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Review

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Copepod cryptic species as aquatic invaders

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ABSTRACT. The dispersal of aquatic organisms has especially increased since the 19th century, mainly due to the introduction of metal ships with ballast compartments or with birds. Along with easily visible aquatic organisms, there are invasions of less noticeable aquatic organisms, like copepods, which can mainly be recognized by experts. A special group is made up of cryptic species for which morphological identification is inaccessible or very difficult. This review is devoted to the identification, description and analysis of the dispersal routes of three copepod cryptic species complexes into waterbodies. Using molecular-genetic methods, *Eurytemora carolleeae* introduction were revealed in 2007. After describing this invader as a new species, its distribution was also studied using morphology. The invasions of *Acanthocyclops americanus* and *Eurytemora caspica* were mainly studied using morphological methods since the species have already been described; however, molecular-genetic methods were also used to confirm their distinctions from local forms. The real distribution of the former "cosmopolitan" species *Eucyclops serrulatus* was studied using a multidisciplinary approach that combined molecular-genetic, cross-hybridization and morphological methods. Judging by the distribution of local *E. serrulatus* sensu stricto populations in coastal waterbodies of most continents, this species can apparently serve as a good marker of the species dispersal processes with ships. The three possible scenarios resulting from cryptic species introductions and their interaction with local fauna were competitive displacement (*A. americanus*), competitive coexistence (*E. carrolleeae*) and independent development without competition (*E. serrulatus*). The role of cryptic species invasion in aquatic biodiversity modification is discussed.

Keywords: cryptic species dispersal, *A. americanus*, *E. carrolleeae*, *E. caspica*, *E. serrulatus*, scenario of introduction, competitive displacement and coexistence, biodiversity

1. Introduction

The study of biological invasions has become one of the leading areas of aquatic ecology since the second half of the 20th century. Biological invasions are also called biological pollution and most often they are the result of human activity. The main mechanism for the intercontinental dispersal of aquatic organisms is the transport of organisms by ballast water of large-tonnage vessels (Gollasch et al., 2002).

The construction of various hydrotechnical structures (e.g., shipping channels, reservoirs, etc.) also violate biogeographic barriers. The introduction of alien species can cause significant and sometimes catastrophic changes in the ecosystem; for example, the introduction of the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 into the Black and Caspian Seas, the zooplankton crustacean *Cercopagis pengoi* (Ostroumov, 1891) into the Baltic Sea or the mollusk *Dreissena polymorpha* (Pallas, 1771) in the Great Lakes of the North American continent. At the same time, most invasions remain unnoticed and usually do not cause any catastrophic events in the invaded community. A special place among invasions is occupied by cryptic invasions or invasions by cryptic species. Cryptic species are practically indistinguishable by morphological characteristics, but have significant differences at the genetic level (Geller et al., 2010). According to Novak (2011) a cryptic invasion is 'the occurrence of a species or genotype that was not previously recognized as alien in origin or not distinguished from other aliens'.

The first mention of cryptic species bioinvasions was back in 1996 in an article by Carlton (1996) where he used the term "cryptogenic species" and defined them as completely different from what we are "the species that are neither clearly native nor exotic in a biocommunity".

Cryptic species can differ in many parameters including physiological ones, and those differences may cause harmful changes in ecosystem function or

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productivity. Population shifts may eventually have important consequences for biodiversity, biogeography, conservation or fisheries management and ecosystem productivity (Knowlton, 1993; Lee, 2000; Gelembiuk et al., 2006; Declerck et al., 2015; Papakostas et al., 2016). Such invasions might also have important implications for disease transmission; for example, copepods are known as median hosts of many parasites and diseases (Arnold and Yue, 1997; Colwell, 2004; Piasecki et al., 2004; Lee et al., 2007).

Cryptic speciation is especially developed in the aquatic environment due to the predominant development of chemosensory systems for recognizing one's own species there rather than morphological characteristics (Morais and Reichard, 2018). Copepoda is a good example of such organisms, and according to Jarić et al. (2019), they have additional preferences for cryptic invasions like small body size, less-accessible habitats (e.g., aquatic or belowground environments), endoparasitism, camouflage, systematically complex and/or poorly studied species group, interspecific morphological homogeneity and taxonomic instability. According to Panov and Caceres (2007), developed dormancy stages are also a facilitating factor for invasions.

There are few publications devoted to cryptic species invasions among Copepoda: one parasitic copepod (Goedknegt et al., 2018) and our publications on the above-described species (Alekseev and Souissi, 2011; Miracle et al., 2013; Sukhikh et al., 2013; Sukhikh and Alekseev, 2013; Sukhikh et al., 2019; Alekseev et al., 2020; Alekseev, 2021). There are additional publications on other Entomostraca, mainly Cladocera (Mergeay et al., 2005; Ishida and Taylor, 2007; Sharma and Kotov, 2015; Kotov et al., 2020; Taylor et al., 2020) and two articles on *Malacostraca* (Roman, 2006; Grabowski et al., 2012). Many other organisms from different taxa are listed as cryptic invaders in reviews such as plants, algae, Annelida, Hydrozoa, Mollusca, Bryozoa, parasitic Platyhelminthes, Pisces, etc. (Miura, 2007; Morais and Reichard, 2018).

