

REVIEW

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Neocosmopolitan distributions of invertebrate aquatic invasive species due to euryhaline geographic history and human-mediated dispersal: Ponto-Caspian versus other geographic origins

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Abstract

Background: Aquatic invertebrate species that have broad salinity tolerances may be pre-adapted for invasion success and biogeographic distributional range expansions, facilitated by human-mediated dispersal (HMD), leading to a trend to become neocosmopolitan across many regions of the world. This pattern appears to characterize many Ponto-Caspian (P-C) aquatic invertebrates, which have a > 100-year history as aquatic invasive species (AIS), spreading throughout much of Eurasia and for some, in North America and beyond. Our study compiles comparative salinity conditions and distributional data for AIS invertebrate species globally versus those originating from the P-C region, to test whether they statistically differ.

Results: Our investigation discerns that a total of 1861 invertebrate AIS taxa have been recorded worldwide, with (A) 70.5% exclusively living in the saline adaptive zone of brackish (0.5–30 ppt; A1) and/or marine waters (> 30 ppt; A2), (B) 20% in the freshwater adaptive zone alone (0–0.5 ppt), (C) 7.5% being euryhaline (across both A and B), and (D) 2% being semi-aquatic in either (D1) freshwater/terrestrial or (D2) saline/terrestrial environments. In contrast, our results indicate the following proportions for AIS invertebrates of P-C origins: (A) 27% exclusively inhabit the saline adaptive zone, (B) 25% are entirely freshwater, (C) 45% are euryhaline, and (D) 3% are semi-aquatic, significantly differing from the global pattern. Euryhaline AIS native to the P-C region thus markedly outnumber (45%) those originating from other regions (7.5%), likely pre-adapting them for widespread establishment in harbors, estuaries, and coastal areas. Moreover, most P-C invertebrate AIS (70%) contain freshwater-tolerant populations (B + C), rendering them very successful invaders of inland water bodies. These broad salinity tolerances of P-C AIS underlie their tremendous invasion successes and growing neocosmopolitan distributions with HMD.

Conclusions: An evolutionary and recent history of broad salinity tolerances of a large proportion of P-C invertebrates appears to enhance their ability to invade, establish, and spread in new regions, especially harbors, estuaries, and freshwaters, leading to their increasing neocosmopolitan distributions. This trend likely will continue—accelerating with climate change and increased global transportation—meriting worldwide conservation agency focus and

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cooperation, along with public education programs aimed to rapidly identify and circumvent new introductions and spread.

Keywords: Aquatic invasive species, Biogeography, Distribution pattern, Euryhalinity, Freshwater adaptive zone, Invasive species, Neocosmopolitan, Nonindigenous species, Saline adaptive zone, Zebra mussel

Background

Human-mediated dispersal (HMD) has played a major role in geographic spread of aquatic invasive species (AIS), with increased waterway connections and growing worldwide transport opportunities over the past century (Lodge et al. 2016; Bullock et al. 2018). In biogeography, cosmopolitan species are defined as those whose populations are widely distributed across many biogeographic regions. The new term “neocosmopolitan” was erected to differentiate species whose range expansions were due to HMD versus those possessing “natural” cosmopolitan distributions, which are termed “eucosmopolitan” (Pociecha et al. 2016; Darling and Carlton 2018). For example, many Ponto-Caspian (P-C) aquatic taxa originally were geographically confined in isolated basin areas, where they evolved under fluctuating environmental conditions, including salinity changes (Audzijonyte et al. 2008, 2009); however, ongoing HMD has facilitated their range increases toward neocosmopolitan distributions (Hutchings and Kupriyanova 2018).

Human-mediated dispersal and invasion opportunities

According to the Convention for Biological Diversity (CBD 1992), over the past century waterway corridors that connected formerly relatively separated water basins have provided the most common pathways for colonization of western Europe and northern Eurasia by AIS originating from the P-C region (see Ricciardi and MacIsaac 2000; MacIsaac et al. 2001; Bij de Vaate et al. 2002; Grigorovich et al. 2003; Holeck et al. 2004; Ricciardi 2006). Whereas it was once relatively difficult for many invertebrates and their larvae to move upstream, vessels readily transport species that are attached to hulls and gear (Ojaveer et al. 2002; Cupak et al. 2014), are onboard as stow-aways, or are uptaken and released in ballast and bilge waters (Ricciardi 2016; Ojaveer et al. 2017) or from tank sediments (Hänfling et al. 2011; Gruska et al. 2013). Many P-C invertebrates, including the fish hook water flea *Cercopagis pengoi* and the zebra and quagga mussels *Dreissena polymorpha* and *D. rostriformis* were transported overseas by ballast water discharges into the North America Laurentian Great Lakes (Mills et al. 1996; Ricciardi and MacIsaac 2000).

Tourism (water sports, gear) and fishing activities (boats, trailers, ropes, nets) also transport AIS long distances among waterbodies (Bącela-Spychalska et al. 2013;

Bącela-Spychalska 2016). For example, overland trailered boats are believed to have spread zebra and quagga mussels from the Great Lakes throughout much of temperate North America (Johnson et al. 2006; Brown and Stepien 2010; Stepien et al. 2013).

Other vectors for AIS spread include aquaculture, aquarium, pet, and bait releases (CBD 1992; Snyder et al. 2020). Notably, P-C crustaceans, including mysids and amphipods, have been transplanted into Eastern European freshwater reservoirs for fish food (Gasjunas 1964). Surveys have shown that releases of unused bait are a common practice, including AIS in the Laurentian Great Lakes that originated from the P-C and other regions (Snyder et al. 2020). Moreover, pond supply stores were found to accidentally house AIS that once originated from the P-C, including zebra and quagga mussels (Snyder et al. 2020). In 2021, live dreissenid mussels were discovered in living “moss ball” algae imported from the P-C region, which the US Fish and Wildlife Service documented were being sold in aquarium and pet stores in 21 US states (USGS 2022).

