



Review

Euryhalinity of Ponto-Caspian invaders in their native and introduced regions

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Abstract

In the past several decades, Ponto-Caspian species have established in freshwater and brackish habitats of the North and Baltic Sea and Great Lakes-St. Lawrence River region in much higher numbers than expected based on introduction effort (i.e. shipping frequency) and environmental conditions between these regions. Several studies have suggested that Ponto-Caspian taxa are euryhaline and might be able to adapt rapidly to changing salinity conditions, and therefore may be more successful colonizers than species from other regions. To determine the realized niche in the native and introduced habitats of Ponto-Caspian invaders and to assess whether they have expanded their salinity tolerance during the invasion process, we conducted a literature search to assess the salinity ranges of 55 Ponto-Caspian species in their native and introduced ranges. Our results confirmed that the majority of those species occupied a wide range of salinity in their native and introduced habitats. Approximately 50% of species were reported from both freshwater and brackish habitats (0–18 PSU) in their native region, occupying a salinity range of at least 10 PSU difference. In general, the number of species tended to decline as salinity increased in both native and introduced habitats. More than 90% of Ponto-Caspian invaders occupied freshwater (< 0–0.5 PSU) habitats, while 18% did not occur above 18 PSU. Overall, 46% of species were reported from a narrower salinity range in their introduced compared to their native region. Consequently, our study revealed significantly broader salinity ranges in native compared to introduced habitats. As our results suggest that the majority of Ponto-Caspian invaders occupy freshwater and brackish habitats in their native region, the recent numerous invasions of freshwater and brackish areas by these species should not be a surprise. Therefore, managers and policy makers should take into account that the majority of Ponto-Caspian invaders originate from fresh water or low salinities and develop new regulations to prevent future invasions from the Ponto-Caspian region, as well as from areas highly invaded by Ponto-Caspian taxa such as Northern Europe.

Key words: salinity tolerance, Ponto-Caspian non-indigenous species, salinity barrier, salinity of native region, salinity of introduced region

Introduction

The increasing number of human-mediated introductions of species is one of the major challenges for aquatic ecosystems and biodiversity (Hulme 2009;

Molnar et al. 2008; Olden et al. 2004). The invasion process comprises multiple stages including transport, introduction, establishment and spread, where transition between stages is affected by propagule pressure (i.e. number of individuals released), environmental

tolerance of individuals during transport and in new habitats, and their capability to integrate into new communities (Blackburn et al. 2011; Briski et al. 2018; Colautti and MacIsaac 2004; Simberloff 2009). As organisms need to maintain homeostasis, salinity is one of the key factors influencing the spread and establishment of aquatic species (Smyth and Elliott 2016). Consequently, species with a broad salinity tolerance may have a higher probability of establishing in new habitats, particularly in variable environments with fluctuating salinities, which often include freshwater conditions such as shipping ports located on river mouths and estuaries (Keller et al. 2011).

In the past few decades, Ponto-Caspian species, i.e. species originating from the Azov, Black and Caspian Seas and adjacent estuaries and rivers, invaded numerous brackish and freshwater habitats of the Baltic Sea and Laurentian Great Lakes (Bij de Vaate et al. 2002; Casties et al. 2016; Reid and Orlova 2002; Ricciardi and MacIsaac 2000). These invasions have occurred in much higher numbers than expected based on shipping frequency and the environmental conditions in these regions (Casties et al. 2016). This gave rise to the hypothesis that Ponto-Caspian taxa may be inherently more successful colonizers than species from other regions due to their euryhalinity and capability to rapidly adapt to a wide range of salinities (Bij de Vaate et al. 2002; Casties et al. 2016; Reid and Orlova 2002; Ricciardi and MacIsaac 2000). Several recent studies suggested that the majority of Ponto-Caspian endemics may be of freshwater ancestry, rather than marine, because of their invasion history of freshwater habitats and their high tolerance for freshwater conditions in experimental testing (Casties et al. 2016; Paiva et al. 2018; Pauli et al. 2018; Reid and Orlova 2002). Approximately 70% of all established species in the Great Lakes since 1985 originate from brackish waters of the Ponto-Caspian region (MacIsaac et al. 2002). Also, in the Baltic Sea the number of Ponto-Caspian species has been constantly increasing over the last few decades (Leppäkoski et al. 2002). The Ponto-Caspian region has a long history of changing sea levels and salinity due to geological processes (Dumont 1998) and those changing conditions are suggested to have selected for euryhalinity of species evolved in the region (Reid and Orlova 2002). The euryhalinity and high adaptation capacity for diverse salinities of Ponto-Caspian species has been shown by a number of studies. Bij de Vaate et al. (2002) reviewed the invasion routes of 22 Ponto-Caspian invaders in Europe and concluded that 15 of them are euryhaline. Grabowski and Pegid (2007) reviewed 13 gammarid species occurring in European waters and determined that Ponto-Caspian species have a broader salinity

tolerance than native European species. In addition, Dobrzycka-Kraheil et al. (2016) revealed that four gammarid species of Ponto-Caspian origin that have established in the Gulf of Gdansk in the Baltic Sea have overcome a salinity barrier from freshwater to mesohaline habitats (< 8 PSU; Venice System 1958). Experimental studies have supported the notion of euryhalinity of Ponto-Caspian species as shown by salinity tolerance experiments demonstrating that different populations of Ponto-Caspian gammarids tolerate wide ranges of salinity and perform well in freshwater conditions (Paiva et al. 2018). Consequently, current literature points to euryhalinity of Ponto-Caspian taxa and hints at the possibility that these species might be able to expand or shift their salinity tolerance in introduced compared to their native regions.

