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# Conrad's false mussel *Mytilopsis leucophaeata* (Bivalvia: Dreissenidae) in the Ponto-Caspian region: a synthesis of data

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ZHULIDOV, A.V., KOZHARA, A.V., GURTOVAYA, T. YU., SHOKHIN, I.V., SHEVERDYAEV, I.V., KOSMENKO, L.S., VOLKOV, I.K. & VELDE, G. VAN DER, 2025. Conrad's false mussel *Mytilopsis leucophaeata* (Bivalvia: Dreissenidae) in the Ponto-Caspian region: a synthesis of data. – *Basteria*, 89 (1): 60-70. Leiden. Published 19 July 2025.

**Keywords:** Conrad's false mussel, Dreissenidae, taxonomy, nonindigenous species, invasion ecology, thermohaline preferences, Ponto-Caspian region.

This study summarizes the available data on the distribution of Conrad's false mussel *Mytilopsis leucophaeata*, a highly invasive North American bivalve, in the Ponto-Caspian region. It provides new records of this species from the Black, Azov and Caspian Sea and gives a synopsis of known information on its taxonomy, invasion history, and ecology, with special regard to temperature and salinity and adaptive potential for further spread in the region. In all three sea basins, *M. leucophaeata* seems to slowly continue extending its invasion range. Its occurrence is strongly associated with the areas of major freshwater input. In the

Sea of Azov, the recorded salinity for this species is much lower than the maximum salinity for the basin, while in the Black and Caspian seas it colonizes biotopes with a salinity close to the respective maximum. In general, the existing pattern of *M. leucophaeata* dispersal can only partially be explained by such limiting factors as salinity and temperature. Whatever the nature of these factors, this species has not yet colonized some water areas, that appear suitable for its expansion, first of all, southern and south-western parts of the Black Sea. Based on the COI gene Conrad's false mussels from all over Europe, including the Ponto-Caspian region, belong to the same haplotype, a cold-tolerant lineage of mid-eastern or northeastern USA origin which can represent a separate (sub)species.

## INTRODUCTION

The Conrad's false mussel *Mytilopsis leucophaeata* sensu lato (Conrad, 1831) (Dreissenidae) is a highly invasive, strictly brackish-water bivalve species with a relatively high tolerance for fresh water input. The species is native to the Atlantic coast of North America and the northern Gulf of

Mexico (Marelli & Gray 1983; van der Velde et al., 2010a; Mackie & Claudi, 2010; Kennedy, 2010; Fernandes et al., 2018), where it mainly occurs in subtropical brackish waters. New information on the taxonomy based on molecular data proved that under the name *Mytilopsis leucophaeata* in fact two species or subspecies are hiding of which a single haplotype occurs on the eastern Atlantic coast of the US and is the one which invaded all over Europe (Fernandes et al., 2018). This haplotype is also known as *Congerina cochleata* (see Fernandes et al., 2022).

Invasions of this species occurred in Europe, Asia Minor and South America (Souza et al., 2005; Fernandes et al., 2018; Lodeiros et al., 2019). In South America it invaded Venezuela and in Brazil the surroundings of Rio de Janeiro (Fernandes et al., 2020, 2022). In Europe its distribution is still expanding (Zhulidov et al., 2015). Because of its widespread distribution it is known under several names, synonyms and common names (see below). *M. leucophaeata* is gradually settling in brackish waters of the Black, Azov and Caspian Sea (also known as the Ponto-Caspian region) expanding its distribution (Zhulidov et al., 2015, 2018, 2021).