Invasion theory and salinity tolerances

Ricciardi and MacIsaac (2000) proposed multiple hypotheses to explain invasion successes, focusing on the invasions of P-C species in the Great Lakes—including invasion corridors, species traits, and invasional meltdown. MacIsaac et al. (2001) expanded on these hypotheses by applying classical invasion concepts, with a focus on the ability of P-C AIS to overcome salinity barriers. Nevertheless, translocation does not guarantee wide distribution of a species or its settlement, survival, and reproductive successes. Establishment and persistence of AIS are determined by many genetic, reproductive, dispersal, dietary, and environmental factors that influence their relative abilities to adapt to new environments and changing conditions.

The adaptive zone constitutes a complex of environmental conditions that underlie the adaptations of a given species across its geographic range of habitats (Simpson 1944). Salinity tolerance is one of the most important adaptations that limits a given AIS’ distribution (Smyth and Elliott 2016), which may vary among its life stages (e.g., egg, larvae, juvenile, adult), and may be especially important during reproduction and development (Karsiotis et al. 2012; Sa-Nguansil and Wangkulangkul 2020).

The saline (A) and freshwater (B) adaptive zones differ in their respective ionic concentrations and compositions. In freshwaters, HCO_3^- and Ca^{2+} are the most abundant respective anions and cations, whereas Cl^- and Na^+ predominate in seawater (Holland 1978). Moreover, ion ratios that are approximately constant in sea water vary considerably among freshwater bodies (Róžańska 1987; Khlebovich 1989, 1990a, b). Freshwater invertebrates maintain higher overall body fluid osmotic concentrations in relation to their diluted external environments. Various adaptations, including relatively impermeable body surfaces, pumping out or excreting excess water, and ion retention enable some freshwater invertebrate species to osmoregulate in euryhaline habitats (Péqueux 1995; Łapucki and Normant 2008). If species cannot osmoregulate, brackish waters from 5 to 8 ppt (part per thousand, salinity) often comprise a ‘critical salinity zone’ that functions as an ecological, physiological, and evolutionary barrier (Khlebovich and Abramova 2000; Khlebovich 1989, 1990a, b). In turn, freshwaters also comprise a physiological barrier to dispersal, colonization, survival, and reproduction for some marine-adapted invertebrates, limiting their geographic distributions (Lee and Bell 1999).

The distribution of a given aquatic species frequently is restricted to a single adaptive salinity zone: either brackish (A1: 0.5–30 ppt), marine (A2: 30–35+ ppt) or freshwater (B, 0–0.5 ppt) (Freshwater Biodiversity Data Portal 2022; WoRMS 2022). Range extensions, within and/or between the adaptive zones, often have occurred via natural migrations. Over the past 200 years, HMD of various AIS has greatly accelerated this process in time and scale (Lee and Bell 1999; Takahashi and Park 2020). Identification and characterization of globally dispersing AIS and the problems associated with their presence are crucial to guide conservation managers and stakeholders about their prevention and mitigation (Lodge et al. 2016; Piria et al. 2017).

Prior studies have indicated that salinity tolerances and geographical origins can be used to predict invasion propensity of amphipod species; notably, about 40% of P-C amphipod species have become invasive to date (Cuthbert et al. 2020; Copilaș-Ciocianu et al. 2021). Our investigation aims to test whether there are significant differences in the relative salinity tolerances of AIS that originated from the P-C region versus other global regions. We evaluate various taxonomic groups of AIS invertebrates (crustaceans, mollusks, cnidarians, and annelids), comparing the salinity regimes of those living in (A) a wide range of brackish to marine waters (A1; 0.5–30 ppt), exclusively saline marine waters (A2; 30–35+ ppt), (B) freshwaters (0–0.5 ppt), and (C) euryhaline ranges across salinities from freshwaters to marine

(0–35+ ppt). We explore the relationship between neocosmopolitanism and euryhalinity, in relation to relatively rapid range expansions.

Objectives, questions, and hypotheses

Neocosmopolitanism remains a key knowledge gap in ecology, with important questions including: (i) Do P-C AIS invertebrate taxa have broader salinity tolerances than do those originating from other geographical regions, which may predispose them toward neocosmopolitanism?, and (ii) What are their distribution patterns, and will they continue to expand their ranges? We thus compile present-day knowledge about aquatic biodiversity of AIS invertebrate taxa globally, along with their salinity tolerances and geographical origins, allowing us to statistically compare these for donor taxa from various biogeographic origins versus those originating from the P-C region. Earlier studies by Cuthbert et al. (2020) and Paiva et al. (2018) focused on salinity tolerance ranges of crustaceans, and Pauli and Briski (2018) reviewed the salinity tolerance ranges for 50 different P-C aquatic species, providing comparative data. Our central hypothesis is that greater proportions of P-C AIS invertebrate taxa are euryhaline in comparison with those from other geographical origins, which likely has facilitated the former’s growing distributional successes.

Approach and methods

Recent HMD of AIS invertebrates in freshwater and saline adaptive zones are analyzed here based on available literature, whose data were downloaded from the Global Register of Introduced and Invasive Species (GRIIS) database in April 2022. The environmental conditions in which the species live and their salinity tolerance ranges, were assigned according to the GRIIS database, the Great Lakes Aquatic Nonindigenous Species Information System (GLANSIS 2022), and the World Register of Marine Species (WoRMS 2022). The salinity categories we use are: (A1) brackish (0.5–30 ppt), (A2) marine (greater than 30 ppt), and (C) freshwater (less than 0.5 ppt), based on Venice System (1958). The species’ geographical origins were found in the scientific literature, the Baltic Sea Non-indigenous Species database (AquaNIS 2022), and the Global Biodiversity Information Facility (GBIF 2022).

The null hypothesis is that the relative proportions of non-indigenous aquatic invertebrate taxa originating from the P-C region and those from other geographical origins are distributed approximately equally, with equivalent representation among the various salinity adaptive zones: (A) saline—(A1) brackish (0.5–30 ppt and (A2) marine, 30–35+ ppt, (B) freshwater, 0–0.5 ppt, (C) euryhaline, freshwater through saline, 0–35+ ppt, or (D) terrestrial and either freshwater (D1) or saline (D2).