Invasion routes and histories of Ponto-Caspian species have been widely studied and discussed, emphasizing canal construction connecting several main European rivers to allow ship transit between the Ponto-Caspian region and Northern Europe as well as ballast water discharge and hull fouling as the main dispersal vectors (Bij de Vaate et al. 2002; Gallardo and Aldridge 2015; Jazdzewski and Konopacka 2002; Leuven et al. 2009; Olenin 2002; Reid and Orlova 2002). However, it has not yet been confidently determined whether Ponto-Caspian invaders have indeed crossed salinity boundaries and expanded their salinity range in their introduced regions. A comprehensive study comparing *in situ* salinity ranges in native and introduced habitats of Ponto-Caspian species may provide valuable information on their invasion potential and help to implement proper management strategies. Thus, in this study we conducted an extensive literature search on 55 Ponto-Caspian species established in the Baltic and North Seas and the Great Lakes–St. Lawrence River region, including surrounding river mouths and estuaries, to determine their *in situ* native and introduced salinity ranges. In addition, we tested the hypothesis that Ponto-Caspian species have crossed salinity boundaries during the invasion process and expanded their salinity range in introduced regions compared to their native habitats.

Material and methods

Literature search

Based on a recent study on non-native species established in Northern Europe and the Laurentian Great Lakes region by Casties et al. (2016), we compiled a list of Ponto-Caspian species to determine their salinity range in their native and introduced habitats. Two species included in the original list by

Casties et al. (2016), the sturgeon *Acipenser oxyrinchus* Mitchill, 1815, and the copepod *Eurytemora affinis* (Poppe, 1880) where not included in the present study as their Ponto-Caspian origin could not be confirmed. Moreover, the Ponto-Caspian origin of the annelids *Paranais frici* Hrabě, 1941, *Potamothrix heuscheri* (Bretscher, 1900), and *P. vej dovskyi* (Hrabě, 1941) is debated in the current literature (Ketelaars 2004; Milbrink 1999; Paavola et al. 2005). However, based on several studies providing evidence for Ponto-Caspian origin of these species, we decided to keep them in the analysis of this study. Another recent invader of European rivers, the racer goby *Babka gymnotrachelus* (Kessler, 1875) was additionally included in our study.

For each of the analysed species three general databases: Web of Science, Scopus, and Science direct (Science direct 2017; Scopus 2017; Web of Science 2017), as well as three databases specific for invasive species: DAISIE, AquaNIS, and GLANSIS (AquaNIS 2012; DAISIE 2017; GLANSIS 2017) were searched. The scientific species name was used as the search term. Taxonomic status of all species was validated following the classification by Worms (WoRMS 2017) and for Actinopterygii by Fishbase (Froese and Pauly 2017). In cases where more than 250 hits were obtained, the term “salinity” was added as a second search term using AND as a connector. In rare cases when this combination still resulted in more than 250 hits, a third term was added (“high” / “low”) within a distance of two words to the term “salinity”. In case the search algorithm resulted in less than ten hits altogether, an additional search in google scholar was conducted (Google 2017). In addition to the literature search, species records from the Geographic Information Systems (OBIS) and the Biodiversity Information Facility (GBIF) were used to compare species distribution to the reviewed literature (GBIF 2017; OBIS 2017). Records found in these systems but not previously obtained in the literature search were accordingly added. Finally, species records from 16 scientific publications reporting species lists and salinity ranges were included in our dataset as well (Bij de Vaate et al. 2002; Ellis and MacIsaac 2009; Glass et al. 2014; Gollasch et al. 2009; Jazdzewski and Konopačka 2002; Jazdzewski et al. 2005; Karatayev et al. 2008; Ketelaars 2004; Leppäkoski et al. 2002; Mills et al. 1993; O’Connor et al. 2008; Paavola et al. 2005; Panov et al. 2007; Reise et al. 1998; Spencer and Hudson 2003; Verdonshot 2007).

Habitat and salinity classification

The three main Ponto-Caspian basins, Azov-, Black- and Caspian Sea including lakes and rivers within

adjacent areas of the following countries: Azerbaijan, Bulgaria, Georgia, Iran, Kazakhstan, Moldavia, Rumania, Russia (area between Ukraine and Kazakhstan), Turkey, Turkmenistan, and Ukraine were considered as the native Ponto-Caspian region. Any distribution beyond this was considered introduced. Direct references to salinity in the literature were used and converted to Practical Salinity Units (PSU) where possible. Species records lacking salinity values but including detailed geographic information were used to track salinity data for the respective location from the World Ocean Atlas (World Ocean Atlas 2013) and the Baltic Climatological Dataset (Feistel et al. 2010). Salinity data from the World Ocean Atlas (WOA) were extracted as the statistical mean of annual salinities averaged over decades per $\frac{1}{4}^{\circ}$ grid. Salinity from the Baltic Climatological Dataset (BCD) was extracted as mean salinity per $1^{\circ} \times 1^{\circ}$ cell for the period from 1900–2005. Records for rivers and lakes were considered freshwater (0–0.5 PSU) unless otherwise stated. Overall, salinity data were lacking for eight species in their native and for one species in its introduced region making our dataset robust enough to provide reliable conclusions (see results section). The primary dataset is available at PANGAEA (doi: 10.1594/PANGAEA.892332).

