

Review

Non-Indigenous Cladocera (Crustacea: Branchiopoda): From a Few Notorious Cases to a Potential Global Faunal Mixing in Aquatic Ecosystems

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Abstract: Non-indigenous species may pose a threat to native ecosystems worldwide. In aquatic environments, invasives may have a negative impact on human food security and livelihoods. Several water fleas (Crustacea: Branchiopoda: Cladocera) are notorious invasive alien species influencing large freshwater lake systems and even inland seas. In the current review, we discuss the state of knowledge regarding non-indigenous species in the Cladocera and their invasiveness potential in different continents. We argue that the potential impacts and occurrence of cladoceran exotics may be higher than generally assumed. We critically review 79 cases from literature sources, involving 61 cladoceran taxa where records outside of their natural distribution ranges were previously interpreted as invasions. We assessed the probability of natural range expansions versus human-mediated introductions and we discuss several major corridors of invasion. We estimate human-mediated transportations for at least 43 taxa (out of 61; ca 70%), while other cases can be seen as natural expansions of their distribution ranges (not necessarily/not likely human-mediated) and/or taxonomical confusion. We confirm non-indigenous presence in recipient regions for at least 41 cladoceran taxa, of which several are true invasives (i.e., with negative impacts on native ecosystems). The majority are zooplankters with effects on pelagic freshwater ecosystems, yet we also report on introductions by littoral taxa. We argue that cryptic introductions of cladocerans are taking place on a global scale, yet they remain under the radar. We highlight several striking case studies, such as the Ponto–Caspian onychopods that have invaded the Baltic Sea and the Laurentian Great Lakes, and several clones of the anomopod genera *Daphnia* and *Bosmina* that have successfully colonised new environments, causing equilibria shifts in native aquatic worlds. At the same time, we dispel some myths about taxa that were misconstrued as invasive in certain localities. Based on our review, the first of its kind for freshwater zooplankton, future environmental monitoring tools including molecular techniques and detailed surveys with rigorous and critical taxonomical assessments may help to provide a clearer picture on the extent of invasiveness of cladocerans.

Keywords: non-indigenous species; water fleas; Cladocera; freshwater ecosystems; invasive alien species



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1. Introduction

Non-indigenous species that have become invasives are often linked to shifts or loss of biodiversity in a wide range of ecosystems; in aquatic ecosystems, the impacts of such invasive alien species may exert strong pressures on indigenous aquatic communities, often with negative effects on aquatic food webs, which may result in economic effects affecting food security [1–4]. While individual aquatic ecosystems may sometimes function

as naturally insular habitats, human traffic and other impacts have increased connectivity between habitats, thereby increasing faunal mixing and facilitating the unintentional introduction of species with invasive potential. As a result, some aquatic ecosystems are heavily affected, such as the Baltic Sea, which harbours over 100 invaders, most of which are invertebrates [5].

Of particular concern are those aquatic non-indigenous species which have become or are becoming invasive right under our radars, either because they are microscopical inconspicuous invertebrates or because they are morphologically entirely cryptic. The Cladocera (Crustacea: Branchiopoda), a pivotal zooplankton group in the aquatic food chain, contain notorious examples of both: alien invasive species with strong effects on entire lake systems or inland seas (e.g., *Bythotrephes* in the Laurentian Lakes [6]), as well as examples of cryptic invasives of exotic clones that may quietly be able to outcompete indigenous genotypes that cannot be separated morphologically (e.g., the *Chydorus sphaericus* group in Australia [7]). Some species have expanded their distribution range recently due to climate warming, natural expansions, or increased accessibility of disturbed water bodies with partly destroyed ecosystems, and short-distance anthropogenic transportation [8,9].

The successful reproduction strategy of cladocerans, including the ability of both parthenogenetic reproduction and gamogenesis (mostly with a dormant stage) [10,11], allows these animals to be effective at having the potential of occupying entire aquatic niches, starting from either a single clone or a diapausing embryo. Diapausing embryos in "resting eggs" (in the order Anomopoda incorporated into an ephippium = a modified exuvium) are easily transported through different natural means (on the feathers and in the midgut of waterfowl, by wind, currents, spring inundations, etc.) as well as anthropogenically mediated (manipulation with aquatic and semi-aquatic plants (e.g., rice), fish stocking, ballast water, etc.) pathways [12–15]. Their key roles as intermediate consumers or as predators, therefore, has a dark side: when cladocerans are invasive, they have the potential to disrupt an entire aquatic ecosystem, which ripples through at all levels of the food chain to eventually potentially affect fisheries [16] and drinking water quality [17]. One cladoceran, *Cercopagis pengoi*, even made IUCN's list of 100 of the worst invasives in the world [18]. However, while having potentially negative effects as invasives on a wide range of waterbody types globally, cladocerans form excellent case study objects for general invasive species biology, as their ecology is well known and as their remains, including diapausing stages, can be traced in lake sediments, allowing in some cases to determine the exact moment of arrival and a proper assessment of ecological impacts (e.g., *Cercopagis* in the Baltic Sea [19–22]).

Much is written about the roles and impacts of specific cladoceran invaders in particular areas [6,23], yet there are very few attempts to critically review all literature on occurrences of non-indigenous cladocerans.

Here, we present a critical literature review functioning as a "road-map" of cladoceran exotics, including the first documented occurrences out of their native ranges, and we examine major patterns and pathways that are human-mediated. We focus primarily on non-indigenous species that are most likely the result of direct human-mediated introductions and we also discuss natural range expansions which may potentially be the result of indirect human effects such as global warming. We highlight taxa recognised by an apparent disjunction between areas that are unlikely to be connected through natural vectors alone, or by a clearly documented series of direct events leading to the introduction.

2. Materials and Methods: Literature Study

Based on a detailed review of cladoceran literature published over 120 years (1900–2022), we found 79 cases of non-indigenous occurrences, in total containing 61 taxa (Appendix A). We critically investigated each of these records and found 52 cases (of 43 taxa, i.e., 70% of the total taxa in Appendix A) with non-indigenous occurrences that are most likely the result of human intervention, but some of these cases are false (often due to taxonomical confusion).

Several of these taxa were shown to have negative impacts in recipient regions as a result of non-indigenous establishment of cladocerans (i.e., invasive alien species or IAS).

Appendix A contains individual comments per case and inputs regarding the first literature occurrence, previous important reviews, phylogeography of the invasion, most recent results about non-indigenous species and other critical notes by us wherever relevant (e.g., if the record is most likely a potential natural range expansion or if we consider it an actual human-mediated disjunction). We distinguished between cases which we consider human-mediated introductions (indicated as long-distance transportation or TR) versus range expansions (RE) that are not necessarily through human-mediated vectors, and we noted which taxa are planktonic (PL) and non-planktonic (NP) in Appendix A.

Based on Appendix A, we discuss key examples and main invasive corridors in the sections below and the major pathways of the introductions. The sections below are structured from well-known “classical” examples of cladoceran invasives (and their negative impacts) to the latest insights into non-indigenous taxa, using molecular approaches. Based on this table, we also assessed the number of cases of introductions in developed versus non-developed/transitional regions.

Information on transportation and range expansions in Cladocera is summarised in the map (Figure 1).

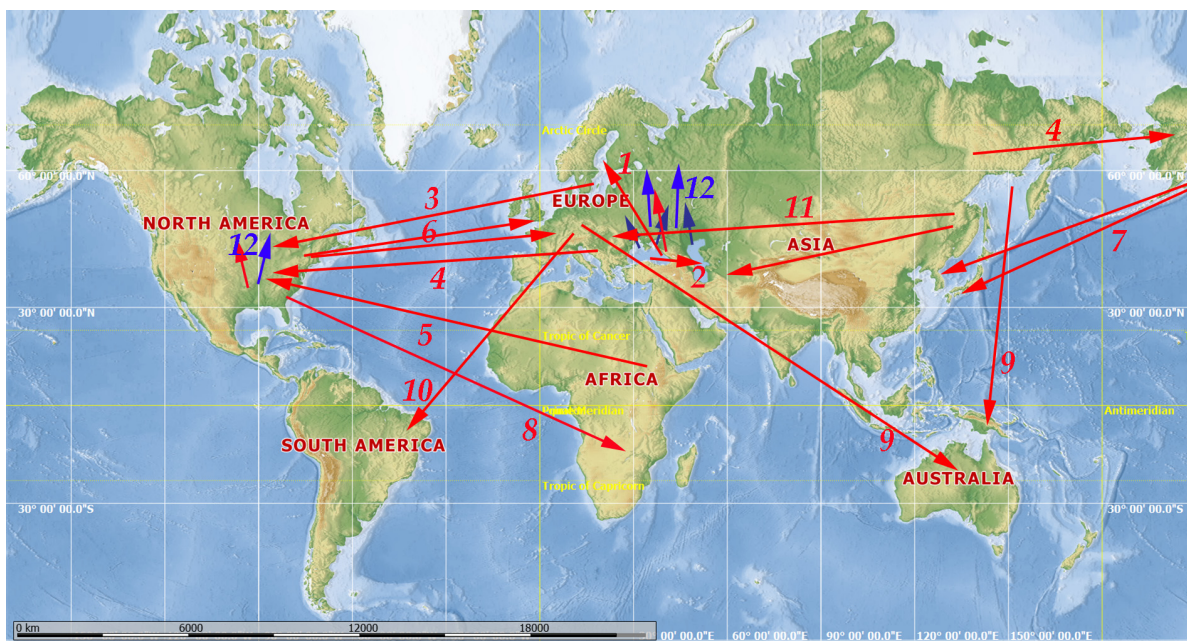


Figure 1. Main pathways of cladoceran long-distance transportation (red arrows) and range expansions (blue arrows) discussed in this study. The base map is from the public domain atlas in the desktop app, Marble 2.2.20 (<https://marble.kde.org/index.php>, accessed on 1 July 2022) [24]. Numbers correspond to the subsections in Section 3 (Results).

