Towards effective conservation and governance of Pontocaspian biodiversity in the Black Sea region

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2

DECLINE OF UNIQUE PONTOCASPIAN BIODIVERSITY IN THE BLACK SEA BASIN: A REVIEW

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Abstract

The unique aquatic Pontocaspian (PC) biota of the Black Sea Basin (BSB) is in decline. Lack of detailed knowledge on the status and trends of species, populations and communities hampers a thorough risk assessment and precludes effective conservation. This paper aims to review PC biodiversity trends using endemic molluscs as a model group. We aim to assess changes in PC habitats, community structure and species distribution in the Black Sea Basin (Bulgaria, Romania, Moldova, Ukraine and Russia) over the past century and to identify direct anthropogenic threats. Presence/absence data of target mollusc species was assembled from literature, reports and personal observations. PC biodiversity trends in the NW Black Sea Basin coastal regions were established by comparing 20th and 21st century occurrences. Direct drivers of habitat and biodiversity change were identified and documented. Our results show that a very strong decline of PC species and communities during the past century is driven by a) damming of rivers, b) habitat modifications negatively affecting salinity gradients, c) pollution and eutrophication, d) invasive alien species and e) climate change. Four out of 10 studied regions, namely, the Danube Delta – Razim Lake system, Dniester Liman, Dnieper-South Bug Estuary and Taganrog Bay-Don Delta contain the entire spectrum of ecological conditions to support PC communities and still host threatened endemic PC mollusc species. Distribution data is incomplete, but the scale of deterioration of PC species and communities is evident from the assembled data, as are major direct threats. PC biodiversity in the BSB is profoundly affected by human activities. Standardised observation and collection data as well as precise definition of PC biota and habitats are necessary for targeted conservation actions. This study will help to set the research and policy agenda required to improve data collection to accommodate effective conservation of the unique PC biota.

2.1 Introduction

Pontocaspian (PC) biota forms a unique, endemic ecological community, that occurs in transitional brackish habitats between freshwater and marine habitats in the Black Sea region (Anistratenko 2007b; Mordukhay-Boltovskoy 1960; Sowinsky 1904). Globally, very little endemic biodiversity exists in brackish water systems due to the lack of longevity of these dynamic habitats. PC biota evolved in anomalohaline lakes and marginal seas of the Caspian-Black Sea region over the past few million years (Krijgsman et al. 2019; Starobogatov 1970). Within the Black Sea Basin (BSB) that includes the Azov Sea, PC species live in river deltas, lowland lakes and estuaries in the northern coastal zones. Current status and trends of PC biodiversity in the BSB is poorly known due to taxonomic uncertainty, lack of standardized observation data and the transient boundaries of PC habitats (Anistratenko et al. 2020; Sands et al. 2020; Son 2011a, b, c, d, e, f; Son and Cioboiu 2011; Wesselingh et al. 2019). This is further hampered by language barriers (Russia, Ukraine, Romania, Moldova and Bulgaria share PC habitats and species in the BSB and reporting has mostly been done in their respective languages and in unpublished reports), and the complex economic and political situation. While a comprehensive view of PC population trends is lacking, it is clear that Black Sea coastal areas have faced a variety of anthropogenic modifications, which were reported to result in strong reductions in PC species numbers and their abundances in various places (Alexenko and Shevchenko 2016; Markovsky 1953, 1954a, b, 1955; Popa et al. 2009; Velde et al. 2019).

The PC biota comprises vertebrate, e.g., fish, as well as a variety of invertebrate taxa, e.g., molluscs, crustaceans and worms. Molluscs are particularly well suited to study the changing fate of the PC biota in the BSB (see e.g. Son et al. 2020; Velde et al. 2019). They are well represented in museum collections, their shells can indicate previous occurrences of species (Fig. 2.1), they occur in all benthic PC habitats and several of the species are good environmental indicators (i.e., sensitive to oxygen, salinity, water flow and sedimentation regimes: e.g., Kijashko (2013); Latypov (2015); Mordukhay-Boltovskoy (1960); Velde et al. (2019); Zhadin (1952)). Within the group, some species are characterized by narrow distribution ranges corresponding to narrow ecological tolerance limits. Other species, such as dreissenid bivalves, are opportunistic and have become major invaders elsewhere (Orlova et al. 2005). The taxonomic status of several PC mollusc species is not resolved due to large morphological variability (see e.g. Fig. 2.2a and b) and is hampered by the paucity or absence of living material for novel DNA-based research (Wesselingh et al. 2019). However, a network of PC mollusc specialists has been established in the past years as part of the EU funded Innovative Training Network "PRIDE" (www.pontocaspian.eu) that is actively targeting taxonomic uncertainties, which is an ongoing effort and provides an essential taxonomic base for this study.

The aim of this paper is to review distribution trends of PC biota (using molluscs as a model group) in the BSB by comparing historical (20th century) and modern (21st century) occurrences. Furthermore, we aim to identify the direct anthropogenic threats to their existence and survival (sensu Díaz et al. 2015), viz. processes and settings resulting from human decisions and actions that have direct implications for turnover/decline of PC biota, such as uncontrolled influx of

Figure 2.1. Shells show the decline of PC biota. (a) Shell beach on Popina Island in northern part of Lake Razim, Romania located in prime PC habitat (LOP, sept. 2015). (b) PC shell residues showing the extinct *Hypanis plicata* (no. 1), extirpated *Adacna fragilis* (no. 2), and declining *Monodacna colorata* (no. 3). In the past decades, freshwater taxa such as Viviparus acerosus (no. 4) and Unio pictorum (no. 5) became very abundant while PC species declined. Length of large Unio valve is c 8 cm.

sewage, invasion of alien species and establishment of large dammed reservoirs in river basins, among others (e.g. Lattuada et al. 2020; Lattuada et al. 2019; Semenchenko et al. 2015; Shiganova 2011). PC biodiversity is also affected by indirect anthropogenic drivers such as the organization and interaction within and between societies, stakeholders and people and their interactions with nature. For the BSB these are treated elsewhere (e.g. Gogaladze et al. 2020a; Gogaladze et al. 2020b). Based on this review we outline follow-up approaches to develop a conservation strategy that applies to the entire PC benthic biota in the BSB.

Figure 2.2. Overview of the PC mollusc species from the Northern and North-Western BSB. (a) *Monodacna colorata* (Eichwald, 1829), typical form. Beglitza beach, Taganrog Bay, Azov Sea (Russia). Photo FPW.

(continuation of Figure 2.2.) L 22 mm. (b) *Monodacna colorata* (Eichwald, 1829), forma pontica. Lake Razim (Romania). Photo FPW. L 20 mm. (c) *Hypanis plicata* (Eichwald, 1829). Lake Razim (Romania). Photo FPW. L 24 mm. (d) *Adacna fragilis* Milaschewitsch, 1908. Merzhanovo, Taganrog Bay, Azov Sea (Russia). Leg. M. Kurkay, 10.2018, photo JJP. L 17.3 mm. (e) *Adacna vitrea glabra* Ostroumov, 1905. Don River, Tsimlyansk Reservoir (Russia). Photo MOS. L 11 mm. (f) *Dreissena bugensis* Andrussov, 1897. Merzhanovo, Taganrog Bay, Azov Sea (Russia). Photo FPW. L 14 mm. (g) *Dreissena polymorpha* (Pallas, 1771). Southern Bug Liman (Ukraine). Photo MOS. L 21 mm. (h) *Theodoxus fluviatilis* (Linnaeus, 1758) Dnieper River, Kherson Region (Ukraine). Photo VVA. W 8.1 mm. (i) *Theodoxus velox* V. Anistratenko in O. Anistratenko et al., 1999. Dnieper River Delta, Zburjevskiy Liman, Kherson Region (Ukraine). Photo VVA. W 8.4 mm. (j) *Theodoxus danubialis* (Pfeiffer, 1828). Gergweis, Vils River (Germany). Photo AFS. W 10.2 mm. (k) *Theodoxus major* Issel, 1865. Astrakhan, Volga River (Russia). Photo AFS. W 5.5 mm. (l) *Laevicaspia ismailensis* (Golikov and Starobogatov, 1966). Lake Kugurlui or Yalpug (Ukraine). Illustration reproduced from Kantor and Sysoev (2006), plate 50, Fig. A. L 5.6 mm. (m) *Laevicaspia lincta* (Milaschewitsch, 1908). Lower Dnieper, Kherson (Ukraine). Photo VVA. H 8.97 mm. (n) *Clessiniola variabilis* (Eichwald, 1838). Lower Dnieper, Kherson (Ukraine). Photo VVA. H 7.10 mm. (o) *Clathrocaspia logvinenkoi* (Golikov and Starobogatov, 1966). Lower Don River near Rostov-on-Don (Russia). Photo VVA. H 1.58 mm. (p) *Clathrocaspia knipowitschii* (Makarov, 1938). Lower Dnieper, Kherson (Ukraine). Photo VVA. H 1.99 mm.

2.2 Methods and background

2.2.1 Pontocaspian mollusc species in the BSB

We define Pontocaspian (PC) mollusc species as extant, endemic, fully aquatic species, which evolved in the Black Sea and Caspian Sea Basins during the Quaternary, where they became adapted to a range of anomalohaline salinity regimes that characterized these basins. Most of the PC species evolved from ancestral species that radiated in the Late Miocene and Pliocene Paratethyan Basins (Krijgsman et al. 2019). The common historical origin of PC species and related ecological adaptations distinguish this group from other groups such as Palearctic freshwater species groups and several opportunistic marine species occurring in the PC region today (Anistratenko 2007b; Sowinsky 1904; Starobogatov 1970; Wesselingh et al. 2019; Zhadin 1952).

The historical distribution of PC mollusc families in the BSB has been subject of various studies, viz. Hydrobiidae (Alexenko and Starobogatov 1987; Anistratenko 2007a, b, 2008; Golikov and Starobogatov 1966, 1972; Grossu 1962; Makarov 1938; Sitnikova and Starobogatov 1999; Wilke et al. 2007); Neritidae (Anistratenko et al. 1999; Anistratenko et al. 2011; Anistratenko et al. 2020; Anistratenko et al. 2017; Golikov and Starobogatov 1966, 1972; Lindholm 1908; Makarov 1938; Mordukhay-Boltovskoy 1960; Sands et al. 2020); Lymnocardiinae (Anistratenko et al. 2011; Borcea 1926a, b; Grossu 1973; Makarov 1938; Milaschewitsch 1916; Munasypova-Motyash 2006; Ostroumov 1898; Popa et al. 2009) and Dreissenidae (Andrussov 1897; Rosenberg and Ludyanskiy 1994; Son 2007b). This review is based on endemic and native PC mollusc species (Table 2.1, Fig. 2.2) that have been reported alive from BSB coastal habitats in the 20th and 21st centuries

Table 2.1. Taxonomic status of PC mollusc species from the Black Sea Basin (BSB) with confirmed living 20th and 21st century occurrences. 1Wesselingh et al. (2019); 2 Sands et al. (2020); 3Son et al. (2020); 4Appendix 2.1.

(Sub) Family	Species	Author	Status
Lymnocardiinae	*Adacna fragilis*	Milaschewitsch, 1908	BSB endemic[4]
Lymnocardiinae	*Adacna vitrea glabra*	Ostroumov, 1905	Caspian invasive[3,4]
Lymnocardiinae	*Hypanis plicata*	(Eichwald, 1829)	PC endemic[1]
Lymnocardiinae	*Monodacna colorata*	(Eichwald, 1829)	BSB endemic (20th century), now invasive in Caspian basin
Dreissenidae	*Dreissena bugensis*	Andrussov, 1897	BSB endemic (<20th century), now global invasive
Dreissenidae	*Dreissena polymorpha*	(Pallas, 1771)	Native[1]
Neritidae	*Theodoxus danubialis*	(Pfeiffer, 1828)	Native[1,2]
Neritidae	*Theodoxus fluviatilis*	(Linnaeus, 1758)	Native[1,2]
Neritidae	*Theodoxus major*	Issel, 1865	PC native[2]
Neritidae	*Theodoxus velox*	V. Anistratenko in O. Anistratenko et al., 1999	PC native[2]
Hydrobiidae	*Clathrocaspia knipowitschii*	(Makarov, 1938)	BSB endemic (20th century), now possibly invasive in Danube catchment[1]
Hydrobiidae	*Clathrocaspia logvinenkoi*	(Golikov and Starobogatov, 1966)	BSB endemic[1]
Hydrobiidae	*Clessiniola variabilis*	(Eichwald, 1838)	PC endemic[1]
Hydrobiidae	*Laevicaspia lincta*	(Milaschewitsch, 1908)	BSB endemic[1]
Hydrobiidae	*Laevicaspia ismailensis*	(Golikov and Starobogatov, 1966)	BSB endemic[1]
Hydrobiidae	*Turricaspia chersonica*	Alexenko and Starobogatov, 1987	BSB endemic

(following taxonomy of Wesselingh et al. (2019) and Sands et al. (2020) with a taxonomical update in Appendix 2.1).

