

Research Article

Status of the invasive brackish water bivalve *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae) in the Ponto-Caspian region

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Abstract

Since 1996, the invasive Conrad's false mussel *Mytilopsis leucophaeata* (Conrad) has been recorded in brackish water bodies in the Ponto-Caspian region, which includes the basins of the Black Sea, Azov Sea, and Caspian Sea. In the Azov-Black Sea basin, where the number of records is increasing, its range currently includes the Dniester, Dnieper-Southern Bug, and Don River estuarine systems, and the mouth of the Tuapse River near the town of Tuapse. In the Caspian Sea basin, *M. leucophaeata* is present in areas near the mouths of the Volga and Ural rivers, and in the south Caspian Sea, near Bandar Anzali town. The present study analyses new records from this region as well as previously published records. All sites in the Azov-Black Sea basin with records of living specimens of *M. leucophaeata* were characterized by changes in the hydrological regime due to the effect of hydraulic engineering (mostly along deep-water shipping canals or for fish ladders). The most probable vector for long-distance dispersal of *M. leucophaeata* is transatlantic shipping to the Black Sea basin; while for secondary spread, coastal and inland shipping across adjacent ports is likely. Introduction of this species to the Caspian Sea could have resulted from specimens first present in the Black Sea or from independent long-distance transfer.

Key words: Azov Sea, Black Sea, Caspian Sea, invasion ecology, invasion pathways, shipping

Introduction

Conrad's false mussel or dark false mussel *Mytilopsis leucophaeata* (Conrad) is an invasive, brackish water bivalve species originating from the North American Atlantic coast and the northern part of the Gulf of

Mexico which occurs mainly in subtropical and warm-temperate regions (Marelli and Gray 1983; Van der Velde et al. 2010a). Certainly, temperature plays a large role in the species' natural and historic distribution patterns, but range expansion relative to its temperature limits is likely a function of climate change



Figure 1. Map of the Ponto-Azov-Caspian region with sampling locations of *M. leucophaeata* (1–6: Earlier records in white circles with black line and numbers; 7–12: New records of this study in black circles with white numbers; 1: Republic of Kazakhstan, Caspian Sea, Atyrau (Guryev), near the Ural River mouth; 2: Ukraine, Dniester Liman, 2001; 3: Ukraine, Dnieper-Bug Liman; 4: Russian Federation, Taganrog Bay of the Azov Sea, close to the Don River delta; 5: Iran, Caspian Sea, Bandar Anzali; 6: Ukraine, Southern Bug River, near Mykolayiv (Nikolaev); 7: Ukraine, Dniester Liman, 2009–2014; 8: Artificial canals between Dniester and Budakskiy limans; 9: Ukraine, Southern Bug River mouth area; 10: Ukraine, Southern Bug Liman; 11: Russian Federation, north-western Caspian Sea, adjacent to the Damchik area of the Astrakhan Biosphere Reserve; 12: Russian Federation, Tuapse River bay of the Black Sea.

and adaptation to local conditions at new colonization sites (Zhulidov et al. 2015). The species is still expanding its distribution in Europe (Zhulidov et al. 2015; Forsström et al. 2016) and this recent spread is of concern because it can cause severe bio-fouling problems in brackish water systems (Mackie and Claudi 2010; Rajagopal and Van der Velde 2012). These problems include fouling of ship hulls, and clogging of cooling water systems and pump houses of power plants and industries (Van der Velde et al. 2010b).

In 1996, three whole empty shells of *M. leucophaeata* were found in the northern Caspian Sea near the Ural River mouth, Atyrau (Guryev) Town, Republic of Kazakhstan (Figure 1) (Boeva et al. 1999).

The first record of live specimens in the Caspian Sea basin was in 2009 (Heiler et al. 2010). In the Azov-Black sea region, *M. leucophaeata* was first recorded in 2001 in the Dniester Liman (lagoon-type river estuary) in the Black Sea basin, Ukraine (Grigorovich et al. 2002; Therriault et al. 2004), and later found in the Azov Sea basin in 2004 (Zhulidov et al. 2015) and the Southern Bug River near the town of Mykolayiv (Nikolaev), Ukraine in 2009 (Heiler et al. 2010).

This paper reviews the published records and provides further evidence of the occurrence and establishment of *M. leucophaeata* in the Ponto-Caspian region based on new records. Furthermore, we discuss the significance of these findings in relation to the ecology, invasion patterns and ecological risks of this species.