Probably, until a sufficient amount of data has been accumulated and methods for studying such cryptic invasions (mainly methods of molecular genetics according to Jarić et al. (2019)) will become more affordable, small organisms like copepods will be studied less in the sense of cryptic invasions. Here, we reviewed four Copepoda cryptic invasions. Each has its own introduction and naturalization scenario, which might be common for other Copepoda invasions.

The aim of our review is to describe three dispersal scenarios of cryptic copepod species into Eurasian water bodies and the related consequences for local ecosystems.

2. Biological invasion of *Acanthocyclops americanus* (Marsh, 1893) from North America to Eurasia

The history of bioinvasion of the North American cyclopoid *Acanthocyclops americanus* (Marsh, 1892), which is a cryptic species of two European species, *Acanthocyclops vernalis* (Fischer, 1853) and *Acanthocyclops robustus* (Sars G.O., 1863), is in some respects opposite to the case of *Eurytemora carolleeae* described below. *Acanthocyclops americanus* was described in the late 19th century as a distinct taxon from the Great Lakes vicinity of North America. At the beginning of the 20th century, it was found in England, which had the closest maritime ties with the United States at the time, and where the most modern ships equipped with ballast compartments had cruised on a permanent basis since 1880. The species was correctly identified and defined as invasive from North America by Lowndes (1926; 1928).

In the middle of the last century it was found on the mainland in water bodies along the Atlantic coast of Europe in France and Spain in a mass form (Dussart, 1967; 1971), then as a dominant species of summer zooplankton in large reservoirs built on the Dnieper and Dniester (Monchenko, 1961), and then in the reservoirs of the Volga cascade (Vijushkova and Kuznetsova, 1974; Alekseev and Kossova, 1976) and the fresh part of the Caspian Sea (Chuykov, 1986). Further study of its distribution in Europe was temporarily interrupted, and the species passed into the category of cryptic due to a taxonomic mistake of the most prominent expert in the field of copepod taxonomy, Prof. Kiefer. He drew attention to the great similarity between the invader and one of the two native Eurasian species, *A. robustus*, which was described much earlier than the American taxon, but the holotype and type material for it were absent. To address this issue, Kiefer visited Oslo, Norway and took a sample from the lake Sars was working on. Comparing the type population from Sars's lake with individuals of *Acanthocyclops* from other water bodies of Europe, where the invader was already dominant, Kiefer became convinced of their complete identity and synonymized the American species with the species described by Sars, thus making it an artificial cryptic species under the name "*A. robustus*".

In our opinion, Kiefer's taxonomic mistake was caused by the rapid dispersal of the American taxon and its aggressiveness as a more active predator than the native forms. Thus, by the time Kiefer visited Oslo, this species had not only been introduced, but had practically displaced the native species from the lake ecosystem. This can be seen from Kiefer's drawings and was subsequently confirmed by a detailed sampling of the lake and its catchment (Miracle et al., 2013; Alekseev et al., 2020). The native species described by Sars still existed in this lake, but only in the mouths of small river tributaries of the lake; it was displaced by the American invader in the entire pelagial and littoral zones of the lake (Alekseev, 2021). To confirm this hypothesis and the actual validity of both the American and European taxa (in fact, to split this artificial cryptic taxonomy of Kiefer), it was necessary to conduct a molecular genetic examination and compare the type populations of American *A. americanus* and the two European taxa described in the 19th century from Norway by Sars and from Russia by Fischer — *A. robustus* and *A. vernalis*.

Two descriptions were added to these undoubtedly valid species from the water bodies of

France and Norway (Mirabdullayev and Defaye, 2002; 2004), which appeared due to attempts to sort out this confusion and turned out to be young synonyms of controversial cryptic species (*Acanthocyclops trajani = A. americanus*; *Acanthocyclops einsle = A. robustus*) (Miracle et al., 2013).

The phylogenetic tree that we made based on the sequences from the database GenBank (Fig. 1) and the original ones from the habitat types of three these *Acanthocyclops* species show that *A. americanus* from the United States, Mexico, the Czech Republic and Spain are practically identical, while the European forms, *A. vernalis* from Russia and *A. robustus* from Norway, are clearly separated from them. It is interesting to note that the distribution of native *Acanthocyclops* species most likely covers the entire Palearctic, which is confirmed by the discovery of forms very close to *A. robustus* in the area of Lake Baikal (see Fig. 1), 5000 km away from Norway and separated by mountain ranges and catchments of several large rivers.

It should be noted that not all copepodologists agreed with Kiefer's revision. In the identification keys in Ukraine and Russia, and hence in the studies of biodiversity in the territory of the former USSR, the dispersal of the American species continued to be recorded (Monchenko, 1974; Alekseev, 1995; 1998; Kruppa, 1998; Alekseev et al., 2002).

It was shown that after its appearance in the Volga delta (Alekseev and Kosova, 1976) and the Northern Caspian Sea (Chuykov, 1986), the main route of seasonal migration of waterfowl nesting in the Arctic zone of Western and Central Siberia, this species was found as an abundant form of summer zooplankton in water bodies of northern Kazakhstan, Crimea, the Trans-Urals and in even reservoirs of the Yenisei River (such as the Bratsk reservoir) (Alekseev, 1998; Kruppa, 1998; Anufriieva et al., 2014; Alekseev et al., 2020).