2.2.2 Habitats of Pontocaspian species and communities in the BSB

PC communities occur(ed) in coastal plains in areas influenced by the Black Sea and Azov Sea, such as lower stretches of rivers, lagoons, delta areas, estuaries/limans and bays (Figs. 2.3 and 2.4). Limans (a particular landform common to the Northern Black Sea) are estuaries or lagoons mostly or entirely separated from the sea by sand barrier systems and have lagoonal, lake, bay and estuarine properties. Some PC groups, such as *Theodoxus* and *Dreissena* species, are tolerant to a wide array of environmental conditions and have far larger distribution ranges than lymnocardiine and/or hydrobiid species - they are abundant in rivers and lakes, also outside the BSB drainage systems (Sands et al. 2020; Zhadin 1952). We define optimum PC habitats as waterbodies (lakes, estuaries, bays, river stretches) where at least one endemic PC species of two different families co-occur (Table 2.1). Our definition will need expansion when other groups in addition to molluscs are included. Optimum PC habitats contain(ed) communities dominated by PC species within the coastal zone, mostly in oligohaline settings (Alexenko and Starobogatov 1987; Anistratenko 2007b; Anistratenko

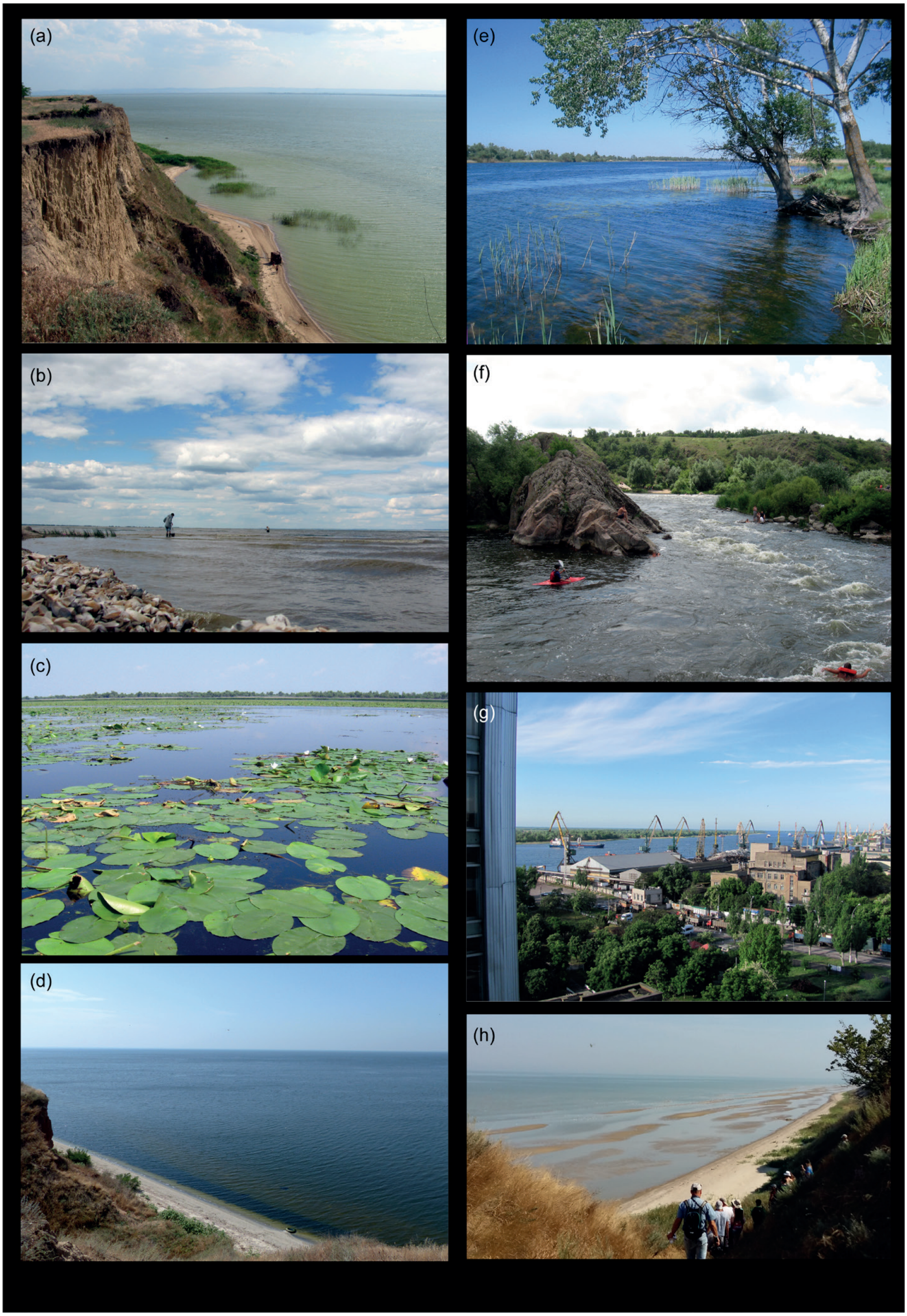


Figure 2.3. Examples of PC habitats in the BSB. (a) Lake Yalpug, Ukraine (Mikhail Son, June 2009). This large lake is still a prime PC habitat, however eutrophication is noticeable. The reed vegetation zone along

(continuation of Figure 2.3.) the shore is a habitat for PC hydrobiid species. (b) Dniester Liman, Ukraine (VVA, June 2016). The small, waves are actively forming shell ridges along the liman near Belgorod-Dnestrovsky that are mainly composed of *Monodacna* and *Dreissena* shells. *Theodoxus* and mostly juvenile *Monodacna* are still living in the area, hydrobiids are represented by fresh empty shells. (c) Lake Beloie in Dniester Delta, Ukraine (photo MOS, July 2009). Smaller deltaic lakes and river floodplain lakes, such as shown in this image, hosted a combination of freshwater and PC species in the past (< 20th century), but PC species have mostly disappeared from these habitats in the past century. (d) Dnieper Liman, Aleksandrovka, Ukraine (VVA, June 2016). Sandy bottom of the distal sector of the liman. Freshwater species are dominant here. Large quantities of empty shells of PC species such as hydrobiid, *Theodoxus* and *Monodacna* spp. are indicative of their former abundance in the region. (e) Dnieper Delta, Konka Branch (MOS, May 2007). Wide riverine channel upstream the estuary. All groups of PC molluscs are present in this habitat. (f) Rapids of the Southern Bug River, Migia Canyon, Ukraine (MOS, July 2009). These rapids form a natural upper boundary for the distribution of most PC taxa. (g) Kherson cargo Harbour, Ukraine (VVA, May 2016). The harbours are important vectors for invasive species and the dredging required to ensure access to sea has various impact on PC habitats in the estuaries and limans. (h) Taganrog Bay at Semibalki, Russia (FPW, September 2017). The view shows the shallow nature of the bay and the sandy character of the sediments. Here, large populations of *Monodacna colorata* and *Adacna fragilis* occur.

et al. 2011; Makarov 1938; Munasypova-Motyash 2006; Starobogatov 1970; Zhadin 1952). Densities of PC molluscs are variable. *Dreissena* and *Monodacna* can dominate communities, but most of the PC hydrobiids have patchy occurrences (Alexenko and Kucheryava 2019; Alexenko and Starobogatov 1987; Anistratenko and Anistratenko 2018).

Three main PC community types have been described during the 20th century from the different regions: (1) *Dreissena* communities, (2) *Dreissena-Monodacna* communities and (3) *Adacna-Hypanis-Monodacna* communities. *Dreissena*-dominated communities are common in rivers (often with *Theodoxus* species present) within and outside the PC region but also occur as secondary species-depleted communities in estuaries in all BSB PC regions (Markovsky 1953, 1954a, 1955; Mordukhay-Boltovskoy 1960; Zhadin 1931). Several *Dreissena* subcommunities have been proposed and all are characterised by the absence of *Monodacna*. The *Dreissena-Monodacna* communities form species-rich communities in freshwater to oligohaline settings at the core of estuaries in all BSB PC regions, and are locally dominated by either *Monodacna* or *Dreissena* species (Markovsky 1953, 1954a, 1955; Mordukhay-Boltovskoy 1960). *Adacna-Hypanis-Monodacna* dominated communities were common in the oligohaline-mesohaline zones in all BSB PC regions (Markovsky 1953, 1954a, 1955; Mordukhay-Boltovskoy 1960; Shokhin et al. 2006; Zhadin 1931). These communities were relatively species poor, contained *Adacna fragilis*, *Monodacna colorata* and *Hypanis plicata* and with the demise of the latter in the BSB these communities vanished. Within the central-eastern parts of the Taganrog Bay today an impoverished version of the community