Table 1. Records of *Mytilopsis leucophaeata* in the Ponto-Azov-Caspian basin.

N	Location and coordinates	Sampling date*	Shell length (mm)	Number of specimens or density**	Salinity (PSU)	Reference
1	Republic of Kazakhstan, Caspian Sea, Atyrau (Guryev), near the Ural River mouth (46.822778; 51.515833)	1996	10.4–11.2	3 whole empty shells	6.1–8.7	Starobogatov in Boeva et al. 1999
2	Ukraine, Dniester Liman (Not known)	2001	No data	2 specimens	No data	Grigorovich et al. 2002; Therriault et al. 2004
3	Ukraine, Dnieper-Bug Liman (46.635358; 31.933425)	July 2003	12.4–14.6	4 whole empty shells	1.2–6.3	Zhulidov et al. 2015
4	Russian Federation, Taganrog Bay of the Azov Sea, close to the Don River delta (46.085389; 39.224314)	August 2004 and August 2005	12.8–15.4	3 specimens (2004), 5 specimens (2005)	0.9–4.1	Zhulidov et al. 2015
5	Iran, Caspian Sea, Bandar Anzali (37.481936; 49.460281)	April 28, 2009	5.5–22.0	Several hundred specimens	12.0–13.0	Heiler et al. 2010
6	Ukraine, Southern Bug River, near Mykolayiv (Nikolaev) (46.98035; 38.967789)	July 3, 2009	No data	No data	No data	Heiler et al. 2010
7	Ukraine, Dniester Liman (46.170833; 30.403611)	Repetitive samples from August 10, 2009 to March 23, 2014	Max. 24.5	2400 individuals per m ² at maximum aggregation	1.0–2.4	This study
8	Artificial canals between Dniester and Budakskiy limans (46.101944; 30.438611)	Repetitive samples from August 10, 2009 to March 23, 2014	Max. 19.0	2400 individuals per m ² at maximum aggregation	No data	This study
9	Ukraine, Southern Bug River mouth area (46.719167; 31.951389)	May 2, 2012	Max. 4.0 ***	7 specimens	2.6	This study
10	Ukraine, Southern Bug Liman (46.644444; 31.938333)	August 13–14, 2013	Max. 7.5	600 individuals per m ² at maximum aggregation	2.7–3.0	This study
11	Russian Federation, north-western Caspian Sea, adjacent to the Damchik area of the Astrakhan Biosphere Reserve (45.636111; 47.714444)	September, 2014	10.2–3.8	7 specimens	5.2–7.6	This study
12	Russian Federation, Tuapse River bay of the Black Sea (44.086389; 39.078611)	October 11, 2014	8.8–10.1	2 specimens	4.7–10.2	This study

*: For repetitive sampling, the year of first record is provided; **: Live specimens unless otherwise indicated; ***: Live juveniles; empty shells of large adults were also present.

Materials and methods

Over the years 2009–2014, several surveys were undertaken to assess the presence of *M. leucophaeata* in the Dniester and Southern Bug rivers, and the Black and Caspian Seas (Table 1). At all locations in the Dniester and Southern Bug rivers (and associated limans), snorkel surveys at depths of 0–2 m were performed and specimens were collected by hand or

with a frame sampler for scraping molluscs from hard substrate. The mussel specimens were deposited at the Institute of Marine Biology, Odessa (former Odessa Branch Institute of Biology of the Southern Seas). An additional survey by snorkelling in the Black Sea (near Tuapse) was performed in October 2014 at a depth of 1.5–2.0 m. A final survey to determine the presence of *M. leucophaeata* was done in the north-western Caspian Sea in September 2014. Samples were collected by hand at depths of 1.5–2.0 m.

The literature records of *M. leucophaeata* were compiled from several independent studies with different goals (Table 1; Zhulidov et al. 2015). Specimens of *M. leucophaeata* were haphazardly sampled in most cases. When possible, the density of mussels at sites with maximum aggregation was recorded. Otherwise, the total number of specimens collected over the sampling period was presented.

Results

Both previously published records of *M. leucophaeata* in the Ponto-Caspian region as well as new records from this study are listed in Table 1. The species was first recorded in 1996, 2001 and 2004 in the Caspian Sea, Black Sea and Azov Sea, respectively. It had been reported from a number of isolated localities over nearly two decades indicating that this species has become definitively established in the Ponto-Caspian region (Table 1, Figure 1).