Such a rapid settlement of the vast territory covering the divided catchments of the largest rivers of Europe and Asia was possible, in our opinion, due to the active transfer of the invader by birds. This was facilitated by a specific form of physiological protection (winter diapause), which is reactivated in the invader only after the water warms to above 16 °C (Alekseev, 2021). As a rule, migrating birds fly north to their nesting sites following the melting of ice in local water bodies when the water temperature even near the shores of lakes and rivers is only a few degrees above zero. While feeding on bottom remains of plants etc. in this zone of waterbodies, birds capture cysts with dormant stages of invaders and then transfer them over considerable distances (geese up to 1000 km per flight). Both local species of this genus, preferring cold water in the beginning of their life cycles, have already been reactivated by this time and lack the physiological and constitutional (cysts) protection to migrate with birds in this way. Examples of external views of similar cysts protecting dormant copepodites can be seen in Figure 2.

Other reasons, along with efficient transportation by birds and often highly toxic ballast waters of ships, which is facilitated by the protective role of diapause, are rooted in the peculiarities of the invader's biology, which determine its advantage in the competitive struggle with native species. Some of the reasons for the displacement of native species by the invader have already been described in our previous paper, which included a higher growth rate, higher fecundity in comparison with both local *Acanthocyclops* species and adaptive behavioural features of its juveniles that reduce the risk of cannibalism (Alekseev, 2021).

Furthermore, one additional feature of the biology of the invader that was not previously considered but is important is the behaviour of adults in the process of hunting and feeding. Many planktonic invertebrates, being active predators, show dominance of hunting instinct over self-feeding (the so-called wolf in a flock of sheep effect, in which a predator kills many more prey than it can eat or carry away) (Monakov, 2003). Our observations on the feeding behaviours of sexually mature females of the invader on the larvae of the fire shrimps hatching from resting eggs showed that one female is capable of killing dozens of larvae in a short time, which is many times greater than her daily food intake (Alekseev and Pugachev, 1978). This phenomenon, called overconsumption, is known in many, mainly pelagic, copepod species. Both native *Acanthocyclops* cryptic species from Eurasia live in the littoral zone or at the bottom of waterbodies and do not show such high hunting activity (Monakov, 2003). In our opinion, this overconsumption feeding behaviour of the invader that allows it to be dominant. (Alekseev et al., 2002; 2020). We observed this domination usually in shallow-pelagic ecosystems such as city ponds in Belgium (Alekseev et al., 2002).

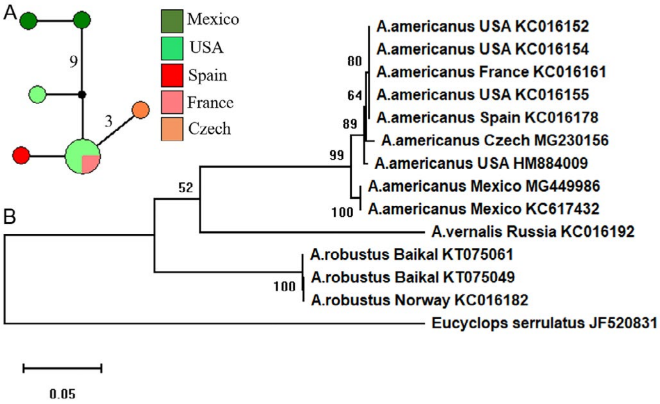

Fig.1. A) Median joining networks of the mitochondrial cytochrome oxidase subunit I (COI) of the mtDNA gene from *Acanthocyclops americanus* (Marsh, 1893) retrieved from GenBank. The black dot indicates the median vector. B) Maximum likelihood phylogenetic tree based on COI sequences of *A. americanus* using 13 sequences retrieved from GenBank. Bootstrap values for maximum likelihood (ML) (≥ 50%) are given for nodes. Accession numbers are given after the species name and geographical location. *Acanthocyclops vernalis* (Fischer, 1853), *Acanthocyclops robustus* (Sars G.O., 1863) and *Eucyclops serrulatus* (Fischer, 1851) are used as outgroups.

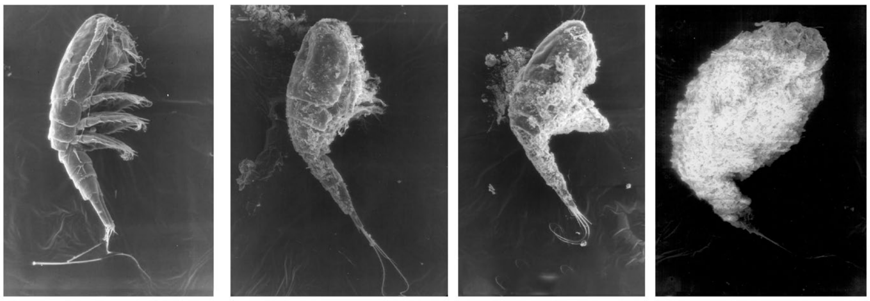

Fig.2. *Diacyclops thomasi* (S. A. Forbes 1882) cysts found by us in the lakes of Quebec at a latitude climatically close to Eurasia.

Such feeding behaviour, along with a high capacity for uncontrolled dispersal, represents, a particular danger of the invading species for Arctic waterbodies such as polygonal tundra lakes, in which the biodiversity of invertebrates is limited to several highly specialized species of crustaceans (Abramova et al., 2017). At present, the dispersal of the invader to the north is apparently limited by a short period of temperatures effective for its life cycle (above 16 °C). As a result, the range of this species does not reach the Polar Circle (64°N) and does not cover the tundra zone (Alekseev, 2021) (Fig. 3).