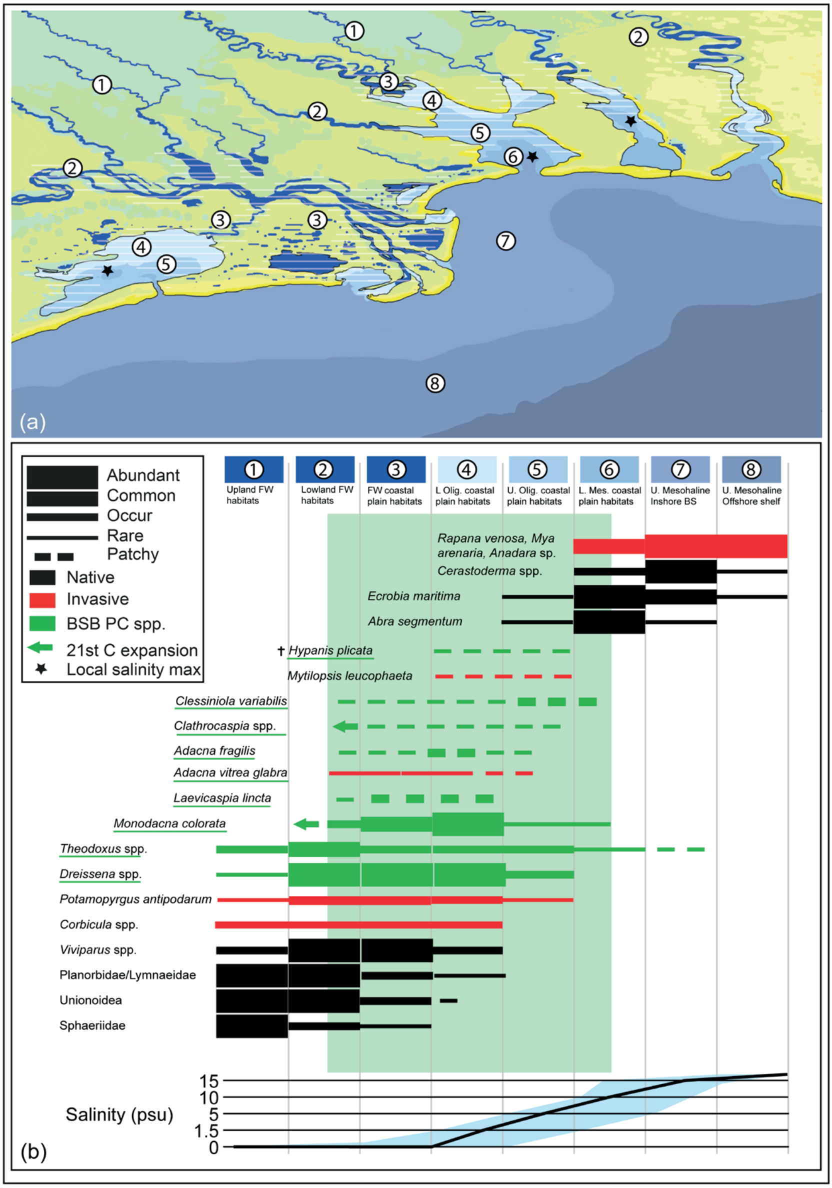
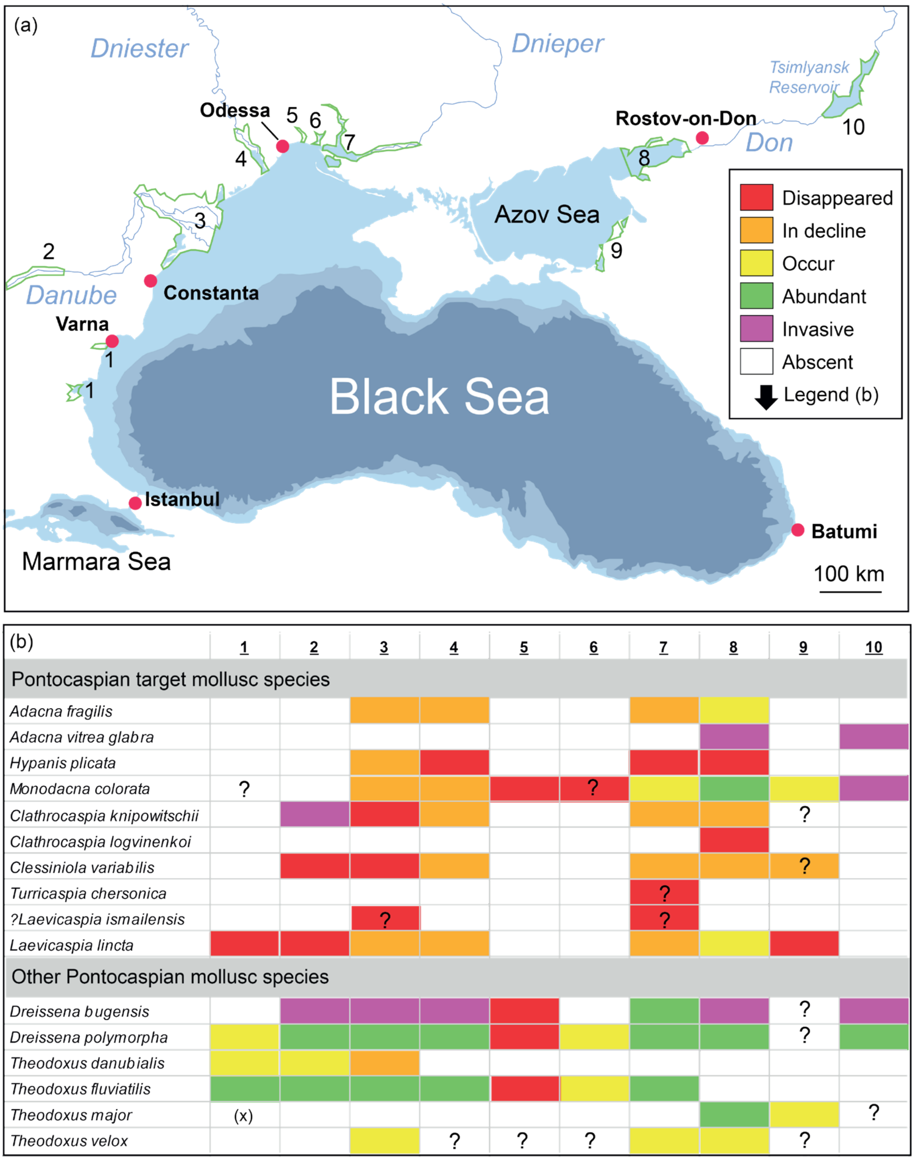


Figure 2.4. Simplified model of coastal landscapes depicting habitats of selected PC (green underlined) and other abundant mollusc species in the north-western Black Sea coastal zone for the 20th-21st century. The optimum PC habitats are shaded (above) and indicated in green (below). FW - fresh water, U - Upper, L - Lower, Olig - Oligohaline, Mes - Mesohaline. Our model summarised personal observations as well as published accounts. In each sub-basin in the BSB the salinity gradients and habitat successions are complex. In some areas local salinity maxima occur that are the result of excessive evaporation rather than a simple freshwater to marine gradient.



(b)	1	2	3	4	5	6	7	8	9	10
Pontocaspian target mollusc species										
Adacna fragilis			🟧	🟧			🟧	🟨		
Adacna vitrea glabra								🟪		🟪
Hypanis plicata			🟧	🟥			🟥	🟥		
Monodacna colorata	?		🟧	🟧	🟥	🟥 ?	🟨	🟩	🟨	🟪
Clathrocaspia knipowitschii		🟪	🟥	🟧			🟧	🟧	?	
Clathrocaspia logvinenkoi								🟥		
Clessiniola variabilis		🟥	🟥	🟧			🟧	🟧	🟧 ?	
Turricaspia chersonica							🟥 ?			
?Laevicaspia ismailensis			🟥 ?				🟥 ?			
Laevicaspia lincta	🟥	🟥	🟧	🟧			🟧	🟨	🟥	
Other Pontocaspian mollusc species										
Dreissena bugensis		🟪	🟪	🟪	🟥		🟩	🟪	?	🟪
Dreissena polymorpha	🟨	🟩	🟩	🟩	🟥	🟨	🟩	🟩	?	🟩
Theodoxus danubialis	🟨	🟨	🟧							
Theodoxus fluviatilis	🟩	🟩	🟩	🟩	🟥	🟨	🟩			
Theodoxus major	(x)							🟩	🟨	?
Theodoxus velox			🟨	?	?	?	🟨	🟨	?	

Figure 2.5. (a) PC species occurrences in the BSB. 1. Bulgarian coastal lagoons and limans, 2. Lower Danube River, 3. Danube Delta – Razim, 4. Dniester Liman, 5. Tiligul Liman, 6. Berezan Liman, 7. Dnieper-Bug Estuary, 8. Taganrog Bay – Don Delta, 9. SE Azov Sea coast, 10. Tsimlyansk Reservoir. (b) Status of PC mollusc species. "Decline" stands for diminished distribution range within an area and/or declining abundances in the past century. "Invasive" stands for 21st century introductions. Question marks denote areas with insufficient observations (such as southeast Azov coast) or taxonomic groups that require re-examination (*Theodoxus* species). *Earlier reports of this species likely to be misidentifications of *Theodoxus fluviatilis* and/or *T. danubialis* (AFS, PO).

exists (lacking *Hypanis*) that is often termed *Monodacna* community (Nekrasova 1972; Stark 1960; Vorobyev 1949). Optimum conditions for that community are fresh or oligohaline (up to 5 psu), sandy, shelly or moderately silty grounds in the bay, and low current areas in the outer Don river indicative of good oxygenation and moderate hydrodynamics. Within the PC habitats previously local very dense aggregates of PC gastropod occurrences existed, that may be interpreted as communities or subcommunities. *Clessiniola variabilis* dominated communities have been mentioned from shallow waters with variable salinities in the Dniester and Dnieper-Bug regions (Markovsky 1953, 1954a) but we have not encountered such aggregates in the past decades. *Laevicaspia lincta* dominated communities (mentioned from Dniester and Kuchurgan Liman, Katlabukh, Yalpug and Dnieper by Markovsky 1953; Markovsky 1954a, 1955; Olivari 1953; and observed in Razim Lake by Wilke et al. 2007 as late as in 2003) were a common feature in freshwater areas and occasionally low oligohaline settings with abundant *Dreissena*.

2.2.3 PC habitat mapping

We retrieved freshwater habitat polygons from HydroLAKES dataset (https://www.hydrosheds.org/pages/hydrolakes) to map the PC habitats in the BSB using QGIS 3.10 "A Coruña". We manually edited those polygons that did not cover the PC habitats, such as swamps and marshes, based on published literature and expert knowledge. We also manually drew lagoons and bays of Pontocaspian habitats which are not part of the HydroLAKES based on published accounts and expert opinion. Given the densely aggregated small lakes in the Danube Delta with surface areas lesser than 0.2 km2 we merged the Chilia branch of Danube River and outer delta lakes both upstream and downstream of Vilkovo (Table A2.2.1 and Appendix 2.3).

2.3 Results

2.3.1 Status and trends of PC species in BSB

Ten regions in the BSB contain 20th and/or 21st century occurrences of endemic PC species (Fig. 2.5). Historical (20th century) and modern (21st century) distributions of PC target taxa are summarised in Appendix 2.2. PC habitat polygon shapefiles as well as the attributes describing historical (20th century) and modern (21st century) distributions of PC target taxa are provided in Appendix 2.3. Data derived from published accounts and personal observations (PO) of the authors (ABP – Ana Bianca Pavel, AFS – Arthur Francis Sands, FPW – Frank P. Wesselingh; LOP – Luis Ovidiu Popa, MOS – Mikhail O. Son, MVV - Maxim V Vinarski, OPP – Oana Paula Popa, OYA – Olga Yu Anistratenko, TT - Teodora Trichkova, TW – Thomas Wilke, VLS – Vitali L. Syomin, VVA – Vitaliy V. Anistratenko).

Bulgarian coastal lagoons and limans

The Bulgarian Black Sea coast contains 31 wetland areas such as lakes, marshes and lower river floodplain areas (Varbanov 2002), from where living PC species and shells have been reported

(Georgiev and Hubenov 2013; Hubenov 2007, 2015; Sands et al. 2019; Appendix 2.2). *Theodoxus fluviatilis* has been reported from more than 15 wetlands (Hubenov 2015), while *Dreissena polymorpha* occurred in about ten wetlands in the past, and currently is confirmed from five of these native habitats (Hubenov 2015; Vidinova et al. 2016). *Theodoxus major* (reported as T. pallasi) occurred in Lake Varna before salinization in the first half of the 20th century (Drensky 1947; Kaneva-Abadjieva 1957) and is now considered extinct in Bulgaria (Hubenov 2015). Living specimens of *Laevicaspia lincta* (reported as *Micromelania lincta*) were recorded in Lake Mandra (June 1944) and Lake Beloslav (August 1945) by Drensky (1947). The species was considered rare for Bulgaria (Drensky 1947), and since then no further occurrences have been recorded (Hubenov 2015). PC cardiids have been reported only as shells in the Bulgarian coastal wetlands. Kaneva-Abadjieva (1957) found single shells of *Monodacna colorata* at different parts and depths of Lake Varna, assuming that the species was present there before salinity regime change in the first half of the 20th century. Shells of *L. lincta*, *M. colorata* and *Hypanis plicata* (reported as *Adacna relicta* and *A. plicata relicta*) have been reported from the Black Sea littoral sediments by Valkanov (1957b), Marinov (1990), and (Hubenov 2015), and shells of *Clessiniola variabilis* – by Genov and Peychev (2001), and (Hubenov 2015). It is unclear whether these littoral shells represent possible 20th century occurrences, as older Holocene and even Late Pleistocene occurrences are well known from shallow deposits in the Black Sea coastal and shelf areas (Velde et al. 2019).

The Bulgarian Black Sea coastal wetlands have been exposed to a variety of strong anthropogenic pressures owing to agricultural, recreational, urban and industrial development over the past two centuries (Hubenov 2015; Trichkova 2007). Increased eutrophication as well as substantial variation in physico-chemical parameters such as salinity, oxygen content, mineral content and temperature in the wetlands have caused very strong changes in benthic invertebrate communities (Trichkova 2007). Some of the past habitats sustaining PC species have completely changed. For example, Lake Varna was connected to the sea through a navigation canal in 1909 and to Lake Beloslav in 1923. Later, in 1975, a bigger canal and a sea port were built, increasing salinity within both lakes, driving the loss of their natural fauna, including PC species (Trichkova 2007; Varbanov 2002). Benthic invertebrate biota in other wetlands (e.g. Durankulak, Shabla-Ezerets, Burgas, Mandra, and Dyavolsko Blato Marsh) declined or vanished due to restriction or complete disconnection from the Black Sea because of damming, and/or due to intensive fish-farming activities, overfishing, and household and industrial pollution (summarised in Hubenov 2015; and Trichkova 2007).