Mytilopsis leucophaeata was collected in the north-eastern Caspian Sea near the Ural River mouth, Atyrau (Guryev) Town, Republic of Kazakhstan in 1996 (Boeva et al. 1999, see Fig. 1, p. 1). Three intact empty shells were collected by hand at a depth of about 1.0 m: the first known record of *M. leucophaeata* based on empty shells in the northern Caspian Sea. It is noteworthy that the simultaneous survey conducted in the north-western part of the Caspian Sea near the Volga River delta (near the Damchik area of the Astrakhan Biosphere Reserve at circa 430 km distance from the Ural River mouth) failed to reveal the presence of this species (Boeva et al. 1999, see p. 11 in Fig. 1). However, in 2014, live specimens of *M. leucophaeata* were found in the same location (Location 11 in Table 1).

Mytilopsis leucophaeata was found in 2001 in the Dniester Liman (Black Sea); however more intensive sampling in 2002 failed to find them again (Stepien et al. 2013; Grigorovich et al. 2002; I.A. Grigorovich, pers. comm.). Initial reports of *M. leucophaeata* in the Black Sea basin were documented by Grigorovich et al. (2002), who listed this species in an extensive literature review on alien species in the Ponto-Caspian region, and Theriault et al. (2004) identified *M. leucophaeata* among specimens collected from the region that were used to define dreissenid phylogeny (the year of collection was 2001; I.A. Grigorovich, pers. comm.). In August 2009, *M. leucophaeata* was recorded in the Dniester liman where populations were quite large (Table 1; Figures 2 and 3). Two live specimens in the Tuapse River bay of the Black Sea were collected in 2014. In the Dniester Liman, *M. leucophaeata* was found exclusively on hard substrates. In the Southern Bug River mouth area the species was sampled from concrete and granite



Figure 2. *Mytilopsis leucophaeata* in the Dniester liman (Photo: M. Son, 12th August 2009).

boulders near the embankment in Mykolayiv Town. In the central stretch of the Southern Bug Liman the species occurred on reed stems, pondweeds and the vertical surfaces of limestone debris.

In the Azov Sea, *M. leucophaeata* was first found in 2004 in Taganrog Bay, close to the Don River delta (Zhulidov et al. 2015). At all mentioned localities, this species was not abundant and no massive aggregations (druses) were found. At all locations, except the location of the first record from the Caspian Sea (Boeva et al. 1999) and of the first record from the Dnieper-Bug Liman (Zhulidov et al. 2015), live individuals of *M. leucophaeata* were recorded.

Discussion

The new records and available literature show that *M. leucophaeata* has definitively established in the Ponto-Caspian region and has recently expanded its range in this area. The number of localities allows us to discuss the pathways for introduction, recent spread and ecology of *M. leucophaeata* in this region, with reference to water temperature, salinity, hydrological conditions, substratum, and oil pollution. The current distribution pattern of this species indicates jump dispersal with gradual expansion from established populations.

Ecology in the Ponto-Caspian region

Water temperature

Most records of *M. leucophaeata* in the Ponto-Caspian region are confined to zones of regular winter freezing (Nazarov 1962; Vinogradov et al. 1966) suggesting