Statistical analysis

For the majority of the reviewed species there were a limited number of studies and data on salinity ranges available, so statistical analysis was conducted only for species with at least three references in each the native and introduced region. This resulted in a total of 18 species, including species of the phyla Arthropoda, Chordata and Mollusca, hereafter referred to as the restricted dataset. For all other taxa, determined salinity ranges were reported, but not statistically analysed. Differences between native and introduced salinity ranges, i.e. the difference between minimum and maximum salinity per species, was tested using a paired Wilcoxon rank-sum test due to non-normal data distribution. Analyses were conducted for all 18 species together and for each phylum separately. The Wilcoxon rank-sum test compared rank sums based on the null hypothesis that the centre of location of native and introduced salinity range is equal. All analyses were performed using the basic stats package in R (R Core Team 2017).

Results

In situ salinity for all species – original dataset

Fifty-five species from the Ponto-Caspian region that invaded the North and Baltic Seas and Great Lakes–

St. Lawrence River region were used in this study to determine their salinity ranges in native and non-native habitats (Supplementary material Table S1). This dataset is hereafter referred to as the original dataset. Overall, there was a trend of a decreasing number of species with increasing *in situ* salinity range (Figure 2). When both habitats are considered together, more than 90% of the species were recorded from fresh water (0–0.5 PSU); 67% in their native and 85% in their introduced habitats. In their native habitats, 53% occurred in freshwater as well as in mesohaline conditions (0.5–18 PSU; Venice System 1958). This applied to 56% in the introduced habitats. In both native and introduced habitats, salinities higher than 18 PSU were recorded for 18% of the species. Only four species were not found in salinities below 10 PSU, two Cnidaria (*Moerisia inkermanica* Paltschikowa–Ostroumowa, 1925 and *Sphaeromyxa sevastopoli* Naidenova, 1970), one Mollusca (*Lithoglyphus naticoides* (C. Pfeiffer, 1828)) and one Arthropoda (*Cornigerius maeoticus* (Pengo, 1879)). All of these species had a rather narrow salinity range in their native habitats with not more than 3 PSU difference (Figure 1; Table S1).

In their native habitats, approximately 50% of species occupied a range with at least 10 PSU difference; in the introduced habitats this reduced to 27% of the species (Figure 1). A narrow sense euryhaline distribution was determined for 15% of the species, meaning that they occurred in salinities from 0 to > 30 PSU (Figure 2; Hutchinson 1960). Overall, 46% of species occupied a narrower salinity range in their introduced compared to their native region (Figure 1; Table S1). In contrast, 25% of species occupied a wider salinity range in their introduced habitats. In total, 17 species occupied either higher or lower salinities in their introduced habitats. Among these, six species expanded their salinity range towards lower salinities, eight towards higher salinities, and three (*P. communis*, *C. caspia* and *M. inkermanica*) in both directions (Figure 1, Table S1).

In situ salinity for restricted dataset

Statistical analysis was conducted for species with at least three references in each the native and introduced region. Almost 95% of these species were recorded from freshwater in their native and introduced habitats. Only the cladoceran *Evadne anonyx* G.O. Sars, 1897 did not occur in fresh water. Almost 89% of the tested species occupied a salinity range with at least 10 PSU difference within their native habitats. In the introduced habitats, this applied to 28% of the species. A narrow sense euryhaline distribution could be assigned only for *Neogobius*

Table 1. Results of the paired Wilcoxon rank-sum test comparing salinity ranges as difference between minimum and maximum salinity in the native and introduced range per phylum. The species with at least three records reported per habitat were used for statistical analysis. Sample size (number of species) for each test was provided, as well. V designates the sum of ranks. Significant values are highlighted in bold.

	Sample size (number of species)	V	p-value
All taxa	18	139	0.021
Phylum			
Arthropoda	9	36	0.129
Chordata	7	24	0.106
Mollusca	2	3	0.5

melanostomus (Pallas, 1814). Overall, 16 species occupied a narrower, while only two a wider salinity range in their introduced compared to their native region (Figure 1; Table S1). When all 18 species were tested together, the Wilcoxon rank sum test revealed significantly broader salinity ranges in native compared to introduced habitats ($p < 0.05$; Table 1). However, when phyla were tested separately, there was no difference between native and introduced habitats for any phyla ($p > 0.05$; Table 1).

Discussion

In recent years, Ponto-Caspian species have invaded both freshwater and brackish habitats of the North and Baltic Sea and Great Lakes–St. Lawrence River regions in higher numbers than expected based on shipping frequency and matching environmental conditions among regions (Bij de Vaate et al. 2002; Casties et al. 2016; Paiva et al. 2018; Reid and Orlova 2002). Thus, it has been suggested that many Ponto-Caspian taxa are euryhaline and able to colonize new habitats more rapidly than species from other regions. Our results demonstrated that the majority of Ponto-Caspian species occupied wide ranges of salinity, with often more than 10 PSU difference. In addition, more than 90% of species were recorded from freshwater habitats, while there was a tendency for a decreasing number of species with increasing salinity. Interestingly, our study did not confirm that Ponto-Caspian invaders shifted their salinity ranges during the invasion process, but that the majority of them occupy a narrower salinity range in their introduced compared to their native region. Still, our study demonstrated that many Ponto-Caspian invaders tolerate wide ranges of salinity, with some of them being true euryhaline species that can tolerate salinities from freshwater up to fully marine conditions of more than 30 PSU.