#### Taxonomic and nomenclatural notes

Initially, the Conrad's false mussel was described as part of the genus *Mytilus* Linnaeus, 1758 – *Mytilus leucophaeatus* Conrad, 1831, from the southern coast of the United States. Later the author classified this species into a separate genus *Mytilopsis* Conrad, 1858 (the journal was dated 1857, but actually published in 1858). Just four years after the description of *Mytilus leucophaeatus* from North America, Nyst (1835) described *Mytilus cochleatus*, a name coined by Kickx. After studying the population in the harbor of Antwerp, he suggested that the species was not a river one, but was brought here by sea vessels. This taxon was later considered (Dunker, 1853) as a member of the genus *Tichogonia* Rossmässler, 1835 (now a synonym of *Dreissena* Van Beneden, 1835). Subsequently, Dunker (1855) reconsidered it as *Dreissena cochleata*. In the same work he described *Dreissena cumingiana* Dunker, 1855 from the Mississippi River, which has subsequently been considered a synonym of *Mytilopsis leucophaeata*. Reeve (1858) described two taxa (*Mytilus americanus* from Florida and *Mytilus tenebrosus* from the Mississippi River) that are considered synonyms of *M. leucophaeata* as well. Sometimes both taxa (*Mytilus leucophaeatus* and *Mytilus cochleatus*) were attributed to the genus *Congerina* Partsch, 1835, described from fossil molluscs and previously grouped with *Dreissena*.

Genetic information should be considered with respect to environmental tolerances such as salinity. Recently, it became clear that with respect to the COI gene of the invasive populations of *M. leucophaeata* in Europe, only one haplotype was involved. This haplotype is the same for the populations along the temperate east Atlantic coast of

North America (Fernandes et al., 2018, 2022; Heiler et al., 2010). This relatively cold-tolerant lineage may be presenting a distinct taxon that originated in the mid-eastern or north-eastern USA and deviating because of past glaciations or the formation of the Labrador Current. This haplotype has colonized Eurasia via harbours by the shipping trade, which function as the hubs for further dispersal (Fernandes et al., 2018). The haplotype can be considered a subspecies or a species separate from *M. leucophaeata* sensu lato. So, it is important to specify the salinity-temperature tolerance of this (sub)species. Shells of *M. leucophaeata* sensu stricto from the Black Sea (Dniester Liman and the Southern Bug river) have been photographed and published (Zhulidov et al., 2018, 2021) just as shells from the Caspian Sea (Bandar Anzali) (Vinarski et al., 2024). The COI gene of specimens from the Black Sea and Caspian Sea was sequenced and compared with other populations in Europe leading to the conclusion that *M. leucophaeata* in Europe represents only one haplotype. This haplotype occurs at the East Coast of North America which is the most likely origin of *M. leucophaeata* in Europe (Fernandes et al., 2018, 2022).

The discovery of *M. leucophaeata* being two or even three (sub)species has consequences for their nomenclature, viz. which one has to maintain the name and what name should be used for the remainder (Fernandes et al., 2018). T.A. Conrad (1803-1877) lived his whole life in Trenton (New Jersey). In his description (1831: 167) he mentions: "Inhabits the southern coast of the U.S.", which is a vague description. This can be the US coast at the Gulf of Mexico, but also the Atlantic coast south of his home. When he established the genus name *Mytilopsis* for the species *leucophaeata* he writes (1857: 167) "inhabits the rivers of Virginia and probably further south". Virginia is a few hundreds of kilometers away south of Trenton. Important is also the word "probably", which means that he has not seen material further southwards (thus not from the US coast of the Gulf of Mexico). So there is no doubt and that the name *leucophaeata* belongs to haplotype 10 and that the name *cochleata* is a junior synonym of *leucophaeata*. The question rises which name the other species of *Mytilopsis* present in the neighboring area of the Gulf of Mexico should bear. A name used in the past is *Dreissena cumingiana* Dunker (1855: 15), type locality "flumine Mississippi Amer. bor.". An older name is possibly *Tichogonia rossmaessleri* Dunker (1852: 89) described from "Brazil". The lectotype of the latter taxon is figured by Fernandes (2018, fig.1e-f). Further studies on a global scale are necessary to unravel the species by a combination of morphological shell characteristics and molecular data.

Common names (according to Falkner, 1990; Prié, 2017; NOBANIS, 2020: with additions made by authors for Russian-language literature) are: Brackish water mussel (English); Conrad's false mussel (English); Dark false mussel (English); Brakwatermossel (Dutch); Brackwasser-Drei-

eckmuschel (German); Brackwasser-Dreikantmuschel (German) (Falkner, 1990); Moules d’Amerique (French) (Prié, 2017); Moule d’eau saumatre (French); Valekirjo-impukka (Finnish); lozhnaya midiya (Russian); lozhnaya midiya Konrada (Russian).

