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1 **Cold-tolerant traits that favour northwards movement and establishment of**
2 **Mediterranean and Ponto-Caspian alien aquatic invertebrates**

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10 **Abstract**

11 Over recent decades, many Mediterranean and Ponto-Caspian aquatic invertebrate species have
12 dispersed northwards and established as non-native species in colder regions. We hypothesized
13 that these species have cold-tolerant traits, which facilitate dispersal into colder climates.
14 Thanks to these traits, Southern European aquatic species are able to cross biogeographic
15 boundaries.

16 We downloaded the list of all alien invertebrate species that were fully aquatic (i.e. lacking
17 terrestrial adults) from the GRIIS database and picked out those Mediterranean and Ponto-
18 Caspian species that have undergone northwards range expansion. We identified traits that may
19 facilitate dispersal to colder climates including: small size; capacity for behavioural
20 thermoregulation; feeding habit (omnivorous, filter-feeders, food generalists); quiescence and
21 dormancy (or diapause); freezing avoidance (presence of cryoprotectants), tolerance to low
22 temperatures or eurythermicity, active dispersal and enhanced reproduction. We statistically
23 tested the null hypotheses that Mediterranean and Ponto-Caspian alien aquatic invertebrate
24 species that dispersed into the north have all of these traits. We used contingency tables
25 populated with raw frequency data with χ^2 - tests and assessed statistical significance at α of
26 0.05.

27 We identified 95 Mediterranean and Ponto-Caspian alien aquatic invertebrate species that have
28 shown northwards range extension, 10 (10%) of which were of Mediterranean origin and 85
29 (90%) of Ponto-Caspian origin. We found that this northwards dispersal from Southern Europe
30 is mainly limited to a few groups of aquatic invertebrates: small crustaceans, molluscs,
31 cnidarians and annelids. Ability to go to diapause, hibernation or resting period, temperature
32 tolerance and small size were the traits most commonly shared by these organisms.

33 We conclude that Mediterranean and Ponto-Caspian aquatic invertebrate species showing
34 northwards range expansion have cold-tolerant strategies. The traits analysed can favour the
35 establishment of the species.

36

37 **Key words:** alien species, climate change, cold environment, cold-tolerant survival strategies,
38 range expansion

39

40 **1. Introduction**

41 Dispersal ability and the ability to successfully establish in new areas influence the range
42 expansion of organisms (Lester et al. 2007). It is generally accepted that the dispersal process
43 comprises several successive stages, namely transport, introduction, establishment, and spread
44 (Briski et al. 2018). Propagule pressure is often a major predictor of the establishment of alien
45 organisms (Lockwood et al. 2005; Hayes and Barry 2008; Johnston et al. 2009; Briski et al.
46 2018).

47 In addition to the need to be transported from their original ecosystems to new ones, alien
48 species have to overcome several barriers (including manmade) to increase their range. A
49 species' intrinsic characteristics, for example being an r-strategist, may favour success, but it
50 has to cope with the full range of new local variability (e.g. climate, physico-chemical and biotic
51 factors) (e.g. Blackburn et al. 2011). Their success will depend on the match between their

52 physiological requirements and the ecological characteristics of the system being invaded.
53 Cold-tolerant traits and resilience strategies (e.g. freezing avoidance and capacity for
54 behavioural thermoregulation) facilitate northern expansion/establishment and are fundamental
55 to cold adaptation (e.g. Lencioni 2004; Wertheim et al. 2005; Gergs and Rothhaupt 2008;
56 Beermann et al. 2015).

57 A newly established species may have significant negative effects on the recipient
58 ecosystem, although the probability of a species turning truly invasive is up for debate (Jeschke
59 and Pyšek 2018), but is likely to exceed the well-known “tens rule” suggested by Williamson
60 (1996).

61 The climatic areas of Europe can be divided into six broad types: polar, boreal, temperate
62 continental, temperate transitional, temperate oceanic and Mediterranean (Schneider et al.
63 2013). The southern edges of Europe, in the Mediterranean climatic zone, being buffered by
64 the sea, are characterized by hot and dry summers and mild winters, and the annual temperature
65 range here is relatively small. Moving north, we encounter the temperate (divided into oceanic,
66 transitional and continental) and the boreal zones, followed by the polar zone. It is these
67 temperate and boreal zones that are of interest to this study, being the recipient areas for
68 migrants with cold-tolerant survival strategies from Southern Europe. These two climatic zones
69 are characterized by colder temperatures and greater temperature variation when compared to
70 the Mediterranean zone.

71 Herein, when we talk about the Ponto-Caspian region, we are referring to a large area that
72 includes the Black, Caspian and Azov Seas. In turn, the Mediterranean region includes the
73 Mediterranean Sea that is bounded by several European countries as well as by many countries
74 located in Africa and Asia. These two regions are considered extremely important as past and
75 future donor hotspots of aquatic invertebrate species moving to Northern Europe.

76 Previous studies have reported poleward movement of e.g. terrestrial plants (Groom
77 2013; Lenoir and Svenning 2015), birds (Bradley et al. 1999), butterflies (Wilson et al. 2005)
78 and fishes (Perry et al. 2005) in Europe. There are also papers addressing the effects of climate
79 changes in some invertebrate distribution ranges at local (e.g. Bruno et al. 2019), national (e.g.
80 Vittoz et al. 2013) and international **scales** (e.g. Heino et al. 2009). Many species retreated from
81 areas that became too warm and expanded into colder areas (Sunday et al. 2012). Odonata have
82 especially experienced significant northward expansion within Europe due to climate change
83 (e.g. Hickling et al. 2006; Heino et al. 2009; Grewe et al. 2013; Lancaster et al. 2015, 2017;
84 Dudaniec et al. 2018; Carbonell et al. 2021). However, northwards expansion has usually been
85 described in the context of native species (Urban 2020). Northwards movements are also
86 happening with alien aquatic invertebrates. However, this is relatively new area of research that
87 requires more attention.

88 Recently, many alien aquatic species of Mediterranean and Ponto-Caspian origin have
89 dispersed northwards and become established (e.g. Dobrzycka-Krahel and Medina-Villar 2020;
90 Kemp et al. 2020) as a result of human-mediated dispersal (HMD). One such species is the
91 isopod *Proasellus coxalis*, which increased its range in Northern Europe (including
92 Scandinavia) after spreading from the Mediterranean region using the network of waterways
93 followed by a probable jump as a stow-away with live fish bait (Spikkeland et al. 2013; Kemp
94 et al. 2020 and references therein). Many Ponto-Caspian species have also gradually dispersed
95 from the Black Sea–Caspian Sea region northwards over Europe (Milbrink and Timm 2001;
96 Dobrzycka-Krahel et al. 2013) using the dense network of man-made waterways, which offered
97 new migration pathways (Galil et al. 2007). Due to such a developed and complex systems of
98 waterways, aquatic alien species can reach the recipient ecosystems either through active
99 movement, drift, and / or as a result of shipping through ballast water discharge and hull fouling
100 (Bij de Vaate et al. 2002; Galil et al. 2007; Leuven et al. 2009; Keller et al. 2011; Gallardo and

101 Aldridge 2015; Kemp et al. 2020). Moreover, shipping routes around the world have given
102 frequent opportunities for numerous alien species to disperse (Carlton and Geller 1993). These
103 Southern European aquatic species are able to cross biogeographic boundaries. The species that
104 successfully establish are often those from environmentally heterogeneous ecosystems and
105 capable of habitat selection and avoidance of less favourable zones, such as the Mediterranean
106 shrimp *Atyaephyra desmarestii* (Vera-Vera et al. 2019).