Lower Danube River

Theodoxus and *Dreissena* are and have been common in the Danube River (Angelov 2000; Russev 1966; Sands et al. 2019; Trichkova et al. 2019). In the Bulgarian sector, PC hydrobiid shells were reported in the 20th century. In June 1958, empty shells of *Laevicaspia lincta* (reported as *Micromelania lincta*) were recorded at Oryahovo (678 rkm) by Russev (1966). Shells of *Clessiniola*

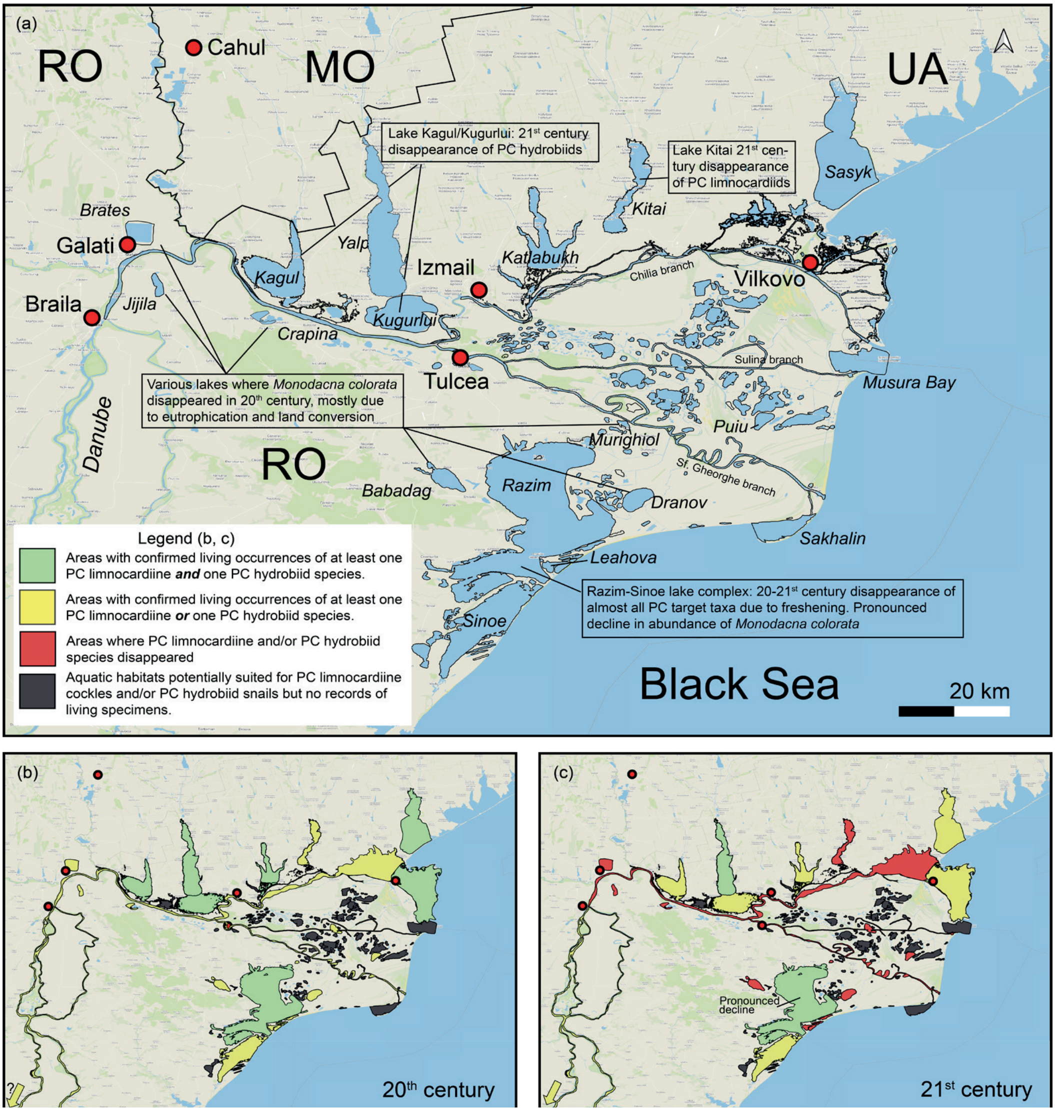


Figure 2.6. PC habitats in the Danube Delta region. (a) Regional overview and major trends, (b) 20th century occurrences, (c) 21st century occurrences. See data in Appendix 2.2, Table A2.2.1, outline of subareas in Fig. A2.2.1. PC taxa still appear in Razim Lake complex in 21st century (hence the green colour), but hydrobiid species have not been reported after 2003 and lymnocardiine species have strongly declined in abundance (Monodacna colorata) or disappeared (*Adacna* and *Hypanis* spp.). Map is projected in EPSG Projection 4326 - WGS 84.

variabilis were found upstream of Lom (474 rkm) in September 1957, at Ruse (493 rkm) in October 1959, and upstream of Silistra (381 rkm) in June 1963 (Russev 1966). No 21st century records exist of these PC hydrobiids from the Bulgarian Danube River stretch. However, recently a *Clathrocaspia* species has been described as Caspia milae in Boeters et al. (2015) from Vardim Island in the Bulgarian sector of the Danube, whose identity is subject to further study (see Appendix 2.1).

The main threats to the aquatic molluscs in general and the PC fauna in the Lower Danube River in particular, are the loss and degradation of habitats, pollution, and introduction of invasive alien species (Trichkova et al. 2019). Throughout the years, the Danube River has been contaminated by urban, industrial and agricultural waste and experienced increasing economic activities such as ship traffic (Russev and Naidenow 1978). A major threat in the 21st century has become the introduction, establishment and spread of invasive alien species (Paunović and Csányi 2018). In recent years, owing to the increase in abundance and biomass of the newly introduced invasive alien mussels *Corbicula fluminea*, *Sinanodonta woodiana*, and *Dreissena bugensis*, benthic habitats in the Bulgarian sector of the Danube River completely changed (Hubenov 2001, 2006; Hubenov and Trichkova 2007; Hubenov et al. 2012, 2013), which may have potential adverse impact on several PC species. Additionally, the invasive mussels may directly impact PC species through competition and fouling.

Danube Delta – Razim

The Danube Delta (up to its apex near Galati), the neighbouring drowned valley lakes both on the Romanian side (e.g., Brates, Crapina, Jijila) and the Ukrainian side (Yalpug, Katlabukh, Kagul, Kitai), as well as the coastal Razim-Sinoe lake complex to the south of the delta and Sasyk lake to the north make up a large (c 6000 km2) and varied area that hosts many PC species (Fig. 2.6). Lake Sasyk was historically separated from the Danube Delta, but was included when, in 1978, a feeder channel from the Danube was constructed. Most of the Danube-Razim region consists of freshwater habitats (river channels, floodplain and delta lakes, drowned river valleys, swamps) but, important, salinity gradients towards mesohaline settings occur in the outer delta and in the coastal lagoons and lakes. The maximum depth within the Razim Lagoon complex is 3.5 metres (Velde et al. 2019).

The Danube Delta region historically harbours a diverse PC mollusc fauna (Markovsky 1955; Mordukhay-Boltovskoy 1960; Popa et al. 2009; Velde et al. 2019) with twelve PC species (Fig. 2.6). Common PC mollusc species are *Monodacna colorata*, *Theodoxus fluviatilis* and *Dreissena polymorpha*. All three lymnocardiine species recorded in the 20th century have disappeared in Romanian lakes, with the exception of the Razim-Sinoe (Popa et al. 2009; Velde et al. 2019), where *M. colorata* and *Adacna fragilis* have 21st century records. However, annual fieldwork in the Razim complex has shown that their abundance has strongly declined in the past 15 years (Popa et al. 2009). One species (*Hypanis plicata*) has not been found alive since 1974. Within the lakes and lagoons very close to the Black Sea coast *A. fragilis* has been a common occurrence in the 20th century (Borcea 1926b; Grossu 1962; Markovsky 1955), but the species has declined recently (Popa et al. 2009). Velde et al. (2019) showed that the Razim communities have almost entirely been

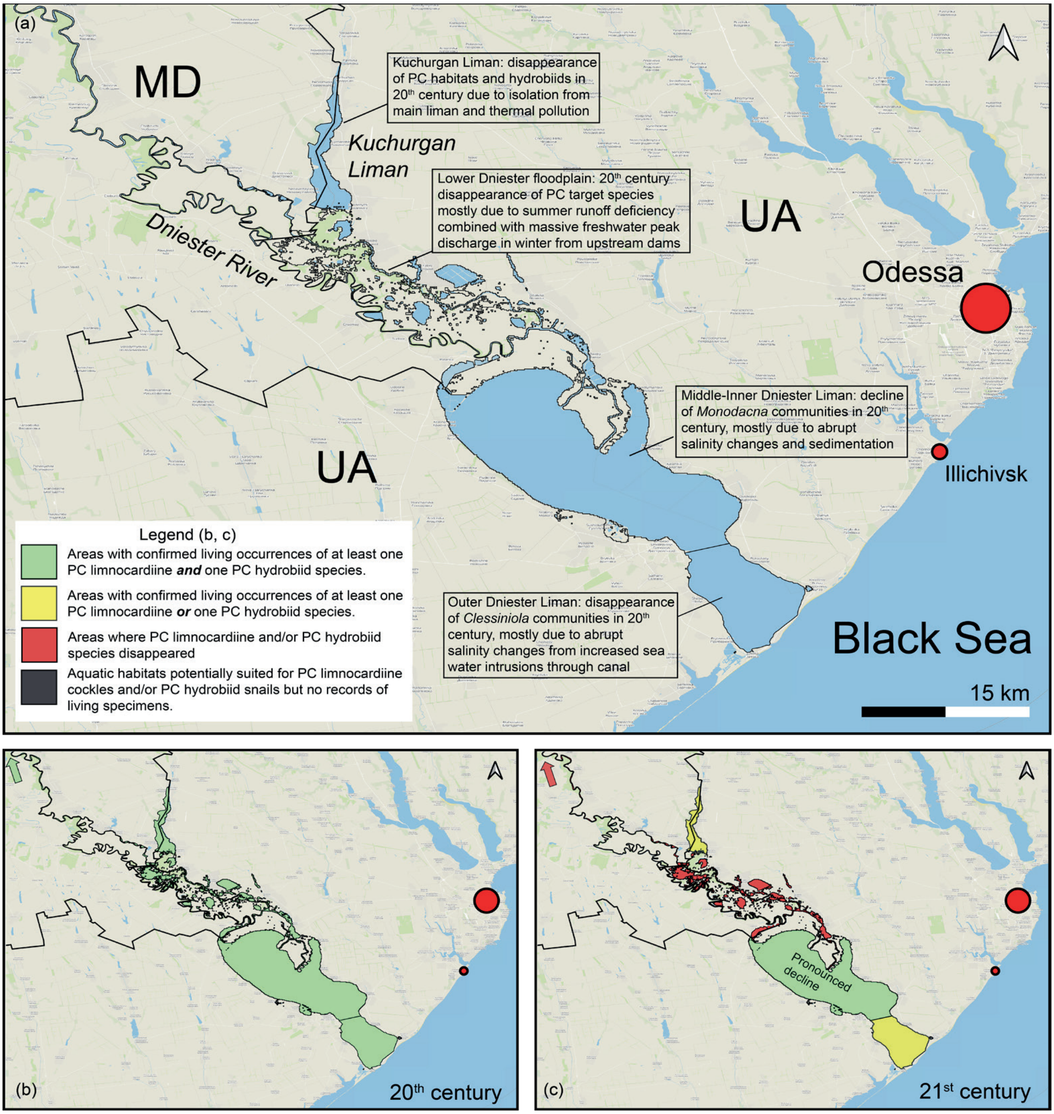


Figure 2.7. PC habitats and trends in the Dniester Liman. (a) Regional overview and major trends, (b) 20th century occurrences, (c) 21st century occurrences. See data in Appendix 2.2, Table A2.2.2, outline of subareas in Fig. A2.2.2. Map is projected in EPSG Projection 4326 - WGS 84.

replaced by freshwater communities in the past decades. In Romania, PC hydrobiid species were reported mostly from the Razim-Sinoe complex and low salinity habitats near the mouth of the Danube distributaries (Grossu 1956). In most cases, these records represent empty shells and their historical distribution (e.g. 20th century occurrence) is not well known. In the past decade no living specimens were encountered apart from a 2003 record of *Laevicaspia lincta* (Wilke et al. 2007).