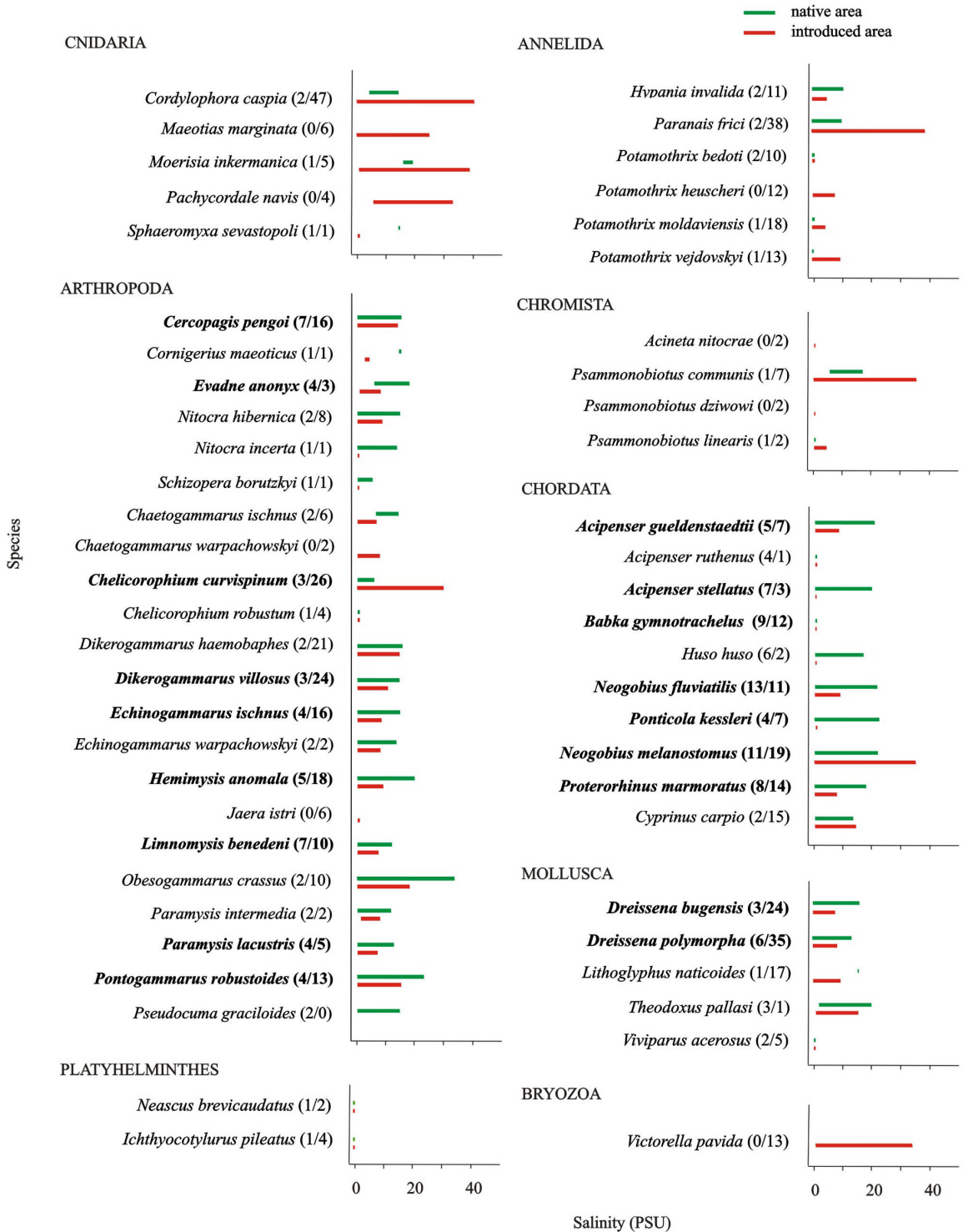


Figure 1. Salinity ranges of the Ponto-Caspian non-native species that invaded the North and Baltic Seas and Great Lakes-St. Lawrence River region grouped by phyla. The numbers in brackets represent the number of search records for native and introduced regions, respectively. Species highlighted in bold were used for statistical analysis.

Our results are supported by a few recent experimental studies that demonstrate the wide salinity tolerance and fast adaptation potential of Ponto-Caspian species, especially to low salinities. Paiva et al. (2018) compared the salinity tolerance (i.e. fundamental salinity niche) of 22 populations of eight gammarid species originating from the Ponto-Caspian, Northern European and Great Lakes–St. Lawrence River regions and revealed that all of those populations tolerate wide ranges of salinity. This study also showed that populations of Ponto-Caspian species, though collected from salinities of 4 PSU and 10 PSU, thrived in freshwater conditions (≤ 0.5 PSU; Venice System 1958), while populations from the other two regions were not able to survive below 0.5 PSU. Moreover, artificial selection experiments on a Ponto-Caspian amphipod collected from 10 PSU demonstrated that selection is possible for lower but not higher salinities, suggesting that the Ponto-Caspian populations that currently inhabit brackish habitats in their native region still contain enough standing genetic variation to establish in freshwater habitats (Dlugosch et al. 2015; Pauli et al. 2018).