However, in the event of further climatic warming, the situation may change and the invader can reach arctic area in the nearest future. In that case the biodiversity and productivity of polygonal lakes of the tundra, which provide the main food for nesting waterfowl and juveniles of valuable fish species in the north, may radically change. So effective predator as *A.americanus* is capable of controlling even so large animals like phyllopods (Alekseev and Pugachev, 1978). The phyllopodsform the basis of nutrition for the juveniles of most waterfowl species in this region. . Apparently, it will not be possible to track further change the distribution of *A.americanus*, but it is necessary to follow the development of these species distribution to the north.

3. Settlement of the Palearctic species *Eucyclops serrulatus* (Fischer, 1851) in coastal waterbodies of other continents and zoogeographic zones

The second example, and also the second variant, of the bioinvasion of cryptic species is the dispersal of *E. serrulatus* along the main routes of navigation, apparently throughout the entire period of the sailing fleet. During this period, water was supplied and renewed in places where the ships sailed, usually the estuaries of rivers on the sea and ocean shores. The water was taken and transported after preliminarily emptying the remains and washing out the wooden barrels. The water in these barrels was not boiled, and the organisms contained in it, which were resistant to a decrease in oxygen content and a lack of food, as well as usually to an increase in temperature, were transported step by step, as local populations formed farther and farther along trade routes, geographical research and the colonial conquesting.

Cyclopids of the subfamily Eucyclopinae occupy a leading place among the relatively small number of species that meet the above requirements. *Eucyclops serrulatus* itself has long been considered cosmopolitan (i.e., living on all continents, against which the leading

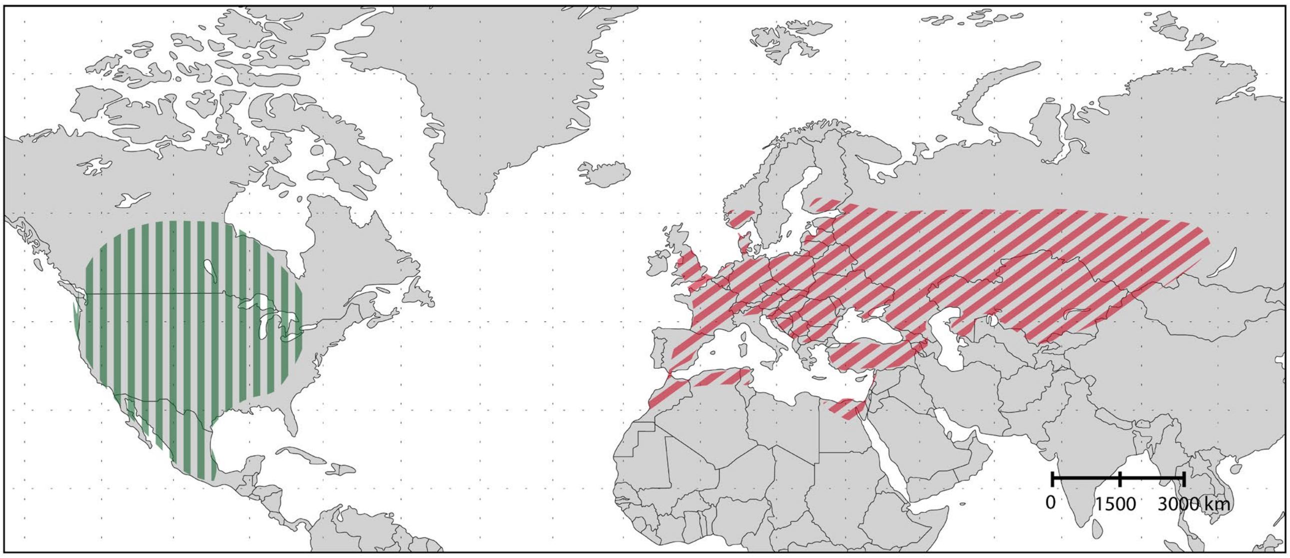

Fig.3. Confirmed native area (in green) of *Acanthocyclops americanus* (Marsh, 1893) and the extent of its invasion in the Palearctic (in red).

taxonomists objected back at the beginning of the last century. Thus, Kiefer explained a phenomenon of cosmopolitanism as a result of insufficient knowledge of species morphology among distant populations.

Indeed, the redescription of a single "cosmopolitanian" type species of *E. serrulatus* sensu stricto using several methods, including hybridization and molecular genetic diagnostics, led to the separation of about 30 species of this complex and, in turn, to the limitation of the natural range of *E. serrulatus* to part of the Palearctic (Alekseev et al., 2006; Alekseev and Defaye, 2011; Fig. 3). At the borders of this area, the species is represented by several subspecies, and outside it is replaced by other taxa, more or less corresponding to their niche properties (eurythermal, polygenerative, meiobenthic, substrate-bound, small collector-detritus eater) (Alekseev, 2019).

At the same time, the study of near-port regions including river deltas and adjacent waterbodies in areas that are very remote from the natural range often reveals the presence (never as dominants, but in a noticeable density comparable to native species) of representatives of the Palearctic species *E. serrulatus* sensu stricto. It has been reliably established (at least at the morphological level) that there are such populations of *E. serrulatus* sensu stricto cut off from the main area of North America, Australia, a number of countries in Southeast Asia (Singapore, Malaysia, Thailand), New Zealand and Tasmania (see Fig. 4).