In the Ukrainian part of the Danube Delta, in the Kitai Lake PC communities have recently disappeared completely and PC species abundances in this lake and in other lakes are decreasing (MOS and VVA, PO). Distribution ranges of *Laevicaspia lincta* and *Adacna fragilis* decreased compared to occurrences reported over a century ago (Markovsky 1953, 1954a, b, 1955; Milaschewitsch 1916; Ostroumov 1898). The latter species became rare in its native NW Black Sea coastal range (Lyashenko et al. 2012; Munasypova-Motyash 2006), but became temporarily abundant (along with *Monodacna colorata*) in Lake Sasyk when the lake was connected with the Danube River, via a canal, in 1978 (Khalaim and Son 2016). Previously, Lake Sasyk hosted marine communities, but after the connection with the Danube River was established, two PC communities became common there, viz. *Dreissena* communities in the shore zones and *Monodacna* communities in deeper parts. *Laevicaspia ismailensis* may have disappeared from lakes Yalpug and Kugurlui (VVA, MOS, PO).

Several causes have been proposed for the decline of PC species and communities in the Danube-Razim region. Eutrophication and conversion of inland lakes were linked by Popa et al. (2009) to the disappearance of lymnocardiine species. Velde et al. (2019) related the breakdown of the salinity gradients in the Razim-Sinoe lake complex, due to rerouting of Danube waters as well as closing Black Sea inlets in the second half of the 20th century, to the collapse of PC communities and disappearance of species. Recently, invasive Corbicula species have been expanding in the Danube Delta area (Pavel et al. 2017) and potential interactions of this successful invasive (Crespo et al. 2015) with PC species is reason for concern.

Dniester Liman

The lower Dniester, comprising the Dniester Delta and Liman as well as the Kuchurgan Liman (Fig. 2.7) and the lower Dniester River up to Dubăsari Dam (Moldova) historically hosts a rich PC fauna with 10 mollusc species (Grinbart 1953a; Markovsky 1953; Son 2007b). The Dniester Liman is about 45 km long, with a surface area of about 400 km2 and maximum depth is 2.7 m. In the 20th century the Liman was subdivided into an inner freshwater-oligohaline zone (up to 0.5 psu), a middle oligohaline zone (up to 4 psu) and an outer mesohaline zone (salinities typically between 4 and 9 psu with episodic lowering during peak floods (Markovsky 1953). Salinity regimes changed due to human interference. A deep-water sea canal has enabled sea water intrusions during storm surges. In the Upper Dniester basin, a system of fish ladders decimated natural flow regimes (Zhulidov et al. 2015). In general, the Lower Dniester basin is characterized by problems of seasonal runoff deficiency and associated degradation of floodplain ecosystems, common to all large PC rivers with cascades of dams (Shevtsova 2000). However, the episodic release of large amounts of fresh water from reservoirs in the feeding rivers causes strong episodic freshening of the inner and middle parts of the Dniester system, thereby sharply steepening the salinity gradient and minimizing optimum salinity areas of PC biota. The Kuchurgan Liman (a part of the Dniester Liman that became cut off by the prograding river delta) was turned into cooling pond for the power station and has thus

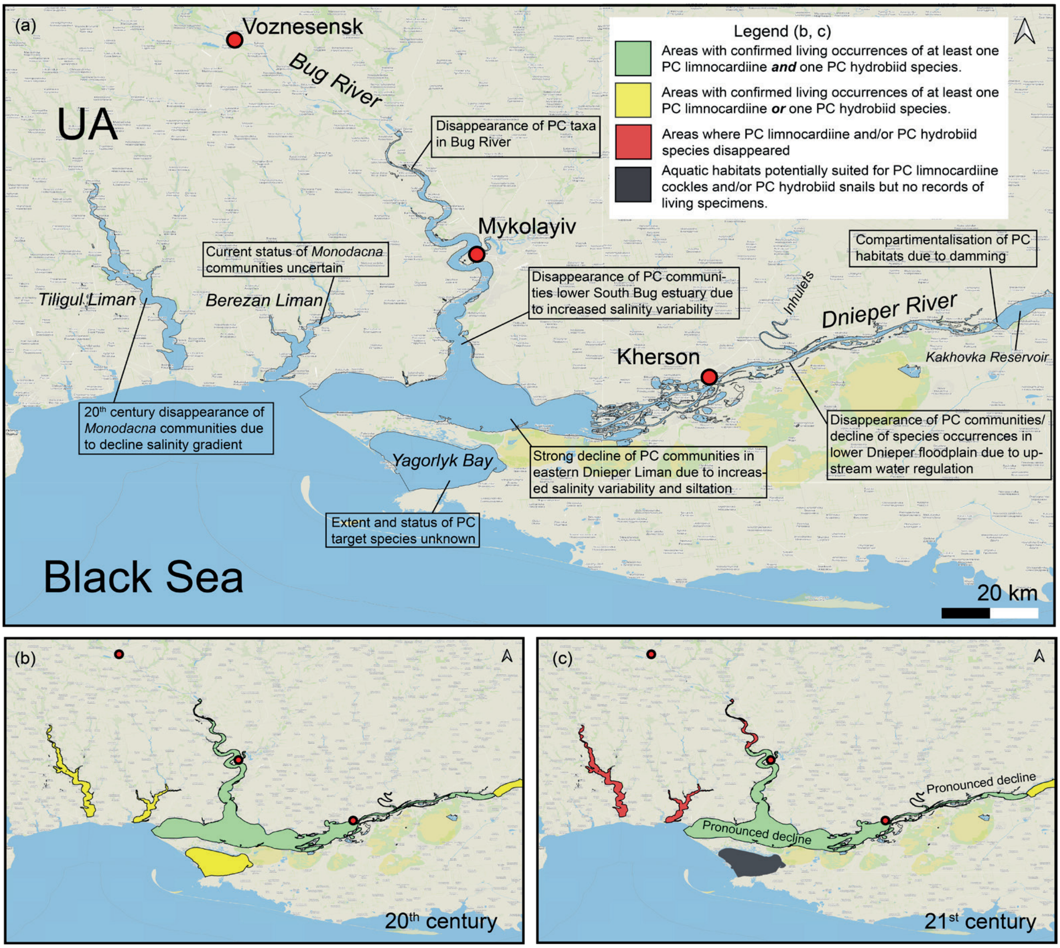


Figure 2.8. PC habitats and trends in the Dnieper-Bug Estuary and adjacent Tiligul and Berezan Limans. (a) Regional overview and major trends, (b) 20th century occurrences, (c) 21st century occurrences. See data in Appendix 2.2, Table A2.2.3, outline of subareas in Fig. A2.2.3. Map is projected in EPSG Projection 4326 - WGS 84.

become impacted by thermal pollution.

The distribution range of PC communities in the Dniester Delta declined in the early 20th century before the start of large-scale anthropogenic modifications, such as construction of dams and canals, and thermal pollution (Grinbart 1953a; Markovsky 1953). According to our observations (MOS, VVA), lymnocardiine and hydrobiid PC species have completely disappeared in floodplain lakes, and among molluscs only the most tolerant *Dreissena* and *Theodoxus* species have survived in river channels. In the past decades, the Dniester Liman communities dominated by *Adacna fragilis* and *Hypanis plicata* have vanished. On species level, *A. fragilis*, *Monodacna colorata* and *Laevicaspia lincta* have very strongly reduced distribution ranges and/or abundances, and

H. plicata and *Clathrocaspia knipowitchii* are possibly extinct in the Dniester area (VVA, PO).

Dam construction has been a major driver for Dniester floodplain ecosystem demise (Shevtsova 2000), which has been further affected by an increase in water extraction, climate change and organic pollution. Increased episodic intrusions of seawater and variability of freshwater inflow from the catchments has severely impacted the salinity gradients. Salinity increase in estuaries under the conditions of climate change and artificial flood-changing constructions is a global trend (Rahel and Olden 2008). In freshwater and oligohaline zones, among numerous alien species, two (the Dnieper-Bug PC species *Dreissena bugensis* and the New Zealand derived Potamopyrgus antipodarum) affected the original PC communities (Son 2007a, 2008). In the lower zone of the Dniester Liman alien species (especially *Mytilopsis leucophaeta*) occupy the vacant niches of PC species, which are not adapted to rapid salinity changes (Zhulidov et al. 2015). These invasive species took advantage of the PC species decline, and have not been demonstrated to drive the decline and disappearance of PC communities.

Tiligul Liman

The Tiligul Liman is an 80 km long estuary that is up to 19 m deep (Fig. 2.8). It was disconnected from the Black Sea in the 18-19th century due to the formation of a coastal barrier, but a canal still provides limited water exchange. In 1960s the liman contained freshwater and brackish mesohaline zones, and salinity increased after canal construction combined with excessive evaporation. The Tiligul Liman drainage consists of steppe rivers that are dry during summer and therefore unsuited for PC species. Historically, Tiligul Liman contained few PC species. The specific ecological community which used to live here was dominated by PC (i.e. *Monodacna colorata*) and marine cardiids (Grinbart 1953b). *Dreissena polymorpha*, *M. colorata* and the *Theodoxus* species that lived in the Liman have disappeared (Moroz et al. 1986; Son 2007b) as a result of a human-driven salinity increase.

Berezan Liman

The Berezan Liman is 26 km long, with a surface area of c 60 km2 and a maximum depth of 26 m, which is connected to the Black Sea by a canal (Fig. 2.8). The liman has many bays that have very different hydrological settings. The Solonets Tuzly Bay became separated and transformed into a hypersaline lake in the 20th century. In several places, dams have been erected to create isolated areas for aquaculture impeding water exchange. Most rivers draining into the Berezan liman are steppe rivers that dry out during summer rendering them unsuitable for PC species with the exception of the lower Berezan River, where *Dreissena polymorpha* occurs (Son 2007b). Salinities within the Berezan Liman historically ranged between about 3–6 psu but was depressed by an influx of low saline waters during peak discharges from the adjacent Dnieper-Bug estuary through a channel connecting the liman to the Black Sea (Grinbart 1955).

Figure 2.9. PC habitats and trends in the Taganrog Bay-Don Delta region. (a) Regional overview and major trends, (b) 20th century occurrences, (c) 21st century occurrences. See data in Appendix 2.2, Table A2.2.4, outline of subareas in Fig. A2.2.4. Map is projected in EPSG Projection 4326 - WGS 84.

In the earlier part of the 20th century Berezan Liman was dominated by *Monodacna colorata*, as well as *Theodoxus* species (Grinbart 1953b), and further contained *Dreissena polymorpha*. In recent times *M. colorata* has disappeared in several visited sites (MOS, PO), but some areas within the estuary have not been explored; other PC species still occur in this liman (Son 2007b).

Dnieper-Bug Estuary

The Dnieper-Bug Estuary contains the South Bug Estuary and Bug River up to Novaya Odessa City, and the Dnieper Liman, Delta and lower Dnieper River up to the Kahovka Dam (Fig. 2.8). The Dnieper Estuary is 55 km long and on the Black Sea side is limited by a constriction at the north end of the Kinburn Spit. To the south side the Yagorlyk Bay may also be included into the Dnieper-Bug complex. The Bug estuary is 47 km long. The Dnieper-Bug estuary has a maximum depth of 22 m. The central areas have mostly silty bottoms and the shore zones are mostly sandy with occasional rocky outcrops. Before the 19th century, the Dnieper-Bug estuary had a salinity gradient similar to the Dniester Liman. Within the outer zone variable salinities occurred with an average 4 psu. However, increased regulation of the river basins and construction of shipping channels resulted in large scale changes of the salinity regimes. Hydropower dam construction in the 1950s restricted freshwater input resulting in strong salinity increase (with freshwater and oligohaline areas badly affected), but also resulted in episodic massive release of fresh water. Afterwards, salinities gradually lowered and the initial gradient more or less returned (Shatova et al. 2009). However, a combination of weak river flow and strong western winds pushes at times mesohaline Black Sea waters through the Bugsko-Dneprovsko-Lymansky Canal upstream to Mykolayiv Port and Kherson Port (Dotsenko and Ivanov 2010). This dramatically changed salinity regimes and increased variability, especially in the narrow Bug Liman.

