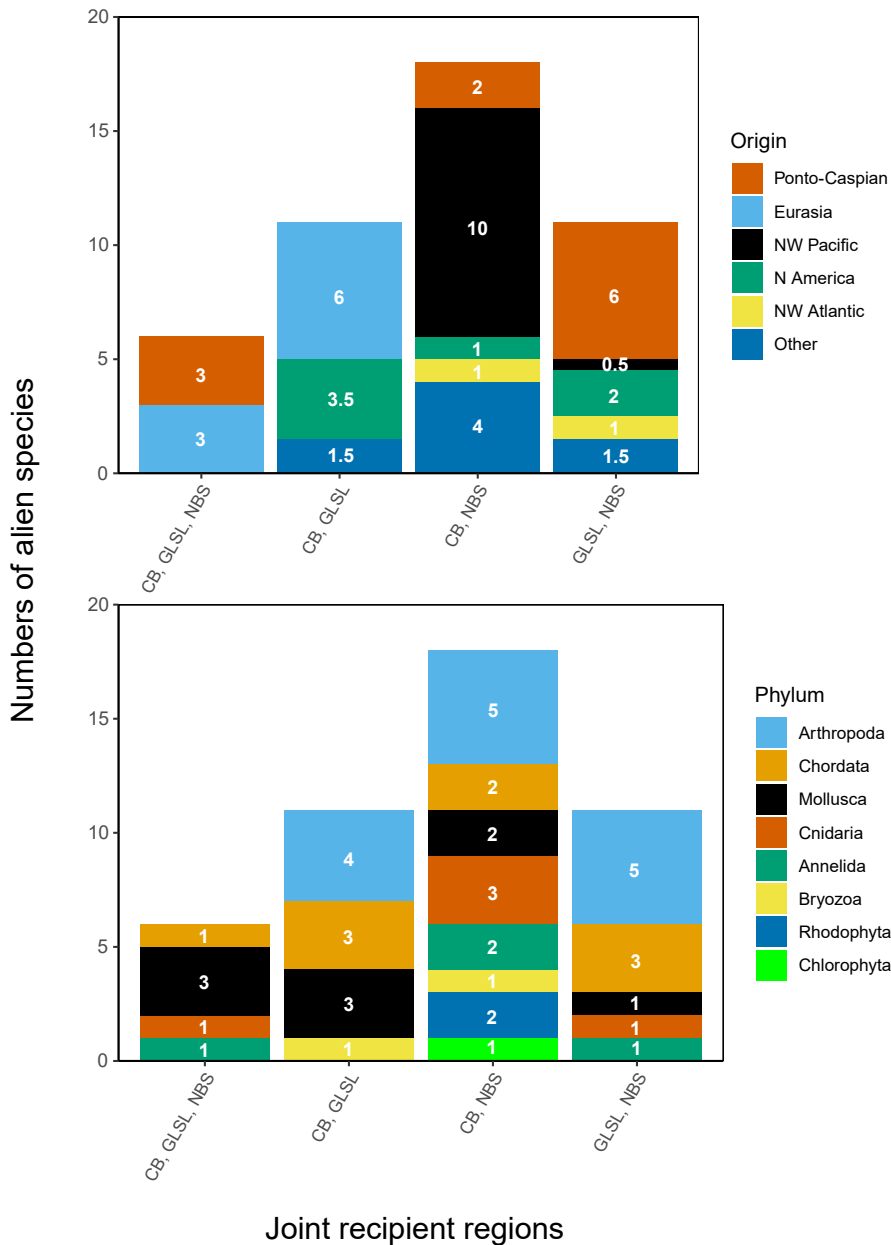


FIGURE 3 Numbers of individual alien species invading more than one recipient region, among Chesapeake Bay (CB), Great Lakes-St. Lawrence River (GLSL) and North and Baltic Seas (NBS). Fills correspond to alien origins (a) and phyla (b). Numbers correspond to the number of species in each fill category. Species in all three regions are not included in bars for two regions. 'Other' includes origins which contributed fewer than two alien species overall. Note that, within regions, if an alien had several origins, the contribution of that species was divided among those origins (i.e. ratio of 1 divided by the origin number)