107 There is no common set of characteristics or universal traits shared by all alien species.
108 Rather, different trait combinations can be successful, depending on the new home of the
109 species. Also, various trait combinations can prove beneficial and provide different ways to
110 establish successfully (Heger et al. 2015). Having said this, there are factors that favour some
111 species over others, such as an ability to survive long-distance dispersal (e.g. in ballast water
112 tanks) and to establish in an area with wide-ranging environmental conditions (Ricciardi and
113 Rasmussen 1998). In addition, r-selected species are usually seen as having a higher probability
114 of spreading than K-selected species. The failure of alien species to establish most often results
115 from their inability to overcome the “environmental resistance” of the receiving ecosystem,
116 caused by, for example, adverse temperature conditions and the biological pressures of the
117 native community.

118 Many recent studies have looked at species dispersal (e.g. Hickling et al. 2006; Travis
119 et al. 2013; Osland et al. 2021), but the species traits that help facilitate dispersal to different
120 climate zones are important and are worthy of a more detailed analysis. The focus of this paper
121 are the Mediterranean and Ponto-Caspian, alien, fully aquatic invertebrate species i.e. lacking
122 the terrestrial stages and long-distance flight capacity of, for example, the Odonata (May 2013).
123 These fully aquatic species have relatively poorly documented behaviour, adaptive significance
124 and ecology of migration, even though they show northwards expansion and are able to
125 establish populations in colder areas outside their original range. The aim of the present paper

126 is to examine the role of morphological, behavioural and physiological traits of these species
127 and how these underpin their **successful** northwards range expansion and establishment. We
128 discuss the processes and consequences of northwards range expansion, topics which have had
129 limited treatment in the literature thus far. There are some important questions concerning the
130 mechanisms and adaptations for determining the success of the northwards expansion of such
131 species: (1) what are the traits of species naturally living in warmer climate which facilitate
132 dispersal into colder climates? and (2) what kinds of cold-tolerant strategies prevail among
133 Mediterranean and Ponto-Caspian alien aquatic invertebrate species spreading into the north?

134

135 **2. Approach**

136 On 21 April of 2021, we downloaded the list of all aquatic invertebrate species from the
137 database GRIIS (2021) (Global Register of Introduced and Invasive Species) which presents
138 validated and verified national checklists of introduced (alien) and invasive alien species at the
139 country, territory and associated island level. GRIIS provides significant support for national
140 governments to identify and prioritise alien species, establishing both national and global
141 baselines (Pagad et al. 2018). We searched the origin of the species in the literature and in GBIF
142 (2021) (Global Biodiversity Information Facility) and identified aquatic Mediterranean and
143 Ponto-Caspian species that have undergone northwards expansion – that dispersed into the
144 north outside their original regions. Based on literature published since 1926, searching the
145 terms “cold tolerance traits”, “cold adaptation”, “freeze tolerance”, we looked for the biological
146 traits that have allowed the expansion of these species northwards, to colder areas (based on
147 Lencioni 2004, with modifications) (Table 1), using Science Direct (2021); Scopus (2021); Web
148 of Science (2021). We also used the DISPERSE database (Sarremejane et al. 2020) to search
149 dispersal and reproductive traits. We statistically tested the null hypothesis that the proportions
150 of each of the cold-tolerant traits in Mediterranean and Ponto-Caspian alien aquatic invertebrate

151 species each are fully distributed among Mediterranean and Ponto-Caspian species and we also
 152 tested affinity between these species from the two geographical regions. We used contingency
 153 tables populated with raw frequency data with χ^2 - tests and assessed statistical significance at
 154 α of 0.05. These analyses were carried out using the STATISTICA 13.1 PL program (StatSoft).
 155

156 **Table 1 Traits of aquatic invertebrate species that enable northwards range expansion and can**
 157 **tolerate cold conditions (based on Lencioni 2004, with modifications)**

Traits	Trait modalities	Score	Description of properties
<i>Morphological</i>			
Normal adult size	small (<1 cm) or small-medium (1-6 cm) (criteria based on Kun et al. 2019)	1	Body size determines metabolic rate and all organism processes (Rio and Karasov 2010). Reduction in size has several advantages: a lower requirement for food in habitats where it is limited; a faster growth rate and development; greater availability of sheltered microhabitats for protection during winter (Lencioni 2004). Small sized animals can warm up quickly to ambient temperature. They can also live in large groups for protection, e.g. gammarids and isopods live in aggregations for long time periods (Wertheim et al. 2005; Beermann et al. 2015).
	medium-large (1-6 cm) or large (>10 cm) (criteria based on Kun et al. 2019)	0	
<i>Behavioural</i>			
Capacity for behavioural thermoregulation		1	Migration to unfrozen habitats by aquatic invertebrates helps to avoid the hazards of freezing (Lencioni 2004). Habitat selection includes the ability to avoid iced/cold habitats, e.g. migration of species to other water columns, choosing a refuge (e.g. vegetation, rocks, sand, and backwater zones). Escape is a normal response of a mobile organism to stressful conditions (e.g. in the case of crustaceans). In contrast, non-mobile species cannot escape.
No capacity for behavioural thermoregulation		0	

Feeding habit (omnivorous, filter-feeders, food generalist organisms)	1	Adaptation to changing environmental temperatures through animals varying diet during temporal changes in food availability. Utilization of organic matter is also beneficial (Gergs and Rothhaupt 2008).
Food specialists	0	
<hr/> <i>Physiological and biochemical</i> <hr/>		
Diapause or resting period	1	Quiescence and dormancy (or diapause) are traits having a strong reduction of the metabolic rate helping to overcome adverse conditions (Lencioni 2004), e.g. hibernation and aestivation in molluscs (Lal Hora 1926), and diapause in crustaceans (Hairston and Cáceres 1996), cocoon production in annelids (Rossi et al. 2016).
No mechanisms of diapause or resting period	0	
Freezing avoidance: presence of cryoprotectants	1	Production of cryoprotectants at lower temperatures decreases metabolism (Gismondi et al. 2012). Cold tolerance is linked to osmoregulatory function (Gerber and Overgaard 2018). Content of different organic substances and ions may help in cold tolerance, including raising the osmotic concentrations of a body.
No or limited ability for production of cryoprotectants	0	
Tolerance of low temperatures or eurythermicity	1	Freezing tolerance and adaptation to low temperatures are crucial (Lencioni 2004).
No tolerance of low temperatures or no eurythermicity	0	
Dispersal aquatic active (from the DISPERSE database)	1	Dispersal as the unidirectional movement of individuals from one location to another (Bohonak and Jenkins 2003).
Aquatic passive (from the DISPERSE database)	0	

Reproduction

Reproduction means sexual and asexual production of offspring providing for the continued existence of a species (Britannica 2022).