### Invasion history

The Conrad’s false mussel *M. leucophaeata* first arrived in Europe probably around 1800, as Oliver (2015) found a collection of shells of this mollusc in Britain, with an estimated collecting date of 1800. In 1835, the false mussel was found in the harbor of Antwerp, Belgium (Nyst, 1835; Verween et al., 2005). In 1872, it was recorded in the Bergues Canal in France (De Guerné, 1873), and in 1895 in Amsterdam, the Netherlands (Maitland, 1897).

In 1928 this species was first discovered in the Kiel Canal, which connects the North and Baltic Sea in Germany (Boettger, 1932; Schlesch, 1937). It was then found before the end of 1939 on the southern coast of the Baltic Sea, in Klaipeda (Memel), Lithuania (Jaeckel, 1962), and in Baltijsk (Pillau), Russia (Steusslof, 1939; Jaeckel, 1962). In Spain, the Conrad’s false mussel was first discovered in 1993 (Escot et al., 2003), in the UK in 1996 (Oliver et al., 1998), and in Finland in 2003 (Laine et al., 2006).

Subsequently, this mollusc continued to be found throughout Europe (Girardi, 2003; Escot et al., 2003; Darr & Zettler, 2000; Dziubinska, 2011; Florin et al., 2013; van der Velde et al., 2010b; Verween et al., 2010; van der Gaag et al., 2014; Forsström et al., 2016; Zulian & Quaggiotto, 2020; van der Gaag, 2021).

In the Black Sea, the Conrad’s false mussel was first discovered in Ukraine’s Dniester Estuary in 2000–2001 (Son, 2007; Grigorovich et al., 2002; Therriault et al., 2004). After that, it was not observed for a while (Son, 2007) until 2009, when it was found near the city of Mykolayiv (Nikolaev) at the mouth of the Southern Bug River (Heiler et al., 2010). In the Sea of Azov, this mollusc was first discovered on the territory of the Russian Federation, not far from Rostov-on-Don, in 2004 (Zhulidov et al., 2015).

In the Caspian Sea, live individuals of *M. leucophaeata* were first recorded in 2009 in the waters of Iran (Heiler et al., 2010), and then, in 2014, in the northern part of the Caspian Sea, on the territory of Russia (Zhulidov et al., 2018). Prior to this, in 1996, empty shells of *M. leucophaeata* were found in the north of the Caspian Sea, near the mouth of the Ural River in Kazakhstan (Boeva et al., 1999; Zhulidov et al., 2018).

In the Black Sea, as far as we know, populations of this mollusc are currently stable and abundant only in the areas around Odessa and Mykolayiv (Zhulidov et al., 2018, 2021). Elsewhere in the Ponto-Caspian region, it is either not found at all (Bulysheva et al., 2020) or is found sporadically, with an apparent expansion of its range in brackish

waters, judging by the number of new findings (Zhulidov et al., 2015, 2018, 2021), extending eastwards in the Black Sea as far as Georgia (Mumladze et al., 2019).

In the future, it can cause serious problems in the Ponto-Caspian region. This is due to the colonization of underwater structures, such as pipes of technical facilities (Mackie & Claudi 2010; Rajagopal & van der Velde 2012; van der Velde et al., 2010b; van der Gaag, 2021) and transformation of local biological communities (Vitousek, 1990; Williamson, 1996; Robinson et al., 2007; Simberloff et al., 2013).

In the present article, we have synthesized all available earlier information on the distribution of *M. leucophaeata* in the Ponto-Caspian region since 1996 (see under references all papers with earlier records and overviews). We present here new unpublished data on the locations where this species was recorded in the Ponto-Caspian region from 2020 until September 2023.

## MATERIALS AND METHODS

### Sampling

In all cases, as in previous studies (Zhulidov et al., 2015, 2018, 2021), living molluscs and/or their empty shells were collected in desalinated areas of the Black, Azov and Caspian Sea (Table 1). Underwater surveys were conducted in all locations (except Azerbaijan and Turkmenistan) at depths of 0–3 m. Living shellfish and/or their empty shells were collected manually or, if the substrate was hard, using a frame sampler. The European Environment Agency habitat classification terminology was used to describe the substrate (European Environment Agency, 2012). Samples of living molluscs were preserved in 96% ethanol for further morphological and molecular analyses and deposited at the Southern Scientific Center of the Russian Academy of Sciences.