All of these territories were included in the circle of possession or influence at the level of colonies of Great Britain, the largest maritime power for centuries. There is some evidence that these isolated colonies are the result of biological invasions of these species from Europe that occurred slowly over several hundred years, starting with the period of geographical discoveries. A reasonable settlement pattern of this kind (from one freshwater intake to another) is described at the beginning of this section. To validate this concept, it is necessary to conduct large-scale molecular genetic studies.

The nucleotide sequences of mitochondrial and nuclear DNA are already available in the database (Sukhikh and Alekseev, 2015; Kochanova et al., 2021) and make it possible to not only identify various haplotypes of the Palearctic species *E. serrulatus*, but also to use them to identify penetration vectors, including other invasive species, into various regions of the Earth (Fig. 5).

Such a dispersal of the species apparently occurs without significant rearrangements in local communities since almost everywhere *E. serrulatus* was found several other species, undoubtedly native, were also found in comparable numbers. It is known that this species coexists within its own range, and apparently diverges very effectively along microniches with several representatives of this genus. This complex in the Palearctic includes *Eucyclops macrurus* (Sars G.O., 1863), *Eucyclops macruroides* (Lilljeborg, 1901), *Eucyclops denticulatus* (Graeter, 1903), *Eucyclops speratus* (Lilljeborg, 1901) and *E. serrulatus*. Together with *E. serrulatus*, these species live in approximately equal numbers in the same biotope in the littoral part of lakes and rivers (Rylov, 1948; Monchenko, 1974). The apparent lack of competition seems to be compared with the well-known Hutchinson's paradox of plankton (Hutchinson, 1961), which states that species similar in ecological requirements and occupied niches coexist in the plankton of lakes without displacing each other. The ecological consequences of such a "cryptic" bioinvasion, an example of which is the resettlement of *E. serrulatus*, remain to be studied.

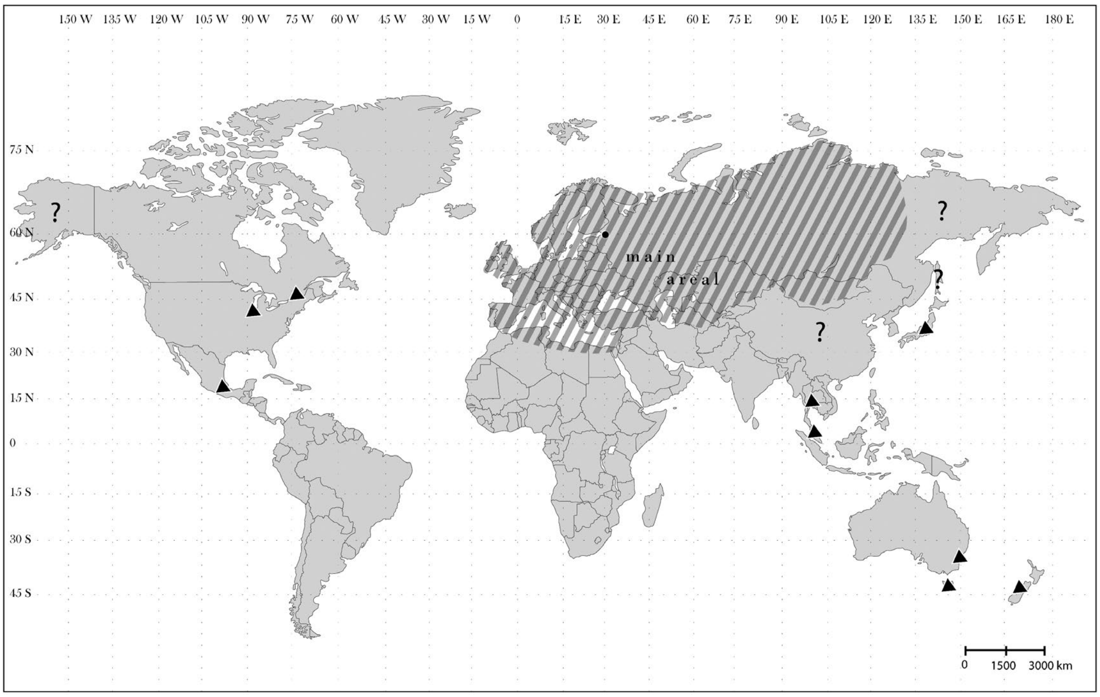

Fig.4. Main range of *Eucyclops serrulatus* sensu stricto (Fischer, 1851) (shaded) and its distant local populations (marked as triangles); the black point indicates the type locality and circles indicate localities of some confirmed findings (Alekseev and Defaye, 2011).

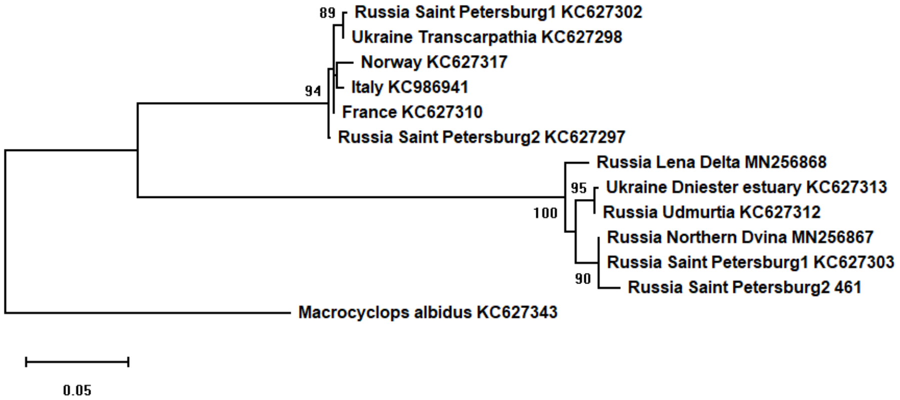

Fig.5. Maximum likelihood phylogenetic tree based on the 13 sequences retrieved from GenBank using the cytochrome oxidase I (COI) mtDNA gene from *Eucyclops serrulatus* (Fischer, 1851). Bootstrap values for maximum likelihood (ML) (≥ 50%) are given for nodes. Accession numbers are given after the species name and geographical location. *Macrocyclops albidus* (Jurine, 1820) was used as the outgroup.