We evaluate this for all invertebrates, and separately for molluscs and crustaceans, since those are the most abundant AIS taxonomic groups. Contingency tables were populated with raw frequency data, and evaluated using χ^2 tests and statistical significance of $\alpha=0.05$, with the STATISTICA 13.1 PL program (StatSoft; www.statistica.com). We conducted contingency tests for all taxa, as well as separately for the most prevalent groups (i.e., crustaceans and mollusks).

The temporal distribution patterns of P-C aquatic invertebrate AIS are evaluated based on the year of first record for each species that documented it as occurring outside of its native range, according to GBIF on 1 April 2022 (GBIF 2022). Their spatial distribution patterns are based on GBIF distribution data available on 1 August 2022 (GBIF 2022), and are mapped here.

Results and discussion

Global biodiversity and salinity zones of AIS invertebrates

Our findings indicate that to date, 1861 invertebrate AIS taxa have been recorded globally (Additional file 1: Table S1), with most—(A) 1312 taxa (70.5%) verified as living in the saline adaptive zone (brackish and/or marine waters), (B) 368 (20%) in the freshwater adaptive zone, (C) 139 (7.5%) in both the fresh and saline adaptive zones, and (D) just 2% are semi-aquatic, with: (D1) 32 (1.7%) in freshwater/terrestrial environments and (D2) 5 (0.3%) in saline/terrestrial environments (Fig. 1). Globally, significantly more invertebrate AIS are reported to inhabit the (A) saline adaptive zone compared to (B) freshwater (B), (C) both freshwater and saline (euryhaline), or (D) freshwater/terrestrial, and the saline/terrestrial zones ($\chi^2 = 171.47$, $df = 4$, $p < 0.001$).

Determining the precise origins, salinity realms, and distributional spread patterns of AIS often are limited by insufficient sampling and the relative paucity of genetic/genomic, biogeographic, and physiological analyses. Additional investigations are needed to determine whether dispersal is ongoing, and to discern its mechanisms and pathways. We found that only a few such studies are available, at present, for relatively few species, including: killer shrimp amphipod *Dikerogammarus villosus* (Rewicz et al. 2015), amphipod *Echinogammarus ischnus* (Cristescu et al. 2004), mysid shrimps *Limnomysis benedeni* (Audzijonyte et al. 2009) and bloody-red shrimp *Hemimysis anomala* (Audzijonyte et al. 2008), fishhook cladoceran waterflea (Cristescu et al. 2003), and zebra and quagga mussels (Brown and Stepien 2010; Stepien et al. 2013).

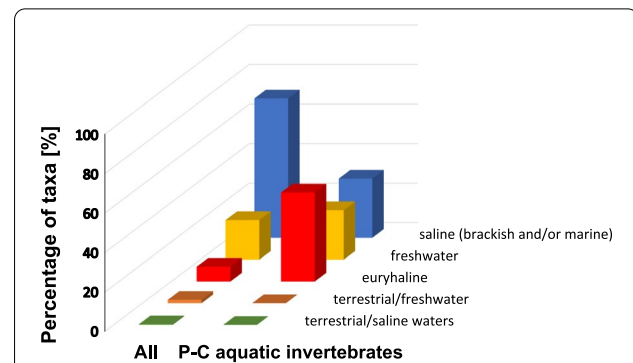


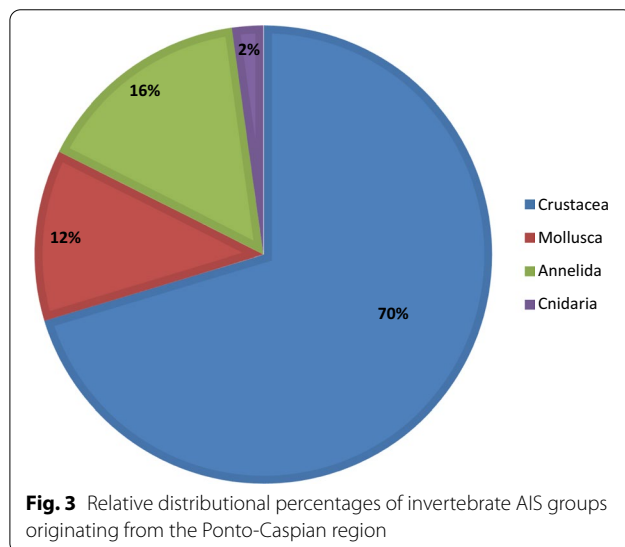
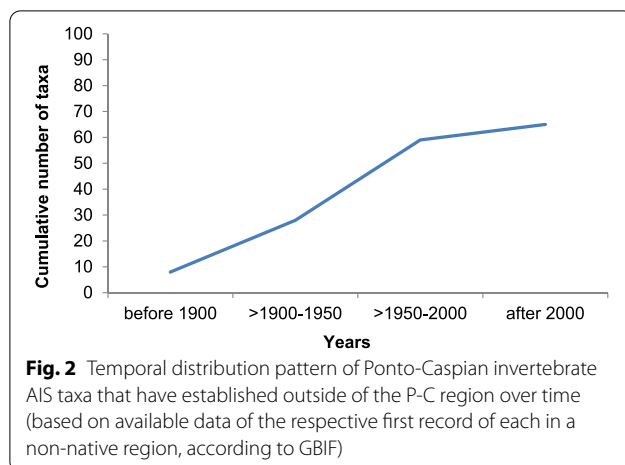
Fig. 1 Proportions of global nonindigenous aquatic invertebrate taxa (left) vs. Ponto-Caspian aquatic invertebrate taxa (right) living in: (A) (top, blue) the saline adaptive zone, i.e., brackish and/or marine waters (0.5–35+ ppt), (B) (yellow) the freshwater adaptive zone, i.e., exclusively in fresh water (0–0.5 ppt), (C) (red) both the freshwater and saline adaptive zones (i.e., being euryhaline, 0–35+ ppt), and (D) (bottom) semi-aquatic, e.g., inhabiting terrestrial and aquatic, either freshwater (D1, brown) or saline (D2, green) habitats, changing with life cycle stage

Ponto-Caspian invertebrate AIS: invasive ranges and salinity trends

In total, our investigation discerns that 91 (5%) of the reported invertebrate AIS taxa have originated from the P-C region. Of these, 41 (45%) of AIS invertebrates are (C) euryhaline, 27 (30%) occur in the (A) saline adaptive zone alone, and (B) 23 (25%) exclusively are found in the freshwater adaptive zone (Fig. 1, Additional file 1: Table S2). Statistical comparisons thus reveal that significantly greater relative numbers of P-C aquatic invertebrate taxa are: (C) euryhaline, living across a range of saline through freshwater habitats, compared to being exclusively (A) saline alone, (B) freshwater alone, or in (D) the freshwater/terrestrial and saline/terrestrial zones ($\chi^2 = 77.5$, $df = 4$, $p < 0.001$). Significantly more euryhaline (C) invertebrate AIS are native to the P-C region than those originating from other geographical regions ($\chi^2 = 312.47$, $df = 4$, $p < 0.001$). This thus indicates a different pattern for P-C taxa versus those from other geographical origins, i.e., the preponderance of euryhalinity for the former.