### Salinity measurements

Water salinity was measured using a ysi Pro Plus handheld multiparameter conductivity meter. The instrument was calibrated using a KCL standard solution with a conductivity of 10 mS/cm as recommended by the manufacturer (for use in brackish water, from brackish to estuarine habitats).

Salinity values were determined based on measured conductivity values in accordance with the 1978 Practical Salinity Scale (Zhulidov et al., 2018). A portable refractometer (RHS-4ATC) was used to measure salinity in estuarine areas where salinity ranged from 6 to 15. In areas where salinity due to seasonal floods was below 3, a manual salinity meter (TDS-3) was used. This was manually calibrated to a range of 0–9990 parts per million (ppm) (Zhulidov et al., 2018).

### Identification of molluscs

*Mytilopsis leucophaeata* can be identified by the presence of an apophysis, a tuberculate structure located under the anterior inner part of the shell where muscles are attached (see fig. 2 in Zhulidov et al., 2021; fig. 3 in Zhulidov et al., 2018; and fig. 105b in Kijashko, 2013). This feature distinguishes *M. leucophaeata* from all other local species of Dreissenidae and Mytilidae in the Ponto-Caspian region.

In this case, it is important to consider the potential invasion of *Mytilopsis sallei* (Récluz, 1849) into the Ponto-Caspian region, since it has expanded to the Mediterranean coast of Israel via the Suez Canal (Galil & Bogi 2009; Fernandes 2018). A characteristic feature that distinguishes individuals of the two species from each other is the

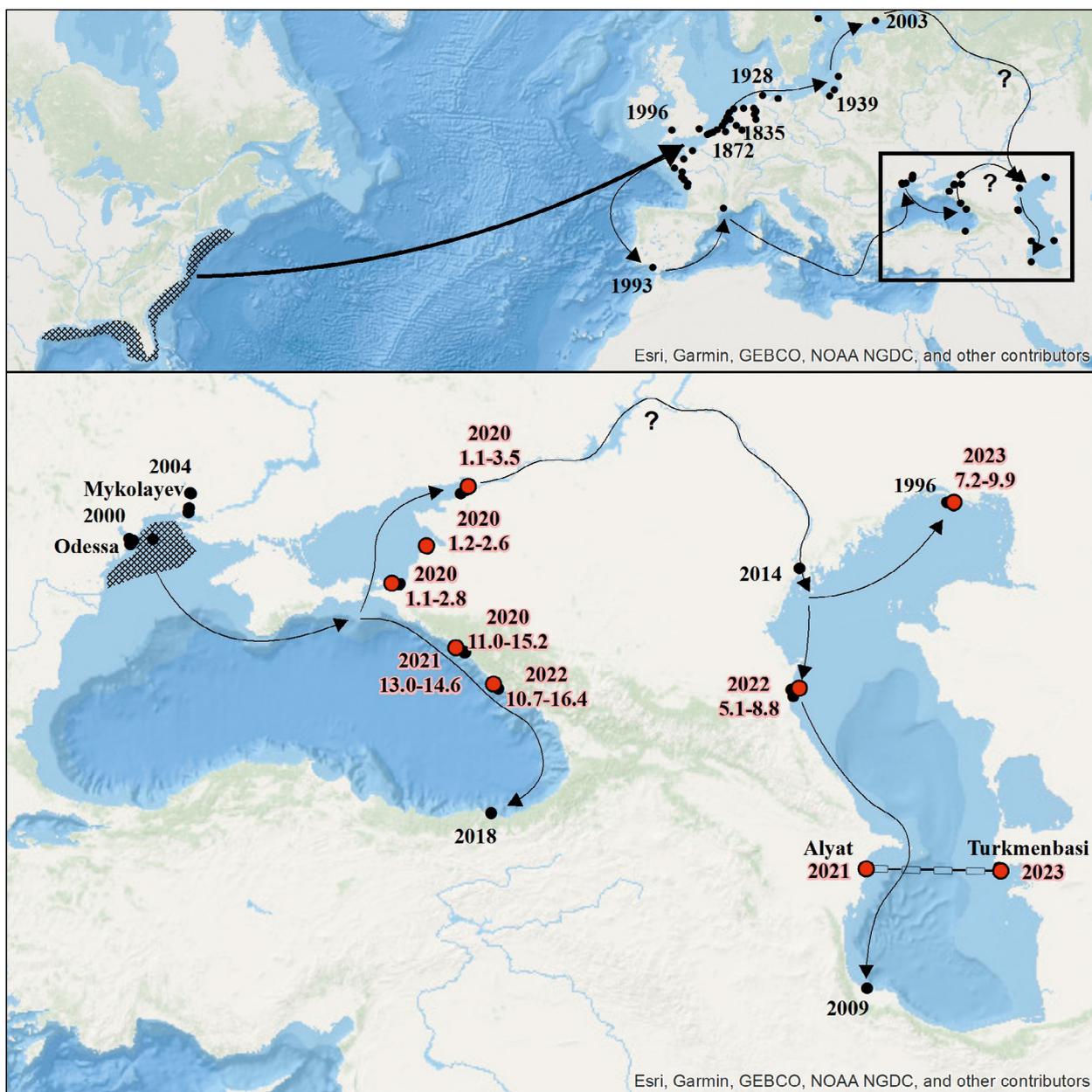
straightened dorsal margin of the shell in *M. leucophaeata* compared to the curved dorsal margin in *M. sallei*. However, this character is not always reliable, especially given the debate in interpretations of *M. sallei* as a taxon - a more reliable diagnostic feature may be the difference in apophysis shape between the two species (Marelli & Gray, 1983, 1985; see also Zhulidov et al., 2021).