The spread of *E. serrulatus* and similar species contributes to the emergence of the phenomenon of “neo-cosmopolitanism” which is not based on the historical reasons for the settlement of species across continents (the existence of Pangea, drift of continents, evolution of the Tethys Sea, etc.), but on human-mediated dispersals.

4. Biological invasions of *Eurytemora carolleeae* Alekseev and Souissi, 2011 and *Eurytemora caspica* Sukhikh et Alekseev, 2013

The *Eurytemora affinis* species complex is a group of species inhabiting the Holarctic (Lee, 1999). Since the first species description by Poppe in 1880, it was clear that the species has a very high level of morphological polymorphism, even in the Baltic Sea that is close to the type locality where few subspecies were described (Sukhikh et al., 2016). Genetic analysis of extensive population samples of *E. cf. affinis* using the mitochondrial genes 16S rRNA and cytochrome c oxidase 1 (CO1) revealed a significant genetic heterogeneity in the northern hemisphere (Lee, 1999; 2000). As a result, *E. affinis* was recognized as a cryptic species complex (Lee, 2000).

Due to the worldwide distribution of the species complex, its euryhalinity and central position in the food web, it has been well studied using morphological characteristics (Lee and Frost, 2002; Alekseev and Souissi, 2011; Sukhikh et al., 2013), genetic tools (Lee, 2000; Winkler et al., 2011; Sukhikh et al., 2013; 2016; 2019; 2020a; 2020b), hybridization methods (Prof. Sami Souissi, personal communication) and searches of physiological features (Knatz, 1978; Hirche, 1992; Devreker et al., 2008; 2010; Beyrend-Dur et al., 2009; Dur et al., 2009; Lloyd et al., 2013; Lajus et al., 2015).

The phenomenon of cryptic speciation was supported by hybridization experiments that showed reproductive isolation among some North American populations (Lee, 2000) and between North American and European populations (S. Souissi, unpublished data). Furthermore, significant ecophysiological differences between one North American and one European population were found (Beyrend-Dur et al., 2009). Nevertheless, no valid species were distinguished in this complex since morphological stasis was established for these species (Lee and Frost, 2002).

However, when a *Eurytemora* population of the Gulf of Finland was studied with molecular-genetic tools in the frame of the project on biological invasions in 2007, the estuarine North American *Eurytemora* was revealed (Alekseev et al., 2009; Sukhikh et al., 2013). These studies provided the basis for detailed morphological analyses. A new set of morphological signs allows us to overcome the limitation of the morphological stasis hypothesis. As a result, the North American *E. cf. affinis* (USA) was described as a new species, *E. carolleeae* Alekseev and Souissi, 2011. Later, the Asian *Eurytemora* population from the Caspian Sea was also described morphologically as a new species, *Eurytemora caspica* Sukhikh and Alekseev, 2013. Thus, the species complex is currently represented by three species: *E. affinis* with a Palearctic distribution; North American *E. carolleeae*; and Asian *E. caspica* Sukhikh and Alekseev, 2013.

It is interesting that, according to pictures and descriptions of *Eurytemora* species in English waters (Gurney, 1931), it seems as though the American invader *E. carolleeae* already inhabited this area of water at the beginning of the 20th century. Perhaps it was an invasion through ship ballast water, similar to the case of *Eurytemora americana* Williams, 1906, which was originally discovered in 1933 in the same area (Lowndes, 1931).

The presence of the invasive *E. carolleeae* species in European waters has only been reported in specific locations, namely the Gulf of Finland, the Gulf of Riga, Amsterdam channels (Sukhikh et al., 2013), the Oder River (Sługocki et al., 2021), Kiel Bight, Mecklenburg Bight, the Arkona Sea, the Bornholm Sea, the Eastern Gotland Sea (Wasmund et al., 2013) and perhaps in British waters (Gurney, 1931) (Fig. 6, Fig. 7).