The Dnieper-Bug Estuary is historically a major centre of PC biodiversity in the Black Sea Basin (Fig. 2.4). A diverse PC fauna containing some local endemic species existed here in the early 20th century (Borcea 1926a, b; Golikov and Starobogatov 1966, 1972; Grossu 1956, 1962; Markovsky 1954a; Milaschewitsch 1916; Mordukhay-Boltovskoy 1960; Scarlato and Starobogatov 1972a). Some PC species, including *Clessiniola variabilis* were recorded in the Yagorlyk bay on the south side of the Dnieper-Bug estuary (Anistratenko 1996) and *Laevicaspia lincta* in the upper Dnieper delta near Kherson (Wilke et al. 2007). The Dnieper Liman has been severely affected by the construction of a cascade of dams along the Dnieper River leading to the severe decline of PC communities. The communities only remained in the eastern part of the Liman adjacent to the delta (Moroz and Alexenko 1983). According to our observations (VVA: 2016-2019), the range of PC communities also decreased in the estuarine part of the southern Bug (Upper South Bug Liman and Lower South Bug River). Communities declined, and some species became very rare or went locally extinct such as *Adacna fragilis*, *Hypanis plicata*, *Turricaspia chersonica*, *Clathrocaspia knipowitchii*.

Since the construction of the cascade of reservoirs on the Dnieper River in the 1930–1970s, the water flow rate decreased markedly and the accumulation of silt increased. Algal blooms have become more frequent in the reservoirs and estuaries of the Dnieper, bottom oxygen content decreased and lead to local anoxic conditions (Romanenko 1987; Zakonnov et al. 2019). Together with progressive siltation at the bottom of reservoirs, the area of hard substrates, on which *Dreissena* associations and communities of higher aquatic vegetation can occur, was reduced too (e.g. Alexenko and Shevchenko 2016). This resulted in a gradual but widespread reduction of habitats suitable for PC gastropod species such as Clathrocaspia species that rely on dreissenid bivalves to deposit their eggs (Alexenko and Kucheryava 2019; Alexenko and Shevchenko 2016).

Taganrog Bay – Don Delta

The Taganrog Bay, adjacent Mius and Yevsk Limans and Don River Delta (Fig. 2.9) form the main PC biodiversity hotspot in the NE Black Sea Basin with a rich fauna and different types of PC-dominated communities (Mordukhay-Boltovskoy 1960). Taganrog Bay is a large (5600 km2) and shallow (0–2 m depth in the eastern part, down to 9–10 m in the west) bay (Ecological Atlas 2019; Zhidkova et al. 2018). It hosts a major salinity gradient from mostly freshwater at its eastern end, to 8–15 psu at the western end. PC communities flourish in fresh water to lower mesohaline settings (0–5 psu) in areas with occasional influx of salinities up to 8 psu. The bay floor is mostly silty in the central areas and sandy in the margins and shell accumulations are common. Near large ports (Taganrog, Mariupol, Yeysk), black jelly-like anthropogenic sediments with high concentrations of petrochemicals and other pollutants occur (Bespalov 2005). The upper sediment layer in the bay is commonly disturbed by storm waves. Wind is a major factor determining water circulation and therefore, salinity distribution in the bay (Matishov and Grigorenko 2017). Strong western storms can push mesohaline waters to the eastern end of the bay and even occasionally flood the adjacent Don Delta with 4-5 psu waters (Matishov and Grigorenko 2017). Other drivers affecting the salinity gradient in the bay are the river flow volume and Black Sea water advections (Matishov and Grigorenko 2017). Two large limans adjoin the bay approximately in its middle. The Mius Liman (33-40 km long and only 1 m deep: Vishnevetskiy and Popruzhniy 2018) to the north is a drowned estuary with average salinities between 0.9-1.8 psu (Kreneva et al. 2013). The Yeysk Liman to the south is an open estuary with hydrological conditions similar to the adjacent Taganrog Bay. Benthic fauna is different here due to small nature of this water body (Nabozhenko and Kovalenko 2011). The Don is a regulated river with a mostly sandy bottom. It has some very deep pits (down to 22 m deep) where PC biota occur, but to date no PC molluscs have been mentioned.

The Inner Taganrog Bay hosts *Dreissena* and *Monodacna* communities. *Adacna fragilis* is also common. In the outer delta areas, a rich PC fauna of 11 species occurred until recently together with freshwater species, e.g. unionid mussels, planorbid snails and Lithoglyphus naticoides. The outer delta-bay transitional zone hosts the only known occurrences of the extremely rare *Clathrocaspia logvinenkoi* (Anistratenko 2007b). Historically PC species were common in the Taganrog Bay and the outer Don River Delta. In early 2000, communities were changing (Shokhin et al. 2006) but later works showed the persistence of, slightly altered but nevertheless diverse, *Monodacna colorata* communities in the inner and central bay area (Nabozhenko 2008) and the Yeysk Liman (Nabozhenko and Kovalenko 2011).

Until recently, Taganrog Bay remained relatively unaffected by invasive species. However, the introduction of three exotic polychaete species in 2013–2015 resulted in considerable changes in the bottom communities of the Taganrog Bay and the Don Delta by 2017–2018 (Bick et al. 2018;

Syomin et al. 2017). Within a few years after introduction, the alien polychaete Marenzelleria neglecta became dominant in PC habitats in the eastern part of the Taganrog Bay. However, its sharp increase so far was not accompanied by considerable shifts in *Monodacna* abundance or species structure of corresponding communities. Corbicula cf. fluminea, which was first found in the Don River in 2017 (Zhivoglyadova et al. 2018), is considered one of the most aggressive invasive species tending to lead to negative environmental consequences (Bespalaya et al. 2018; Crespo et al. 2015) and can therefore be potentially hazardous exotic species for PC molluscs in the fresh and oligohaline zones. Recently, the brackish water mussel Mytilopsis leucophaeta was reported from the inner Taganrog Bay (Zhulidov et al. 2015), which, if capable to survive low winter temperatures, can disrupt PC habitats similar as in the Dniester Liman.

The Taganrog Bay and the Don River are located in a densely populated area with intensive shipping, agricultural and industrial activity. Dredging and dumping are common in the eastern Taganrog Bay, where artificial fairways subject to permanent siltation are present. Continuous dredging also occurs in the Don River, especially in the delta. The Lower Don and the Taganrog Bay waters are strongly eutrophicated due to the sewage discharge and terrigenous nutrients from agricultural fertilizers (Matishov 2005; Moses et al. 2012). Large industrial ports – Taganrog and Mariupol – are sources of local toxic contamination as well. A considerable threat is the Bagayevskiy waterworks facility which is planned to be put into operation in 2023 (http://bguzel.ru/). According to preliminary estimates, it will lead to wide-scale changes in the Lower Don ecosystem (Dubinina and Zhukova 2016; Krivoshey 2016).

SE Azov Sea coast

The area includes the coastal zone of the Temryuk Bay northwards to Primorsko-Akhtarsk, and the estuaries and channels of the Kuban Delta. The marine part has typical features of the southern Sea of Azov, with mesohaline conditions and faunas, sandy beaches and silty and shelly sediments at depths over 2 m (Simonov and Altman 1991). The estuaries and channels of the Kuban Delta contain waters from fresh-lower mesohaline, and are mostly shallow (average depth within 0.5-1.8 m), with various bottom sediments (e.g. silt, shells and sand) (Nagalevsky and Nagalevsky 2013). Little recent information is available on the PC species occurrences from the area. *Monodacna colorata* was recorded in environmental impact assessments for oil exploration from the Kurchanskiy, Konovalovskiy, Kulikovskiy and Polyakov Limans (Korpakova et al. 2007) and the Temryuk Bay itself (Korpakova et al. 2008). Also, *Dreissena polymorpha* communities with relatively high biomass of the dominant species were mentioned across the area (Korpakova et al. 2010). No recent records of PC hydrobiid species are known from the region, even though their general presence in the area was reported by Golikov and Starobogatov (1972).

As the PC species occurrences are poorly known, we have no insights into their trends, but the area is subject to severe anthropogenic modifications. These include invasive species (Syomin et al. 2020), oil/gas exploration and production in Temryuk Bay whose infrastructure caused considerable habitat damage (Nagalevsky and Lobko 2017), and the shallowing and siltation in the estuaries of the Kuban Delta area resulting from hydraulic engineering and pollution by the drainage waters from the rice fields released into the water system. Some limans have been transformed in aquaculture ponds losing PC habitats.

Tsimlyansk Reservoir

A recent expansion of *Monodacna colorata* and *Adacna vitrea glabra* upstream into the Tsimlyansk Reservoir in the Don River has been documented by Son et al. (2020). The latter species was imported by ship traffic from the Caspian Sea through the Volga-Don Canal. *Monodacna colorata* expanded from Taganrog Bay and has now moved through the Volga-Don Canal upstream in the Volga River (AFS and MVV, PO 2017). Species-rich *Dreissena* communities with high biomass containing PC crustaceans, bryozoans, polychaetes and hydrozoans are common on hard and sandy substrata in the reservoir (Bulysheva et al. 2019).

2.3.2 Threats

Five direct threats have been shown or postulated to drive the decline of PC communities and species (for references see below). These are a) damming of rivers, b) modification of marine and freshwater influx in coastal areas, c) invasive alien species, d) pollution/eutrophication and e) climate change.

Damming of rivers

Damming of rivers (IUCN threat category 7.2 Dams & water management/use) is common in almost all major PC rivers. The construction of dams and large-scale water irrigation systems resulted in modifications of river flow regimes that affected PC species and communities (Lyashenko et al. 2012; Semenchenko et al. 2015; Son 2007b). Many PC species are sensitive to oxygen availability and river flow regimes (Mordukhay-Boltovskoy 1960). The newly built structures, such as cascades at reservoir dams, and cement-lined canals and riverbanks, provided new habitats for some *Theodoxus*/*Dreissena* species (Semenchenko et al. 2016; Semenchenko et al. 2015; Son 2007b). At the same time, soft-bottom or vagile species that are dependent on intermittent flow regimes (e.g. hydrobiids) declined with the newly erected barriers (Son 2007a). In river networks, the damming resulted in compartmentalisation and disappearance of small river basins and the degradation of floodplains and deltas of larger rivers. Within the estuaries damming led to isolation, local salinization resulting in reduction of prime PC habitat. Silt accumulation and loss of hard substrate and vegetation as a result of restricted river flow by damming has created adverse conditions for PC communities in the Dnieper River (Romanenko 1987; Zakonnov et al. 2019) resulting in declining habitat area (Alexenko and Kucheryava 2019; Alexenko and Shevchenko 2016). Such deterioration also applies to other rivers of the NW Black Sea region (South Bug, Dniester), as well as the lower Don River and Taganrog Bay (Anistratenko et al. 2011; Shokhin et al. 2006). Siltation should be considered as an important, perhaps even a key factor triggering habitat reduction threatening PC biota.