3. Results: Major Pathways of Transportations and Range Expansion

3.1. Introduction of Ponto–Caspian Onychopods in Europe

Onychopoda, the most speciose predatory order in the Cladocera, have a wide native distribution in freshwater and marine ecosystems [25]. A significant proportion of the taxa in this order has a broad salinity tolerance, while several are confined to each end of the ecological spectrum in either pure freshwater or marine environments [25]. As efficient pelagic predators, most onychopods easily compete with other invertebrate and even vertebrate consumers in the aquatic food chain, exerting strong top-down effects on zooplankton communities. Onychopods radiate in the Ponto–Caspian region [9,25,26].

Human-mediated range expansions of several onychopods deep into the river systems of the Ponto–Caspian basin were among the first recorded non-indigenous cladocerans

that attracted the attention of hydrobiologists. Since the first reports of non-indigenous populations of *Cercopagis pengoi* and *Cornigerius maeoticus* in the 1950s [27,28], the study of the subsequent dispersal of a number of Ponto–Caspian invaders became important in general zooplankton monitoring studies. In the second half of the 20th century, several Ponto–Caspian onychopods significantly expanded their distribution ranges, reaching the Kama Reservoirs (Volga basin; ca. 55–59° N).

New exotics such as *Podonevadne trigona* and *Cornigerius bicornis* were recorded from the lower reaches of the Volga, Don, Dnieper and Danube Rivers [9,29]. These expansions are associated with introductions of *Cercopagis pengoi* and several aquatic copepod species of Ponto–Caspian origin follow the same mechanisms [30].

The Caspian and Black seas are well known for their complex history with invasive aquatic animals [31,32]. Penetration of the Ponto–Caspian taxa towards the north was significantly catalysed by large hydrological works during Soviet times when main river basins were interconnected by canals (firstly, the Volga–Don Canal) and when several dammed lakes were constructed (with the hydrological regime of a lake, not a river), intensifying upstream shipping [33]. Upstream ships would therefore have the potential to transport diapausing embryos of onychopods in ballast water [9]. As most Ponto–Caspian Onychophora are not able to swim against river currents, their expansion was therefore strongly facilitated by human activity. These cladocerans confirm that “*The Ponto-Caspian region is among the most notable donor regions for aquatic invasive species in Europe*” [34].

Their presence as invasives may affect entire aquatic trophic webs [6]. Now non-indigenous crustaceans form 24–29% of the taxa and 14–25% of the total biomass of zooplankton in the Volga–Kama basin [33,35]. “*Among the Ponto-Caspian cladocerans living in the Volga and Kama, the largest and most prominent invasive species was Cercopagis pengoi*” [35]. The latter changes zooplankton structure significantly by eliminating small-sized zooplankton filtration which increases the incidence of algal blooms; in addition, the species causes difficulties for fishery by clogging nets and may even cause an allergic reaction in people [32].

3.2. Transportation of Oceanic Cladocerans from the Black Sea to the Caspian Sea

While the first Ponto–Caspian invasions took place towards the west, human-mediated transportation of cladocerans also occurred in the other direction (Figure 1). Two indigenous inhabitants of the World Ocean, *Pleopis polyphemoides* and *Podon intermedius* were established in the Caspian Sea [8,36]. Most likely, they were transported from the Black Sea in ballast water by ships moving through the Volga–Don Canal, although this scenario has not been assessed by molecular methods yet (however, there is such data for fish [37]). No information on their negative impacts is available to date, while these crustaceans became an additional food source for indigenous fishes [36]; they are now incorporated into the food web of the Caspian ecosystem.

3.3. The Baltic Sea Region as a Hub for Intercontinental Transportation and Further Expansion of Invaders in North America

Transportation of the Ponto–Caspian taxa to the Baltic Sea has shown that the latter has functioned both as a harbour and a stepping stone, facilitating the potential westward range expansion through ships over the Atlantic Ocean [38,39] (Cristescu et al., 2001; Bailey et al., 2003). This is also the case for other aquatic invertebrates, as the Baltic Sea is a notorious hub for invasives [5].

Intense shipping from the Ponto–Caspian basin to the Baltic Sea in the last decades has led to the transportation of several non-indigenous taxa (not only crustaceans). Such faunal exchanges were strongly facilitated through the expansion of the interconnected river systems in Russia and by the transport of diapausing stages in the ballast waters of ships.

The most notorious example of a cladoceran invasive species is the spiny water flea. *Bythotrephes* species are considered among the world’s best-studied invasive zooplankters [6, 40,41]. Initially originating from the Ponto–Caspian Basin, *Bythotrephes* was transported

to North America, probably, from Lake Ladoga [42] which is also a part of the Baltic Sea Region and interconnected with the Sea itself. Populations of the spiny water fleas were first detected in Lake Ontario in 1982 [43], from where they rapidly spread to the other Great Lakes [6,40,44]. By 2010, the spiny water flea was reported from over 150 lakes in North America and Canada (important reviews include a special issue on these animals [6]).

Recently, the taxonomical status of basic *Bythotrephes* species and hybrids, including *B. cederstroemii* and *B. longimanus* was revised in detail, based on Eurasian and North American populations and using morphology [45–49]. The latter revealed that the general naming in the literature of this widely distributed animal in the North American Lakes had been erroneous for many years—the Eurasian species that is most widespread in Canada and North America is *B. cederstroemii*, not *B. longimanus* [48].

Other notorious invasives used the Baltic as a stepping stone. The first findings of the onychopod *Cercopagis pengoi* in the Baltic Sea dated to the 1990s [19,20], and then two new Ponto–Caspian onychopod predators appeared in the Baltic Sea: *Cornigerius maeoticus* [25,50,51] and *Evadne anonyx* [25,52]. It is well-known that *Cercopagis* and *Cornigerius* have a strong effect on zooplankton communities, but, at the same time, *Cercopagis* became a new important food item for local fish [21]. Information on these cladoceran invasives and the negative impacts on the Baltic ecosystem were discussed in several publications [22,29,31,32,38,53]. Subsequently, *C. pengoi* was detected in the Great Lakes [38,54].

The Baltic Sea was also a source of other invaders to North America, not related to harbouring Ponto–Caspian taxa. Together with the destructive onychopods, at least two very common European anomopods were also transported: *Bosmina* (*Eubosmina*) cf. *coregoni* [55–58] and *Daphnia galeata* [59,60]. Subsequently, these two taxa greatly expanded their ranges throughout the USA and Canada, although their effects on the indigenous communities can be considered relatively less destructive than that of the onychopods.

It is important to note that the Baltic Sea region became a natural laboratory for the adaptation of some cladocerans to wide ranges of salinity, re-enforcing their invasive potential. This is the home of *Bosmina* (*Eubosmina*) *coregoni maritima* which was regarded as a separate species adapted to life in the Baltic Sea but is now regarded as a Baltic population of *B. (E.) coregoni* s.lat. [61].

3.4. Other European Invaders in North America

Several cladocerans have reached North America by other modes other than ballast waters and from other areas than the Baltic Sea. Their populations were established in isolated water bodies, not through intensive trans-continental shipping. There are two species of *Daphnia* that colonised North American waters this way: *D. (Daphnia) curvirostris*, found in some lakes on the Atlantic Coast of the USA and in Mexico [62–67] and the “European” phylogroup of *D. (Ctenodaphnia) magna*—while the indigenous “American” phylogroup of the latter is also present in North America [68]. The “European” phylogroup most probably represents an escaped laboratory clone [68]. Only two European cladocerans from other families were detected in North America to date: *Moina macrocopa macrocopa* in Mexico [69] and *Alonella excisa* (clade I2) which is a possible invader in Canada from Asia [70]. These cases could be regarded as cryptic invasions: the exotic status of the populations only became obvious after applying recent molecular methods, while morphological identification of such invaders is very problematic due to the unstable taxonomy of these genera and species groups. No destructive influence of these taxa on indigenous ecosystems has been revealed to date.

3.5. Transportation of African Cladocerans to North America

The best-known case with evidence of impacts is the establishment of *Daphnia lumholtzi* [65, 71–73] from Africa attributed to aquaculture (inaccurate manipulations with exotic fish). This taxon rapidly expanded its range recently in North America and penetrates South America from the former region [74–76]. The invasion has strong economic effects as *D. lumholtzi* “outcompetes native zooplankton populations during their normal peak abundance in late

summer" [77]; this may adversely impact planktivorous fish relying on critical native food sources but which are unable to tolerate *D. lumholtzi*'s spines [41]. Moreover, a selective avoidance of *D. lumholtzi* by predators (fish) may increase predation pressure on native zooplankton [78].

There is a chance that "*D. brooksi* Dodson, 1985" in Utah (USA) and Michoacán (Mexico) in reality represents a non-indigenous population of African *Daphnia barbata* [65,73], but this needs to be confirmed by molecular tools.