Potential number of reproductive cycles per year 1 or >1 (from the DISPERSE database)

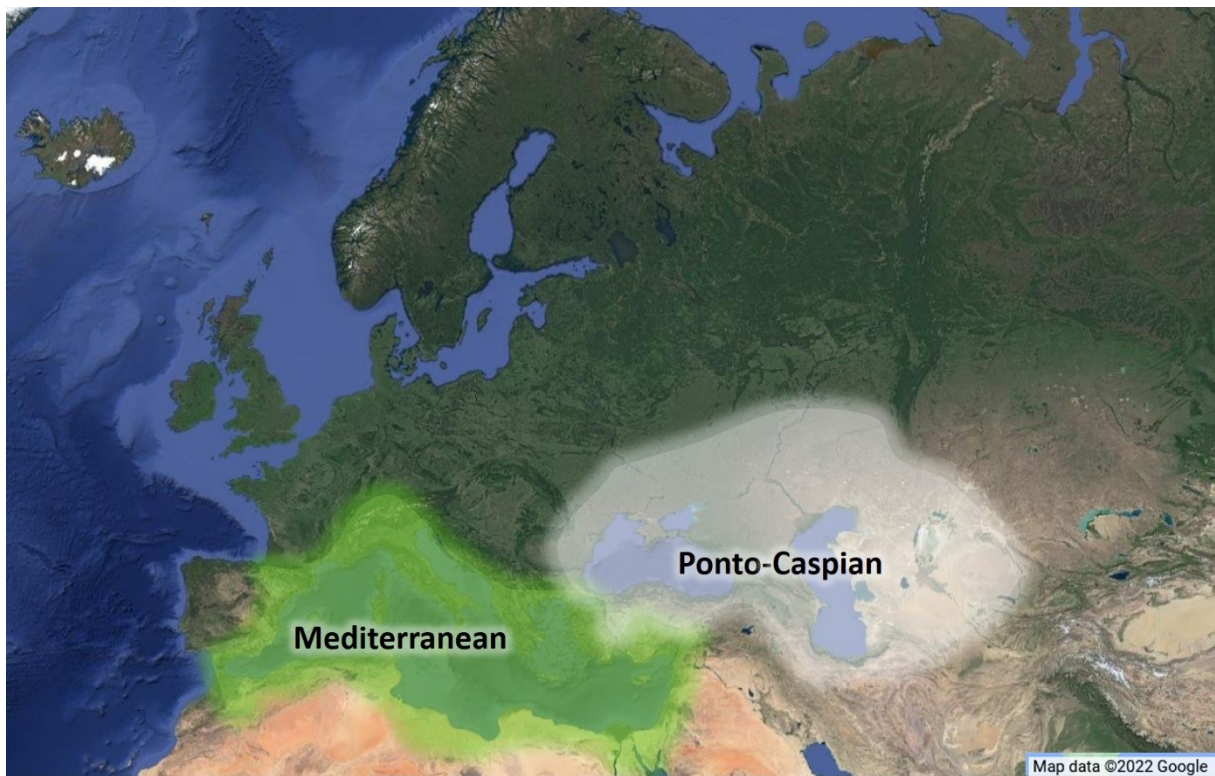
1

Potential number of reproductive cycles per year <1 (from the DISPERSE database)

0

158

159



160

161 **Fig. 1 Location of the Mediterranean and Ponto-Caspian regions**

162 **3. Results**

163

164 **3.1. Mediterranean and Ponto-Caspian alien aquatic invertebrate species characterised**
165 **by northwards expansion**

166 The biogeographical regions highlighted here which are donors of aquatic invertebrates (Fig.
167 1) are situated in relatively warm climate zones. The percentage share of different groups of
168 cold-tolerant Mediterranean and Ponto-Caspian alien aquatic invertebrate species expanding
169 northwards into colder areas, are presented in Fig. 2. Mediterranean and Ponto-Caspian alien
170 aquatic invertebrate species characterized by northwards dispersal are given in Tables 2 and 3
171 (small crustaceans, molluscs, cnidarians and annelids).

172

173 **3.2. Mediterranean and Ponto-Caspian alien aquatic invertebrate species are well adapted**
174 **to life in the northern latitudes**

175 The Mediterranean species examined here (Table 2) were all characterized by the ability to go
176 into diapause, resting stage or hibernation, had feeding habits which included omnivorous,
177 filter-feeding or food generalist strategies, presence of cryoprotectants and high reproductive
178 capacity. Small size, temperature tolerance and capacity for behavioural thermoregulation were
179 observed in 9 (90%) of these Mediterranean species. Active dispersal was observed in 7 (70%
180 of them). More details are given in Supplementary material.

181 All of the included Ponto-Caspian species (Table 3) had small size, temperature tolerance and
182 were able to go into diapause, hibernation or resting period. These cold-tolerant strategies
183 prevail among the Ponto-Caspian species and facilitate their dispersal into the north. 77 Ponto-
184 Caspian species (90.58%) were omnivorous, filter-feeders or food generalists. 72 (84.70%) of
185 Ponto-Caspian species were able to produce cryoprotectants. 72 species (84.70%) had the

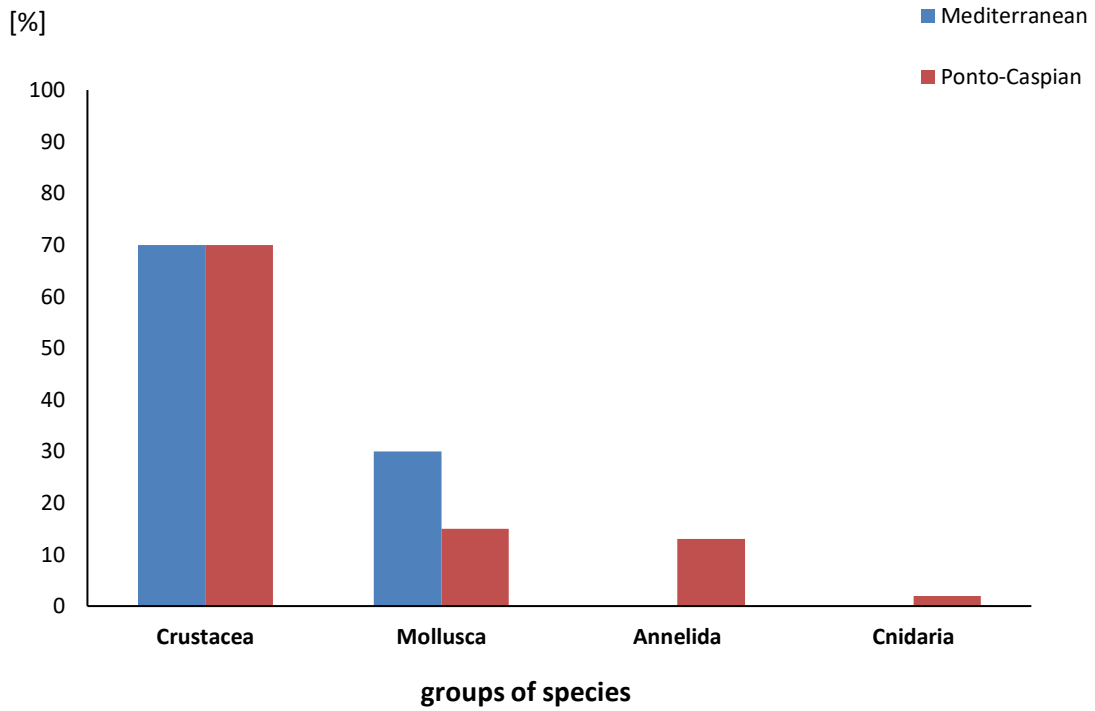
186 ability to select habitat. Active dispersal was observed in 76 species (89.41%) of Ponto-Caspian
187 species and enhanced reproduction in 82 species (96.47%).