### RESULTS

The results obtained between 2020 and September 2023 are presented in Table 1 and Fig. 1.

Location	Coordinates (Latitude N and longitude E)	Sampling date	Salinity (PSU)	Substrate	Number of live molluscs and / or empty shells; shell length (mm)
The Sea of Azov					
Primorsko-Akhtarsk surroundings, Russia	46.02 N 38.14 E	June 25, 2020	1.2 – 2.6	Mixed sediments, silty sand, shelly ground	15 live specimens and 1 empty shell; 6.8 – 12.7
Temryuk Bay, Taman Peninsula, seaport area in the mixing zone of the Kuban River waters and the waters of the Sea of Azov, Russia	45.333 N 37.336 E	July 30, 2020	1.1 – 2.8	Mixed sediments, silty sand, shelly ground	7 live specimens and 5 empty shells; 9.5 – 13.4
Taganrog Bay, close to the Don River delta, Russia	47.044 N 39.209 E	September 5, 2020; June 25, 2022	1.1 – 3.5	Mixed sediments, silty sand, gravel, shelly ground	5 live specimens and 1 empty shell; 10.2 – 15.1
The Black Sea					
Tuapse Bay, suburbs of Tuapse Town, Russia	44.09 N 39.062 E	August 15, 2020	11.0 – 15.2	Mixed sediments, sand, pebble	1 live specimen and 3 empty shells; 7.9 – 9.2
Tuapse Bay, suburbs of Tuapse Town, Russia	44.086 N 39.073 E	September 5, 2021	13.0 – 14.6	Mixed sediments, sand, pebble	4 live specimens and 1 empty shell; 7.1 – 10.3
Suburbs of Adler City, Russia	43.412 N 39.926 E	August 23, 2022	10.7 – 16.4	Mixed sediments, sand, pebble	5 live specimens; 9.2 – 14.4
The Caspian Sea					
Surroundings of Sulak settlement, Dagestan, Russia	43.349 N 47.481 E	June 12, 2022	5.1 – 8.8	Shelly ground, mixed sediments	6 live specimens and 1 empty shell; 10.1 – 15.0
Sea/ferry port of Alyat (70 km from Baku City), Azerbaijan	39.952 N 49.441 E	September 20, 2021	No information available	Mixed sediments	2 live specimens and 4 empty shells; 6.8 – 8.0
Turkmenbashi port surroundings, Turkmenistan	40.006 N 52.903 E	May 18, 2023	No information available	No information available	3 empty shells; 7.7 – 9.2
The Ural River delta area, Kazakhstan	46.865 N 51.552 E	September 8, 2023	7.2 – 9.9	Mixed sediments	3 live specimens and 2 empty shells; 6.8 – 8.0

**Table 1.** New locations of *Mytilopsis leucophaeata* in the Ponto-Caspian region from 2020 to September 2023, with information about the locations and coordinates, the date of their discovery, water salinity in the sampling sites (PSU), and the number of alive mussels (or empty shells) found with their shell length range (mm) in the Ponto-Caspian region from 2020 to September 2023.