3.6. Transportation of North American Taxa to Europe

Probably the first American taxon detected in Europe was the small daphniid *Daphnia ambigua*, initially described in the Royal Botanic Gardens, Kew in London [79,80]. It was shown that this is a North American taxon that was introduced in Europe during WWII [81,82]; the same scenario is known for the similar-looking *Daphnia parvula* [81,83]. Both taxa strongly expanded their ranges in Europe [65,84,85].

A few American non-daphniid taxa were recently recorded in Europe; the North-American *Chydorus brevilabris* was found in Belgium, Luxembourg and France [86,87]. *Moina affinis* in Italy was reported as an American invader [84,88–90], but this hypothesis needs to be checked (Appendix A). No information on their impact on indigenous ecosystems is available, but *D. ambigua* and *D. parvula* can be locally highly abundant in eutrophic European waters.

3.7. Transportation of North American Taxa to the Far East of Asia

The introduction of North American anomopods was also recorded in the Far East of Asia. *Daphnia* cf. *pulicaria* was found in Japan [91] and a rapid expansion of an American *Daphnia pulex* × *pulicaria* clone was detected in this country as well [92]. There is a strong chance that *Daphnia ambigua* in Japan [93,94] is also a North American species instead of an indigenous taxon. Finally, the North American chydorid *Biapertura ossiani herricki* is now detected in Korea and is thought to have been introduced during the Korean War [95].

3.8. American Taxa in Africa

The best-recorded case of American taxa invading the Afrotropics is the transportation of an American *Daphnia pulex* × *pulicaria* asexual clone to East Africa, followed by its expansion in the entire African continent [23,96,97] and appearance in Southern Europe [23,98–100]. This species introduction was not strongly destructive (as far as we know) for the communities in newly colonised water bodies, but it did lead to a replacement of the indigenous *D. pulex* by the non-indigenous taxon and full extinction of the former in such water bodies; this story is well-supported by paleolimnology [23].

3.9. Transportation of Several Taxa from the Holarctic to Australia/New Zealand and Subsequent Expansion of Their Ranges

Recently, New Zealand and continental Australia became important regions for the study of cladoceran invasions. Two boreal colonists have rapidly expanded their ranges and are now found in New Zealand: *Daphnia galeata* [101] as well as the "American" *Daphnia pulex* × *pulicaria* clone [102,103]. Estimates from genomic data imply a colonisation time for the South Island population of the latter of ca. 60 years ago, due to the introduction of salmonid fishes from North America [103]. As in the case of the African invaders, the latter two non-indigenous species are replacing indigenous taxa in some lakes [104].

At the same time, several European taxa have appeared in most urbanised southern Australia: *Daphnia* cf. *obtusa* [105], *Daphnia galeata* [106], *Bosmina longirostris* [107] and *Chydorus sphaericus* [7,108]. The latter are not likely to be a result of long-distance dispersal but introductions. Their impact on the freshwater communities is not studied to date, but *D. galeata* is known as a strong competitor and could also replace native taxa [106].

3.10. European Taxa in South America

Few cases of introductions of European taxa into South America are known: *Moina macrocopa* which is now widely distributed there [69,109,110] and *Eurycercus lamellatus* in Brazil [111,112]. No information on a potential impact has been obtained to date.

3.11. Transportation of Far Eastern Taxa to Europe and Middle Asia Due to Aquaculture and Rice Crops

Some taxa are regarded as transported from the Far East due to rice production and aquaculture activity: *Diaphanosoma macrophthalma* to Kazakhstan, Uzbekistan, Pre-Caucasus [53,113] and *Moina weismanni* to Italy and then to other countries of Southern Europe [84,114–116]. However, in reality, this hypothesis needs to be checked genetically, as for the incidental introduction of fish [117,118] and bivalve mollusks [119]. No information on the negative impact has been obtained to date.

3.12. General Range Expansions towards North and South of Europe and North America Due to Natural Factors Re-Enforced by Human Activity

Few cases of the appearance of a taxon far north from its natural range are known from the USA. These include the finding of *Daphnia exilis* in New York State [64,65,120]. Two earlier non-registered taxa of *Diaphanosoma* were found recently in the Great Lakes: *Diaphanosoma fluviatile* [121] and *D. brevireme* [122], and new records are quite expected. These are likely human-mediated introductions which, due to a warmer climate, are able to maintain populations far more north beyond their natural ranges.

Since the 1990s, in several European and North American countries, hydrobiologists recorded range expansions of some Cladocera. For example, *Bythotrephes brevimanus* has appeared in The Netherlands and Belgium where it was absent a century ago [123]. It is proposed that *Latonopsis australis* and *Wlassiscia pannonica* have appeared in Italy [84,90,124], but such records must be checked (see Appendix A). Conclusions on the appearance of *Bosmina* (*Eubosmina*) *coregoni* in Slovakia, Volga and Dnieper Rivers basins [84] are dubious because it was demonstrated that such morphotypes of *B. (Eubosmina)* are forming independently in different water bodies [61]. At the same time, the appearance of *B. (E.) coregoni* in the Iberian Peninsula [125] seems to be a real range expansion, as no taxa of this subgenus have been recorded in (well-studied) Spain [126] before.

New records are found south of their previous ranges concerning several taxa in European Russia and some other countries: *Diaphanosoma orghidani* and *Diaphanosoma mongolianum* in the Volga basin [127,128], *Limnoscia frontosa* in the Volga, Dniepr basins, and Czech Republic [84]; *Diaphanosoma dubium* in Kazakhstan, Uzbekistan, lower reaches of the Volga, Pre-Caucasus, Ukraine [129–132]; *Moina micrura* in the Volga basin and the Baltic Sea [133,134]. A range expansion of some taxa towards the south seems to have taken place, but it is necessary to be accurate when interpreting such new records as “invasions”, keeping in mind the recent changes in the taxonomy of many cladoceran groups and the difficulty of identification using morphology [53,130,132]. In some obvious cases, such as the finding of *Ilyocryptus spinifer* in the Middle Volga River [135], the interpretation is more adequate, but it is unknown if these populations are stable in time.

No information on a significant negative impact of such non-indigenous populations is obtained to date, and non-indigenous species coexist with indigenous ones in the Volga basin [33,136].

3.13. Occasional Anthropogenic Transportation of Unpredictable, Chaotic Directionality

There are single cases of introductions that do not follow any pattern. These include the finding of a South American taxon *Scapholeberis yahuarcaquensis* in Belgium [137], an African taxon *Disparalona striatoides* in Europe [84,87,116,138,139], and *Evadne nordmanni* in the North American Great Lakes (the latter coming from the World Ocean) [140,141]. The population of *Daphnia inopinata* in Germany could be also non-indigenous, but its origin is actually unknown [142].

A non-indigenous haplotype of *Daphnia magna* is detected in Sevan Lake (Armenia) [68,143], which led to changes in the fish population [144], as often happens with the introduction of alien species of invertebrates [145]. Such cases are singular, and it is impossible to separate each directionality of the invasion for each case. No information on the negative impact of such cases has been obtained to date, but they add to the occurrences of cladoceran faunal mixing.

3.14. Developed vs. Developing Countries and More Cases of Planktonic Invaders

It is very important to note here that cases of non-indigenous species establishment (both long-distance transportation and local range expansion) are mainly reported in developed countries while developing countries are almost not touched by such studies (Figure 2a). Moreover, the relative number of false cases is higher in developing countries (Figure 2b) and few cases of range expansions are detected there (Figure 2c). In general, we found fewer cases of local range expansion than human-mediated long-distance transportation (Figure 2d). Finally, most records of long-distance transportation and local range expansion are present for planktonic cladocerans, while inhabitants of the littoral zone almost fully escape the attention of aquatic biologists (Figure 2e).