188 Trait combinations within the pool of all species, facilitating northwards expansion were: ability
189 to go to diapause, hibernation or resting period (100%), wide temperature tolerance (98.95%)
190 and small size (98.95%). And also important were: enhanced reproduction (97.89%), generalist
191 feeding habit (93.44%), dispersal (88.42%), presence of cryoprotectants (86.32%) and habitat
192 selection (85.26%).

193 The distribution of traits among Mediterranean and Ponto-Caspian species is presented in Fig.
194 3.

195 There were no significant statistical differences between the frequency of traits among tested
196 species and expected frequency (100%), so we assumed the null hypothesis that Mediterranean
197 and Ponto-Caspian aquatic invertebrate species dispersing into the north have cold-tolerant
198 traits. We obtained for Mediterranean species $\chi^2=12.00$, $df=7$, $p=0.100563$ and for Ponto-
199 Caspian species $\chi^2=6.813371$, $df=7$, $p=0.448569$ at α of 0.05.

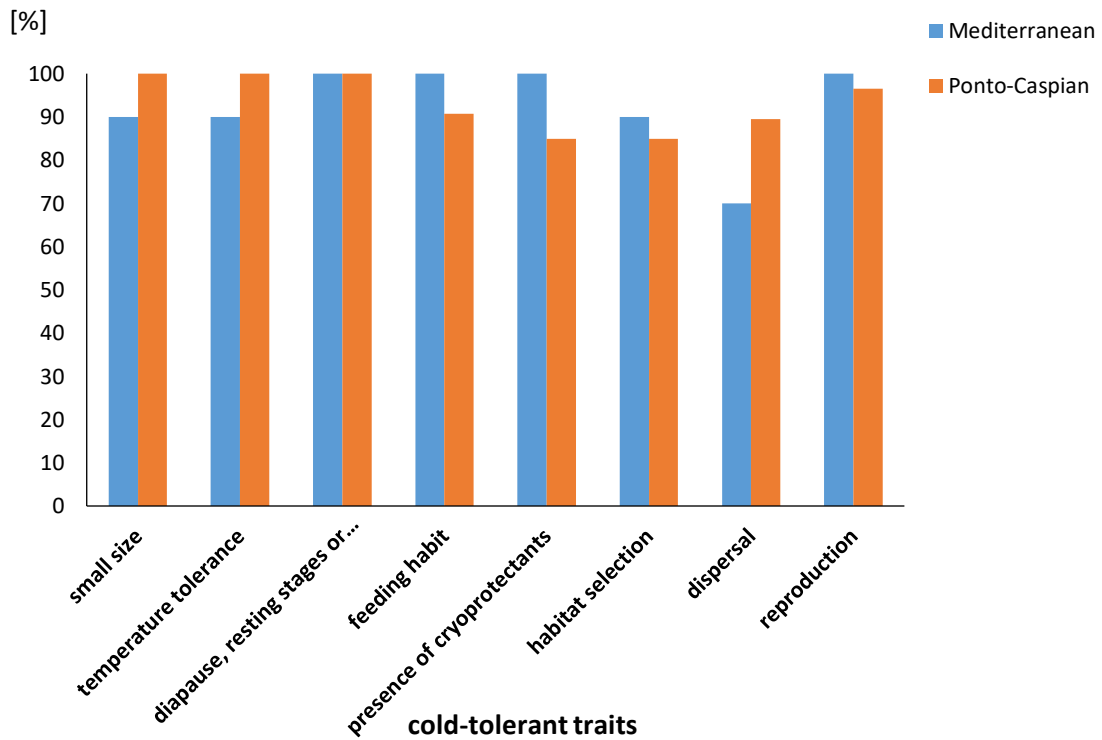
200 We statistically tested affinity between the Mediterranean and Ponto-Caspian species at α of
201 0.05 which was statistically not significant (we obtained $\chi^2=10.41574$, $df=7$, $p=0.166217$).



202

203 **Fig. 2 Percentage share of different groups of cold-tolerant Mediterranean and Ponto-**
 204 **Caspian species that are expanding northwards**

205



206

207 **Fig. 3 Distribution of cold-tolerant traits among Mediterranean and Ponto-Caspian**
 208 **species that disperse into the north**

209 **Table 2 Mediterranean aquatic invertebrate species that are characterized by northwards extension and can**
 210 **tolerate cold conditions (based on GRIIS, WORMS and literature search)**
 211

Species	Taxonomic position (Order)	Northern range	Impact	
<i>Aporrhais pespelecani</i> (Linnaeus, 1758)	Littorinimorpha	F, N, Sp, U	No	212 213 214
<i>Atyaephyra desmarestii</i> (Millet, 1831)	Decapoda	A, B, C, CR, F, G, Gr, I, L, Ne, P, Po, Sp, Sw	No	215 216
<i>Brachynotus sexdentatus</i> (Risso, 1827)	Decapoda	F, Sp, UK	No	217 218
<i>Echinogammarus berilloni</i> (Catta, 1878)	Amphipoda	B, F, G, L, Ne, Sp, Sw	No	219 220
<i>Gammarus pulex</i> (Linnaeus, 1758)	Amphipoda	B, F, G, Ir, Ne, S, UK	Yes (Ir)	221 222
<i>Gammarus roeselii</i> Gervais, 1835	Amphipoda	A, B, F, G, I, Ne, P	No	222 223
<i>Mytilus galloprovincialis</i> Lamarck, 1819	Mytilidae	Ca, F, Ir, UK, US	No	
<i>Proasellus coxalis</i> (Dollfus, 1892)	Isopoda	B, CR, D, F, G, I, N, Ne, S, Sw	No	
<i>Proasellus meridianus</i> * (Racovitza, 1919)	Isopoda	B, D, F, G, I, N, Ne, Po, S, Sp, Sw	No	
<i>Tritia corniculum</i> (Olivi, 1792)	Neogastropoda	F, I, Po, Sp	No	

224
 225 A-Austria, B-Belgium, Ca-Canada, C-Croatia, CR-Czech Republic, D-Denmark, F-France, G-Germany, Gr-Greece, I-
 226 Italy, Ir-Ireland, L-Luxemburg, Ne-Netherlands, N-Norway, P-Poland, Po-Portugal, Sp-Spain, S-Sweden, Sw-
 227 Switzerland, UK-United Kingdom, US-United States, U-Ukraine.