Experimental studies comparing the fitness traits (development time, clutch size and longevity) of *E. affinis* (from the Seine estuary, France) and *E. carolleeae* (from St. Lawrence salt marshes, Canada,

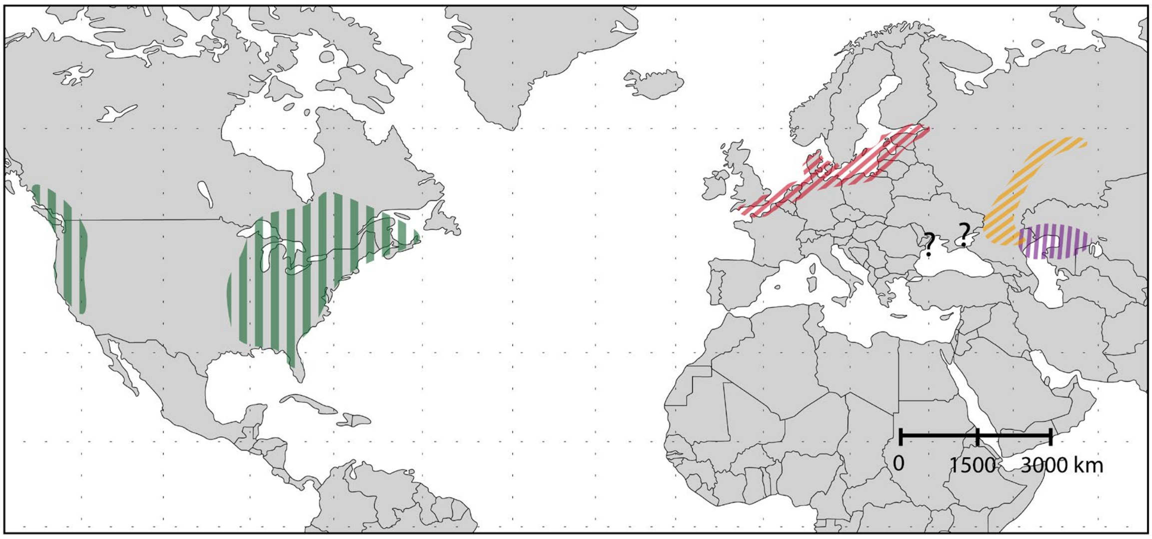

Fig.6. Confirmed native area of *E. carolleeae* Alekseev and Souissi, 2011 (in green) and *E. caspica* Sukhikh et Alekseev, 2013 (in violet) and the extent of the invasions in the Palearctic for *E. carolleeae* (in red) and *E. caspica* (in orange). Question marks are questionable areas for *E. caspica*.

and Chesapeake Bay, USA) have confirmed the higher fitness of the North American population (Beyrend-Dur et al., 2009; Devreker et al., 2012) compared to the European one (Dur et al., 2009; Devreker et al., 2012). In addition, field measurements have suggested that, in both populations, egg production decreases when temperatures rise above 18 ˚C (Lloyd et al., 2013; Pierson et al., 2016). This corroborates results from laboratory experiments (Devreker et al., 2012).

The population dynamics of both species coexisting in the Gulf of Finland are largely parallel and exhibited one or two summer population density peaks at the same time. Invasive *E. carolleeae* is usually second to *E. affinis* in terms of density (the invader accounts for about 30% of the total adult species density for the two species). It was observed that the invasive species has a larger body size and different reproductive traits that could facilitate displacing native *E. affinis* species by alien *Eurytemora* (Sukhikh et al., 2019). Moreover sometimes only *E. carolleeae* was observed in samples; this suggests a major shift in zooplankton populations, featuring a replacement of *E. affinis* by invasive *E. carolleeae*. However, the shift in zooplankton was temporary since samples devoid of *E. affinis* were recorded only two times in the summers of 2010 and 2015. These seasons featured unusual temperatures — hot in 2010 and cold in 2015 (https://en.wikipedia.org; https://en.wikipedia.org/wiki/2010_Northern_Hemisphere_summer_heat_waves). Summer in 2021 was even hotter than in 2010 and water in the Russian part of the Gulf of Finland at the end of July reached 25 ˚C (http://weatherarchive.ru/Pogoda/Lomonosov/July), whereas the yearly mean water temperature in the eastern part of the Gulf of Finland usually varies between 0 (winter) and 18–20 ˚C (summer) (http://weatherarchive.ru/Sea/Ust-luga/July). We did not find total loss of the native species in this year, but density of the alien *E. carolleeae* was six times higher than *E. affinis*, which is abnormal for the Gulf of Finland community (unpublished data). These uncommon temperature conditions probably negatively affected native *E. affinis* populations without reducing population densities of invasive *E. carolleeae*. The temperature tolerance of the invasive copepod species is possibly wider as water temperatures in its native Chesapeake Bay range between 5 ˚C and 25 ˚C (Kimmel et al., 2006). *Eurytemora carolleeae* is also characterized by high egg productivity in the same food conditions (Pierson et al., 2016; Sukhikh et al., 2019), which could favour its rapid spread in the area. Invasive species may be more successful than native ones in fast-changing

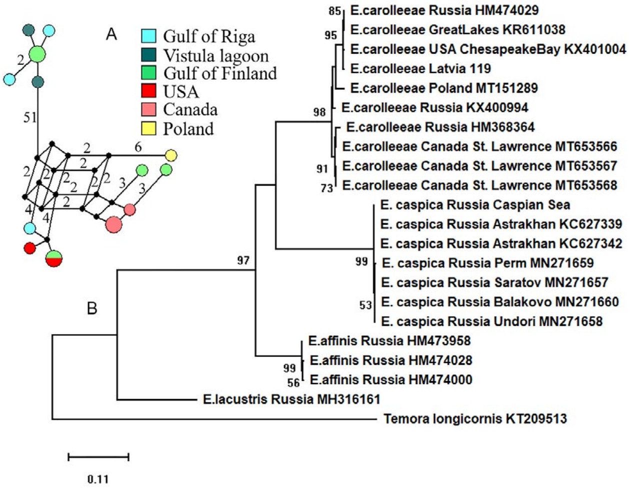

Fig.7. A) Median joining networks of the mitochondrial cytochrome oxidase subunit I (COI) mtDNA gene from *Eurytemora affinis* (Poppe, 1880) (upper) and *Eurytemora carolleeae* Alekseev et Souissi, 2011 (lower) retrieved from GenBank. Black dots indicate median vectors. B) Maximum likelihood phylogenetic tree based on COI sequences of *E. carolleeae, E. affinis* and *Eurytemora caspica* Sukhikh et Alekseev, 2013, constructed using the 22 sequences retrieved from GenBank. Bootstrap values for maximum likelihood (ML) (≥ 50%) are given for the nodes. Accession numbers are given after the species name and geographical location. *Eurytemora lacustris* (Poppe, 1887) and *Temora longicornis* (Müller O.F., 1785) were used as outgroups.