The study by Paiva et al. (2018) revealed significant differences in salinity tolerance among different populations of the same species raising the question which populations of Ponto-Caspian species have become invaders and whether the same populations have invaded the North and Baltic Seas, European rivers and the Great Lakes–St. Lawrence River regions. Previous studies suggested that the most likely pathway for Ponto-Caspian species to the Great Lakes is a secondary introduction from Northern Europe (Leppäkoski et al. 2002; Ricciardi and MacIsaac 2000). However, Casties et al. (2016) revealed that half of the Ponto-Caspian species in the Great Lakes are not established in the North and Baltic Seas, though they did not take into account European rivers. As the North and Baltic Seas are predominantly brackish habitats, while the Great Lakes are freshwater systems, a plausible explanation might be that different populations invaded the two systems. Consequently, stepping stone introduction to the Great Lakes from Northern Europe may provide a parsimonious explanation, but probably from Northern European rivers, not from the North and Baltic Seas. In addition, our study demonstrated a narrower salinity range in introduced compared to invaded regions. This may be because populations inhabiting higher salinities in their native region did not have much opportunity to be transported outside their native region as the majority of shipping traffic in the Ponto-Caspian region is in northern estuaries of the Black Sea (Kaluza et al. 2010; Seebens et al. 2013). Osmoregulatory and population genetic studies

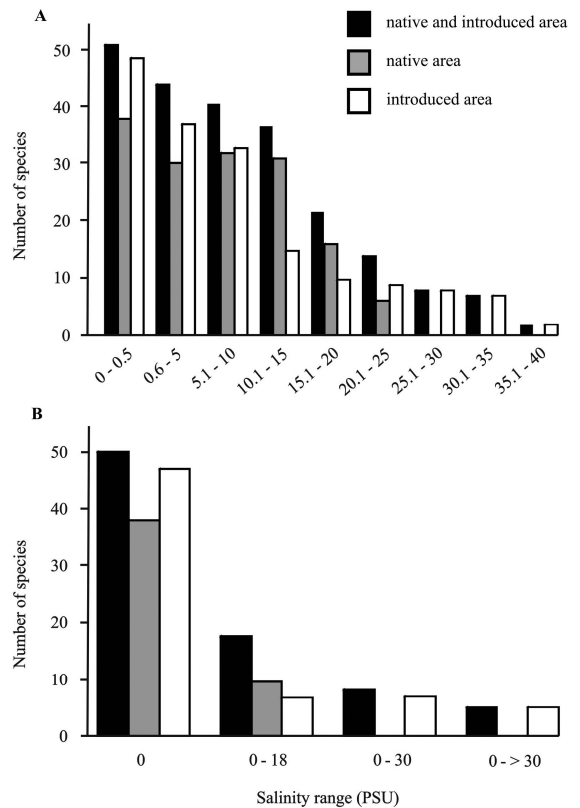


Figure 2. Number of species per salinity range. (A) Number of species in freshwater ($0 < 0.5$ PSU), oligohaline conditions (0.5–5 PSU) and from that on in 5 PSU steps. (B) Number of species that occupy freshwater habitats, and freshwater and saline habitats based on Venice System (1958). Note that the number of species is not cumulative; the same species may occur in more than one salinity range.

are needed to elucidate the invasion pathways and origins of invading populations, such as that of Spidle et al. (1994) that demonstrated that the quagga mussel *Dreissena bugensis* (Andrusov, 1897) likely came to the Great Lakes directly from the Black Sea drainage of Ukraine.

As the Ponto-Caspian region is understudied compared to Northern Europe and the Great Lakes regions, we emphasize that our assembled dataset for Ponto-Caspian species is probably not demonstrating the complete realized salinity niche of Ponto-Caspian taxa in their native habitats because many species may occur in habitats which have never been sampled or studied. This may be, in particular, the case for higher salinities in native habitats as they are predominantly in the southern areas of the region (Casties et al. 2016). Our two types of datasets, original and restricted, further confirm this assumption as our results demonstrated that only 18% of species in the

original, but 38% in the restricted dataset occurred in salinities higher than 18 PSU in their native region. Similarly, our study revealed that 85% and 94% of species occurred in freshwater conditions, respectively. In the introduced habitats, the difference between the two datasets was less pronounced, with 18% and 11% of species occurring in salinities above 18 PSU, respectively. Consequently, there is the possibility that our data obtained from literature where scientists measured salinity during sampling underestimated, while those extracted from the World Ocean Atlas and the Baltic Climatological Dataset overestimated, the realized salinity niche of those species, not only in their native region but also in introduced regions. Further uncertainties in our study might come from the fact that river estuaries in Northern Europe, as well as in the Ponto-Caspian region, often show high spatial heterogeneity and salinity gradients due to tidal influence and dams. Moreover, species with a long invasion history have had a higher chance of entering, establishing and adapting to new habitats with varying salinity than those with a short invasion history. Salinity records for species which are in their early invasion phase might also be biased towards lower salinities when entering *via* river systems or released in freshwater ports.