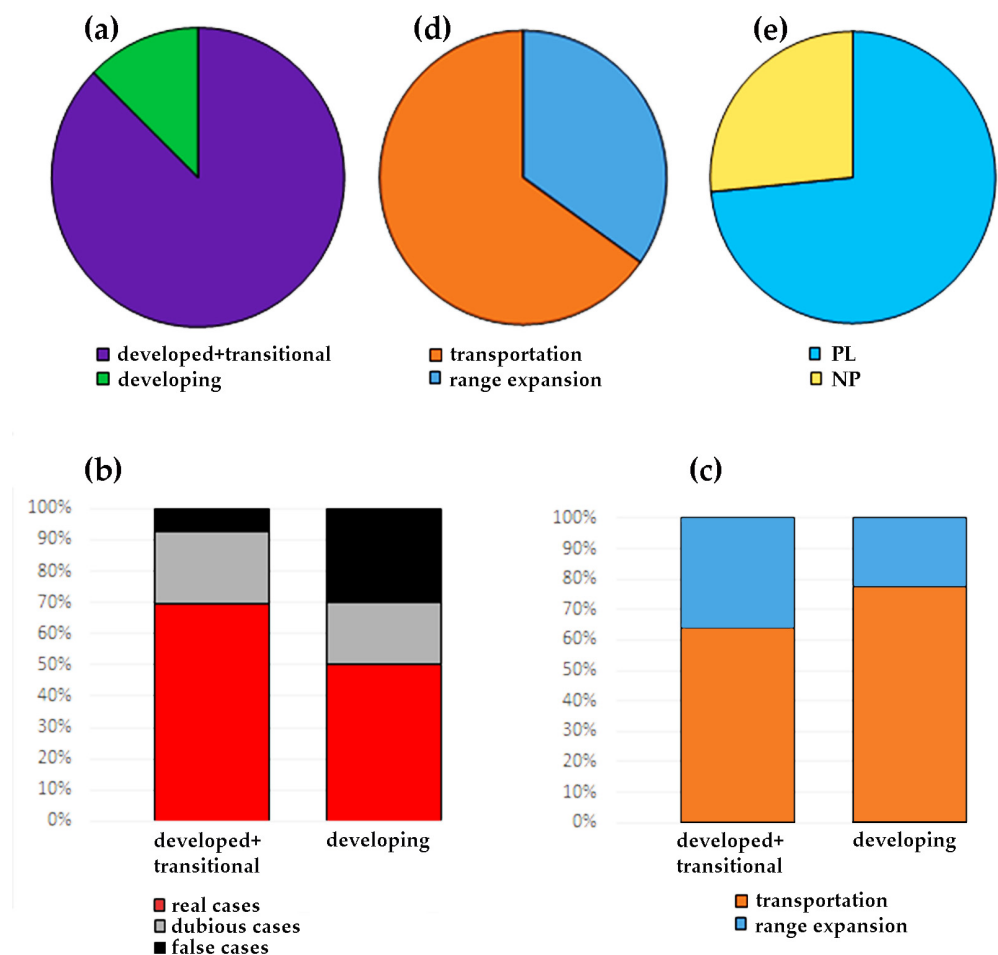


Figure 2. Analysis of data on non-indigenous taxa of Cladocera from our literature study (79 cases, 61 taxa; see Appendix A). (a) Proportion of cases of revealed transportation+range expansion in developed+transitional vs. developing countries; (b) Proportion of true, dubious and false identification of non-indigenous taxa in developed+transitional vs. developed countries; (c) Rate of cases of transportation vs. range expansions in developed+transitional vs. developed countries; (d) Global proportion of transportation vs. range expansion cases; (e) Rate of planktonic (PL) vs. non-planktonic (NP) taxa recorded as non-indigenous elsewhere.

4. Discussion: Recent Insights in Cladoceran Exotics

4.1. Dispelling Myths: Some Cases May Not Be Exotics after All

During the last decade, there has been a rapid increase in the amount of morphological and molecular data in the Cladocera, in particular in the Anomopoda. Such new data allow for a more rigorous identification of taxa, a comparison with similar morpho- and genotypes, and more detailed knowledge of the natural phylogeographical patterns, to understand the deviations from such patterns through direct or indirect human intervention.

Unfortunately, we need to conclude that many cases of cladoceran “invasions” are false. New morphological and/or molecular explorations do not help to identify cryptic exotics, in fact, the exact opposite can happen. A so-called exotic, leading to new hypotheses of new anthropogenic introductions, may appear to be something entirely different. Such cases are possible and occur in the Cladocera, in particular in the chydorids which are hard to identify. It is a consequence of how we initially recognise exotics by morphology, which should be critically assessed, and because we are lacking comparative molecular data for the majority of the exotics that we wish to identify. We highlight a few such cases below.

Already more than four decades ago, E. Kubersky [146] proposed a very sophisticated hypothesis on introductions of the resting eggs of *Alonopsis* from Europe to North America by the first European colonists in the ballast water of their ships; this now seems to be unrealistic as the European and North American populations are now revised, and clearly belong to separate taxa [147].

Until recently, researchers have assumed that the presence of the main water flea dominating the temporary and permanent aquatic environments of Easter Island in the Pacific Ocean, represented a man-mediated introduction from the subantarctic region. Easter Island populations of a chydorid were identified as *Alona weinecki*, a taxon originally described from the subantarctic islands, including Marion Island and the Kerguelen [148,149]. Based on sediment cores in Easter Island, the potential subantarctic aquatic element was attributed to the human-mediated introduction by Dutch or British ships through ballast water in the late 18th century [150]. This idea of a subantarctic chydorid on Easter Island spread widely and the hypothesis has led to the occurrence becoming a textbook important example of microcrustacean non-indigenous species in aquatic ecosystems worldwide [151,152]. However, we now know that this is not the case. Detailed morphological revision of chydorid populations from the Subantarctic islands and from Easter Island, as part of a general revision of the lump taxon *Alona* Baird, 1843, showed that these populations belong to two clearly different species. The apparent similarity is one of the many cases of external phenotypic convergence in chydorids [153,154] and the separation of the taxa was a result of a rapid improvement of our understanding of the detailed morphologies of the group. The subantarctic *Alona*-like chydorid populations have now been placed under the name *Ovalona weinecki* [155] and the Easter Island species was subsequently described as new, *Ovalona pascua* [156]. The origin of the latter and connection to the nearest mainland is unclear, but it is quite different from other species in the genus; it may even be an Easter Island endemic [156]. Other species, such as an unidentified *Daphnia*, were also found here, clearly a result of long-distance dispersal. Therefore, even in aquatic organisms on extremely remote islands, the understanding of exotic or non-exotic can depend on detailed morphological or molecular revision.

Another well-known non-exotic case of cladocerans is that of the chydorid *Pleuroxus denticulatus* in Eurasia. Based on morphology, recent records of western and central European populations attributed to this species were identified as human-mediated introductions from North America, where the taxon was originally described [116,157–159]. However, no detailed morphological revision of these populations was carried out, and as with many chydorid species, there are morphological indications that *P. denticulatus* is not a single widespread species but a species complex with considerable cryptic diversity. Based on morphology, more than one species had been recognised in its *terra typica* in North America [160]. The European populations belong to another taxon, which is also present in the Mediterranean [126]. The newly observed presence in northwestern Euro-

pean territories and mountain areas is most likely part of a northward range expansion within the area. Potentially natural range expansions (e.g., because of climate warming) and cryptic diversity, should be taken into account for such new records. For another chydorid taxon, *Disparalona* cf. *leei*, ideas on invasive status [84] were most probably wrong as these populations could belong to a special and relatively widely distributed Eurasian taxon instead of the North American congener [161].

Besides cryptic diversity and taxonomical confusion, there is also a potentially cryptic lifestyle. Several chydorids are very rare or have very specific ecologies. Their so-called former absence may just be a case of these species having been overlooked in a certain region and a sudden discovery could then be misconstrued as an anthropogenic introduction. Hudec and Illiová [158] presented a Slovakian record of the chydorid *Rhynchotalona falcata* as either a rare native species or a potential introduction from northwestern regions in Europe. Their human introduction hypothesis from northwestern regions is not likely. As a psammophilic species living in relatively specific ecological conditions and with a widespread but sporadic occurrence all over Europe, often in dystrophic waters [81], *R. falcata* is easily overlooked, and it may well be actively distributed through natural ways. Another species of the same genus in Scandinavia, *Rhynchotalona latens* [162], was thought to be extinct. Recent intensive surveys in Finnish lakes made it clear that the extant populations had just been overlooked [163,164]. Similar observations can be made for so-called appearances [84,124] of *Phreatalona protzi*; this is a genus with a very specific, mainly hyporheic ecology that was only recently revised [165]. A so-called new record of “*Alona*” *rustica* (according to [166] this belongs to *Flavalona*) [90,167] in Italy is also a clear case of improved sampling efforts rather than former absence in Italy, as this is a very specific sphagnophilic species (i.e., found mainly in littoral *Sphagnum* moss) of dystrophic waters that can be easily missed. It is likely that such species have just been overlooked by researchers, or confused with other *Alona*-like taxa before, purely on morphological confusion and undersampling.

Several conclusions on the appearance of some non-indigenous species in Appendix A are made based on studies of artificial water reservoirs [168–171]. However, species colonisation and community succession in man-made water bodies during earlier years of their formation are well-known. Monitoring of reservoirs is a special task of some Institutions, such as the Papanin Institute for Biology of Inland Waters Russian Academy of Sciences in Russia, where cladoceran “invaders” were studied in detail many years ago [25,172]. Such processes in man-made reservoirs could be regarded as a part of the invasive thematic, but they are not real invasions; such changes are analogous to that which we see in many cores of bottom sediments. In reality, this is a “natural” succession process. At the same time, it is known that urbanisation increases the biotic homogenisation of zooplankton communities [173,174], similarly to the invasions which are a kind of faunal mixing [175].

Very interesting for our understanding of the colonisation of newly made water reservoirs, are observations of Spanish hydrobiologists who found that the construction of large dams in Spain resulted in their colonisation by several taxa previously not recorded in this country: *Diaphanosoma mongolianum*, *Daphnia galeata*, *D. parvula*, *D. cucullata*, and *Ceriodaphnia cornuta* [176,177]. The same probably happened in the case of the “invasive *Daphnia exilis*” in Chilean water reservoirs [168,170]: this population most probably belongs to a South American congener of the former (see [178]), and its appearance in a newly created reservoir is very predictable.

Many published single reports on “invasions” seem to be dubious, such as the appearance of the Australian *Daphnia longicephala* in the Great Lakes [141], which is most likely a misidentification. New records of rare taxa such as *Ceriodaphnia rotunda*, *Campptocercus uncinatus*, *Leberis diaphanus* and the above-mentioned “*Alona*” *rustica* and *Phreatalona protzi* in Italy [84,90,124,167], several of which live in specific (undersampled) habitats, most probably reflect previous insufficient sampling efforts instead of true invasions. Any ideas on invasions of taxa from the genera *Ceriodaphnia* and *Simocephalus* [124,169], with an imperfect taxonomy

and outdated keys, should also be regarded with skepticism because a correct identification by morphology is really difficult; molecular tools can be of great help here.