**Fig. 1.** Map of the Ponto-Azov-Caspian region with sampling locations of *Mytilopsis leucophaeata*. Red circles – samples collected from 2020 to 2023 (Table 1), black circles – earlier collections, arrows – dispersal routes. On the cutaway, the general scheme of *M. leucophaeata* dispersal is presented. Salinity ranges are presented at various locations.

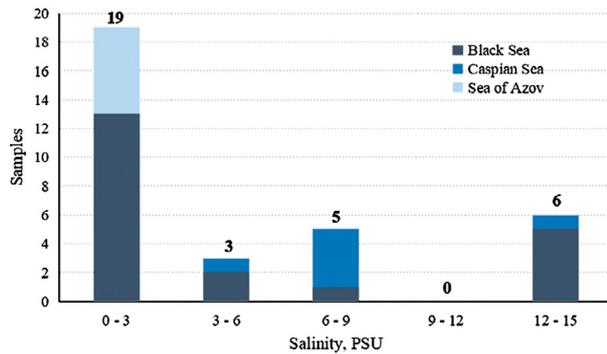
## DISCUSSION

### Dispersal patterns and salinity

The data presented in Table 1 and Fig. 1 for 2020 - 2023, as well as earlier data (Zhulidov et al., 2015, 2018, 2021; Mumladze et al., 2019) suggest that *M. leucophaeata* is still successfully expanding its range in the Ponto-Caspian region, colonizing exclusively brackish-water biotopes (including estuarine ones), but in a wide range of salinities. Thus, in the Ponto-Caspian region, this species was found in brack-

ish biotopes with salinities ranging from 0.9 to 4.1 PSU (in the Sea of Azov), from 0.6 (which is the boundary between fresh and sea water) to 16.4 (in the Black Sea) and from 4.2 to 13.0 (in the Caspian Sea) (see Table 1, Fig. 2 and also Zhulidov et al., 2018, 2021). Meanwhile, water salinities in the biotopes where *M. leucophaeata* was searched for, but could not be found, ranged from 0.9 to 3.2 PSU in the Azov Sea, from 0.8 to 15.1 in the Black Sea and from 2.4 to 11.0 in the Caspian Sea.

It should be noted that in brackish-water biotopes, espe-



**Fig. 2.** Frequency distributions of salinity at the sampling locations of *Mytilopsis leucophaeata*, with reference to particular sea basins. According to the aggregated data from Zhulidov et al. (2015, 2018, 2021) and this study. For sites with salinity range indicated instead of a single value, mean ranges were used.

cially in zones of active mixing of sea and fresh waters, water salinity can vary greatly with time due to hydrological and external factors such as surge processes. As a result, it can be difficult to determine an “optimal” salinity based on field measurements taken at a specific location and time. Anyway, the histogram of the preferred salinities (Fig. 2) allows to spot some general patterns. In particular, in all of three sea basins, *M. leucophaeata* is evidently confined to freshened parts of the respective water areas. However, in the Caspian and Black seas the false mussel colonizes habitats with salinity close to the maximum for the basin (13 and 18 PSU, respectively) while in the Azov Sea (up to 12-13 PSU) it occurs in waters with a lower salinity.

The fact that only empty shells of *M. leucophaeata* were collected in the area of the port of Turkmenbashi, Turkmenistan, does not allow us to conclude that this species has already reached the eastern coast of the Caspian Sea. Nevertheless, given the following:

- that *M. leucophaeata* larvae may have a higher tolerance to water salinity compared to the benthic stage (see: Siddall, 1980; Mackie & Claudi, 2010; van der Gaag, 2021, as well as the literature cited in Zhulidov et al., 2015, 2018, 2021),
- as well as the fact that the distance between the port of Alyat, Azerbaijan (western coast of the Caspian Sea) and the port of Turkmenbashi, Turkmenistan (eastern coast of the Caspian Sea) is only about 300 km and there is also a regular rail ferry service operating between these ports,
- and also, that the individuals of *M. leucophaeata* are able to colonize ports in brackish waters by way of shipping (Leuven et al., 2009; Zhulidov et al., 2018, 2021),

we believe that there is a high chance that this mollusc has already reached the eastern coast of the Caspian Sea.