The figure illustrating temporal distribution patterns of P-C origin aquatic invertebrates (Fig. 2) shows that some were recorded outside of their native area prior to 1900, with most appearing in 1900–1950 due to construction of canals and intensified global shipping. Maps depicting the spatial distribution patterns of P-C AIS invertebrates, prepared from GBIF data are presented in Additional file 1: Fig. S3. These indicate that the P-C origin species are widespread in nearshore temperate regions.

Expansions of P-C AIS freshwater-adapted invertebrates throughout European water corridors with passive



and active HMD likely have been facilitated by increases of chloride ions (from industrial pollution) and increased water salinity over the last 100 years (Bij de Vaate et al. 2002; Jażdżewski et al. 2004; Schulz 2011; Dobrzycka-Kraheil and Graca 2014). Additional studies are needed to determine invertebrate AIS salinity tolerances and the physiological, genetic, genomic, and phenotypic factors that regulate them.

Crustacean P-C AIS

Crustaceans have been very successful invaders of European inland waters, constituting the majority of P-C aquatic invertebrate AIS taxa based on GRIIS (2022) (Fig. 3, Additional file 1). During the twentieth century, many P-C crustaceans rapidly colonized European rivers that became newly linked by water corridors (Bij de Vaate et al. 2002), whose establishments led to significant changes in European freshwater macroinvertebrate

communities, displacing indigenous species (Dick and Platvoet 2000). Several crustaceans in Table 1 are so widely distributed across today's freshwater habitats that they have mistakenly been referred to in the scientific literature as originally being freshwater species (Guerlet et al. 2008; Kinzler et al. 2009; Jermacz et al. 2015). Their populations today are broadly distributed across (C) euryhaline habitats, from freshwater through brackish/marine conditions (Kobak et al. 2017; Dobrzycka-Kraheil and Graca 2018). Gammarid amphipods are the primary group of P-C crustaceans (53% of them) that have successfully invaded the freshwater through saline adaptive zones, exhibiting euryhalinity (C). In our investigation, contingency-based analyses also indicate that significantly much greater numbers of euryhaline crustacean invertebrate AIS have originated from the P-C region in comparison with crustacean AIS having other geographical origins ($\chi^2 = 137.86$, $df = 4$, $p < 0.0000001$).

Laboratory experiments found that salinity >20 ppt is lethal for many P-C crustacean species (Bruijs et al. 2001; Ovcarenko et al. 2006), with some P-C gammarid amphipod species readily osmoregulating up to 20 ppt (Dobrzycka-Kraheil and Surowiec 2011; Dobrzycka-Kraheil and Graca 2014; Dobrzycka-Kraheil et al. 2015). Field studies of gammarids in their native ranges indicated that the P-C killer “shrimp” *D. villosus* occurs at salinities up to 17 ppt (Grigorovich et al. 2003), *Pontogammarus robustoides* (Sars, 1894) to 13 ppt (Romanova 1959), and the demon “shrimp” *D. haemobaphes* to 8 ppt (Ponomareva 1975). Meßner and Zettler (2018) discerned the P-C gammarids *D. villosus* and *Obesogammarus crassus* (Sars G.O., 1894) in waters to 8 ppt. These P-C species thus are broadly adapted to euryhaline conditions, which likely predicates their invasive successes.

Bivalve Mollusk P-C AIS

Mollusks constituted about 12% of the P-C AIS invertebrate taxa in our survey results (Fig. 3, Additional file 1). Dreissenid bivalve mussels are among the most widespread AIS, with the zebra mussel *D. polymorpha* recorded in 39 countries and the quagga mussel *D. rostriformis* in 18 (Table 1, Additional file 1). Our results show that significantly more euryhaline mollusk invertebrate AIS have originated from P-C region than from other geographical region origins ($\chi^2 = 943.8$, $df = 4$, $p < 0.0000001$).

Rapid invasions by dreissenids have been facilitated by their abilities to disperse during all life stages (Stepien et al. 2013), including as juveniles and adults while attached to ship hulls or drifting objects, and being able to survive while out of water for up to several days (Ackerman et al. 1994; Collas et al. 2014). Their pelagic larval

Table 1 Ponto-Caspian AIS invertebrate taxa having populations in freshwater (0–0.5 ppt), brackish (0.5–30 ppt), and marine (30–35+ ppt) environments (scientific nomenclature with authors according to WoRMS—World Register of Marine Species 2022), based on GRIS (Global Register of Introduced and Invasive Species 2022)