Some of the “invasions” and “range expansions”, i.e., in the review of Dexter and Bollens [179] are misinterpretations apparently dealing with normal new records for regions [15,180,181], or even microcosm experiments with non-indigenous taxa in particular water bodies [182].

Therefore, care should be taken before labeling a new record as a potential exotic cladoceran, considering cryptic diversity, taxonomical confusion and a specific ecology. In-depth knowledge of the taxonomy and biogeography of these taxa, and a reliable comparative molecular database, are key.

4.2. Next Stage: Understanding Invasions Using Molecular Tools

Molecular methods have turned a new page in the studies of non-indigenous taxa. Such works have started in cladocerans as phylogeographic investigations of mainly the most scenic invaders [42,56,59,183]. In the 21st century, molecular methods became cheaper and more widely used, becoming the most efficient tools in understanding biological invasions in cladocerans.

A genetic approach was used for studying resting eggs in ship ballast water, a pathway recognised as a potential dispersal mechanism for plankton since the late 1890s [39]. A large number of cladocerans are able to survive in ballast sediments [12]. Now resting eggs of water fleas are detected in ballast waters by molecular methods [184,185]; it is confirmed this mechanism is the main vector of inter-continental introductions of the Cladocera, and that domestic shipping is a way of their further dispersal [186].

A great resource for revealing non-indigenous taxa are sequences deposited in the NCBI GenBank [187] and BOLD [188] by different authors from different countries. Using such data demonstrates all advantages of an international collaborative approach, as detailed studies focused on separate countries [189,190] can rely on these sequences (and add more). However, a mass deposition of sequences to international databases (frequently as “direct submissions” without an accompanying publication) has now led to a situation when many of them need to be “decoded” (i.e., attributed to a proper species after improper initial identification) for their subsequent application in genetic identification of indigenous and non-indigenous taxa [70,191]. Identification using barcoding should therefore always include a critical interpretation of the comparative sequences from the databases, to avoid mistakes.

It is obvious that the detection of non-indigenous taxa is becoming easier in well-explored macrotaxa and species groups after their revisions, based on traditional taxonomy combined with molecular phylogeny, such as in *Daphnia*. Genetic data confirmed the presence of European *D. curvirostris* [67] and *D. magna* s.str. [68] in North America and *D. galeata* to southern Australia [106]. Special investigations are aimed at tracing the invasion histories of cladocerans in different regions of the planet [92,103]. Moreover, we can conclude based on genetic data that some cases of anthropogenic transportation are unsuccessful, although these can have genetic consequences such as the presence of “invader” mitochondrial DNA in populations of indigenous taxa [192].

With great regret, we need to conclude that, unfortunately, non-indigenous taxa are recorded in nearly all recent phylogeographic studies in non-*Daphnia* genera with wide regional coverage: *Scapholeberis* [191], *Alonella* [70], and *Chydorus* [7]. All these invasions are cryptic as these groups are often overlooked and the invaders do not change the communities significantly (as far as we know) and do not have serious economic effects.

A special task is revealing the non-indigenous taxa and haplotypes in large datasets of phylogeographic studies. A universally accepted methodological basis for discrimination of indigenous/non-indigenous phylogroups and haplotypes is not developed yet, but some ideas are already proposed [192].

Obviously, recently, metabarcoding and eDNA studies will help to reveal the biological invasions in freshwaters [193–195]. For scenic cladoceran taxa, such methods are already proposed [196,197].

4.3. Paleolimnological Study as the Final Evidence of a Past Invasion

The species composition of a particular lake is not always stable. Paleolimnological studies provide us with numerous cases of community changes, but also with examples of sudden appearance and disappearance of particular taxa [198]. Long-term observations on a particular water body can put such population “flashes” in context. For example, Nikolai Smirnov studied the littoral zone of Glubokoe Lake in the Moscow area (European Russia) since the 1970s, but only during a single year did he observe a massive appearance in the littoral zone of a very rare chydorid species, *Pleuroxus pigroides* Lilljeborg, 1901, which fully disappeared the next year [199]. Since that time the taxon was never recorded in the (closely monitored) lake again. Kotov [200] observed the presence of *Daphnia magna* Straus, 1820 in the zone of floating leaves in the littoral of the same lake, but soon this taxon also disappeared. Therefore, conclusions about invasions and range expansions must be made based on long-term monitoring.

A good help in revealing past invasions and confirmation of hypotheses is a paleolimnological study. Indeed, studying the remains in cores taken from waterbody sediments is a good realistic way to confirm the appearance of a non-indigenous cladoceran taxon and even to estimate the time of colonisation [120,201–203]. However, unfortunately, not all (actually, only some) cladocerans are well-represented in lake sediment cores [204,205]. Based on a paleolimnological study in the Great Lakes basin, a recent study [203] has questioned if *Bythotrephes* arrived in this area in the 1980s, as generally assumed, because remains were found in the sediment layers dated as pre-1650s.

Such studies in the future could be greatly reinforced by the extraction of DNA from resting eggs [23,206,207]. We expect that eDNA from bottom sediments [208,209] will be also applied in such studies in the future, but such technologies are only recently being fine-tuned (and a proper taxonomically curated database of comparative sequences is vital).

4.4. General Analysis of Revealed Cases

Based on our literature review, we can discuss general patterns and ideas on cladoceran exotics for the first time in a wider context. Dexter and Bollens [179] previously concluded that approximately half of the publications on “invasive, exotic, non-indigenous or introduced” zooplankters published in 2000–2018 concern only four taxa, among which three are cladocerans (*Bythotrephes longimanus*, *Cercopagis pengoi* and *Daphnia lumholtzi*). Therefore, studies on invasive water fleas contribute significantly to a general pool of literature on invasive problems, which is extremely fashionable now. Such a trend (and funding availability related to the former) has led already to some over-enthusiasm in the detection of several “non-indigenous” taxa which are in fact false cases (see above and Appendix A).

Major geographical pathways through which recorded invasions have taken place in the Cladocera are shown in Figure 1. Most cases of non-indigenous occurrences that were identified based on morphological methods are known from particular regions or lakes with long-term cladoceran studies and a developed system of “standard” monitoring of zooplankton, such as in Italy [124], Slovakia and the Danube basin [116], the Volga basin [127,210], and the Baltic Sea in Europe, the Great Lakes in North America [44,54], or New Zealand [101,103]. After the discovery in the 1980–1990s of some textbook examples of very destructive and economically harmful cladoceran invaders (*Daphnia lumholtzi*, *Bythotrephes cederstroemi*, *Cercopagis pengoi*), the search for potential non-indigenous taxa became a special task of long-term monitoring. We can even say that the efforts to find new records of non-indigenous species became an important part of hydrobiological monitoring and single records were easily accepted as publications. Such efforts sometimes were over-enthusiastic, and some records of “invaders” were dubious and even apparently wrong (see Appendix A). Some taxa “introduced to Europe from North America” in reality represent separate species that are congeners of the American taxa. Some records, especially of rare taxa with very specific ecologies, could be explained by insufficient previous sampling efforts, and other records of so-called exotics have appeared following changes in Cladocera taxonomy after global and local revisions of several macro-taxa.

For example, before 1995, the main key book for identification of water fleas in Russia [211] (Manujlova, 1964) did not recognise *Daphnia galeata* as a valid taxon. After the publication of a more proper and recent monograph [212], *D. galeata* was immediately observed as an “invader” of many water bodies in Russia, but this was just a matter of increased resolution of the observations. The situation with several taxa of the genus *Diaphanosoma* Fischer, 1850 is similar. Before the 1990s, almost all populations from the northern portion of European Russia and South Europe were identified as *D. brachyurum* Liévin. After the publication of recent keys [130,213], it became possible to identify other taxa there (see Appendix A). In reality, we cannot be entirely certain if these taxa truly expanded their ranges, or if they were not properly identified in the past—standard monitoring and ecological surveys tend to easily oversee taxonomically difficult taxa (while it is crucial to identify non-indigenous as well as indigenous taxa correctly).

Over 50% of the literature on invasive cladocerans in previous studies concerns North American water bodies [179]. Looking at the map (Figure 1), we need to conclude that most cases of long-term transportation and range expansions are recorded in developed countries (Figure 2). The latter are primary recipient as well as donor areas for invasions. Such a phenomenon has two main explanations: (1) developed countries are best studied for Cladocera (and other organisms) due to a long tradition in science and organisation of long-term monitoring of at least some larger water bodies, i.e. this is “a mirror of global distribution of wealth” [179]; (2) transportation between highly urbanised developed countries are more intensive as compared to developing countries or countries with transitional economies. To date, developing and transitional countries are almost unexplored (with few exceptions, e.g., cladoceran studies in Mexico [69,109,214], Argentina [110,173] and Brazil [215,216]), leaving such high-biodiversity areas under-evaluated regarding the impacts of invasives. We expect that many cases of introduction and establishment by non-indigenous species have already taken place in developing countries yet have been overlooked to date. For example, Africa is almost unexplored (in relative terms).

Even in western areas, many supposedly “harmless” exotics remain under the radar because of strong morphological similarities with native species and taxonomical difficulties. Still, the outdated cosmopolitanism concept in the Cladocera (assuming that most widespread species groups are single taxa occurring all over the world) [217] remains a widespread, stubborn idea that does not help to assume to recognise exotics when one does not expect it; in fact, regionalism is now understood as being a more common natural pattern in cladocerans. An example is *C. sphaericus*—originally thought to be all over the world [218,219], now thanks to molecular approaches, it seems that the situation is far more complex: including some regionalism [220,221], some wide natural distribution, and some actual invasions [7]—if we wish to understand invasive species in the cladocerans, we must acknowledge the complexity of their biogeographical patterns.