228 * *Proasellus meridianus* is thought to originate in western rather than southern Europe (and be spreading east and north),
 229 but could still be considered as a Mediterranean species as its supposed native range includes Portugal and Spain.
 230

231
232
233
234

Table 3 Ponto-Caspian aquatic invertebrate species that are characterized by northwards extension and can tolerate cold conditions (based on GRIIS, WORMS and literature search)

Species	Taxonomic position (Order)	Northern range	Impact
<i>Abra segmentum</i> (Récluz, 1843)	Cardiida	Az	No
<i>Amathillina cristata</i> G.O.Sars, 1894	Amphipoda	Hu, U	Yes (U)
<i>Amathillina pusilla</i> G.O.Sars, 1896	Amphipoda	U	Yes (U)
<i>Blackfordia virginica</i> Mayer, 1910	Leptothecata	Bu, Fr, Ne, Po, Ro, U, US	Yes (Ro)
<i>Cardiophilus marisnigrae</i> Miloslawskaya, 1931	Amphipoda	Hu	No
<i>Caspiobdella fadejewi</i> (Epshtein, 1961)	Rhynchobdellida	A, B, Fr, G, Ne, P, R, Sw	No
<i>Caspiocuma campylaspoides</i> (G.O. Sars, 1897)	Cumacea	Hu, Mo	No
<i>Cercopagis pengoi</i> (Ostroumov, 1891)	Onychopoda	Ca, D, E, G, La, Li, P, R, RK, Ro, S, US	Yes (La, Li, P, R)
<i>Chaetogammarus placidus</i> (G.O.Sars, 1896)	Amphipoda	Hu	No
<i>Chaetogammarus warpachowskyi</i> Sars, 1897	Amphipoda	Hu, Li, U, UK	No
<i>Chelicorophium chelicorne</i> (G.O.Sars, 1895)	Amphipoda	Hu, U, UK	Yes (U)
<i>Chelicorophium curvispinum</i> (G.O. Sars, 1895)	Amphipoda	A, B, Be, BH, C, CR, E, Fr, G, Hu, I, L, La, Li, Ne, P, R, Se, Slo, Sw, U, UK	Yes (B, BH, G, Hu, Ne, P, R, Se, Sw, U)
<i>Chelicorophium maeoticum</i> (Sowinsky, 1898)	Amphipoda	Hu, Mo, U	Yes (U)
<i>Chelicorophium mucronatum</i> (G.O.Sars, 1895)	Amphipoda	Hu, U	Yes (U)
<i>Chelicorophium nobile</i> (G.O.Sars, 1895)	Amphipoda	Hu, U	Yes (U)
<i>Chelicorophium robustum</i> (G.O.Sars, 1895)	Amphipoda	B, Fr, G, Hu, Ne, Slo, U	Yes (Hu)

<i>Chelicorophium sowinskyi</i> (Martynov, 1924)	Amphipoda	Hu, Ne, R	Yes (Hu)
<i>Compactogammarus compactus</i> (G.O.Sars, 1895)	Amphipoda	Hu	No
<i>Cordylophora caspia</i> (Pallas, 1771)	Anthoathecata	A, Be, D, F, G, L, Li, N, P, Pa, Po, R, S, Sp, UK	Yes (Li, P, Po, R, UK)
<i>Cornigerius bicornis</i> (Zernov, 1901)	Onychopoda	U	No
<i>Cornigerius lacustris</i> (Spandl, 1923)	Onychopoda	U	No
<i>Cornigerius maeoticus</i> (Pengo, 1879)	Onychopoda	R, S, U	No
<i>Dikerogammarus bispinosus</i> Martynov, 1925	Amphipoda	A, C, Fr, Hu, Slo	Yes (Hu)
<i>Dikerogammarus haemobaphes</i> (Eichwald, 1841)	Amphipoda	A, B, Be, C, Fr, G, Hu, P, R, Slo, Sw, UK	Yes (Hu, UK)
<i>Dikerogammarus villosus</i> (Sowinsky, 1894)	Amphipoda	A, B, Be, C, CR, F, Fr, G, Hu, P, R, Se, Slo, Sp, Sw, UK	Yes (B, F, G, Hu, P, Se, Sw, UK)
<i>Dreissena polymorpha</i> (Pallas, 1771)	Myida	A, B, Be, Bu, C, Ca, CR, D, E, F, Fr, G, Gr, Hu, I, La, Li, Ne, P, Po, R, RK, S, Se, Sl, Sp, Sw, U, UK, US	Yes (B, Bu, C, Ca, CR, D, F, Fr, G, Hu, I, La, Li, Ne, P, Se, Sl, Sp, UK, US)
<i>Dreissena rostriformis</i> (Deshayes, 1838)	Myida	Fr	No
<i>Dreissena rostriformis bugensis</i> Andrusov 1897	Myida	Bu, Ca, G, Hu, Mo, Ne, Po, R, RM, Ro, S, U, UK, US	Yes (Bu, Ca, Hu, Mo, Ne, Ro, S, U, UK)
<i>Echinogammarus ischnus</i> syn. <i>Chaetogammarus ichnus</i> (Stebbing, 1899)	Amphipoda	A, B, Fr, G, Hu, Li, Ne, P, Slo, Sw, U, UK	Yes (Hu)
<i>Echinogammarus trichiatus</i> (Martynov, 1932)	Amphipoda	A, Be, G, Hu, Ne, P, Slo, Sw	Yes (Hu, Ne)
<i>Echinogammarus warpachowskyi</i> (G.O.Sars, 1894)	Amphipoda	S	Yes (S)
<i>Ectinosoma abrau</i> (Krichagin, 1877)	Harpacticoida	U	No
<i>Euxinia sarsi</i> (Sowinsky, 1898)	Amphipoda	Hu	No
<i>Euxinipyrgula lincta</i>	Littorinimorpha	U	No

(Milaschewitsch, 1908)			
<i>Euxinia weidemanni</i> (G.O.Sars, 1896)	Amphipoda	Hu	No
<i>Evadne anonyx</i> G.O. Sars, 1897	Onychopoda	F, P, S	No
<i>Hemimysis anomala</i> G.O. Sars, 1907	Mysida	A, Be, C, F, Fr, G, Hu, I, Li, P, RM, S, Se, Slo, Sw, U, UK	Yes (Hu, I, Li, Sw, UK)
<i>Heterocope appendiculata</i> Sars G.O., 1863	Calanoida	U	No
<i>Heterocope caspia</i> Sars G.O., 1897	Calanoida	U	No
<i>Hypania invalida</i> (Grube, 1860)	Terebellida	A, B, Be, G, P, R, Se, Sw, U, UK	Yes (G, UK)
<i>Hypaniola kowalewskii</i> (Grimm in Annenkova, 1927)	Terebellida	R, U	No
<i>Hypanis colorata</i> (Eichwald, 1829)	Cardiida	U	No
<i>Hypanis fragilis</i> (Milashevitch, 1908)	Cardiida	U	No
<i>Hypanis glabra</i> (Ostroumoff, 1905)	Cardiida	U	Yes (U)
<i>Hypanis pontica</i> Eichwald, 1838	Cardiida	U	No
<i>Iphigenella acanthopoda</i> G.O.Sars, 1896	Amphipoda	Hu	No
<i>Isochaetides michaelseni</i> (Lastockin, 1937)	Tubificida	E	No
<i>Jaera istri</i> Veuille, 1979	Isopoda	A, B, C, Fr, G, Ne, P, Sw	No
<i>Jaera sarsi</i> Valkanov, 1936	Isopoda	Fr, Hu, P, Slo, U	Yes (Hu)
<i>Katamysis warpachowskyi</i> G. O. Sars, 1893	Mysida	A, Cr, Hu, RM, Se, Slo, U	Yes (Hu)
<i>Kuzmelina kusnezowi</i> (Sowinsky, 1894)	Amphipoda	U	Yes (U)
<i>Lanceogammarus andrussowi</i> (G.O.Sars, 1896)	Amphipoda	Hu, U	Yes (U)
<i>Limnomysis benedeni</i>	Mysida	A, B, Be, C, Fr, G, Hu, Li, Slo, Sw, Uz	Yes