Taxonomic group	Species and naming authority	Countries where the species is present (based on GRIS and personal collections)	Salinity regime (based on GRIS and GLANSIS)	References that confirm presence in freshwater and saline adaptive zones
Crustacea Arthropoda	<i>Amathillina cristata</i> Sars, 1894	HU, UA	Freshwater/brackish	Ozbek and Ozkan (2010), WoRMS (2022)
	<i>Cardiophilus marisnigrae</i> Miloslawskaya, 1931	HU	Freshwater/brackish	Copilaş-Ciocianu and Sidorov (2021), WoRMS (2022)
	<i>Caspiocuma campylaspoides</i> (Sars, 1897)	MD, HU	Freshwater/brackish/marine	Jaume and Boxshall (2008), WoRMS (2022)
	<i>Cercopagis pengoi</i> (Ostroumov, 1891)	CA, DK, EE, DE, LV, LT, PL, RU, SE, US, FI, UA	Freshwater/brackish/ marine; also, in freshwater Great Lakes (GLANSIS)	Gusynskaya and Zdanova (1978), Panov et al. (2007)
	<i>Chelicerophium chelicone</i> (Sars, 1895)	HU, UK	Freshwater/brackish	Uryupova and Mugue (2007)
	<i>Chelicerophium curvispinum</i> (Sars, 1895)	AT, BY, BE, HR, EE, DE, HU, IE, Lit, PL, RU, RS, CH, NL, FR, U, GB, CR, LV	Freshwater/brackish	Bij de Vaate et al. (2002), Herkül et al. (2009)
	<i>Chelicerophium maeoticum</i> (Sowinsky, 1898)	HU, RM	Freshwater/brackish	Ozbek (2004)
	<i>Chelicerophium mucronatum</i> (Sars, 1895)	HU, UA	Freshwater/brackish	Uryupova and Mugue (2007)
	<i>Chelicerophium nobile</i> (Sars, 1895)	HU, UA	Freshwater/brackish	Uryupova and Mugue (2007)
	<i>Chelicerophium robustum</i> (Sars, 1895)	BY, DE, HU, FR, NL, SK, UA	Freshwater/brackish	Bernauer and Jansen (2006), Uryupova and Mugue (2005)
	<i>Chelicerophium sowinskyi</i> (Martynov, 1924)	NL, HU, RU	Freshwater/brackish	Uryupova and Mugue (2007)

Table 1 (continued)

Taxonomic group	Species and naming authority	Countries where the species is present (based on GRIS and personal collections)	Salinity regime (based on GRIS and GLANSIS)	References that confirm presence in freshwater and saline adaptive zones
	<i>Dikergammarus haemobaphes</i> (Eichwald, 1841)	AT, BY, HR, FR, DE, HU, PL, RU, CH, GB, SK, MD, NL, UA, SE	Freshwater/brackish	Bij de Vaate et al. (2002), Dobrzycka-Kraheil and Rzemkowska (2010)
	<i>Dikergammarus villosus</i> (Sowinsky, 1894)	AT, BY, BE, HR, CR, FI, FR, DE, HU, PL, RU, RS, SK, ES, CH, GB, NL, IT, MD, SE, UA	Freshwater/brackish	Bij de Vaate et al. (2002), Dobrzycka-Kraheil and Rzemkowska (2010)
	<i>Echinogammarus berilloni</i> (Catta, 1878)	BE, CH, DE, FR	Freshwater/brackish/marine	Schmidt-Drewello et al. (2016)
	<i>Echinogammarus ischnus</i> (Stebbing, 1899)	AT, DE, HU, SK, CH, BY, GB, LT, PL, SE, U, BE, FR, NL	Freshwater/brackish and also in freshwater Great Lakes (GLANSIS)	Bij de Vaate et al. (2002), Cristescu et al. (2004)
	<i>Echinogammarus warpachowskyi</i> (Sars, 1894)	SE	Freshwater/brackish	Bij de Vaate et al. (2002)
	<i>Echinogammarus trichiatus</i> (Martynov, 1932)	AT, BE, DE, HU, PL, SK, CH, BY, FR, NL, UA, SE, BY	Freshwater/brackish	Bernauer and Jansen (2006), Gollasch and Nehring (2006)
	<i>Evadne anonyx</i> Sars, 1897	FI, PL, SE	Freshwater/brackish/marine	Fedonenko and Yakovenko (2016), Panov et al. (2007)
	<i>Hemimysis anomala</i> Sars, 1907	AT, BE, HR, FI, FR, DE, HU, IE, LT, PL, RU, MX, RS, SK, SE, CH, UA, GB, EE, NL	Freshwater/brackish	Gasjunas (1964), Salemaa and Hietalahti (1993)
	<i>Obesogammarus crassus</i> (Sars, 1894)	BY, DE, LT, PL, RU, HU, UA	Freshwater/brackish	Bij de Vaate et al. (2002), Dobrzycka-Kraheil and Rzemkowska (2010)
	<i>Pontogammarus robustoides</i> (Sars, 1894)	BY, FI, DE, LT, PL, RU, SE, MD, EE, HU, UA	Freshwater/brackish	Bij de Vaate et al. (2002), Dobrzycka-Kraheil and Rzemkowska (2010)
	<i>Stenogammarus carausui</i> Derzhavin and Ptakova, 1962	HU	Freshwater/brackish	WoRMS (2022)
	<i>Stenogammarus compressus</i> (Sars, 1894)	HU	Freshwater/brackish	Soheil et al. (2018)
	<i>Stenogammarus macturus</i> (Sars, 1894)	HU	Freshwater/brackish	Copilaş-Ciocianu and Sidorov (2021)
	<i>Stenogammarus similis</i> (Sars, 1894)	HU	Freshwater/brackish	WoRMS (2022)
	<i>Uroniphargoides spinicaudatus</i> (Caraus, 1943)	HU	Freshwater/brackish	Copilaş-Ciocianu and Sidorov (2021)
	<i>Yogmelina limana</i> Karaman and Barnard, 1979	HU	Freshwater/brackish	Copilaş-Ciocianu and Sidorov (2021)
Bivalvia, Mollusca	<i>Dreissena polymorpha</i> (Pallas, 1771)	AT, BY, BE, BG, CA, HR, CR, DK, EE, FI, FR, DE, GR, HU, IE, IQ, JM, LV, LT, NL, PL, PT, KR, RU, RS, SI, ES, SE, CH, U, GB, US, AZ, ID, IT, LU, MX, NL	Freshwater/brackish; also, in freshwater Great Lakes (GLANSIS)	Bij de Vaate et al. (2002), Panov et al. (1997)

Table 1 (continued)