Now more cases of biological invasions in developing countries are recorded, and this is a reflection of the rise of national programs in biodiversity studies worldwide but perhaps also of the intensification of transportation between countries with developing economies. It is well-known that rapid economic growth immediately stimulates biological invasions [222]. A boom of records in those countries with growing economies is expected recently. The faunal mixing is a part of the global biodiversity crisis, characteristic of developed and developing countries [223,224].

The clear dominance of planktonic cladocerans among reported cases of cladoceran introductions (Figure 2, Appendix A) is obvious as well as expected. We need to remember that non-planktonic groups such as chydorids and macrothricids have entirely different strategies of dispersal than planktonic cladocerans [225]. Moreover, resting egg resistance to stress is very different among different cladoceran taxa [11,226]: the ephippia of *Daphnia* or *Moina* are able to survive total desiccation, but it is not true for the planktonic *Bosmina* [227] or for the onychopods [228]. We cannot say that ephippia/resting eggs of the planktonic cladocera are more protected in comparison to the littoral forms.

Mostly, the prevalence of the pelagic zooplankters among the non-indigenous taxa in our list clearly reflects a general trend of recent studies: most aquatic biologists deal with the actual plankton (even with a few model planktonic taxa!), while anything beyond the pelagic zone is studied rarely and many events there are often overlooked. Additionally, note that most cases of real biological invasions were revealed for the onychopods and different representatives of the genus *Daphnia* [179], which are planktonic. However, again, non-indigenous taxa and haplotypes of the littoral cladocerans were also revealed in each global phylogeographic study similar to the planktonic forms. We believe that the global faunal mixing in reality is severe in both planktonic and non-planktonic cladocerans.

5. Conclusions

Cladocera is a group of microscopic animals living in freshwater that is well-adapted for easy passive dispersal by means of their resting eggs. They can be excellent invaders which, due to their key roles in aquatic ecosystems, have a high potential to change entire ecosystems. Their current and potential impacts should be closely monitored. Recent studies, and this review, are showing that the width of their coverage is larger than expected, as illustrated by cryptic genotypes: invaders are found in many global phylogeographic studies in the Cladocera. However, more genetic studies and improvement of monitoring tools are necessary. Moreover, developing countries and their huge territories are inadequately studied to date, and we expect a mass presence and detection of non-indigenous taxa and haplotypes here after applying adequate methods to future cladoceran studies (but also the indigenous fauna in such countries should be studied better first). Even in developed countries, the interpretation of some cases remains dubious because of several factors, including unstable cladoceran taxonomy, improper identification during monitoring, and sometimes the absence of adequately identified vouchers in international genetic databases (wrong barcodes). For final confirmation of a non-indigenous status besides the application of molecular tools, a paleolimnological approach can be used where possible, to trace the dispersion history combined with a phylogeographic approach.

We need to be aware that major human interventions (through ballast water of ships, fish stocking/fish food culturing, rice aquaculture, artificial connections between waterbodies, military transport, etc.) will definitely increase the spread of cladocerans. To date our prognosis is quite pessimistic: the faunal mixing in freshwater faunas will increase in the closest future. Recently, we are at a new stage of invasion studies in the Cladocera (and, most probably, in all freshwater microcrustaceans), leading to a better understanding of the width of the problem. Unfortunately, we need to conclude that the speed of the faunal mixing in freshwaters is increasing, and the chance of stopping this process in the Anthropocene is quite low. “Silent” mixing of faunas is already happening, sometimes resulting in the entire replacement of a native genotype by an introduced one. We do not even know at this moment, what the effects are of such mixing (or entire genotype replacements) for the native ecosystems. We also do not know whether further mixing is a big risk or if it has already happened (i.e., in huge unexplored territories). Moreover, very little is known about the correlation between cladoceran invasives and in-habitat biodiversity [229–231], and this study is a necessary task for the future. Additional references on the cases discussed in this review, are included in Appendix A ([232–248]).

It is important to underline that we already know some cases of non-indigenous species introductions due to military activity, firstly, accompanying the wars which are destructive not only for humans but also for nature, including freshwater bodies and their faunas.

Our recommendation for the future is to identify clearly high-risk taxa and areas using examples and patterns, shown in this review, and to increase the efforts in revealing exotics in unexplored territories by a wide usage of genetic methods as well as improved monitoring in the regions where they were already detected or can be expected. The current review is a first “road-map” to the literature on these micro-crustaceans and a discussion of new patterns in the hope that it will help future monitoring programs and provide a better understanding of the impacts of cladoceran introductions on native aquatic ecosystems worldwide.

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Appendix A

A brief overview of 79 cases concerning 61 taxa in the literature herein assessed as human-mediated introductions versus range expansions in the Cladocera. TR—long-distance transportation; RE—range expansion; PL—planktonic, NP—non-planktonic.

№	TR/RE	PL/NP	Taxon	Region of Non-Indigenous Species Appearance (Recipient Region)	Donor Region	Fist Records of Invasion/Range Expansion	Last Reviews	Our Comments (with Reference to Last Source If We Agree with That Conclusion)
CTENOPODA—SIDIDAE								
1	TR	PL	<i>Diaphanosoma brevireme</i> Sars, 1901	Great Lakes	Neotropics and Southern regions of North America	[122]	[130]	The taxon is widely distributed from Argentina to Florida [130], but its appearance in the Great Lakes seems to be a case of anthropogenic transportation (if the identification is correct).
2	TR	PL	<i>Diaphanosoma dubium</i> Manujlova, 1964	Kazakhstan, Uzbekistan, lower reaches of Volga, Pre-Caucasus, Ukraine	East Asia	[129,131]	[130,132]	Hypothesis on a recent expansion of the distribution range in the south of European Russia, Ukraine, and Middle Asia is realistic [130,132].
3	TR	PL	<i>Diaphanosoma fluviatile</i> Hansen, 1899	Great Lakes, North America	Neotropical zone	[121]		Anthropogenic transportation (less likely, natural range expansion) [121].
4	TR	PL	<i>Diaphanosoma macrophthalmum</i> Korovchinsky et Mirabdullaev, 1995	Kazakhstan, Uzbekistan, Pre-Caucasus	East Asia	[113]	[130,132]	Possibly, occasionally introduced to Middle Asia due to fish introduction as this species is found predominantly in fishponds [130].
5	RE	PL	? <i>Diaphanosoma mongolianum</i> Ueno, 1938	Volga basin	more southern regions	[128]	[130]	The ideas on distribution range changes could be a reflection of previous imperfect state of taxonomy.

№	TR/RE	PL/NP	Taxon	Region of Non-Indigenous Species Appearance (Recipient Region)	Donor Region	Fist Records of Invasion/Range Expansion	Last Reviews	Our Comments (with Reference to Last Source If We Agree with That Conclusion)
6	RE	PL	? <i>Diaphanosoma orghidani</i> Negrea, 1982	Volga basin, European Russia	more southern regions	[127,232]	[130]	The ideas on distribution range changes could be a reflection of previous imperfect state of taxonomy.
7	RE	NP	? <i>Latonopsis australis</i> Sars, 1888	Italy	more southern regions	[124]	[84,90]	Conclusion on human introduction is dubious as this rare taxon had a good chance to be missed in previous studies. This “tropical” species is known from some localities in South Europe [130].
8	RE	PL	? <i>Limnosida frontosa</i> Sars, 1862	Volga, Dniepr basins, and Czech Republic	more eastern regions		[84]	Conclusion on wide range expansion is dubious. The introduction of fish ponds in Czech Republic seems more realistic [130,233].
CTENOPODA—HOLOPEDIIDAE								
9	RE	PL	? <i>Holopedium gibberum</i> Zaddach, 1855	Lena Delta	?	[181]	[179]	Misinterpretation [179]. A new record was made for the region [181], without interpreting the natural range expansion. <i>H. gibberus</i> is very common in North Eurasia.
ANOMOPODA—DAPHNIIDAE								
10	TR	PL	<i>Daphnia ambigua</i> Scourfield, 1947	Europe	Eastern North America	[79]	[65,81,82,84]	Human-mediated transportation with subsequent range expansion confirmed genetically [82].
11	TR	PL	<i>Daphnia ambigua</i> Scourfield, 1947	Japan	North America	[93]	[94]	Possible invader from North America, or secondary introduction from Europe.
12	TR	PL	? <i>Daphnia barbata</i> Weltner, 1897 = “ <i>D. brooksi</i> Dodson, 1985”	Utah (USA) and Michoacán (Mexico)	Africa	[73]	[65]	Possibly an anthropogenic invasion initially from Africa and then North America [73], but this should be checked using molecular methods.
13	TR	PL	<i>Daphnia curvirostris</i> Eylmann, 1887	Mexico and Atlantic Coast of USA	Eurasia	[62–64]	[65,67]	Anthropogenic transportation from Eurasia confirmed genetically [67].
14	TR	PL	<i>Daphnia exilis</i> Herrick, 1895	New York State (USA)	Southern USA and Mexico	[64,120]	[65]	Anthropogenic transportation ca. 1000 km north of the boundary of its natural distribution range.
15	RE	PL	? <i>Daphnia exilis</i> Herrick, 1895	Chile	North America?	[168,170]	[65,178]	In reality, South American <i>D. spinulata</i> Birabén, 1917 is a very common species in southern South America. It is a close congener of <i>D. exilis</i> [178]. Most probably, the authors mixed the two taxa. It is likely that they have observed colonisation of the single man-made water reservoir by a local species, which is a very common process.