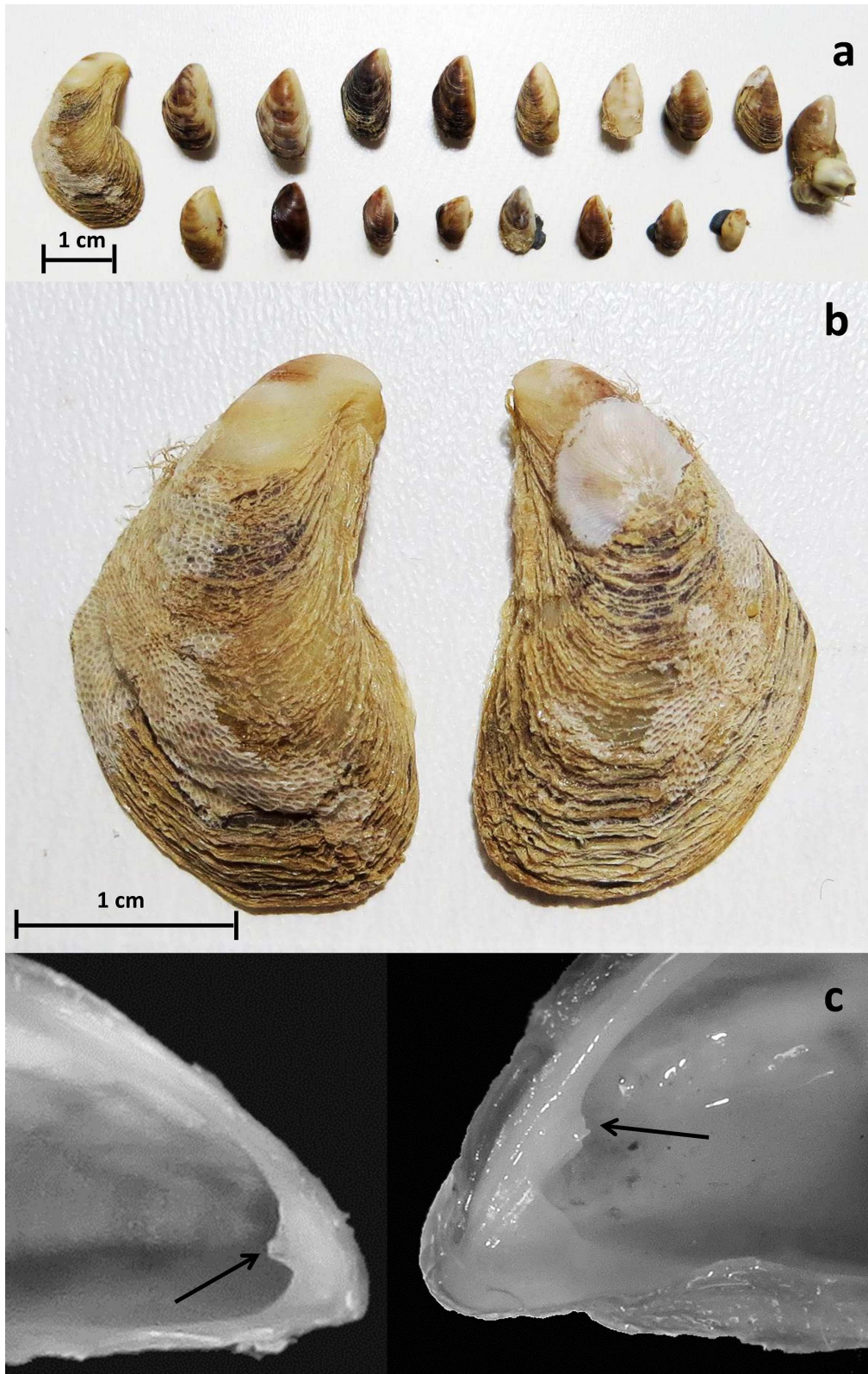


Figure 3. *Mytilopsis leucophaeata* collected from the Dniester liman (An arrow indicates the apophysis, a tubercle under the beak of the shell, where the foot muscles are attached; Photo: M. Son).

a higher tolerance of this species to low water temperatures than earlier reported (Van der Velde et al. 2010a; Van der Gaag et al. 2014, 2018; Zhulidov et al. 2015). Similarly, this species was found in the northern Baltic Sea, a region also subject to winter freezing (Forsström et al. 2016).

Hydrological conditions

Mytilopsis leucophaeata was mostly collected in estuaries in the Azov-Black Sea region with variable and disturbed hydrological regimes. All living specimens from this region were collected in biotopes that were subject to hydro-engineering activities, mostly along deep-water sea canals or fish ladders which lead to larger changes in salinity than would naturally occur in Azov-Black Sea estuaries (limans). All semi-closed “bottle-like” estuaries (especially Dniester Liman) are protected from marine intrusion by sand spits or other accumulative forms making these water bodies function like closed lagoons (Mikhailov 2004; Mikhailov and Gorin 2012). An important habitat modification affecting estuarine ecosystems in these regions is the construction of deep-water shipping canals that require regular dredging of sediments, hence promoting massive intrusion of seawater into estuaries and river deltas during storm surges causing rapid salinity fluctuations. The impact can be magnified due to large-scale water withdrawal upstream from these estuaries and river deltas. These specific regional types of man-made disturbances in non-tidal sea basins (Dotsenko and Ivanov 2010) may result in changes in communities and, especially, expansion of alien and native species uncommon for these local habitats (Vinogradov et al. 2012, 2014).