Taxonomic group	Species and naming authority	Countries where the species is present (based on GRIIS and personal collections)	Salinity regime (based on GRIIS and GLANSIS)	References that confirm presence in freshwater and saline adaptive zones
Cnidaria	<i>Dreissena rostriformis (bugensis)</i> Andrusov 1897	CA, DE, PT, MD, RO, HU, RU, UA, US, ES, FR, AZ, BE, BG, GB, NL, SE	Freshwater/brackish; also, in freshwater Great Lakes (GLANSIS)	Orlova et al. (2004), Woźniczka et al. (2016)
	<i>Hypanis glabra</i> (Ostroumoff, 1905)	UA	Freshwater/brackish	WoRMS (2022)
	<i>Lithoglyphus naticoides</i> (Pfeiffer, 1828)	BE, BY, DE, FR, HU, LT, PL, RS, UA, RU, SE	Freshwater/brackish	Falniowski and Szarowska (2012)
	<i>Cordylophora caspia</i> (Pallas, 1771)	AT, AU, BE, CA, CL, DK, FI, DE, LT, LU, MX, NO, PA, PL, PT, RU, ES, SE, TR, GB, US, EE, FR, HU, NL, NZ, UA, IT	Freshwater/brackish; also, in freshwater Great Lakes (GLANSIS)	Bij de Vaate et al. (2002), Olenin and Lep-päkoski (1999)
Annelida	<i>Caspiobdella fadjejewi</i> (Epshtein, 1961)	NL, AT, BY, CH, DE, FR, PL, RU	Freshwater/brackish/marine	Bielecki (1990)
	<i>Hypania invalida</i> (Grube, 1960)	AT, BY, BA, DE, PL, RU, RS, CH, UA, GB, NL	Freshwater/brackish	Bij de Vaate et al. (2002), Woźniczka et al. (2011)
	<i>Isochaetides michaelsoni</i> (Lastockin, 1937)	EE	Freshwater/brackish	Borkhanuddin et al. (2014)
	<i>Potamothrix bavaricus</i> (Oschmann, 1913)	BY, EE, PL, US	Freshwater/brackish	Timm (2013)
	<i>Potamothrix hammoniensis</i> (Michaelson, 1901)	PL	Freshwater/brackish	Timm (2013)
	<i>Potamothrix heuscheri</i> (Bretscher, 1900)	RU, SE, BY, EE, PL	Freshwater/brackish	Bij de Vaate et al. (2002), Panov et al. (1997)
	<i>Potamothrix moldaviensis</i> (Vejdovsky and Mrázek, 1903)	BY, IE, PL, SE, EE, US	Freshwater/marine	Poznańska et al. (2017), Milbrink and Timm (2001)
	<i>Potamothrix vejdoskyi</i> (Hrabě, 1941)	BY, IE, PL, RU, US, SE	Freshwater/brackish	Bij de Vaate et al. (2002), Panov et al. (1997)
AT Austria, AU Australia, AZ Azerbaijan, BY Belarus, BE Belgium, BA Bosnia and Herzegovina, BG Bulgaria, CA Canada, CL Chile, HR Croatia, CR Czech Republic, DK Denmark, EE Estonia, FI Finland, FR France, DE Germany, GR Greece, HU Hungary, IE Ireland, ID Indonesia, IT Italy, IQ Iraq, JM Jamaica, LV Latvia, LT Lithuania, LU Luxembourg, MX Mexico, NO Norway, NL Netherlands, NZ New Zealand, PA Panama, PT Portugal, RU Russian Federation, MD Republic of Moldova, RK Republic of Korea, RO Romania, SE Sweden, RS Serbia, SI Slovenia, SK Slovakia, ES Spain, CH Switzerland, TR Turkey, UA Ukraine, GB United Kingdom, US United States, UZ Uzbekistan				

stages swim and are transported by water currents and tidal movements, as well as being uptaken and released in ballast and bilge waters of vessels (Van der Gaag et al. 2016; Marshall and Stepien 2019).

Salinity tolerances of zebra and quagga mussels appear limited to about 5 ppt in situ in their North American invasive range (Spidle et al. 2011). However, native *Dreissena* populations in the Black Sea region of Ukraine showed greater acclimation to salinity extremes, attributed to the long-term euryhaline conditions in their native range compared to their more recent colonization of North American freshwaters (Mills et al. 1996) and/or due to genetic characters of their inoculant populations (Stepien et al. 2013). Laboratory experiments (Wright et al. 1996) showed that salinity tolerances of North American zebra and quagga mussels increased with larval age, with the zebra mussel being more tolerant; embryos of both species were negatively affected by salinities ≥ 4 ppt, whereas larval and juvenile metamorphosed zebra mussels tolerated up to 10 ppt.

Some native zebra mussel populations in the Caspian Sea survive salinities up to 10.2 ppt (NAS 2022). The maximum survival duration of zebra mussels in long-term mesocosm experiments was 318 days at a salinity of 3.2 ppt, which would be equivalent to a lengthy ship voyage through many ports (van der Gaag et al. 2016). Introduced zebra mussel populations have not yet colonized waters >6.5 ppt in Baltic Sea regions, where salinity appears to comprise an effective barrier (Orlova et al. 2004; Wolnomiejski and Woźniczka 2008; Chubarenko and Margoński 2008; Kotta et al. 2008; Chušev et al. 2012). However, under conditions of hyperosmotic stress, zebra mussels will osmoconform in laboratory experiences (Dietz et al. 2015). Thus, various populations of zebra mussels across the world appear to differ in their salinity tolerances, which may facilitate their colonization and persistence across their AIS ranges.

The quagga mussel currently occurs in almost all Dnieper River reservoirs and tributary deltas in eastern and southern Ukraine (Mills et al. 1996). It also has become widespread in the North American Great Lakes (beginning in 1988), and has established in western U.S. reservoirs, including the Colorado River system, where it was transported by overland trailered boats (Brown and Stepien 2010) and has been reported from Mexico (Wakida-Kusunoki et al. 2015). Quagga mussels usually occur in salinities up to 1 ppt; they can reproduce in salinities <2 ppt, and salinities >6 ppt have been reported as lethal for them (Setzler-Hamilton et al. 1997). Laboratory tolerance experiments by Hofius et al. (2015) showed that quagga mussels from inland lakes of North America remained healthy in brackish

waters of 4 ppt salinity for a maximum of 2 weeks. However, more saline waters killed quagga mussels in 70 h at 21.3 ppt, and they did not survive for long at 15.3 ppt (Hofius et al. 2015). It thus appears likely that the quagga mussel will not be as successful at colonizing euryhaline estuarine waters, in comparison with zebra mussel.