№	TR/RE	PL/NP	Taxon	Region of Non-Indigenous Species Appearance (Recipient Region)	Donor Region	Fist Records of Invasion/Range Expansion	Last Reviews	Our Comments (with Reference to Last Source If We Agree with That Conclusion)
16	TR	PL	<i>Daphnia galeata</i> Sars, 1863	North America	Eurasia	[59]	[60]	Anthropogenic transportation and subsequent hybridisation with an indigenous congener confirmed genetically [59].
17	TR	PL	<i>Daphnia galeata</i> Sars, 1863	New Zealand	Eurasia	[101]		Anthropogenic transportation. Initially, the species was identified as <i>D. dentifera</i> Forbes, 1893, but then the identification was improved [15] and confirmed genetically [106].
18	TR	PL	<i>Daphnia galeata</i> Sars, 1863	South Australia	Eurasia	[106]		Apparently, anthropogenic transportation from Eurasia to eutrophied lakes confirmed genetically [106].
19	TR	PL	<i>Daphnia inopinata</i> Popova et al., 2016	Germany (single locality)	Unknown	[142]		It is, most probably, a non-indigenous taxon from an unknown locality as it was found in a military training area, but no other locality for this species is known worldwide [142].
20	TR	PL	<i>Daphnia korovchinskyi</i> Kotov et al., 2021	Samara Area in European Russia	Far East of Russia	[234]		Most probably, transportation of ephippia attached to car wheels. <i>Daphnia korovchinskyi</i> has produced hybrids with indigenous <i>D. curvirostris</i> , but the latter went locally extinct [234].
21	TR	PL	? <i>Daphnia longicephala</i> Hebert, 1977	Great Lakes (USA)	Australia?	[141]		Very dubious record of inadequately described Australian species from North America, most probably a misidentification.
22	TR	PL	<i>Daphnia lumholtzi</i> Sars, 1885	North America	Eastern hemisphere	[71,72]	[65,73]	Transportation with subsequent great range expansion (next entry), well-studied genetically [72].
23	TR	PL	<i>Daphnia lumholtzi</i> Sars, 1885	Brazil and Argentina (South America)	North America	[74,75]	[76]	Anthropogenic transportation from North American populations confirmed genetically [75,76].
24	TR	PL	<i>Daphnia magna</i> Straus, 1820	North America	Eurasia	[68]		Commercial clone escaped from a laboratory, confirmed genetically [68,192].
25	TR	PL	<i>Daphnia magna</i> Straus, 1820	Sevan Lake (Armenia)	More southern regions	[143]	[68]	<i>D. magna</i> already existed in Sevan Lake (Armenia) in the past, but, indeed, together with an indigenous haplotype, this site was colonised by a haplotype from Central Russia—this is an apparent case of anthropogenic transportation confirmed genetically [68].

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26	TR	PL	<i>Daphnia</i> cf. <i>obtusa</i> Kurz, 1874	Australia	?	[105]	[65]	Transportation, but the exact donor region is unknown as many <i>D. obtusa</i> -like taxa are known in different continents [235].
27	TR	PL	<i>Daphnia parvula</i> Fordyce, 1901	Western and Southern Europe	North and South America	[83]	[65,81,84]	Transportation by military amphibian vehicles during WWII followed by range expansion in Europe [83,84].
28	RE	PL	? <i>Daphnia pulex</i> (Linnaeus, 1758)	A lake in Masurian LakeDistrict, Poland	?	[182]	[179]	Misinterpretation by [179]. In reality, these specimens were artificially taken from another water body where they are indigenous and placed in the microcosms.
29	TR	PL	American <i>Daphnia pulex</i> × <i>pulicaria</i> clone	East Africa, then whole Africa	North America	[96,97]	[23]	Transportation to Rift Valley lakes and then range expansion confirmed genetically [23,97].
30	TR	PL	American <i>Daphnia pulex</i> × <i>pulicaria</i> clone	New Zealand	North America	[102]	[103]	Transportation following a rapid range expansion; well-studied genetically. Likely imported by accompanying introduction of salmonid fishes, confirmed genetically [103].
31	TR	PL	American <i>Daphnia pulex</i> × <i>pulicaria</i> clone	Japan	North America		[92]	Transportation confirmed by genetic methods [92].
32	RE	PL	American <i>Daphnia pulex</i> × <i>pulicaria</i> clone	Sardinia, North Italy, Spain	North America	[23,98,99]	[100,207]	Range expansion after transportation from North America confirmed by genetic methods [207].
33	TR	PL	<i>Daphnia</i> cf. <i>pulicaria</i> Forbes, 1893	Japan	North America	[91]		Transportation confirmed genetically [91].
34	RE	PL	? <i>Daphnia sinensis</i> Gu, Xu, Li, Dumont et Han, 2013	Ethiopia	Ethiopia	[142,171]	[179]	Misinterpretation by [179]. In reality, the authors have studied the colonisation of man-made reservoirs by a local species of the <i>D. similis</i> group, widely distributed in Africa [142]. This is a very common process in artificial water reservoirs due to colonisation by indigenous taxa.
35	RE	PL	? <i>Ceriodaphnia dubia</i> Richard, 1894	Two artificial reservoirs in Brazil	?	[169]		We consider this a misidentification. Very likely, this is a common case of a <i>Ceriodaphnia</i> appearing in a man-made water reservoir. <i>Ceriodaphnia</i> cf. <i>dubia</i> is an unusual taxon in tropical South America [236]. The species of this genus are very hard to identify.

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36	RE	PL	? <i>Ceriodaphnia rotunda</i> Sars, 1862	Italy	Other countries of Europe?	[124]	[84,90]	Not likely an anthropogenic introduction; this rare European taxon [81] had a good chance to be missed in previous studies due to misidentification. <i>Ceriodaphnia</i> is not easy to identify.
37	TR	NP	<i>Scapholeberis yahuaracaquensis</i> Andrade-Sossa, Buitron-Caicedo et Elías-Gutiérrez, 2020	Belgium	South America	[137]		Anthropogenic introduction, revealed genetically [137].
38	TR	NP	? <i>Simocephalus hejlongjiangensis</i> Shi and Shi, 1994	Italy	SE Asia	[124]	[90]	This can be a misidentification. Unfortunately, the taxonomy of <i>Simocephalus</i> is outdated now, and any conclusions on the non-indigenous status of this taxon seem premature.
39	TR	NP	? <i>Simocephalus vetulus</i> (O.F. Müller, 1776)	New Zealand	?	[15]	[179]	Misinterpretation by [179]. Ref. [15] originally stated that there is an “uncertain status in New Zealand” for <i>S. vetulus</i> , a species group with naturally occurring representatives in Australasia.
40	RE	NP	? <i>Simocephalus vetulus</i> (O.F. Müller, 1776)	Poland	?	[182]	[179]	Misinterpretation by [179]. In reality, specimens were artificially taken from one water body and placed in a microcosm of another water body.
ANOMOPODA—MOINIDAE								
41	TR?	PL	? <i>Moina affinis</i> Birge, 1893	Italy and Sicily	North America	[88,89]	[84,90]	European populations of <i>M. affinis</i> had a chance to appear due to transportation from North America – it is possible. However, note that <i>M. cf. affinis</i> is present in the Far East of Asia as well [237,238]. Records in Italy and Sicily could belong to a separate taxon or also be another, eastern invasive [239]. The non-indigenous status of European and Far Eastern populations of <i>Moina</i> need to be checked by molecular tools.
42	RE	PL	<i>Moina micrura</i> Kurz, 1875	Volga basin, Baltic Sea	More southern regions?	[133]	[134]	Range expansion north.
43	TR	PL	<i>Moina macrocopa</i> (Straus, 1820)	South America	Eurasia	[109,110]	[69]	Intercontinental transportation confirmed genetically [69].

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44	TR	PL	<i>Moina macrocopa</i> (Straus, 1820)	Mexico	Eurasia	[69]	[69]	Multiple intercontinental transportations of <i>M. macrocopa macrocopa</i> confirmed genetically [69].
45	TR?	PL	? <i>Moina weismanni</i> Ishikawa, 1896	Italy and then other countries of Southern Europe	Far East of Asia	[114–116]	[84]	European populations have appeared after transportation from East Asia. Numerous populations of this taxon were found in Central Asia [240] and southern portion of European Russia and authors concluded that it could have a very wide natural distribution range in South Asia, reaching South Europe. Moreover, [239] confirmed the status of some populations from European Russia as <i>M. weismanni</i> s.str. The taxon must be studied by phylogeographic/ molecular methods.
ANOMOPODA—ILYOCRYPTIDAE								
46	TR?	NP	<i>Ilyocryptus spinifer</i> Herrick 1882	Middle Volga River	Far East of Asia	[135]		Possible anthropogenic transportation or natural introduction of ephippia by waterfowl [135].
ANOMOPODA—MACROTHRICIDAE								
47	RE	NP	? <i>Wlassiscia pannonica</i> Daday, 1904	Italy	?	[241]	[84,90]	This rare <i>Macrothrix</i> -like taxon had a good chance to be missed in previous studies. Italy is within its natural range in Europe.
ANOMOPODA—BOSMINIDAE								
48	TR	PL	<i>Bosmina (Eubosmina)</i> cf. <i>coregoni</i> Baird, 1857 (including <i>B. maritima</i> P. E. Müller, 1867)	North America	Europe (e.g., Baltic)	[55]	[56–58]	Transportation from Europe and then range expansion. Different species of <i>B. (Eubosmina)</i> were recorded from North America, but they form a lineage with recent speciation. Introduction is confirmed genetically [61].
49	RE	PL	? <i>Bosmina (Eubosmina)</i> <i>coregoni</i> Baird, 1857	Slovakia, Volga and Dniepr Rivers basins	Europe		[84]	Such “range expansion” needs to be accurately studied genetically; this is a widespread taxon and different <i>B. (Eubosmina)</i> morphotypes occur in different water bodies independently [61].
50	RE	PL	<i>Bosmina (Eubosmina)</i> <i>coregoni</i> Baird, 1857	Iberian Peninsula	Europe	[125]		Most probably, it is a true range expansion: penetration into the Iberian Peninsula where <i>B. (Eubosmina)</i> was apparently absent [126].