Czerniavsky, 1882			(B, Hu, Li)
<i>Lithoglyphus naticoides</i> (C.Pfeiffer, 1828)	Littorinimorpha	B, Be, Fr, G, Hu, Li, P, R, S, Se, U	Yes (B, Hu, Se)
<i>Niphargogammarus intermedius</i> (Carausu, 1943)	Amphipoda	Hu	No
<i>Niphargoides corpulentus</i> G.O.Sars, 1895	Amphipoda	Hu	No
<i>Niphargus hrabei</i> S.Karaman, 1932	Amphipoda	A	No
<i>Obesogammarus crassus</i> (Sars G.O., 1894)	Amphipoda	B, G, Li, P, R	Yes (B, Li)
<i>Obesogammarus obesus</i> (G.O. Sars, 1894)	Amphipoda	A, B, C, G, Hu, Ne, R, Slo, U	Yes (Hu, U)
<i>Paramysis lacustris</i> (Czerniavsky, 1882)	Mysida	Li, R	Yes (Li)
<i>Paraniphargoides motasi</i> (Carausu, 1943)	Amphipoda	Hu	No
<i>Pontogammarus abbreviatus</i> (Sars G.O., 1894)	Amphipoda	R	No
<i>Pontogammarus aestuarius</i> (Derzhavin, 1924)	Amphipoda	Hu	No
<i>Pontogammarus borceae</i> Carausu, 1943	Amphipoda	Hu	No
<i>Pontogammarus maeoticus</i> (Sovinskij, 1894)	Amphipoda	Hu, U	Yes (U)
<i>Pontogammarus robustoides</i> (Sars, 1894)	Amphipoda	B, F, G, Li, P, R	Yes (Li, P, R)
<i>Potamothenrix bavaricus</i> (Oschmann, 1913)	Tubificida	B	No
<i>Potamothenrix bedoti</i> (Piguet, 1913)	Tubificida	B, F	No
<i>Potamothenrix hammoniensis</i> (Michaelson, 1901)	Tubificida	P	No
<i>Potamothenrix heuscheri</i> (Bretscher, 1900)	Tubificida	F, R, S	No
<i>Potamothenrix moldaviensis</i> Vejdovský & Mrázek, 1903	Tubificida	B, I, P, S	No
<i>Potamothenrix vej dovskyi</i>	Tubificida	Be, I, P, R, S	No

(Hrabe, 1941)			
<i>Psammoryctides moravicus</i> (Hrabe, 1934)	Tubificida,	Be, E, P	No
<i>Shablogammarus chablensis</i> (Carausu, 1943)	Amphipoda	Hu	No
<i>Shablogammarus subnudus</i> (G.O.Sars, 1896)	Amphipoda	Hu, U	Yes (U)
<i>Stenogammarus carausui</i> Derzhavin & Pjatakova, 1962	Amphipoda	Hu, U	No
<i>Stenogammarus compressus</i> (Sars G.O., 1894)	Amphipoda	Hu	No
<i>Stenogammarus macrurus</i> (Sars, 1894)	Amphipoda	Hu	No
<i>Stenogammarus similis</i> (Sars, 1894)	Amphipoda	Hu	No
<i>Tubifex newaensis</i> (Michaelsen, 1903)	Tubificida	B, E, U	No
<i>Tubificoides diazi</i> Brinkhurst & Baker, 1979	Tubificida	US	Yes (US)
<i>Turcogammarus aralensis</i> (Uljanin, 1875)	Amphipoda	U	Yes (U)
<i>Uroniphargoides spinicaudatus</i> (Carausu, 1943)	Amphipoda	Hu	No
<i>Viviparus acerosus</i> (Bourguignat, 1862)	Architaenioglossa	G	No
<i>Yogmelina limana</i> Karaman & Barnard, 1979	Amphipoda	Hu	No

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A-Austria, Az-Azerbaijan, B-Belarus, Be-Belgium, BH-Bosnia and Hercegovina, Bu-Bulgaria, Ca-Canada, C-Croatia, CR-Czech Republic, D-Denmark, E-Estonia, F-Finland, Fr-France, G-Germany, Gr-Greece, Hu-Hungary, Ir-Ireland, I-Italy, La-Latvia, Li-Lithuania, L-Luxemburg, Mo-Moldova, N- Norway, Ne-Netherlands, P-Poland, Po-Portugal, RK-Republic of Korea, Ro-Romania, R-Russian Federation, Se-Serbia, Slo-Slovakia, Sl-Slovenia, Sp-Spain, S-Sweden, Sw-Switzerland, UK-United Kingdom, US-United States, U-Ukraine, Uz-Uzbekistan.

241 4. Discussion

242 4.1. Mediterranean species

243 Currently, Mediterranean alien aquatic invertebrate species are relatively rare in
244 introduced areas and are classed as “no impact” rather than invasive (Table 2). We examined
245 10 Mediterranean species that are on the way to the north and found that seven species (70%)
246 are crustaceans and three species (30%) are molluscs.

247 *Atyaephyra desmarestii* is not considered a threat to native fauna and inhabits rivers,
248 canals, lakes, and impoundments (Grabowski et al. 2005). The amphipod *Gammarus roeselii*
249 occurs in rivers of slow current, lakes, and artificial canals but does not exhibit a high invasive
250 potential (Jażdżewski and Roux 1988; Jażdżewski and Konopacka 1995; Grabowski et al.
251 2007). The decapod *Brachynotus sexdentatus* lives on substrates of mud and sand (Ateş 1999).
252 *Echinogammarus berilloni* is currently observed in the running waters of Central Europe,
253 thanks to the dense network of waterways (Pinkster 1993; Schmidt-Drewello et al. 2016).
254 *Gammarus pulex* is common e.g. in a Rhine tributary in Germany (Kley and Maier 2015), and
255 in smaller rivers in France (Chovet and Lecureuil 1994; Piscart et al. 2007). *Proasellus coxalis*
256 inhabits both freshwater (e.g. in Rhine River, Germany) and brackish water (e.g. in the German
257 part of the Szczecin Lagoon) (Wittfoth and Zettler 2013). *Proasellus meridianus* is spreading
258 along rivers and inhabits slow-flowing waters (Von Vaupel Klein and Schram 2000; Gherardi
259 2007). Both *Proasellus* species have also made an overseas hop to Scandinavia (Kemp et al.
260 2020). The gastropod *Aporrhais pespelecani* lives on the surface of the mud (Perron 1978). The
261 Mediterranean mussel *Mytilus galloprovincialis* spreads to new locations through ballast water
262 and through its use in aquaculture (GISD 2021). *Tritia corniculum* is a small gastropod species
263 spreading most probably via shipping (Crocetta et al. 2020).