The biological and physical characteristics of the Ponto-Caspian basins have been characterized by a complex geology during the last ten million years (Mordukhai-Boltovskoi 1964; Zenkevich 1963). Those complex changes in salinity and successions of the basins were influenced by several connections and disconnections of the basins with the Mediterranean Sea and freshwater flooding after ice melting at the end of each Glacial Maximum (Zenkevich 1963). Nowadays, the salinity gradient in the Ponto-Caspian region ranges from fresh water in the east to more saline in the west, with an average sea-surface salinity in the Black Sea between 17.5–19 PSU and 22 PSU in deeper waters (Reid and Orlova 2002). The species that have endured these complex changes over millions of years evolved euryhalinity with most of them settling in estuaries, lagoons and the lower courses of rivers (Mordukhai-Boltovskoi 1964; Zenkevich 1963). Consequently, Ponto-Caspian biota may consist of relict freshwater euryhaline species inhabiting these regions for several millions of years and of marine ones entering the system after each connection with the Mediterranean Sea (Mordukhai-Boltovskoi 1964; Zenkevich 1963), with both groups of species adapting to the current intermediate salinity of the majority of the Ponto-Caspian region.

Several recent studies have suggested that Ponto-Caspian species might be of freshwater ancestry, able to tolerate brackish and mesohaline conditions

(Paiva et al. 2018; Pauli et al. 2018). Though our study cannot provide cues for the ancestry of the reviewed species, our results revealed that more than 90% of Ponto-Caspian invaders occupy freshwater habitats in their native or introduced habitats. Moreover, our results showed that some species are able to expand their salinity tolerance towards lower salinities in the introduced habitats. These findings could further support the notion of a freshwater euryhaline ancestry of Ponto-Caspian invaders (Gurevitch et al. 2018). If so, the recent numerous invasions of freshwater and brackish habitats by these species (Bij de Vaate et al. 2002; Casties et al. 2016) should not be a surprise, and management strategies to prevent future invasions should take special concern to regulate vectors coming from this region.

Future studies investigating the fundamental salinity tolerance of Ponto-Caspian taxa, such as those conducted by Paiva et al. (2018), accompanied by studies on osmoregulatory mechanisms to elucidate differences in the osmoregulatory capability between Ponto-Caspian taxa and species from other regions such as the study of Dobrzycka-Kraheil and Graca (2018) are needed. In addition, the genetic background of Ponto-Caspian invaders using state-of-the-art techniques, particularly for functional genes responding to salinity conditions, as well as population genetics studies on different populations should be conducted to shed light on the great invasion success of Ponto-Caspian invaders. Finally, managers and policy makers should take into account the fact that the majority of Ponto-Caspian invaders may be freshwater taxa able to tolerate brackish conditions, and develop new regulations and require more stringent control of vectors, such as ships' ballast tanks and transport of aquaculture stocks, to prevent future invasions from the Ponto-Caspian region, as well as from areas highly invaded by Ponto-Caspian taxa such as Northern Europe.

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References

- AquaNIS (2012) Information system on aquatic non-indigenous and cryptogenic species. <http://www.corpi.ku.lt/databases/index.php/aquanis> (accessed 9/25/2017)
- Bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1159–1174. <https://doi.org/10.1139/f02-098>

- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339, <https://doi.org/10.1016/j.tree.2011.03.023>
- Briski E, Chan FT, Darling JA, Lauringson V, MacIsaac HJ, Zhan A, Bailey SA (2018) Beyond propagule pressure: importance of selection during the transport stage of biological invasions. *Frontiers in Ecology and the Environment* 16: 345–353, <https://doi.org/10.1002/fee.1820>
- Casties I, Seebens H, Briski E (2016) Importance of geographic origin for invasion success: A case study of the North and Baltic Seas versus the Great Lakes–St. Lawrence River region. *Ecology and Evolution* 6: 8318–8329, <https://doi.org/10.1002/ece3.2528>
- Colautti RI, MacIsaac HJ (2004) A neutral terminology to define ‘invasive’ species. *Diversity and Distributions* 10: 135–141, <https://doi.org/10.1111/j.1366-9516.2004.00061.x>
- DAISIE (2017) Delivering Alien Invasive Species in Europe. <http://www.europe-aliens.org/> (accessed 9/25/2017)
- Dlugosch KM, Anderson SR, Braasch J, Cang FA, Gillette HD (2015) The devil is in the details: genetic variation in introduced populations and its contributions to invasion. *Molecular Ecology* 24: 2095–2111, <https://doi.org/10.1111/mec.13183>
- Dobrzycka-Krahel A, Graca B (2018) Effect of salinity on the distribution of Ponto-Caspian gammarids in a non-native area – environmental and experimental study. *Marine Biology Research* 14: 183–190, <https://doi.org/10.1080/17451000.2017.1406666>
- Dobrzycka-Krahel A, Majkowski W, Melzer M (2016) Length-weight relationships of Ponto-Caspian gammarids that have overcome the salinity barrier of the southern Baltic Sea coastal waters. *Marine and Freshwater Behaviour and Physiology* 49: 407–413, <https://doi.org/10.1080/10236244.2016.1244948>
- Dumont HJ (1998) The Caspian Lake: History, biota, structure, and function. *Limnology and Oceanography* 43: 44–52, <https://doi.org/10.4319/lo.1998.43.1.0044>
- Ellis S, MacIsaac HJ (2009) Salinity tolerance of Great Lakes invaders. *Freshwater Biology* 54: 77–89, <https://doi.org/10.1111/j.1365-2427.2008.02098.x>
- Feistel R, Weinreb S, Wolf H, Seitz S, Spitzer P, Adel B, Nausch G, Schneider B, Wright DG (2010) Density and absolute salinity of the Baltic Sea 2006–2009. *Ocean Science* 6: 3–24, <https://doi.org/10.5194/os-6-3-2010>
- Froese R, Pauly D (2017) FishBase. www.fishbase.org (accessed 12/06/2017)
- Gallardo B, Aldridge DC (2015) Is Great Britain heading for a Ponto-Caspian invasional meltdown? *Journal of applied Ecology* 52: 41–49, <https://doi.org/10.1111/1365-2664.12348>
- GBIF (2017) Global Biodiversity Information Facility. <https://www.gbif.org/> (accessed 9/25/2017)
- GLANSIS (2017) Great Lakes Aquatic Nonindigenous Species Information System. <https://www.glerl.noaa.gov/glansis/index.html> (accessed 9/25/2017)
- Glass WR, Mandrak NE, Koops MA (2014) Application of the ecologically significant species criteria to the aquatic community of the Bay of Quinte, Lake Ontario. DFO Canadian Science Advisory Secretariat, Research Document 2014/043, 32 pp
- Gollasch S, Haydar D, Minchin D, Wolff WJ, Reise K (2009) Introduced aquatic species of the North Sea coasts and adjacent brackish waters. In: Rilov G, Crooks JA (eds), Biological invasions in marine ecosystems: Ecological management, and geographic perspectives. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 507–528, https://doi.org/10.1007/978-3-540-79236-9_29
- Google (2017) Google scholar. <https://scholar.google.com> (accessed 12/13/2017)
- Grabowski M, Pegid V (2007) New data on the distribution and checklist of fresh- and brackish water Gammaridae, Pontogammaridae and Behningiellidae (Amphipoda) in Bulgaria. *Lauterbornia* 59: 53–62
- Gurevitch J, Koricheva J, Nakagawa S, Stewart G (2018) Meta-analysis and the science of research synthesis. *Nature* 555: 175–182, <https://doi.org/10.1038/nature25753>
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Hutchinson G (1960) On evolutionary euryhalinity. *American Journal of Science* 258: 98–103
- Jazdzewski K, Konopacka A (2002) Invasive Ponto-Caspian species in waters of the Vistula and Oder basins and the Southern Baltic Sea. In: Leppäkoski E, Gollasch S, Olenin S (eds), Invasive aquatic species of Europe. Distribution impacts and management. Springer Netherlands, Dordrecht, pp 384–398, https://doi.org/10.1007/978-94-015-9956-6_39
- Jazdzewski K, Konopacka A, Grabowski M (2005) Native and alien Malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth Century. *Oceanological and Hydrobiological Studies* 34 Suppl. 1: 175–193
- Kaluza P, Kölzsch A, Gastner MT, Blasius B (2010) The complex network of global cargo ship movement. *Journal of the Royal Society Interface* 7: 1093–1103, <https://doi.org/10.1098/rsif.2009.0495>
- Karatayev AY, Mastitsky SE, Burlakova LE, Olenin S (2008) Past, current, and future of the central European corridor for aquatic invasions in Belarus. *Biological Invasions* 10: 215–232, <https://doi.org/10.1007/s10530-007-9124-y>
- Keller RP, Drake JM, Drew MB, Lodge DM (2011) Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Diversity and Distributions* 17: 93–102, <https://doi.org/10.1111/j.1472-4642.2010.00696.x>
- Ketelaars HAM (2004) Range extensions of Ponto-Caspian aquatic invertebrates in Continental Europe. In: Dumont H, Shiganova TA, Niemann U (eds), Aquatic Invasions in the Black, Caspian, and Mediterranean Seas: The Ctenophores *Mnemiopsis leidyi* and *Beroe* in the Ponto-Caspian and other Aquatic Invasions. Springer Netherlands, Dordrecht, pp 209–236, https://doi.org/10.1007/1-4020-2152-6_13
- Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic - a sea of invaders. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1175–1188, <https://doi.org/10.1139/f02-089>
- Leuven RSEW, van der Velde G, Baijens I, Snijders J, van der Zwart C, Lenders HJR, Bij de Vaate A (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions* 11: 1989–2008, <https://doi.org/10.1007/s10530-009-9491-7>
- MacIsaac HJ, Robbins TC, Lewis MA (2002) Modelling ships’ ballast water as invasion threats to the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1245–1256, <https://doi.org/10.1139/f02-090>
- Milbrink G (1999) Distribution and dispersal capacity of the Ponto-Caspian tubificid oligochaete *Potamothrix heuschleri* (Bretscher, 1900) in Scandinavia. In: Healy BM, Reynoldson TB, Coates KA (eds), Aquatic Oligochaetes: Proceedings of the 7th International Symposium on Aquatic Oligochaetes held in Presque Isle, Maine, USA, 18–22 August 1997. Springer Netherlands, Dordrecht, pp 133–142, <https://doi.org/10.1023/A:1003752621110>
- Mills EL, Leach JH, Carlton JT, Secor CL (1993) Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19: 1–54, [https://doi.org/10.1016/S0380-1330\(93\)71197-1](https://doi.org/10.1016/S0380-1330(93)71197-1)
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6: 485–492, <https://doi.org/10.1890/070064>
- Mordukhai-Boltovskoi (1964) Caspian fauna beyond the Caspian Sea. *Internationale Revue der gesamten Hydrobiologie* 49: 139–176, <https://doi.org/10.1002/iroh.19640490105>
- OBIS (2017) Ocean Biogeographic Information System. <http://www.iobis.org/> (accessed 9/25/2017)
- O’Connor M, Hawkins C, Loomis DK (2008) A manual of previously recorded non-indigenous invasive and native transplanted animal species of the Laurentian Great Lakes and