In the north-western part of the Black Sea there is a huge cluster of major sea ports situated along large river estuaries and connected with the open sea by deep-water shipping canals allowing marine waters to flow upstream, such as those at Belgorod-Dnestrovsky, Mykolayiv and Kherson Cities (Dotsenko and Ivanov 2010; Vinogradov et al. 2012, 2014). Deep-water canals provide corridors for spread of Black Sea species in the Azov Sea basin and the Tuapse River bay system (Matishov 2006; Vinogradov et al. 2012).

Salinity

Black Sea estuaries of the “liman” type have steady gradients of salinity and are only weakly dependent upon marine hydrological processes (Zhulidov et al. 1997; Mikhailov and Gorin 2012). Physiological features of the species inhabiting these types of estuaries are different from those in tidal estuaries

where, for most brackish fauna species, the range of salinity tolerance (obtained in experiments) is much wider than the actual range of salinity in their habitats (Kinne 1957). However, in non-tidal seas with a wide salinity gradient and relatively constant local salinity of the bottom water layer (Ponto-Caspian basin, Baltic Sea), many species tend to occupy all possible habitats within their tolerance ranges (Khlebovich 1974). Such a contrast in the fauna of tidal estuaries is because populations inhabiting the latter type are exposed to regular but short-term salinity changes outside the ecological optimum that do not require permanent local adaptations. *Mytilopsis leucophaeata* is classified as a mainly intertidal species and is known to first populate intertidal zones when invading new geographic locations (De Souza et al. 2005). However, in The Netherlands *M. leucophaeata* occurs in stagnant brackish water such as canals with salt intrusion via sluices with only slight daily fluctuations, but sometimes large annual fluctuations (Wolff 1969; Van der Gaag et al. 2016).

Unlike the tidal estuaries group, populations of Ponto-Caspian species have to perform all of their biological functions at constant salinity that can range from optimal to extreme (Khlebovich 1974). The populations of the Ponto-Caspian species existing at the upper limit of their salinity tolerance are more negatively affected, compared to brackish tidal estuarine species, during rapid salinity fluctuations.

Alterations of salinity regimes induced by human activities in Ponto-Caspian water bodies transform them into systems similar to tidal estuaries allowing for invasions of Atlantic brackish water species, such as *M. leucophaeata* (Orlova 1987; Orlova et al. 1998). Such artificially transformed estuaries can be considered as potential stepping-stones for further dispersal of this species.

Densities

It seems likely that the inability of *M. leucophaeata* to form druses limits the number of occurrences in undisturbed ecosystems of the region, because areas with optimal salinity are mostly found in offshore areas that characteristically have a deficit of hard substrates. However, this species may be common on various technical constructions that are often inaccessible for researchers, such as inlets of power plants and quays of industrial facilities.

Substratum and biofouling

The lack of hard substrates for suitable attachment is probably connected with hydrological regime. In tidal estuaries, substrates such as littoral and sublittoral rocks, boulders and gravel stones are

washed and cleaned of sediment by strong tidal currents, but substrates in non-tidal Ponto-Caspian estuaries are mostly silted, and only a narrow belt of “mid-littoral” hard substrates is kept clean by wave oscillation. In the sublittoral zone, natural hard substrates include mostly dreissenid shells, reed and pondweed.

In highly industrialized brackish water harbour areas in The Netherlands and Belgium *M. leucophaeata* reached high densities due to the wide availability of hard substratum (e.g., rip rap and stones protecting bank erosion, hydraulic structures) and optimal habitat conditions (Rajagopal and Van der Velde 2012; Van der Gaag et al. 2017, 2018). Despite acting as a hazardous biofouling species in these areas, *M. leucophaeata* seems not to cause severe biofouling problems in the Ponto-Caspian basin because of low population densities in most locations (Table 1).