The modification of marine and freshwater influx in coastal areas

Modification of marine and freshwater influx in coastal areas (IUCN threat category 7.3 Other ecosystem modifications) affects natural salinity regimes and gradients that sustain(ed) PC species and communities in the coastal zone. It concerns (a) restriction of Black Sea water input through coastal barrier erection and closing of inlets, (b) increasing freshwater influx through diversion canals from adjacent rivers, (c) increased river discharge variability as a result of upstream water withdrawal and episodic release (worsened by increased summer droughts and peak flooding) and (d) increased marine influx through the construction and dredging of shipping lanes and breaching of coastal barriers. Each region contains a specific combination of factors affecting salinity gradients and regimes that sustain PC species and communities, but overall, the variability has strongly increased. In many of the PC areas, (episodic) influx of mesohaline Black Sea waters increased as a result of canal and shipping lane construction and dredging. Especially deep-water shipping canals that require regular dredging, resulted in massive seawater intrusion into estuaries and river deltas during storm surges causing rapid salinity fluctuations. The impact may be magnified due to large-scale water withdrawal upstream from these estuaries and river deltas. In several regions, breaching of sand barriers and spits resulted in a strong salinity increase and break down of the pre-existing stable gradients (Mikhailov and Gorin 2012). Other estuaries and bays have become isolated hypersaline lakes as a result of their separation from the major limans either by natural or by man-made interventions (Vinogradov et al. 2014). These hypersaline lakes (including the entire Tiligul Liman) are hostile to PC species. The break-down of salinity gradients in Danube coastal lake systems due to closing of Black Sea inlets and river diversion has been a major factor driving the demise of PC species and communities there (Son 2007b; Velde et al. 2019). PC species in the non-tidal Black Sea basin estuaries live in a wide salinity gradient but often occur in the relatively constant salinity regimes of the bottom water layers (Khlebovich 1974). Populations of PC species have local acclimatization optima and are negatively affected by rapid salinity fluctuations even when occurring within the limits of their autecological tolerance (Orlova 1987; Orlova et al. 1998; Zhulidov et al. 2018). Increasing salinity variability is especially beneficial to generalist alien and native species (Shiganova 2011; Zhulidov et al. 2018).

Invasive alien species

Invasive species (IUCN threat category 8.1 Invasive non-native/alien species/diseases) are an ongoing concern for PC biota and (Alexandrov et al. 2007; Bij de Vaate et al. 2002; Son 2007a). PC communities have been replaced by communities dominated by invasive *Mytilopsis leucophaeata, Potamopyrgus antipodarum*, *Rhithropanopeus harrisii* and other euryhaline species (Son 2008; Son et al. 2013; Zhulidov et al. 2018) in the outer part of the Dniester Liman and upper Bug-Ingul estuarine zone in areas previously inhabited by *Clessiniola*, limnocardiine and other PC species. Community turnover can be very rapid, as shown by Syomin et al. (2017) for the Taganrog Bay. In some of the lower estuaries, increased salinity has resulted in the replacement of PC communities by marine communities deriving from the Black Sea (Zhulidov et al. 2018). These marine communities are heavily affected by three invasive mollusc species, especially in the NW Black Sea: Mya arenaria, Rapana venosa and *Anadara* sp. (see for taxonomy discussion of the latter Anistratenko et al. (2014); Anistratenko and Khaliman (2006); Krapal et al. (2015)). In areas with strong freshening, such as the Razim-Sinoe system, freshwater mollusc species including non-native bivalves (*Sinanodonta woodiana*, *Corbicula fluminea*) and viviparids expanded at the cost of PC species (Popa and Murariu 2009; Velde et al. 2019). Some PC species have become invasive themselves. The Quagga mussel *Dreissena bugensis*, expanded in the second half of the 20th century from its native NW BSB range into all PC habitats, but also into all major western-central European inland water systems and even North America (Lyashenko et al. 2012; Son 2007a, b). The BSB species *Monodacna colorata* has recently been introduced into the Volga and Caspian basins as well as Lake Balkash (Kazakhstan) (Son et al. 2020; Wesselingh et al. 2019). A native Caspian subspecies, *Adacna vitrea glabra* recently expanded into the Don River drainage and has a large impact on local benthic species and communities (Son et al. 2020). Increased shipping activity between the Volga and Don river systems increase the introduction risk of Caspian PC species in the BSB.

Pollution and eutrophication

Pollution and eutrophication (IUCN threat categories 9.3.1 Nutrient loads, 9.3.3 Herbicides & pesticides, 9.6.2 Thermal pollution) are rampant throughout the region, resulting from large-scale industrial and agricultural activities in the PC river basins (Lyashenko et al. 2012; Semenchenko et al. 2015). Organic pollution and eutrophication negatively affect PC communities and species that are sensitive to oxygen regimes (Mordukhay-Boltovskoy 1960; Popa et al. 2009). Thermal pollution is a local threat to Kuchurgan Estuary and the lower Dnieper River by simultaneously affecting the PC species communities and creating preferable conditions for alien species (Protasov et al. 2013; Son 2007a; Son et al. 2013). Eutrophication has been proposed as a driver for the demise of lymnocardiine species in many lakes in the Danube Delta area (Popa et al. 2009) and also appears to negatively affect communities in Lake Sasyk at the northern end of the Danube Delta, yet pollution levels in the Razim-Sinoe system were found to be low (Catianis et al. 2018).

Climate change

Direct impact of climate change (IUCN threat categories 11.1 Habitat shifting & alteration, 11.2 Droughts, 11.4 Storms & flooding) on PC communities and habitats has been demonstrated in the BSB. In the Taganrog Bay, influx of mesohaline Black Sea waters increased as a result of shortage of freshwater flow due to insufficient river flow regulation at the background of climate change (Matishov et al. 2017). Increased summer droughts as well as peak flooding is making inflowing river discharge more unpredictable and during prolonged summers rivers may even cease to deliver fresh water to the PC habitats. This is already affecting areas within the Dniester and Dnieper regions and the Tiligul and Berezan Limans. Projected climate change with higher temperatures, increased periodic drought as well as very high peak discharge in the catchments can be expected to further increase the instability of PC habitats. Additionally, projected sea level rise will affect coastal lagoons and estuaries (Velde et al. 2019).

2.4 Discussion – towards effective conservation of PC biota in the BSB

The combined evidence of this review paper indicates a decline of PC mollusc species and their communities throughout the BSB. However, while the decline seems evident, its ecological consequences are not. It is largely unknown to what extent the species associated with the PC taxa (e.g. their parasites or predators) may be affected by their demise. The decline in abundance and apparent fragmentation (and isolation) of populations is a problem in itself, but may drive genetic depletion, which should also be another reason for concern. Data on genetic diversity of PC species in the BSB is scarce, and little understanding exists on patterns and processes of gene flow between populations, even though it may be an important determinant of PC biodiversity maintenance (Audzijonyte et al. 2017; Audzijonyte et al. 2006).

The first step towards effective conservation is improving a) scientific knowledge on PC biodiversity at community, species and genetic levels, and b) understanding population and community dynamics as well as species distributions and their ecological tolerances (Cardoso et al. 2011). Recurring and standardised collection and observation efforts are paramount as a basis for establishing trends. These efforts shall be cross-country collaborative efforts given the transnational character of the PC species and habitats. Furthermore, an improved taxonomical base from integrated morphological-genetic studies is required, whenever the limited amount of living specimens allow for such approaches. Such studies should extend beyond mollusc species and include other groups of PC invertebrate and vertebrate taxa. For many important PC invertebrate groups (such as copepods, amphipods, decapods) no up-to-date taxonomic overview exists (Table 2.2) and they contain disputed species. Historical distribution data are often imprecise and also hampered by uncertainty in identifications (see Appendix 2.1). Updated taxonomy will enable targeted research into autecological tolerances and species responses to disturbances. Furthermore, the extinction risk of species should be updated through IUCN assessments, as many of the taxa concerned are currently data deficient to perform such analyses (e.g. see Wesselingh et al. 2019). New data on PC populations, species and communities will enable a more inclusive and comprehensive definition of PC habitats and their inclusion in conservation schemes.

Secondly, our proposed optimum PC habitats shall be validated using the quantitative data on up-to-date PC population sizes, and standardised threat analyses shall be performed such as conducted by Lattuada et al. (2019) for the Caspian Sea, and Birstein et al. (2006), and Vassilev (2006) for sturgeon habitats. Threat analyses should focus on four PC regions in the BSB (Danube

Table 2.2. Approximate species richness for various invertebrate PC groups in the BSB.

PC group	Number of species	Author
Cnidaria	2-4 spp.	(Mordukhay-Boltovskoy, 1960)
Crustacea – Amphipoda	40-45 spp.	(Mordukhay-Boltovskoy, 1960)
Crustacea – Copepoda	12 spp.	(Monchenko, 2003)
Crustacea – Cumacea	11 spp.	(Mordukhay-Boltovskoy, 1960)
Crustacea – Decapoda	2 spp.	(Policar et al., 2018)
Crustacea – Mysidae	9 spp.	(Audzijonyte, Daneliya, Mugue, & Väinölä, 2008)
Hyrudinea	1 sp.	(Mordukhay-Boltovskoy, 1960)
Mollusca – Bivalvia	6 spp.	This work
Mollusca – Gastropoda	10 spp.	This work
Polychaeta	3 spp.	(Kiseleva, 2004)

Delta – Razim Lake system, Dniester Liman, Dnieper-South Bug Estuary and Taganrog Bay-Don Delta) that contain target species and environmental conditions which can, and in cases do support the survival of PC communities (Table 2.1, Fig. 2.2). Quantitative knowledge on population sizes of PC species is lacking both for molluscs and other groups. Especially, crustaceans contain large numbers of PC species (Table 2.2), and their inclusion would greatly improve the definition of optimum PC habitats. Our proposed optimum PC habitats are therefore indicative for the moment.

The final step should be assessing some of the indirect anthropogenic drivers of PC biodiversity change that are causing the identified direct drivers of decline, such as institutional arrangements and legal landscape, following the IPBES Conceptual Framework (Díaz et al. 2015). Institutional alignment and responsibilities to address PC biodiversity conservation and governance has been studied by Gogaladze et al. (2020a); Gogaladze et al. (2020b), which showed that this biota is not a priority for conservation planning in Ukraine and Romania. Future studies are required to understand legal arrangements of countries sharing the PC biodiversity and their outcomes for conservation. Currently, some parts of optimum PC habitats are covered by national and/or large transnational protected areas such as the Danube Delta Biosphere Reserve shared by Ukraine and Romania. Other parts are covered by Emerald sites (https://emerald.eea.europa.eu/), Natura 2000 sites (https://Natura2000.eea.europa.eu/) and/or by Ramsar sites (https://www.protectedplanet.net/166893). Coverage of optimum PC habitats by protected areas may provide (incidental) protection to PC communities and species, but has not resulted in targeted conservation to date. Assignment of optimum PC habitats to IUCN category IV: Habitats/species management area (Dudley 2008) can be a useful approach. The IUCN protected area management categories provide a global framework for sorting the variety of protected area management aims. Category IV aims to "maintain, conserve and restore species and habitats" (https://www.iucn.org/theme/protected-areas/about/protected-areas-categories/category-iv-habitatspecies-management-area). Such categorization can take place in different phases of establishing a protected area, such as the initial phase: before the protected area is established and category has to be decided, or in later phase: after the protected area has already been established and category decided, but management aim is to address emerging conservation priorities (Dudley 2008). Managing and mitigating the wholesale decline of the unique PC biota in the BSB will require longstanding commitment from various stakeholders in the specific PC countries.

2.5 Conclusions

PC mollusc species and communities in the Black Sea Basin have suffered a severe decline over the past century. Five major drivers for the decline are identified. However, basic distribution data and integrated approaches to mitigate the decline are lacking. Some species have gone extinct and several others are under increased risk of extinction and entire communities have vanished as well. The identification of optimum PC habitats will enable targeted conservation action. Sustained, transnational collaboration is required to improve conservation of PC species, communities and their habitats in the BSB. Only then can the effective conservation of the unique and threatened PC biota be achieved in the Black Sea Basin.

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Data accessibility statement

All data that support the findings of this study are provided in supplementary files. PC habitat polygon shapefiles as well as the attributes describing historical (20th century) and modern (21st century) distributions of PC target taxa are available at https://figshare.com/s/5400c1df29da026c399f (private link).

Appendices

Appendix 2.1 - Update on the taxonomic status of BSB Pontocaspian mollusc species
Appendix 2.2 - Pontocaspian species occurrences in the BSB in 20th and 21st centuries
Appendix 2.3 - Pontocaspian habitat polygon shapefiles

Appendix 2.1. Update on the taxonomic status of BSB Pontocaspian mollusc species

The Pontocaspian mollusc species list (Wesselingh et al. 2019) listed and discussed species whose status at the time were agreed upon ("accepted") by the various authors, and species whose status was considered to be uncertain, based on a review of existing data. Currently several taxonomic studies have been completed or are under way that will provide further clarification. Here a brief summary of the taxonomy of the BSB PC mollusc species is given.