264 Some of the above mentioned species (e.g. *G. roeselii* and *P. coxalis*) are present in the
265 Baltic Sea estuaries (Meßner and Zettler 2018).

266 **4.2. Ponto-Caspian species**

267 We identified 85 species of Ponto-Caspian origin on the way to the north (Table 3). Ponto-
268 Caspian alien aquatic invertebrate species in introduced areas are often invasive newcomers
269 with known “impacts” confirmed in many places (GRIIS 2021). Among them 60 (70%) are
270 crustaceans, 11 (13%) molluscs, 13 (15%) annelids, and 2 (2%) cnidarians (Fig. 2). The Ponto-
271 Caspian region is home to a spectacular diversity of crustaceans (Cristescu et al. 2003), which
272 are common newcomers worldwide (e.g. Bielecka et al. 2014; Dobrzycka-Kraheil and Graca
273 2018; Pauli and Briski 2018; GLANSIS 2021). Ponto-Caspian crustacean species currently
274 inhabit near shore zones of freshwater and / or brackish ecosystems. Ponto-Caspian molluscs
275 are also common worldwide (Pauli and Briski 2018; GLANSIS 2021), especially *Dreissena*
276 *polymorpha*.

277

278 **4.3. Temperature as an important environmental factor for the establishment of species** 279 **in new areas**

280 Temperature is probably the most important environmental factor influencing the performance
281 of species, especially for ectotherms which are the majority of species on Earth (Jiménez-
282 Valverde and Lobo 2011). Aquatic invertebrates are poikilotherms, i.e., animals lacking the
283 power of thermal regulation. Thus, the central temperature of these animals passively undergoes
284 the thermic fluctuations in the environment. It is therefore unsurprising that tolerance to wide
285 temperature variations tends to be a characteristic of successfully established alien species
286 (Grabowski et al. 2007).

287 Temperature is very important from an ecological point of view and all organisms require a
288 certain temperature or range of temperatures to carry on their metabolic processes. Low
289 temperatures decrease the rate of biochemical reactions and consequently reduce the organisms'
290 metabolism (Boscolo-Galazzo et al. 2018). Very high temperatures denature enzymes and

291 destroy their activity (Ahnoff et al. 2015). Somewhere between **these** extremes, organisms will
292 find their optimal temperatures for living.

293 The wide thermal preferences and high resistance to extreme temperatures of Mediterranean
294 and Ponto-Caspian species listed in Tables 2 and 3 (Kititsyna 1980; Jażdżewski and Konopacka
295 1990; Iwanyzki and McCauley 1992; Pinkster 1993; Aladin 1995; Spidle et al. 1995;
296 Gorokhova et al. 2000; Pöckl et al. 2003; Wijnhoven et al. 2003; Romanenko et al. 2014) will
297 have helped their establishment.

298 In the coastal waters in northern latitudes, water temperatures range between 0°C in winter and
299 >20°C in summer. Consequently, most of the species, listed in Tables 2 and 3, would have a
300 potentially very wide geographic distribution if temperature was the only factor limiting their
301 occurrence.

302 Ecophysiological constraints prevent species from occupying the entirety of abiotic
303 gradients present in nature and restrict them to just a portion lying between their tolerance
304 limits, beyond which they cannot survive (Arribas et al. 2019). These environmental restrictions
305 are the first factor that demarcates the geographic regions that a species can inhabit. Alien
306 species are more able to survive if they are introduced to areas with climatic conditions that are
307 similar to those in their native range, with temperature being a key factor for survival, growth
308 and reproduction (Walther et al. 2009). Climatic warming will extend the potential ranges of
309 many species, accelerating the establishment process and will favour species moving from
310 southern to northern latitudes in Europe (Dobrzycka-Kraheil and Medina-Villar 2020), in search
311 of more favorable thermal conditions compared with those existing in the original area.

312

313 **4.4. Preadaptation in the native area**

314 Although the current climate of Northern Europe may appear to be a barrier, many species
315 originating from Southern Europe are primed for range expansion, due to preadaptation in their

316 native, original areas. For a species to increase its range, it must arrive in a new location and
317 survive to reproduce. Having a wide range of environmental tolerances helps a species to both
318 survive the journey and thrive on arrival. It appears that, due to the complex geological history
319 of the Mediterranean and Ponto-Caspian areas, much of their aquatic fauna is tolerant to a wider
320 than usual range of environmental parameters and thereby “pre-adapted” to potential new
321 environments. The Mediterranean Sea has a complex paleogeography and heterogeneous
322 environment, making it particularly diverse on the world-scale and with a high proportion of
323 endemic species (Bianchi and Morri 2000; Reid and Orlova 2002; Coll et al. 2010; Fanelli et
324 al. 2021). It comprises just 0.32% of the volume of the world’s oceans but contains between 4
325 and 18% of all macroscopic marine species of which almost 25% are endemic (Bianchi and
326 Morri 2000). The Mediterranean basin, itself made up of different seas, each with their own
327 characteristics, has had, over millions of years, changing connections and temperature and
328 species arrival from many different bioregions, leading to its current high diversity (Bianchi
329 and Morri 2000; WWF/IUCN 2004; Patarnello et al. 2007).

330 For example, the success of *A. desmarestii* in establishing populations in new aquatic
331 environments is very likely due to its euryecious and eurythermic characteristics as mentioned
332 by several researchers (0-21°C, Redeke 1936; 4-30°C, Packa Tchissambou 1979; 5-30°C,
333 Descouturelle 1980; 6.3-24.8°C, Fidalgo 1985; 2-27°C, Meurisse-Génin et al. 1985; 5-34°C,
334 Ferreira et al. 2002). Over millions of years, the Ponto-Caspian area has also been home to a
335 shifting complex of lakes and seas, varying both spatially and temporally, in terms of
336 parameters such as salinity, temperature, volume, and connectedness. Indeed, species of Ponto-
337 Caspian origin are highly over-represented in the list of non-native aquatic species already
338 successfully established in North America and Northern Europe (Reid and Orlova 2002). Cold-
339 tolerant survival strategies noted in some Mediterranean and Ponto-Caspian species include
340 morphological, behavioural, physiological and biochemical adaptations. Physiological studies

341 of Ponto-Caspian taxa confirm their ability to survive under variable conditions. For example,
342 Maazouzi et al. (2011) compared the temperature tolerance of *Dikerogammarus villosus* and *G.*
343 *pulex* and found that although *G. pulex* could actually survive at higher temperatures and across
344 a wider temperature range (5) 10-20 (30) °C, compared to 5-15 (25) °C (numbers in brackets =
345 extreme limits), *D. villosus* had a higher body glycogen content and lower basal metabolic rate.
346 This may be interpreted as an adaptation to unpredictable and challenging environments and
347 given that Maazouzi et al. (2011) found that *D. villosus* was more comfortable than *G. pulex* at
348 lower temperatures, the northwards spread of *D. villosus* is likely to continue apace.
349 Of nearly 100 alien aquatic invertebrate species that have shown northwards range extension,
350 the vast majority (90%) were Ponto-Caspian in origin rather than Mediterranean. This could be
351 because the Mediterranean region differs more from northern regions than the Ponto-Caspian
352 area and / or because the Ponto-Caspian area has a greater diversity of potential migratory
353 species.