Pathways and vectors for introduction

Lack of evidence for natural dispersal indicates vectors for dispersal are most likely related to vessel traffic through marine or inland waterways. *Mytilopsis leucophaeata* can disperse as larvae by ballast water uptake and discharge, or as a fouling organism on ship hulls (Van der Gaag et al. 2016 and literature therein). Records of *M. leucophaeata* in estuary ports are often associated with inland shipping involving river-marine vessels (Therriault et al. 2004; Heiler et al. 2010). This vector is relevant for the introduction and spread of alien species in all major invasion corridors of Europe (Panov et al. 2009). Three invasion corridors related to inland waterways connect the Ponto-Caspian basin with areas where *M. leucophaeata* was previously recorded (Bij de Vaate et al. 2002; Leuven et al. 2009): (1) The Northern corridor, connecting the catchments of the Black, Azov and Caspian seas with the Baltic Sea basin via the Volga-Don Canal, Volga and Don rivers, and the Volga-Baltic Canal and the river Rhine with the Baltic Sea; (2) The Central corridor, connecting the Black Sea basin with the Baltic Sea region via the Dnieper River and the Bug-Prpyat Canal and with the North Sea basin via an extensive network of waterways; and (3) The Southern corridor, linking the Black Sea basin with the North Sea basin via the Danube-Main-Rhine waterway.

Expansion through the Central Corridor is improbable, because when *M. leucophaeata* was first found in the Ponto-Caspian basin there were no open routes for sea-river cargo vessels through the canals connecting the Dnieper River basin with the Baltic Sea basin (Karatayev et al. 2008). Similarly, expansion through the Southern Corridor from the North

Sea to the Black Sea also seems unlikely. The Southern Corridor became functional as a dispersal vector once the Main-Danube Canal was opened in 1992. This technically allowed direct navigation to and from the North Sea ports in the Rhine River delta and ports in the Danube River delta (Leuven et al. 2009). Even so, long-distance vessel traffic was hardly possible for heavy transport vessels because of difficult navigation conditions on the Danube River. This promoted extensive use of lightering (transferring cargo to shallow-drafted vessels) forming a barrier for brackish-water migrants such as *M. leucophaeata*. Even if *M. leucophaeata* passed this barrier, it likely would have appeared first near estuarine river ports of Ukraine or Romania. During the 2000s, these areas were thoroughly investigated by biologists (Alexandrov et al. 2007; Skolka and Preda 2010) and this species was not found.

According to Boeva et al. (1999) and Laine et al. (2006), *M. leucophaeata* was found in the vicinity of inland ports along the Northern Corridor (from the Baltic Sea to the Caspian Sea) later than in the Ponto-Caspian basin. However, there are much earlier records of *M. leucophaeata*, before World War II, in Baltic inland ports at Klaipeda (Memel) in Lithuania and Baltiysk (Pillau) in Russia (Steussloff 1939; Jaeckel 1962; Schütz 1969). It is unclear if these earlier populations disappeared or were neglected during ensuing years because nobody investigated these areas again. Recently, *M. leucophaeata* was recorded in the Vistula Delta (Brzana et al. 2017). Thus expansion through the Northern Corridor from the Baltic Sea to the Caspian Sea cannot be excluded.

The Black Sea is a principal recipient of shipping-related invasions by brackish and marine species with a notable presence of naturally spreading Lessepsian migrants (Nunes et al. 2014). In the last few decades, there has been a constant increase in ship traffic to ports of the northern Black Sea region, in the volume of ballast water exchange, and in the number of alien species introduced (Alexandrov et al. 2007). On the whole, most direct, long-distance transportation between the northern Black Sea region and different regions of Atlantic and North Europe are made through large open sea ports like the Port of Odessa, while the estuarine ports have narrower specialization.

The first records of *M. leucophaeata* in the Dniester Liman do not match the most probable place of first invasion of this species to the Black Sea. Initial invasions to the Dnieper-Southern Bug estuarine system seem far more credible as a place of greater concentration of shipping infrastructure. The Southern Bug River mouth and the Black Sea are connected by the Bugsko-Dneprovsko-Lymansky

Canal (BDLC), providing access to a number of significant sea ports near the town of Mykolayiv. In its turn, the BDLC is connected by the Kherson Sea Canal with the Dnieper River delta, where important Kherson ports are located. During the supposed establishment of *M. leucophaeata* in the Black Sea basin (from late 1990s to early 2000s), these ports had regular shipping traffic to other regions where *M. leucophaeata* had been introduced. For example, the Mykolayiv Merchant Sea Port in the Southern Bug River mouth was a long-term source for grain export to Belgium and other European regions where *M. leucophaeata* was recorded (Ilnitsky 2005).

The assumption of primary establishment of *M. leucophaeata* in the Southern Bug Liman is fully consistent with its expansion in the Black Sea. It is connected with the Dniester Liman by coastal shipping and with the Port of Tuapse by marine trans-shipment of petroleum products from the Tuapse Refinery through the Tuapse oil terminal (Anonymous 2018a). Ukraine, as a part of the former USSR, remains an important recipient of oil and oil products from the Russian Federation. Import and transfer of oil products is one of the specializations of the Mykolayiv Merchant Sea Port (Anonymous 2018b). The Tuapse bay is one of the locations with a new record of *M. leucophaeata* (Location 12 in Figure 1).