Environmental factors contributing to the range expansion of *M. leucophaeata* beyond its native range have been described in detail (Therriault et al., 2004; Kennedy, 2010;

Zhulidov et al., 2015, 2018; van der Gaag et al., 2016; van der Gaag, 2021). The available information on the distribution of *M. leucophaeata* in the Ponto-Caspian region and its successful colonization of biotopes in the Dniester River estuary, the lower reaches of the Southern Bug River and in the Don River delta area (which are subject to regular winter freezing), demonstrate the ability of this species to withstand winter temperature minimums in natural conditions. At the same time, in experiments, a high mortality rate of this species was noted at temperatures around 0 °C, up to the complete death of individuals (see van der Gaag et al., 2016; van der Gaag, 2021 and the literature cited therein). Thus, our data on the distribution of *M. leucophaeata* in the Ponto-Caspian region indirectly confirm the assumption (Zhulidov et al., 2015) that adaptive processes in populations of these molluscs can facilitate their dispersal, especially in the region under study.

Note that Forsström et al. (2016) subsequently came to a similar conclusion based on findings of *M. leucophaeata* in the relatively cold-water conditions of the northern and eastern Baltic Sea, namely in the waters of Sweden and Finland. In addition, this species was found in the Gulf of Gdańsk, where the minimum water temperature is -0.4°C (Brzana et al., 2017), which also suggests a greater tolerance to winter temperatures than could be expected from experiments and earlier phases of the mollusc’s distribution in the area of invasion.

The dynamics of the spread of *M. leucophaeata* in the Ponto-Caspian region is noteworthy. The slow rate of expansion is similar to that of another dreissenid species, *D. rostriformis bugensis* Andrusov, 1897 (*D. bugensis* auctorum) in the Azov-Black Sea region. For a long time, these molluscs were restricted in their distribution to a small area in the Dnieper-Bug estuary of the Black Sea. However, in the second half of the 20th century they unexpectedly began to expand their range (Zhulidov et al., 2010; Matthews et al., 2014). As already indicated, it is likely that the intensification of international shipping, as well as increased hydraulic engineering in this and neighboring regions, played a significant role in the dispersal of both species (Leuven et al., 2009).

The fact that individuals of *M. leucophaeata* in the Black Sea have established themselves in large numbers only in the areas of Odessa and Mykolayiv, while they are found sporadically in other parts of the sea and do not form large clusters, is most likely due to differences in international shipping activity. After the collapse of the Soviet Union, international shipping was more intense in the territorial waters of Ukraine, especially in the area of the ports of Odessa and Mykolayiv, than in other parts of the Black Sea (Zhulidov et al., 2018). It is very likely that the areas of these ports were those where *M. leucophaeata* first arrived and successfully adapted to local conditions, forming stable and numerous populations.

Considering the thermohaline dynamics of the Ponto-Caspian region, we can observe a rapid increase in salinity in the Sea of Azov after 2007, from about 10 to 15 PSU (Berdnikov et al., 2023), especially in its more freshwater part, the Taganrog Bay, due to a period of low river discharge of the Don and Kuban rivers. Additionally, the water temperature has risen (up to 1°C since the 1980s), accompanied by a decrease in ice coverage and the duration of the ice season in winter (Yaitskaya & Magaeva, 2018). These changes appear to improve the living conditions for *M. leucophaeata*. For the Black Sea's northern part, similar trends in salinity can be seen due to a decrease in river flow from the Dnieper River (Podymov et al., 2021; Gazyetov & Dyatlov, 2021). However, these changes are less significant for the Black Sea as a whole, as there has been no significant decrease in river discharge from the Danube River or the rivers on the southern coast during the recent period. The Caspian Sea is also characterized by a slight decrease in the duration of ice cover, accompanied by minor desalination (Yaitskaya & Magaeva, 2020). This seems to indicate a stable condition for the *M. leucophaeata* population in this regional sea.