354

355 **4.5. Morphological traits**

356 Morphological adaptations may include reduction in size. Size is a centrally important
357 trait which influences all aspects of an organism's physiology and relation to its environment.
358 Smaller organisms need less food than larger ones so small size is beneficial in environments
359 where food is limited (Lencioni 2004). Temperature affects metabolic rate and reduction in size
360 can be energetically beneficial to organisms. Animals of small size are able to warm up quickly
361 to ambient temperature. They may also gain protection by living in large groups, e.g. gammarids
362 and isopods live in aggregations for long time periods (e.g. Wertheim et al. 2005; Beermann et
363 al. 2015; How Animals Survive in Cold Conditions. Science of the Cold 2021). Smaller
364 organisms can grow faster, reproduce earlier and more quickly, which may enhance success in
365 colder climates. The high reproductive performance may help to explain the high impact of

366 some new species in invaded ecosystems as well. The potential for reproduction at relatively
367 low temperatures increases the probability of species survival. Some non-native invasive
368 species begin to reproduce at smaller sizes, e.g. in *P. meridianus* overwintering females become
369 mature at about 3 mm and begin to reproduce early. Therefore small *P. meridianus* females
370 mature at lower temperatures than those of indigenous *Asellus aquaticus* and this will give
371 impetus to the spring reproductive output of the former (Chambers 1977), although they found
372 that reproductive output of the two species across the season was similar. Ovigerous females of
373 *G. roeselii* were sampled from the Pielach River in the mild winter of 1986–87 (Pöckl 1993).
374 Some eggs of *G. roeselii* developed successfully in the laboratory at a constant temperature of
375 4°C (Pöckl and Humpesch 1990).

376

377 **4.6. Behavioural traits**

378 Behavioural adaptations include feeding habits and habitat selection. Survival, growth
379 and reproductive success of invertebrates depends on the quantity and nutritional quality of
380 their food sources (e.g. Basen et al. 2011). Studies of several non-native invasive gammarids,
381 e.g. *D. villosus* (Mayer et al. 2008), *E. berilloni* (Mayer et al. 2012), and *G. roeselii* (Mayer et
382 al. 2009) demonstrated that these species were able to feed on a wide variety of food sources.
383 This adaptability to take advantage of whatever food is available increases the chances of
384 survival in new or changing environments.

385 Utilization of organic matter, an important and readily available food source in aquatic
386 environments, is beneficial for the zebra mussel *D. polymorpha* as well as for many non-
387 indigenous amphipods e.g. *D. villosus*, *G. roeselii*, and others (Gergs and Rothhaupt 2008).

388 The freshwater shrimp *A. desmarestii* is a detritivore decapod that consumes a variety of
389 foods, such as microalgae, microcrustaceans, mud, fecal pellets, carcasses and plant detritus
390 (Margalef 1953; Fidalgo 1985; Fidalgo and Gerhardt 2003; Duarte et al. 2012). In this species

391 the micromorphology of the mandibles is particularly suited to the consumption of these types
392 of foods (Huguet 2015). The high feeding plasticity of *A. desmarestii* gives it an important role
393 in energy transfer at different trophic levels of the grazing and detrital food chains. Moreover
394 this freshwater shrimp also represents an important food item for many fish species (García-
395 Berthou and Moreno-Amich 2000a, b).

396 Another important trait in colder conditions is freezing avoidance. During the coldest
397 parts of the year, under surface-ice in reservoirs, some aquatic invertebrates are able to avoid
398 unfavorable conditions by habitat selection and / or by migration to different habitats. For
399 example, gammarids, including Ponto-Caspian species, can move from shallow,
400 environmentally unstable areas to central bottom sediments with more constant conditions
401 (Poznańska et al. 2009).

402

403 **4.7. Physiological and biochemical traits**

404 Physiological adaptations can include the ability to greatly reduce the metabolic rate and
405 enter to diapause. In unfavorable conditions (e.g. in low temperatures and / or in short-day
406 photoperiods) some crustaceans may enter diapause and resting periods (Sutcliffe 1993) and
407 can therefore resist unfavorable conditions. This phenomenon may alter reproduction and
408 dispersal capability. Prolonged diapause is more common among small crustaceans than among
409 larger ones. It occurs in Malacostraca, including the decapods, euphausiids, amphipods, isopods,
410 and also Branchiopoda such as the cladocerans, conchostracans, anostracans, and notostracans,
411 and the Maxillopoda (e.g. copepods, ostracods), which increases fitness in a temporally varying
412 environment (Hairston and Cáceres 1996).

413 Physiological and biochemical adaptations to cold may include cold avoidance or cold
414 tolerance. At lower temperatures some animals produce cryoprotectants and have lowered

415 metabolism e.g. *G. roeselii* (Gismondi et al. 2012). Reproducing females of e.g. gammarids
416 accumulate and store lipids as the ovaries mature (Sutcliffe 1993).

417 For some species, changing ambient temperatures and modification of hydrological
418 cycles can be important drivers boosting their dispersal into new areas. Usually, r-selected
419 species rather than k-selected species have a higher probability of expanding their distribution.
420 Another factor that can determine the successful expansion of species into new areas is
421 euryoeciousness, i.e., their ability to tolerate wide range to environmental conditions (Ricciardi
422 and Rasmussen 1998), especially eurythermicity which indicates wide tolerance of temperature.

423 Alien species are also characterized by high fecundity, early maturity and elevated
424 reproductive rate (large numbers of generations per year), which facilitate establishment in new
425 areas (Kley and Maier 2003).

426 Most organisms do not occupy all of their potential area in terms of environmental
427 conditions due to limitations to their dispersal ability. In fact, organisms may reach a new area
428 through passive or active transport, but many of them do not succeed to establish in the
429 receiving ecosystem due to abiotic or biotic reasons (such as competition and predation).
430 Passive or active transport is important to overcome different barriers as well as to colonize
431 other water bodies or colonize and re-colonize streams after drought events that will be more
432 frequent in a climate change scenario (Banha and Anastácio 2012). However, in other cases, if
433 they are transported outside their normal range, they may survive, reproduce and spread.
434 Dispersion of organisms can represent a response to cope with scarcity of food resources,
435 changes in local ecological conditions (e.g. pollution, eutrophication) or climate change (e.g.
436 warming, drought events).

437

438

439 **5. Conclusions**

440 The dispersal of species into new geographical areas may be connected with risk of their
441 disappearance in a considerable part of their original ranges due to climate change (Abeli et al.
442 2018; Bolotov et al. 2018). Therefore, it is possible that many cold-tolerant Mediterranean and
443 Ponto-Caspian taxa may shift from one environment to another and decrease in abundance or
444 disappear from their native range. Some of this movement northwards may then be viewed as
445 both inevitable and even desirable, but a significant number of Ponto-Caspian species in
446 particular have behaved invasively in their new areas leading to profound ecosystem change
447 and destabilisation.

448 This work focuses on human-mediated northwards range expansion, both in the sense
449 that a warming climate will enable southern pre-adapted, cold-tolerant species to move
450 northwards, as well as the human role in helping the organisms to disperse through waterways
451 joined by canals and by shipping. The topic of movement of alien species under climate change
452 is a relatively new area of research that requires more attention. These species movements will
453 have economic, health and conservation consequences.

454

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459

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463

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