Other P-C AIS invertebrates

Many other P-C invertebrate groups, including annelid worms (Additional file 1, Table 1) have been successful AIS across various salinities, leading to their increasing neocosmopolitan distributions. For example, the euryhaline (0–12 ppt) polychaete bristle worm *Hypania invalida* (Grube, 1860) has spread widely in Europe throughout the Volga, Dnieper, and Danube river catchments over several decades (Woźniczka et al. 2011 and references therein). More recently, this species was reported from the Baltic and North seas (Pabis et al. 2017), as well as Great Britain (Gallardo and Aldridge 2015). It is a popular fish bait and is used as food in aquaculture and aquariums, likely aiding its spread (Pabis et al. 2017). Our results indicate that significantly greater numbers of euryhaline invertebrate AIS taxa (classified as “other”, i.e., not crustaceans or mollusks), have originated from the P-C region than from other geographical regions ($\chi^2 = 276.04$, $df = 4$, $p < 0.0000001$).

Immigrations of P-C annelid oligochaete worms into new locations have resulted from ballast water exchanges in harbors, along with large-scale passive dispersal (Milbrink and Timm 2001). For example, Naididae (which includes the former family Tubificidae) have been regularly dispersing throughout European waters (Milbrink 1999; Milbrink and Timm 2001; Dumnicka 2016), where *Potamothenis hammonensis* has been reported to significantly alter indigenous benthic community composition (Dumnicka 2016).

The P-C colonial cnidarian hydroid *Codylophora caspia* has become globally distributed due to ballast water transport (Roos 1979; Bij de Vaate et al. 2002; Folino-Rorem 2015). According to Roy et al. (2020), it has been present in the Baltic Sea from the early 1800s, in Ireland from 1842, in Australia from 1885, in the Panama Canal since 1944, and the U.S., including California since the 1930s, Florida in the 1950s, the North American Great Lakes in the 1950s, and other regions since 1990 (Fuller et al. 2020). Today it occurs in temperate and tropical coastal regions of every continent and in many freshwater areas, significantly contributing to biofouling throughout its range (Pucherelli et al. 2016). It survives in salinities of 0 to 35 ppt, including full oceanic conditions, and also inhabits fast-flowing, well-oxygenated freshwaters

containing Ca^{2+} , Mg^{2+} , Na^+ , Cl^- and K^+ ions. It further tolerates wide temperature ranges and is predicted to thrive under growing climate change, to the detriment of native zooplankton species (Meek et al. 2012).

Overall euryhalinity and neocosmopolitan ranges of P-C AIS

Our investigation discerns that the relative proportion of AIS invertebrates originating from the P-C that are euryhaline significantly exceeds the relative proportion of euryhaline AIS that have originated from other geographical regions. These P-C taxa evolved and survived under unstable habitat conditions for millions of years, experiencing wide salinity fluctuations (Reid and Orlova 2002; Bürger and Gimelfarb 2002; Paiva et al. 2018). Their evolutionary history appears to have selected for broad euryhaline tolerances, pre-disposing them to neocosmopolitan distribution expansions, with HMD and climate change.

Paiva et al. (2018) further suggested that since most shipping ports in the P-C are located in estuaries whose salinities fluctuate with tidal cycles, rainfall, drought, and river discharges, P-C taxa tend to be more frequent and more successful invaders in comparison with AIS from other geographic regions. Estuaries are especially susceptible to invasions, being centers for HMD activities, e.g., shipping. Estuaries also are areas where ballast water is exchanged, organisms settle on the hulls of ships or hide onboard, and attach on docks and fishing gear, as well as house releases from aquaculture, aquaria, fishing bait, and live seafood catches (Williams and Grosholz 2008). Estuaries comprise transitional zones located between freshwater and marine habitats (encompassing the freshwater through saline adaptive zones), which provide beneficial conditions for both freshwater and for salt-tolerant organisms. They often have unsaturated ecological niches, housing fewer indigenous species (Nehring 2006); these factors render estuaries amenable for AIS to invade, become established, and persist.

Our investigation reveals that 25% of P-C AIS invertebrate taxa occur in (B) freshwaters and (C) 45% are euryhaline; thus, 70% of all P-C AIS contain freshwater-adapted populations. Pauli and Briski (2018) noted that about 8% of P-C taxa do not occur in salinities > 18 ppt. According to Paiva et al. (2020), P-C juveniles frequently are best adapted to lower saline and freshwater conditions, accounting for their greater invasion successes in those habitats. Most AIS species in the freshwater Great Lakes were once native to the P-C region (MacIsaac and Grigorovich 1999). We thus conclude that P-C taxa generally appear to be widely adaptable to freshwater and estuarine aquatic environments, a trend that likely will continue given transport and establishment opportunity.

Human-mediated salinization of inland waters likely has facilitated dispersal of euryhaline-adapted taxa, including those of P-C origins. Ions (mainly chlorides and sulphates) discharged from coal and salt mining, irrigation, vegetation clearance, dryland farming, and industry in general (e.g., Braukmann and Bohme 2011; Schulz 2011; Motyka and Postawa 2000; Korycińska and Królak 2006) have increased the salinity of many inland waters across the world (Bäthe and Coring 2011; Braukmann and Bohme 2011; Petruk and Stoffler 2011). In cold temperate regions, freshwater salinities have been increasing due to road salts used for de-icing; this constitutes a growing concern for the Great Lakes region (Roy and Malenica 2013; Mackie et al. 2022). Across North America, 44% of freshwater lakes have undergone long-term salinization (Dugan et al. 2017).

Increasing salinity conditions have led to the replacement of some salt sensitive species by euryhaline-adapted taxa, including AIS (Piscart et al. 2005). MacIsaac et al. (1999, 2001) advanced the hypothesis that increasing salinity of inland waters has been an important factor facilitating the success of P-C AIS in the Great Lakes and European freshwaters, including the fish-hook cladoceran water flea and dreissenid mussels. The effect of increasing salinity on native and invasive species thus may favor euryhaline-adapted species in the future if the trend continues, enhancing the spread of AIS.