The distribution of the Conrad's false mussel in the Ponto-Caspian region suggests that this species has not yet colonized multiple water areas, that appear suitable for its expansion. These include adjacent waters near which it has previously been recorded. This may indicate that there are factors that evidently prevent its more active and more successful spread in the waters of the Ponto-Caspian region and, in our case, these are neither salinity, nor water temperature. According to our data (Zhulidov et al., 2018, 2021) *M. leucophaeata* is mostly confined to areas with variable and disturbed hydrological regimes. Most records of living individuals of this species were made in estuaries subject to hydrological fluctuations due to hydro-engineering and other human activities or near the mouths of mountain rivers, viz Tuapse River and Mzymta River in the Black Sea or Sulak River in the Caspian Sea. In all cases, there are irregular fluctuations with time intervals much larger than a day and the range of oscillations varying to a large extent. Although *M. leucophaeata* usually occurs on hard substrates, our findings indicate that it is able to occupy other substrates in the absence of typical biotopes colonizing diverse localities with a broad range of fluctuating conditions.

Despite of the above limitations, this species seems to exhibit high resilience that could be a prerequisite for its further invasion success. Previously, Therriault et al. (2004) explained the possibility of *M. leucophaeata* spreading in the Ponto-Caspian region by the ability to adapt to a wide range of environmental conditions and by the presence of routes for invasion. The genetic potential for adaptation in this species has not yet been studied, but it may play an

important role in its ability to expand and colonize new water areas and biotopes (Czarndowski et al., 2010; Flegr, 2013).

The maximum salinity of the Black Sea populations corresponds well with that of the North Sea Canal population near Amsterdam in the Netherlands. Tolerance experiments demonstrate that the found maximum tolerance of the North Sea Canal population (18 PSU; van der Gaag et al., 2016) was similar with the maximum salinity values found for *M. leucophaeata* in the Ponto-Caspian region, indicating also that European populations in the whole continent are belonging to only one haplotype (van der Gaag et al., 2024) as demonstrated by molecular biological studies for the populations of Odessa and the Caspian Sea and west European populations in relation to the east Atlantic populations in North America (Fernandes et al., 2018, 2022).

A clear contrast with the pattern in the Mediterranean Sea basin where, to our knowledge, only two occurrences of *M. leucophaeata* have been hitherto known (Girardi, 2003; Zulian & Quaggiotto, 2020), apart from two other findings at the south Iberian coast (Escot et al., 2003; Alvarez et al., 2023) is of special interest. Despite of almost twofold higher salinity in the Mediterranean as compared to the Black Sea, there seems to exist many possibly suitable stable freshened water bodies throughout the basin, such as coastal lagoons or river estuaries, not to mention the intensity of ship traffic facilitating the invasive bivalve dispersal. This question calls for further investigation.

## CONCLUSIONS

After almost a two century-long latent phase *M. leucophaeata* started to move south-eastwards from the sites of primary invasion and in quite a short time spread almost all over the Ponto-Caspian region, with barely settled Mediterranean left in its rear. The overall distribution and dispersal pattern of the Conrad's false mussel in the Ponto-Caspian region together with biotopes characteristics is consistent with relative uniformity of biological and ecological features of this species throughout the whole invasion area in Eurasia, first of all, its tolerance to cold water environments. Taking into consideration molecular genetic evidence (Fernandes et al., 2018, 2022) supporting the existence of two distinct lineages of *Mytilopsis leucophaeata* with different invasion vectors, from which the cold-tolerant one (of mid-eastern or northeastern USA origin) have colonized Europe and reached the Caspian Sea basin, we believe that this lineage can represent a separate (sub) species. Reduced genetic diversity of this population system, with only single haplotype for the COI mitochondrial marker, probably needs further confirmation for the Ponto-Caspian region.

## ACKNOWLEDGEMENTS

The study was funded by the state assignment research of the Southern Scientific Centre of the Russian Academy of Sciences (SSC RAS) (projects No. FMRE-2025-0072, No. 125012100503-4 and No. 125011200143-4) and was carried out under the sections No. 124032500016-4 and No. 124032100075-5 of the State Task of the Institute for Biology of Inland Waters of the Russian Academy of Sciences. We thank Ruud Bank for constructive critical remarks which have led to improvement of the paper.

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