Chesapeake Bay. This suggests that the supposed disproportionate contribution of Ponto-Caspian taxa is not uniform across aquatic ecosystems, and other context dependencies are at play that influence invasibility. Furthermore, whilst certain phyla contributed high numbers of aliens, we identified substantial differences in alien species compositions at more granular taxonomic scales, with 83% of alien species only establishing in one aquatic region. This may reflect the fact that most invasions represent discrete establishment events. Accordingly, very few species have invaded multiple regions, suggesting the anomalous ones that do so may be exceptionally predisposed to succeed, have had sufficient time to spread or been introduced intentionally. Overall, the seeming lack of generality across all three regions suggests that species origin and taxonomy are not universal characteristics that inform invasion success, and that management actions should seek to limit invasions from a broad range of source pools and taxonomic groups. Equally, a more limited

approach that considers region-specific invasion contexts, from certain geographic origins or taxonomic groups, may aid finer scale predictive efforts.

The high levels of Eurasian origin species establishing in both North American systems probably arise from the strength of connection between North America and Europe considering global shipping (Kaluza et al., 2010; Seebens et al., 2013). In turn, ballast water likely permitted increased introductions of Arthropoda and Mollusca, which are able to produce dormant life stages and/or occupy pelagic areas of waterbodies (Briski, Bailey, et al., 2011, Briski, Ghabooli, et al., 2011) and can sometimes withstand ballast water treatment (Lin et al., 2020). The burgeoning numbers of Chordata introduced, mostly fish (85%), are primarily intentional additions for recreational angling or fisheries, plus some movements through canals (Ricciardi, 2006), with few stowaways associated with shipping. In general, the larger numbers of invaders in the North and Baltic

Seas likely also reflect differences in the size of that aquatic system relative to those examined from North America. These higher numbers may also reflect historical trade patterns associated with colonialism by Europe, facilitating alien species to accrue earlier than in North America.

Salinity tolerance is a major environmental context that influences invasion success and aquatic ecosystem structuring (Paiva et al., 2018; Stern & Lee, 2020). The very few inland Eurasian taxa established in the North and Baltic Seas may reflect salinity patterns that negate the success of freshwater taxa, whereas brackish or marine origin species from the more saline Ponto-Caspian, Northwest Pacific and Northwest Atlantic regions were the commonest invaders there. Whilst often indicative of intentional introductions from these regions for aquaculture (e.g. Pacific oysters), this pattern also reflects the fact that many Eurasian species are also native to that basin, with most of the alien species from Eurasian waters in the North and Baltic Seas reportedly east Asian in origin. The opposing salinity patterns may also explain the lack of invaders between the North and Baltic Seas and the Great Lakes-St. Lawrence River, despite the historic linking of those systems through the shipment of wheat to the USSR (Kelly et al., 2009), and existing canals. Interestingly, of those species native to the Great Lakes-St. Lawrence River taxa with an invasion history, six invaded Chesapeake Bay and none the North and Baltic Seas, yet this again largely reflects intentional fish introductions and geographic proximity. Alternatively, it may reflect unevenness in the direction of trade and ballast exchange between North America and Europe, with potentially less ballast delivery to the North and Baltic Seas. More broadly, the very few introductions from regions such as the Southwest Pacific, Southwest Atlantic, Yangtze River, New Zealand and Australia likely reflect fewer pathways and opportunities for introduction associated with global trade and transport to the North Atlantic thus far (Kaluza et al., 2010).

Differences in vectors of introduction were also likely pervasive determinants of the composition of alien species in each system. The North and Baltic Seas are extensively connected to the Ponto-Caspian region through a large series of canals, promoting opportunities for invasion from high to low salinities. Similarly, the Great Lakes system is connected to the Mississippi and Atlantic coasts by canals, whereas Chesapeake Bay has had only brief historical canal connections to the Great Lakes, and existing canal connections to other Atlantic estuaries. Ballast water in the North and Baltic Seas is also disposed of in a range of freshwater, brackish and marine ports, promoting establishment of species with ranging salinity tolerances, whereas ballast water in Chesapeake Bay is predominantly discharged in higher salinity areas (e.g. Norfolk), which might constrain the establishment of Ponto-Caspian taxa that perform better at lower salinities (Paiva et al., 2018).