The suggested pathways for introduction and spread of *M. leucophaeata* in the Ponto-Caspian region could be tested with phylogeographic studies using genetic markers to confirm whether proposed routes are consistent with genetic data.

Ballast water and oil pollution

Preventive measures for minimizing the effects of ballast water exchange according to the International Ballast Water Convention and Regional Action Plans for the Black Sea have only been ratified and implemented very recently by countries in the Ponto-Caspian Region (Kideys 2008). *Mytilopsis leucophaeata* could be transported in isolated ballast water and ballast water from oil tanks. Isolated ballast water is exchanged when passing from marine to riverine conditions or vice versa. The waterway between the Black and Caspian Seas is a complex transport corridor that includes a number of sea canals and freshwater river sections forcing ships to repeatedly change isolated ballast water. For example, by the time of entry to the Caspian Sea, ballast water would have originated from the Don River. Likewise, ships returning from the Caspian Sea have ballast water from the Volga River delta. Oil is exported from the Caspian Sea area to ports in the Black Sea. Ballast water in oil tanks is taken at the import port in the

Black Sea and is changed near the export port in the Caspian Sea. Regulations prohibit discharging oil-contaminated waters in freshwater sections of the Volga and Don rivers, where *M. leucophaeata* cannot establish (Gard 2007). Therefore, oil exporting ports in the Caspian Sea have a greater risk of being subject to biological invasions. There have been no studies on the survival of *M. leucophaeata* in oil-contaminated ballast tanks, but a related species, *M. sallei* (Récluz), is able to live in oil polluted harbours (Mohan and Prakash 1998). It is important to note that the oil fraction forms a thin film on the water surface and hence the remaining water may be unaffected. For estuarine alien species, which are transported in ballast waters of oil tanks, the key recipient areas in the Ponto-Caspian region would be around the Azov-Don Canal (for transportation from the Black Sea to the Azov or Caspian Sea basins) and the Volga-Caspian Canal (for transportation from the Caspian Sea).

The scenario of transport and introduction of *M. leucophaeata* via ballast water is in agreement with known records. Anzali Port, where *M. leucophaeata* was found in 2009 (Location 5 in Figure 1), is one of the key oil-exporting Caspian ports which has connections with the Black Sea and other parts of *M. leucophaeata*'s range. Transit from Anzali Port to the Astrakhan Sea Port beginning in the 2000s became part of North-South (Nostrac) cargo route from India to European countries. During transportation ships change ballast water in the Volga-Caspian Canal (see records near Astrakhan in 2014, Location 11 in Figure 1). The records of *M. leucophaeata* in the area around the Azov-Don Canal can be attributed to transportation from the Black Sea.

The finding of empty shells of *M. leucophaeata* near the Republic of Kazakhstan does not seem to be related to transportation in ballast waters of commercial ships but likely to fouling. The Black Sea, Asov Sea and Caspian Sea are extensive brackish water areas (Kosarev and Yablonskaya 1994; Mandych 1995), which are potentially suitable for the colonization of *M. leucophaeata* as this species tolerates a salinity of 0.2–17.5 PSU (Van der Gaag et al. 2016).

Conclusions

Mytilopsis leucophaeata has become established in estuarine systems throughout the Ponto-Caspian region, and this species has strong potential for further dispersal in the basin. Despite a widespread distribution, this species has not yet reached high numbers in these areas and apparently has not become a dominant species. Therefore spatial distributions and habitats of this species relative to its

population dynamics are of special interest and need further investigation and monitoring.

An important prerequisite for *M. leucophaeata* naturalization in non-tidal estuaries in the region is probably construction of deep-water canals for shipping. This allows changes of salinity due to intrusions of sea water through canal beds during storm surges. Fish ladders can exert a similar effect. These man-made habitat changes likely emulate fluctuating environmental conditions that compare to conditions found in native habitats of this species. Among all possible dispersal vectors and pathways, the dispersal pattern of *M. leucophaeata* in the Ponto-Caspian region is most consistent with long-distance shipping between large sea ports. In such areas, this species could potentially create a major biofouling problem if it reaches high densities.

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