AIS primarily have originated from temperate regions, particularly shallow nearshore areas and low saline waters, colonizing new geographic areas that possess similar environmental conditions (Table 1; Dedju 1980; Poznańska-Kakareko et al. 2013; Dobrzycka-Kraheil and Graca 2018). Such similarity of environmental niches is a key concept in invasion ecology (Bello et al. 2020), underlying the increasingly neocosmopolitan distributions of P-C AIS invertebrates. However, since conditions in deeper water areas have been relatively poorly investigated (Gan et al. 2020), those species distributions may be underestimated. Because estuarine and coastal waters have been recognized as hot spots for AIS (Williams and Grosholz 2008), research efforts mostly have concentrated on those nearshore areas, which often are more readily, regularly, and easily surveyed and sampled. Thus, further explorations of deeper water habitats and their species compositions are warranted.

Ecological consequences of P-C neocosmopolitan AIS

Introductions of AIS into new environments may exert unpredictable consequences, including new or disrupted trophic interactions (David et al. 2017). For example, P-C crustaceans comprise key food sources for many fishes and macroinvertebrates, yet can negatively impact biodiversity, food web interactions, habitat quality, and/

or environmental conditions as AIS (Arbaciauskas et al. 2010). For example, the bloody-red mysid shrimp *Hemimysis anomala*, which was introduced to the North American Great Lakes provides food for native fishes, but has reduced the overall abundance and species diversity of the zooplankton community (Ricciardi et al. 2012). The cladoceran fish-hook waterflea *Cercopagis pengoi* (Ostroumov, 1891) is a very efficient predator on a variety of zooplankton taxa, possessing an euryhaline distribution (Lehtiniemi and Linden 2006). However, its individuals clump together, attaching to fishing gear and clogging nets and trawls, resulting in significant gear costs across its invasive range (Leppäkoski and Olenin 2000). Deterious effects of P-C AIS amphipods have included extirpations of native gammarid amphipods (Surowiec and Dobrzycka-Kraheil 2008). For example, the aggressive P-C AIS killer “shrimp” amphipod *D. villosus* readily outcompetes other invertebrates due to its omnivory, euryhalinity, broad temperature tolerance, large size, and rapid reproduction (Dick and Platvoet 2000). In contrast, some P-C AIS also have some positive ecosystem effects, including ‘bottom cleaning’ by some benthic P-C gammarid amphipods, with resonating ecological effects (Dedju 1980).

P-C bivalve mollusks often compete for space and food with native filter-feeding species. Notably, zebra and quagga mussels cause severe habitat alteration as bio-fouling organisms that damage piers, pipes, anchors, water intakes, ships and other vessels, as well as accumulate on the shells of native unionid bivalves, killing them (GISP 2008), thereby exerting significant ecological and economic impacts (McLaughlan et al. 2014; Strayer and Smith 1996; Marshall and Stepien 2019). Economic losses caused by zebra and quagga mussels were estimated at US\$ 50 billion over the 2001–10 decade (Cuthbert et al. 2021). The quagga mussel frequently outcompetes the zebra mussel in regions of sympatry, including many invaded European rivers (Heiler et al. 2013) and North American ecosystems, with significant ecological differences found between these two species (Stepien et al. 2013; Marshall and Stepien 2019, 2021).

Moreover, dreissenid mussels form hard substrates across soft benthos, acting as ecosystem engineers in providing habitat for many different species that settle on their shells and in their interstices (Stepien et al. 2013). Their presence—especially the zebra mussel—often increases water clarity due to their prodigious filtering capacity (Barbiero and Tuchman 2004), along with marked reduction of the standing stock of primary producers and zooplankton (Richardson and Bartsch 1997; De Stasio et al. 2018). Dreissenid mussels provide food for birds and fishes, but reduce the amount of available zooplankton for larval fishes and

macroinvertebrates (Stańczykowska et al. 1990; Watzin et al. 2008). Overall, there are both positive and negative effects for many AIS, whose growing neocosmopolitan spread likely will increase with changing conditions of climate, temperature, salinity, nutrients, shipping and other transport opportunities, and biological interactions during the coming decades.

Conclusions

Invertebrate AIS worldwide primarily have been documented from the (A) saline adaptive zone, whereas those living exclusively in the (B) freshwater adaptive zone or (C) being euryhaline, living across these adaptive zones were previously believed to be less common. However, as shown by the results of our investigation, P-C invertebrate AIS more frequently are (C) euryhaline, inhabiting a wide distributional range of salinities, than those originating from other geographic regions worldwide. Broad salinity tolerance over their evolutionary history likely has predisposed them to be successful invaders across neocosmopolitan biogeographic ranges, when provided with HMD opportunities. Moreover, most P-C species (70%) include (B) freshwater-adapted populations, which explains their tremendous success in invading and expanding in freshwater systems.

Prevention and management of dispersal and transport vectors of P-C AIS are important management concerns. The present study illustrates the scale of this problem, and hopefully scientists, managers, stakeholders, and the public-at-large will benefit from this review paper that evaluates causes and consequences of increasing worldwide dispersal of invaders from the P-C region. Prevention measures against the large-scale dispersal of AIS include the treatment and disposal of ballast water and cleaning of ship hulls, as well as environmental education about cleaning of overland boats and fishing and recreational gear, and the prevention of bait, pet, and aquarium releases.

Supplementary Information

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Additional file 1: Table S1. Nonindigenous aquatic invertebrates based on Global Register of Introduced and Invasive Species (GRIIS 2022). **Table S2.** Ponto-Caspian nonindigenous aquatic invertebrate taxa based on Global Register of Introduced and Invasive Species (GRIIS 2022). **Figure S3.** Distributions of Ponto-Caspian aquatic invertebrates (based on GBIF-Global Biodiversity Information Facility, data available on 1 August 2022).

Author contributions

Each author made substantial contributions to the conception and design of the work: ADK created the original idea, provided the main hypotheses of the

work and interpretation of analyzed data, CAS has significantly reformulated the hypotheses, added to the ecological theory, redrafted the work, and substantively revised and edited it, ZN analyzed data and helped to draft the work. All authors read and approved the final manuscript.

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Competing interests

The authors declare there are no competing interests.

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