Research has suggested that Ponto-Caspian origin taxa are evolutionarily predisposed to invade (Bij de Vaate et al., 2002; Leppäkoski et al., 2002; Ricciardi & Maclsaac, 2000), owing to historic environmental heterogeneities that permit tolerance to a wide range of aquatic environments (Reid & Orlova, 2002; Paiva et al., 2018; but see Paiva et al., 2020). Recent works have also highlighted

the dominance of salt-tolerant taxa from the Ponto-Caspian region in freshwater invasions (Cuthbert et al., 2020), and shown that their invasion success is significantly higher than expected based on shipping intensity and environmental match (Casties et al., 2016). However, our results suggest that these proposed general patterns of invasion frequency by region are not observed for another highly connected aquatic ecosystem in North America, Chesapeake Bay. Just six of the 79 known established aliens in Chesapeake Bay were of Ponto-Caspian origin, and five of these species also invaded the Great Lakes-St. Lawrence River and/or North and Baltic Seas regions. This indicates that their invasion to Chesapeake Bay may be secondary in source from other 'stepping stone' regions, or vice versa. Whilst Ponto-Caspian taxa are highly tolerant to freshwater and brackish conditions (Paiva et al., 2018; Pauli et al., 2018), this lack of invasion to the extensively brackish Chesapeake Bay suggests that other ecological or socioeconomic (e.g. trade and transport patterns) context dependencies are at play in mediating invasion success, and these require further elucidation. It is also possible that seasonal fluctuations in salinity regime in Chesapeake Bay, and higher salinity regimes at key ports, preclude the establishment of Ponto-Caspian taxa that show decreased performance at higher salinities (Paiva et al., 2018). Accordingly, whilst Ponto-Caspian species have undoubtedly been disproportionately successful invaders to certain aquatic ecosystems (Casties et al., 2016), this does not appear to be a phenomenon that can be extended to all brackish, coastal aquatic systems—at least at the present time. Notably, shipping does not constitute the only pathway through which Ponto-Caspian species can become established, with canalization in Europe also permitting increased connectivity and invasibility of the Baltic Sea (Bij de Vaate et al., 2002)—perhaps playing an equal or larger role to ballast water—coupled with reported intentional species introductions to biologically enhance man-made ecosystems (Arbačiauskas et al., 2010).

Despite the dominance of a few geographic origins and taxonomic groups, at the species level, invasions were found to be largely unique in each of the three regions. Over eight-tenths of established aliens were only reported in one region, despite the intensive interconnection between these three North Atlantic systems (Kaluza et al., 2010; Seebens et al., 2013). Globally, invasions are expected to increase markedly in the future (Seebens et al., 2021) owing to the increased availability of novel source pools that permit alien species translocations (Seebens et al., 2018). With aquatic invasive species also accumulating rapidly (Bailey et al., 2020), it is possible that many species simply have not had sufficient chances to invade multiple systems considering propagule and colonization pressures (Briski et al., 2012, 2014; Maclsaac & Johansson, 2017). Equally, abiotic and biotic characteristics might entirely negate invasion success in certain systems. In any case, this seemingly random distribution of alien species among regions thus points to a substantial propensity for future invasions. This is because the numbers of 'chances' to invade will rise as globalization and diversification of trade and transport networks ensue, coupled with often inadequate biosecurity protocols

for addressing vectors (Coughlan et al., 2020)—although rapid adoption of ballast water management in many countries may impede certain aquatic invasions (but see Lin et al., 2020).

A further critical consideration in the types of analyses reported here is that, depending on the region of study, the concomitant history of biological and ecological investigations and the availability of taxonomic expertise, many groups of aquatic invasive species remain to be assessed relative to whether they are native, cryptogenic or introduced (Carlton, 2009; Carlton & Fowler, 2018). A very large number of often smaller bodied taxa, such as protists, rotifers, nematodes, flatworms, hydroids, benthic copepods, ostracods and algae, remain largely or entirely unexplored for their invasion status; Carlton (2009) referred to this as the 'smalls rule' of invasion ecology. Even larger bodied taxa (such as polychaete worms) that occur, for example, in both the Western and Eastern Atlantic, may be classically treated as naturally amphiatlantic without consideration as to whether they may in fact have been introduced centuries ago (Carlton, 2003). The extent to which the underestimation of alien species diversity has influenced our understanding of invasion patterns remains largely to be investigated. Furthermore, our intentional exclusion of particular taxa (i.e. flowering plants, insects and mammals) in order to standardize species lists resulted in a conservative estimation of known aliens. This also highlights a wider issue of heterogeneity in the reporting of semiaquatic alien taxa in aquatic environments, with different habitat definitions for such taxa pervasive in databases. It is thus important to consider that there are inevitable differences between regions in the taxonomic and biogeographic assessment of taxa for the presence of introduced species—which we limited by homogenizing the datasets.