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51	RE	PL	? <i>Bosmina longirostris</i> (O. F. Müller, 1776)	Lake El Tobar (Spain)	?	[180]	[179]	Misinterpretation. This is not an anthropogenic invasion, but colonisation of a new water body by a taxon indigenous to the region.
52	TR	PL	<i>Bosmina longirostris</i> (O. F. Müller, 1776)	New South Wales, Australia	Holarctic	[107]		Possible introduction from an unknown Holarctic locality mediated by fish transportation [107].
ANOMOPODA—EURYCERCIDAE								
53	TR	NP	<i>Eurycercus lamellatus</i> (O.F. Müller, 1776)	Brazil	North Eurasia	[111]	[112]	Transportation from North Eurasia [111].
ANOMOPODA—CHYDORIDAE								
54	RE	NP	? <i>Acroperus harpae</i> (Baird, 1834)	Lena Delta	?	[181]	[179]	Misinterpretation by [179]. Ref. [181] made a new record for the Lena Delta, but <i>A. harpae</i> is very common in Eurasia [242].
55	TR	NP	<i>Alonella excisa</i> (Fischer, 1854) clade I2	Canada	Pacific Asia	[70]		Possible transportation revealed genetically [70].
56	TR	NP	<i>Biapertura ossiani herricki</i> (Sinev, 2013)	Korea	North America	[95]		Transportation, possibly during the Korean War [95].
57	RE	NP	? <i>Camptocercus uncinatus</i> Smirnov, 1971	Italy	Asia	[167]	[84,90]	This rare taxon had a good chance to be missed in previous studies. This taxon is known from Europe so range expansion is likely [218,243].
58	TR	NP	<i>Chydorus brevilabris</i> Frey, 1980	Belgium, Luxembourg, France	North America	[86]		Possible transportation from North America, followed by range expansion.
59	TR	NP	<i>Chydorus sphaericus</i> (O.F. Müller, 1776)	Australia	North Atlantic (Iceland, Greenland)	[108]		Anthropogenic transportation confirmed genetically [108]. However, some populations could have appeared before the Europeans by means of long-term transportation by birds [7].
60	RE	NP	<i>Disparalona cf. leei</i> (Chen, 1970)	Slovakia and the Danube River basin	South Europe	[116,158]	[84]	We consider this a range expansion in Europe. Most probably, this is a separate Eurasian taxon instead of North American <i>D. leei</i> s.str. (needs molecular confirmation).
61	TR	NP	<i>Disparalona striatoïdes</i> (Šrámek-Hušek 1946)	Europe	Africa	[87,116,138]	[84,139]	The taxon was first described in the Czech Republic [138] but then found to be common in Africa [139]. A suggestion of its introduction from Africa [116] is realistic.

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62	RE	NP	? " <i>Alona</i> " <i>rustica</i> (Scott, 1895)	Italy	?	[167]	[84,90]	This rare taxon had a good chance to be missed in previous studies. The species is quite common in Europe but in specific habitats [81,166]. Note: sometimes placed under <i>Flavalona</i> [166].
63	RE	NP	? <i>Leberis diaphanus</i> (King, 1853)	Italy	Tropics of the Old World	[244]	[90]	We consider this a misidentification. Name confusions in <i>Leberis</i> (former <i>Alona diaphana</i> group) are common; North African populations of naturally occurring <i>Leberis</i> can be expected in the Mediterranean; in Africa, <i>L. diaphanus</i> does not occur, but recently revised <i>L. punctatus</i> (Daday, 1898) is widely spread in the Old World [245].
64	RE	NP	<i>Pleuroxus</i> cf. <i>denticulatus</i> Birge, 1879	Slovakia, European Russia	Central Europe	More southern regions?	[158,246]	Ref. [158] speculated that the taxon was possibly introduced in Europe from North America, but this version is dubious as no revision of the <i>P. denticulatus</i> group was performed. Its appearance in Central Europe (i.e. Slovakia and relatively northern localities of European Russia) is most likely a local range expansion of a native species of the <i>P. denticulatus</i> group.
65	TR	NP	? <i>Ovalona weinecki</i> (Studer, 1878)	Easter Island	Subantarctic islands	[150]	[156]	Misidentification. In reality, the population from Easter Island belongs to a separate endemic taxon, <i>Ovalona pascua</i> Van Damme, 2016 [156].
66	RE	NP	<i>Phreatalona protzi</i> Hartwig, 1900	Italy	?	[124]	[84,90]	This rare taxon had a good chance to be missed in previous studies. The species is known from Europe [218] and it lives in unusual habitats; the genus was revised recently, allowing easier identification [165]; Italy is well within its natural range.

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ONYCHOPODA—CERCOPAGIDIDAE								
67	TR	PL	<i>Bythotrephes cederstroemii</i> Schödler, 1877 (earlier misidentified as “ <i>B. longimanus</i> ”)	Great Lakes and then in other water bodies of North America	North-Western European Russia	[40,43,44]	[6,48,203]	Transportation following a range expansion. Korovchinsky and Arnott [48] concluded that invasive populations belong to a single taxon, <i>B. cederstroemii</i> (not <i>B. longimanus</i>). There are some data on earlier colonisation of the Great Lakes basin [203], but they must be rechecked, the recent invasion version is a more plausible hypothesis so far.
68	RE	PL	<i>Bythotrephes brevimanus</i> Lilljeborg, 1901	The Netherlands and Belgium	Circumbaltic region of Europe	[123]	[49,130]	The natural range of this species may have recently expanded westward and colonised water bodies of The Netherlands and Belgium. It may be a natural expansion but there may also be a contribution (or facilitation) by human-mediated transport.
69	TR	PL	<i>Cercopagis pengoi</i> (Ostroumov 1892)	Baltic Sea and the Neva River Estuary	Ponto-Caspian basin	[19,20]	[32,38,132]	Well-documented invasion. Transportation by ship (in ballast water) confirmed genetically [38]. A clear example of human introduction, also clear appearance of resting eggs in Baltic sediments in the 1990s using paleolimnology.
70	RE	PL	<i>Cercopagis pengoi</i> (Ostroumov 1892)	Volga, Don, and Dniepr Rivers basins	Black Sea	[9,27]	[32,38,132]	Range expansion confirmed genetically [38], i.e., after artificial connection of earlier isolated river basins.
71	TR	PL	<i>Cercopagis pengoi</i> (Ostroumov 1892)	North American Great Lakes	Baltic Sea (invasive range)	[54]	[38,132]	Transportation by ships (ballast water) from invasive range in the Baltic Sea confirmed genetically [38].
ONYCHOPODA—PODONIDAE								
72	RE	PL	<i>Cornigerius maeoticus</i> (Pengo, 1880)	The Danube, Dnieper, Don, and Volga Rivers	Ponto-Caspian basin	[9,28]	[29,132]	Range expansion.
73	TR	PL	<i>Cornigerius maeoticus</i> (Pengo, 1880)	Baltic Sea	Ponto-Caspian basin	[25,50,51]	[29,132]	Transportation by ship (in ballast water). According to later records [247], this species has not been observed in the Baltic Sea for years.
74	TR	PL	<i>Cornigerius bicornis</i> (Zernov, 1901)	The lower reaches of the Dnieper, Don, and Volga Rivers	Ponto-Caspian basin	[29]	[132]	Range expansion.
75	TR	PL	<i>Evadne anonyx</i> Sars, 1897	Baltic Sea	Ponto-Caspian basin	[52]	[29,132]	Recent introduction from Ponto-Caspian basin into the Gulf of Finland [52].
76	TR	PL	<i>Evadne nordmanni</i> Loven, 1836	Great Lakes (USA)	World Ocean	[140]	[141]	Transportation by ship (ballast water). This species is also native to the Baltic Sea.

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77	TR	PL	<i>Podon intermedius</i> Lilljeborg, 1853	Caspian Sea	Black Sea	[36]		Transportation through the Volga–Don Canal by ship (ballast water).
78	TR	PL	<i>Pleopis polyphemoides</i> (Leuckart, 1859)	Caspian Sea	Black Sea	[8]	[132]	Transportation through the Volga–Don Canal by ship (ballast water).
79	TR	PL	<i>Podonevadne trigona</i> (Sars, 1897)	Lower reaches of the Dnieper, Don, and Volga Rivers	Ponto-Caspian basin	[9]	[29,132]	The appearance of this species in Eastern Europe was attributed to transportation, e.g., in Romania [228,248] combined with natural range expansion

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