environmental and temperature conditions. Another parameter confirming more favourable environmental conditions for the invader in the Baltic is fluctuating asymmetry (FA). Lajus et al. (2015; 2020) compared levels of FA for populations of *E. carolleeae* from their native Chesapeake Bay and for the native and invasive species in the Gulf of Finland. FA is often used to monitor stress of different origins (Zakharov, 1989; Graham et al., 2010; Beasley et al., 2013). FA was larger for native *E. carolleeae* (Chesapeake Bay) compared to invasive *E. carolleeae* (Gulf of Finland). Interestingly, *E. affinis* from the Gulf of Finland has almost the same FA as the invasive *E. carolleeae* species. This may be the result of generally less stressful environmental conditions in the Gulf of Finland compared to the Chesapeake Bay. The Gulf features different temperature conditions and fewer salinity changes due to the absence of tides. FA of *E. caspica* from the Caspian Sea was minimal within all studied populations (Lajus et al., 2015).

Caspian *Eurytemora* is not as well studied in terms of physiology. According to Krupa (2020), its optimum temperature range is 21–22 °C, which is higher than the values given for *E. affinis* populations in European waterbodies. Initially, the species' area was rather restricted and was represented by northern Caspian Sea and lower Volga River. However, due to the construction of a chain of large water reservoirs along the Volga River, every year the species occupies more and more northern parts of the Volga River and its tributaries up to Perm (Fig. 6 and Fig. 7). Today *E. caspica* reaches the 58th latitude compared to its original range, which was around the 40th–50th latitude (Lazareva, 2018; 2020; Sukhikh et al., 2020b). Considering global warming and ship connections, we can expect further distribution of the species. *Eurytemora caspica* also occurs in central and eastern Kazakhstan (Krupa et al., 2016; Krupa, 2020) and in the Volga-Don channel built in the middle of last century (Lazareva, 2020; 2021). According to the published pictures the species under other names (*E. affinis* and *Eurytemora hirundoides* (Nordquist, 1888)), *E. caspica* is also found in the Black Sea and Sea of Azov (Samchishina, 2005), possibly due to previous invasions via the Volga-Don channel (Lazareva, 2021).

Concluding our review of the introduction of the American species into European waters, we should point out a relatively stable ratio of of its population compared to the native species, which is violated in favour of the invader in years with extreme temperatures. The simultaneous resettlement of the Caspian endemic, which has taken place recently, is due, in our opinion, to hydro-construction (reservoirs on the Volga River) and the creation of navigable canals between the basins of the Black, Caspian and Baltic Seas. The observed tendency of *E. caspica* to move further north allows us to expect to find this species in the Gulf of Finland of the Baltic Sea in the near future.

5. Conclusions

The described examples of biological invasions of cryptic species make it possible to distinguish at least three types of interactions with closely-related species in invaded waterbodies:

- Effective competition, leading to the rapid displacement of native species from their niches, which may be accompanied by taxonomic problems, among other things. Example: *Acanthocyclops americanus* as invader from North America to Eurasia.
- Division of the existing niche between two competitors of practically equal strength and maintenance of a constant relationship between them for a long time, accompanied by periodic changes in the position of one or the other due to fluctuations in environmental conditions (e.g., meteorological conditions). Example: the invasion of *Eurytemora carolleeae* into the Baltic Sea and the Atlantic coast of Europe.
- "Easy" joining of the invader to the community of closely-related species that are similar in ecological requirements and a new community is not formed as observed in the case of *Eucyclops serrulatus* invasion.

Biological invasions can increase biological diversity, leave it unchanged, cause the replacement of one species by another or reduce its population in the event of the penetration of active predators and effective competitors. The dispersal of invasive species of continental hydrofauna, initially based on anthropogenic transportation after crossing serious zoogeographic barriers (such as oceans), can subsequently develop rapidly using local biological routes of dispersal, for example waterfowl. The rate of dispersal in this case can be very high, especially when transportation occurs during the diapause stage of an organism with increased resistance to unfavourable environmental conditions. In our opinion, in recent years a new phenomenon of the distribution of species over distant continents has begun, which should be called "neo-cosmopolitanism". This neocosmopolitanism is based not on the historical reasons for the settlement of species across continents, but on human-mediated dispersals.

Despite the fact that to date, confirmed invasions of cryptic copepod species have been identified only among *Eurytemora* and *Acanthocyclops*, this rather reflects the level of Copepoda research from the point of cryptic bioinvasion, and in many genera of the order there are potential candidates for cryptic invaders (almost all taxa showing cryptic species). This project may be especially pertinent in the context of global climate warming and growing anthropogenic pressure on aquatic ecosystems.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

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