Nonetheless, those few taxa that have hitherto invaded more than one of the focal regions might be especially successful due to life-history traits and environmental tolerances. Indeed, half of the six species that established in all three regions were of Ponto-Caspian origin, such as the 'hyper-successful' zebra mussel *Dreissena polymorpha* (Sousa et al., 2014). These three widely successful Ponto-Caspian species (*Cyprinus carpio*, *D. polymorpha* and *Cordylophora caspia*), but also Eurasian species (*Corbicula fluminea*, *Cipangopaludina chinensis* and *Branchiura sowerbyi*), have broad salinity tolerances spanning fresh and brackish waters. However, a few highly successful, notorious invaders from one origin is arguably insufficient evidence for generalizing invasion dynamics. Likewise, the large numbers of joint Ponto-Caspian invasions to the Great Lakes-St. Lawrence River and North and Baltic Seas may reflect secondary invasions, whereby the North and Baltic Seas act as a 'stepping stone' for further introduction to the more geographically disparate North American systems (Casties et al., 2016). Yet, the large numbers of Ponto-Caspian species established only in the Great Lakes-St. Lawrence River somewhat refutes this hypothesis, indicating numerous direct invasion events. The sharing of invasions between Chesapeake Bay and the Great Lakes-St. Lawrence River, particularly by Arthropoda, Mollusca and Chordata, may also reflect secondary introductions given the geographical proximity of these systems and connection via canals (e.g. Erie and Champlain

canals). In turn, joint invasions to Chesapeake Bay and the North and Baltic Seas were most numerous overall, and largely comprised taxa of marine origin that were so far unable to invade the extensive freshwaters of the Great Lakes. Overall, these invasion dynamics point to complex patterns, suggesting a predominance of individual aquatic invasion events from a broad range of geographic origins and taxonomic groupings. Use of species lists in combination with risk models based on propagule supply and trade could yield further resolution and inform upon invasion dynamics. Considering these systems, there is no strong evidence for globally generalizing invasion probability from specific geographic origins or taxa, although a more limited approach that predicts invasion success in certain regions of certain species from specific sources may prove to be a powerful tool.

5 | CONCLUSIONS

Burgeoning global invasion rates (Bailey et al., 2020; Seebens et al., 2017) necessitate improved understandings of species redistributions to inform predictions and effective management. Our results demonstrate that invasions to three major and interconnected aquatic systems are dominated by just a few geographic origins and taxonomic groups, with Ponto-Caspian, Eurasian, Northwest Pacific, Northwest Atlantic and North American origins commonest, but with the presence of many others suggesting a growing diversity of alien species source pools. This may reflect strong historic trade links among these regions. Of particular interest, Ponto-Caspian taxa were very successful in the Great Lakes-St. Lawrence River and North and Baltic Seas, but relatively rarely invaded Chesapeake Bay, suggesting additional context dependencies mediate invasion success. Moreover, whilst well-studied phyla such as Arthropoda, Chordata and Mollusca were dominant overall, the vast majority of invasions were by single species represented in only one invaded aquatic region, notwithstanding a few 'hyper-successful' taxa that invaded several systems concurrently. These findings suggest largely disparate pattern of invasions at more granular taxonomic scales, pointing to a high potential for invasions to continue rising in future from novel source pools and pathways (Seebens et al., 2018). Accordingly, our results continue to strongly support a vector-based approach that seeks to reduce the number of arriving species—whatever they are, and from wherever their source. Further work is needed to examine invasion patterning with origins and taxonomies across a broader range of recipient regions.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

All authors conceptualized the study. Syrmalena G. Kotronaki, James T. Carlton, Gregory M. Ruiz and Paul Fofonoff collected and curated the data. Ross N. Cuthbert analysed and visualized the data, and led the writing of the manuscript. All authors revised and contributed critical intellectual content to the manuscript and approved submission.

DATA AVAILABILITY STATEMENT

Initial versions of the underlying data for the Great Lakes-St. Lawrence River and North and Baltic Seas are published in Casties et al. (2016) and Chesapeake Bay in Fofonoff et al. (2020). The final, refined dataset used for analyses is available at PANGAEA (<https://doi.org/10.1594/PANGAEA.938254>).

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SUPPORTING INFORMATION

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