- coastal United States. NOAA Technical Memorandum NOS NCCOS 77, 82 pp
- Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19: 18–24, <https://doi.org/10.1016/j.tree.2003.09.010>
- Olenin S (2002) Black Sea-Baltic Sea invasion corridors. Alien marine organisms introduced by ships. CIESM Workshop Monographs n°20, Istanbul, Turkey, pp 29–33
- Paavola M, Olenin S, Leppäkoski E (2005) Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine, Coastal and Shelf Science* 64: 738–750, <https://doi.org/10.1016/j.ecss.2005.03.021>
- Paiva F, Barco A, Chen Y, Mirzajani A, Chan FT, Lauringson V, Baltazar-Soares M, Zhan A, Bailey SA, Javidpour J, Briski E (2018) Is salinity an obstacle for biological invasions? *Global Change Biology* 24: 2708–2720, <https://doi.org/10.1111/gcb.14049>
- Panov VE, Rodionova NV, Bolshagin PV, Bychek EA (2007) Invasion biology of Ponto-Caspian onychopod cladocerans (Crustacea: Cladocera: Onychopoda). *Hydrobiologia* 590: 3–14, <https://doi.org/10.1007/s10750-007-0752-0>
- Pauli N-C, Paiva F, Briski E (2018) Are Ponto-Caspian species able to cross salinity barriers? A case study of the gammarid *Pontogammarus maeoticus*. *Ecology and Evolution* 8: 9817–9826, <https://doi.org/10.1002/ece3.4461>
- R Core Team (2017) R: A Language and Environment for Statistical Computing, vs. 3.3.3
- Reid DF, Orlova MI (2002) Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1144–1158, <https://doi.org/10.1139/f02-099>
- Reise K, Gollasch S, Wolff WJ (1998) Introduced marine species of the North Sea coasts. *Helgoländer Meeresuntersuchungen* 52: 219–234, <https://doi.org/10.1007/BF02908898>
- Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology and Evolution* 15: 62–65, [https://doi.org/10.1016/S0169-5347\(99\)01745-0](https://doi.org/10.1016/S0169-5347(99)01745-0)
- Science direct (2017) <http://www.sciencedirect.com/> (accessed 9/25/2017)
- Scopus (2017) <https://www.scopus.com/search/form.uri?display=basic> (accessed 9/25/2017)
- Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters* 16: 782–790, <https://doi.org/10.1111/ele.12111>
- Shiganova T (2010) Biotic homogenization of inland seas of the Ponto-Caspian. *Annual Review of Ecology Evolution, and Systematics* 41: 103–125, <https://doi.org/10.1146/annurev.ecolsys.110308.120148>
- Simberloff D (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 40: 81–102, <https://doi.org/10.1146/annurev.ecolsys.110308.120304>
- Smyth K, Elliott M (2016) Effects of changing salinity on the ecology of the marine environment. In: Solan M, Whiteley NM (eds), Stressors in the marine environment. Oxford University Press, Oxford, UK, pp 356, <https://doi.org/10.1093/acprof:oso/9780198718826.003.0009>
- Spencer DR, Hudson PL (2003) The Oligochaeta (Annelida, Clitellata) of the St. Lawrence Great Lakes Region: an update. *Journal of Great Lakes Research* 29: 89–104, [https://doi.org/10.1016/S0380-1330\(03\)70418-3](https://doi.org/10.1016/S0380-1330(03)70418-3)
- Spidle AP, Marsden JE, May B (1994) Identification of the Great Lakes quagga mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the basis of allozyme variation. *Canadian Journal of Fisheries and Aquatic Science* 51: 1485–1489, <https://doi.org/10.1139/f94-148>
- Venice System (1958) Symposium on the classification of brackish waters, Venice, April 8–14. *Archives Oceanography and Limnology* 11: 1–248
- Verdonschot PFM (2007) Spatial and temporal re-distribution of Naididae (tubificoid naids and naids s.str., Annelida, Clitellata) in Europe due to climate change: a review based on observational data. *Acta Hydrobiologica Sinica* 31: 116–138
- Web of Science (2017) https://apps.webofknowledge.com/WOS_GeneralSearch_input.do?product=WOS&search_mode=GeneralSearch&SID=W1XOJGzJGhPRk7Jv2s&preferencesSaved= (accessed 9/25/2017)
- World Ocean Atlas (2013) https://www.nodc.noaa.gov/OC5/woa13/woa13_data.html (accessed 9/25/2017)
- WoRMS (2017) World Register of Marine Species. <http://www.marine-species.org> (accessed 9/25/2017)
- Zenkevich LA (1963) Biology of the Seas of the U.S.S.R. London. George Allen and Unwin Ltd. Great Britain, 235 pp

Supplementary material

The following supplementary material is available for this article:

Table S1. Salinity ranges of the Ponto-Caspian non-native species that invaded the North and Baltic Seas and Great Lakes-St. Lawrence River region.

Appendix 1. References for Table S1.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Pauli_Briski_etal_SupplementaryMaterial.xlsx