Neritidae – The recent revision of *Theodoxus* species (Sands et al. 2020) clarified the species delimitation of this genus and showed the presence of four *Theodoxus* species in the BSB (*T. danubialis*, *T. fluviatilis*, *T. velox* and *T. major*, the latter listed as *T. pallasi* in Wesselingh et al. (2019)). However, they also showed that discrimination based on shell morphology is not always sufficient and that some historical records should be re-evaluated. Especially, the confirmation of *T. major* and *T. velox* occurrences in the BSB can be expected to change with further study.

Hydrobiidae – The taxonomic status of PC hydrobiid snails is subject of a number of ongoing studies that will lead to further clarification for species boundaries (e.g. Anistratenko/Neubauer et al. in prep.). A molecular study on the identity of BSB *Clathrocaspia* species is currently under way to assess the status and potential synonymy of four species listed by Wesselingh et al. (2019) (TW & VVA, pers. comm.). The status of two of the smooth PC hydrobiid species listed from the BSB by Wesselingh et al. (2019) (?*Laevicaspia ismailensis* (accepted) and *Turricaspia chersonica* (uncertain)) requires further study involving molecular analyses and study of type material to assess possible conspecifity and establish the generic assignemnt (VVA, pers. comm.). The status of *Laevicaspia lincta* and *Clessiniola variabilis* is undisputed.

Cardiidae – After Wesselingh et al. (2019) published the PC species list, further material of BSB *Adacna fragilis* has been inspected in order to assess its status (listed as uncertain in the publication). The range of morphological variation of the BSB material (especially the almost equilateral shell, the pallial sinus not extending the vertical midline, the more pronounced and well demarcated ribs, especially on the median part of the shell, and the smaller adult size) as well as the salinity preferences differ from the resembling Caspian *Adacna laeviuscula* and merits a separation of the two species. There is full agreement to change the status of *Adacna fragilis* to accepted species among the authors. The species *Adacna glabra* reported by Son et al. (2020) from the Don River was considered as an uncertain status subspecies of *Adacna vitrea* by Wesselingh et al. (2019), who argued for molecular confirmation. However, a review of the distribution range, ecological tolerance and shell characters shows that it is likely that *A. glabra* is closely related to, but at the same time distinct from *A. vitrea*. *Adacna glabra* differs by having somewhat stronger developed ribs with a rather pointed rib crest and the often whitish colour of the shell. We adopt for the moment the distinction proposed by Kijashko (Kijashko in Bogutskaya et al. (2013)) and consider *A. vitrea* vitrea and *A. vitrea glabra* as subspecies whose status will need molecular corroboration.

Dreissenidae – The taxonomy and status of the two BSB dreissenid species (*Dreissena polymorpha* and *D. bugensis*) is undisputed.

Appendix 2.2. Pontocaspian species occurrences in the BSB in 20th and 21st centuries.

Table A2.2.1. Sub-areas within the Danube-Razim and Bulgarian coastal wetlands. ID numbers of the sub-areas are used in Figures A2.2.1-4 for display (see below). + indicates the presence and – the absence of the relevant PC mollusc target taxa in 20th and 21st centuries. C stands for century. PO stands for personal observation. PC habitat map of the Danube Delta region (Fig. 2.6 in the manuscript) and the Danube Delta shapefile (Appendix 2.3) are based on the data in this table.

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
UA	1	Lake Kagul	+ Markovsky (1955)	+ Markovsky (1955)	+ Dzhurtubaev et al. (2017); Munasypova-Motyash (2006)	- Dzhurtubaev et al. (2017)	
UA	2	Northern floodplain lakes west of Izmail	- Markovsky (1955)	- Markovsky (1955)	- MOS (PO)	- MOS (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
UA	3	Lake Yalpug	+ Markovsky (1955); VVA (PO)	+ Markovsky (1955); VVA (PO)	+ Munasypova-Motyash (2006); MOS, VVA (PO)	+ MOS (PO)	
UA	4	Lake Kugurlui	+ Markovsky (1955)	+ Markovsky (1955)	+ Dzhurtubaev et al. (2018)	- Dzhurtubaev et al. (2018)	
UA	5	Lake Katlabukh	+ Markovsky (1955)	+ Markovsky (1955)	+ MOS (PO)	- MOS (PO)	
UA	6	Lake Kitai	+ Markovsky (1955)	- Markovsky (1955)	- MOS (PO)	- MOS (PO)	
UA	7	Lake Sasyk	+ Markovsky (1955)	+ Markovsky (1955)	+ Khalaim and Son (2016); Munasypova-Motyash (2006); MOS, VVA (PO)		Limnocardiid invasion end 20th
UA	8	Northern floodplain lakes east of Izmail	- Markovsky (1955)	- Markovsky (1955)	- MOS (PO)	- MOS (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
ROU, BG	9	Upstream Danube River, Brailla-Gura Vai section	- Ignat et al. (1997), Vădineanu et al. (2000)	- Ignat et al. (1997), Vădineanu et al. (2000); + Likely present (dead shells) Russev (1966)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	+ Boeters et al. (2015); ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013); - ABP (PO)	PC taxa Romania: (*Dreissena*, *Theodoxus*) present (Angelov 2000; Drensky 1947; Russev 1966; Wohlberedt 1911); TT (2012-2019, PO); ABP (PO)
ROU	10	Danube River, Braila-Tulcea section	+ Popa et al. (2009)	- Markovsky (1955); Ignat et al. (1997); Vădineanu et al. (2000)	- Popa et al. (2009); ABP (PO); ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)
ROU, UA	11	Chilia branch and outer delta lakes, upstream from Vilkovo	+ Markovsky (1955)	- Markovsky (1955), - Ignat et al. (1997); Vădineanu et al. (2000)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)

(Continuation Table A2.2.1.)

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
ROU, UA	12	Chilia branch and outer delta lakes downstream from Vilkovo	+ Markovsky (1955)	+ Markovsky (1955)	+ MOS (PO)	- MOS (PO)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)
ROU	13	Sulina branch of Danube River	+ Likely present (dead shells) ABP (PO)	- Ignat et al. (1997); Vădineanu et al. (2000)	- ABP (PO); ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)
ROU	14	Sf. Gheorghe branch of Danube River	+ Popa et al. (2009)	- Ignat et al. (1997); Vădineanu et al. (2000)	- Popa et al. (2009); ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013), ABP (PO)	- ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013), ABP (PO)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)
ROU	15	Lake Brates	+ Popa et al. (2009)	Data deficient	- Popa et al. (2009)	Data deficient	
ROU	16	Lake Jijila	+ Popa et al. (2009)	Data deficient	- Popa et al. (2009)	Data deficient	
ROU	17	Lake Crapina	+ Popa et al. (2009)	Data deficient	- Popa et al. (2009	Data deficient	
ROU	18	Floodplain lakes between Chilia and Sulina branches	- Ignat et al. (1997); Vădineanu et al. (2000)	- Ignat et al. (1997); Vădineanu et al. (2000)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	- ABP (PO) 2015, Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present
ROU	19	Floodplain lakes between Sulina and Sf. Gheorghe branches	- Ignat et al. (1997); Vădineanu et al. (2000)	- Ignat et al. (1997); Vădineanu et al. (2000)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)
ROU	20	Lake Puiu	+ Popa et al. (2009)	- ABP (PO)	- Popa et al. (2009)	- ABP (PO)	
ROU	21	Floodplain lakes south to Sf. Gheorghe branch	- Ignat et al. (1997); Vădineanu et al. (2000)	- Ignat et al. (1997); Vădineanu et al. (2000)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	- ABP (PO), ICPDR (2008, 2015); Stoica et al. (2014); Stoica et al. (2012); Stoica et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present ABP (PO)

(Continuation Table A2.2.1.)

Country	**ID**	**Sub-area**	PC Cardiidae 20th C	**PC Hydrobiidae 20th C**	**PC Cardiidae 21st C**	**PC Hydrobiidae 21st C**	**Remarks**
ROU	22	Lake Murighiol	+ Popa et al. (2009)	- ABP (PO)	- Popa et al. (2009)	- ABP (PO)	
ROU	23	Lake Dranov	+ Popa et al. (2009)	- ABP (PO)	- Popa et al. (2009)	- ABP (PO)	
ROU	24	Sakhalin area	- Gomoiu and Skolka (1996); Gomoiu and Skolka (1998)	- Gomoiu and Skolka (1996); Gomoiu and Skolka (1998)	- Pavel et al. (2019)	- Pavel et al. (2019)	
ROU	25	Musura Bay	- Gomoiu and Skolka (1996); Gomoiu and Skolka (1998)	- Gomoiu and Skolka (1996); Gomoiu and Skolka (1998)	- Pavel et al. (2019)	- Pavel et al. (2019)	PC taxa (*Dreissena*, *Theodoxus*) present Pavel et al., 2019
ROU	26	Lake Razim-Golovita	+ Popa et al. (2009); Teodorescu-Leonte et al. (1956); Teodorescu-Leonte (1966); Teodorescu-Leonte and Leonte (1969); Teodorescu-Leonte (1977).	- Grossu (1986); + Velde et al. (2019)	+ Popa et al. (2009), + ABP (PO); Paraschiv et al. (2010a); Paraschiv et al. (2010b); Velde et al. (2019)	+ Wilke et al. 2007; - ABP (PO)	PC taxa (*Dreissena*, *Theodoxus*) present ABP, FPW (PO); PC hydrobiids have only been reported once in 21th century (2003; Wilke et al. 2007) and not found in later years
ROU	27	Lake Sinoe	-+ Popa et al. (2009); Teodorescu-Leonte et al. (1956); Teodorescu-Leonte (1966); Teodorescu-Leonte and Leonte (1969); Teodorescu-Leonte (1977).	- Velde et al. (2019)	+ Popa et al. (2009), + ABP (PO); Paraschiv et al. (2010a); Paraschiv et al. (2010b)	- ABP (PO)	
ROU	28	Lake Babadag	+ Popa et al (2009)	Data deficient	- Popa et al. (2009), - ABP (PO)	- ABP (PO)	
ROU	29	Lake Leahova	+ Popa et al (2009)	Data deficient	- Popa et al. (2009), - ABP (PO)	- ABP (PO)	
ROU	30	Coastal lakes near Sinoe	Data deficient	Data deficient	Data deficient	Data deficient	
BG	NA	Lake Durankulak	- Angelov (2000); Kovachev et al. (1999)	- Angelov (2000); Kovachev et al. (1999)	- Hubenov (2015); Vidinova et al. (2016)	- Hubenov (2015); Vidinova et al. (2016)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Kovachev et al. 1999); TT (2010, 2014, PO)
BG	NA	Lake Shabla-Ezerets	- Angelov (2000); Kovachev et al. (1999)	- Angelov (2000); Kovachev et al. (1999)	- Hubenov (2015); Vidinova et al. (2016)	- Hubenov (2015); Vidinova et al. (2016)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Kovachev et al. 1999; Valkanov 1941); TT (2010, 2014, PO)
BG	NA	Lake Beloslav	-- Drensky	- Drensky	Hubenov	Hubenov	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Drensky 1947; Valkanov 1957a)
ROU	30	Coastal lakes near Sinoe	Data deficient	Data deficient	Data deficient	Data deficient	

(Continuation Table A2.2.1.)

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
BG	NA	Lake Durankulak	- Angelov (2000); Kovachev et al. (1999)	- Angelov (2000); Kovachev et al. (1999)	- Hubenov (2015); Vidinova et al. (2016)	- Hubenov (2015); Vidinova et al. (2016)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Kovachev et al. 1999); TT (2010, 2014, PO)
BG	NA	Lake Shabla-Ezerets	- Angelov (2000); Kovachev et al. (1999)	- Angelov (2000); Kovachev et al. (1999)	- Hubenov (2015); Vidinova et al. (2016)	- Hubenov (2015); Vidinova et al. (2016)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Kovachev et al. 1999; Valkanov 1941); TT (2010, 2014, PO)
BG	NA	Lake Beloslav	-- Drensky	- Drensky	Hubenov	Hubenov	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Drensky 1947; Valkanov 1957a)
BG	NA	Lake Varna	+ Kaneva-Abadjieva (1957)	- Kaneva-Abadjieva (1957)	- Hubenov (2015); Vidinova et al. (2016)	- Hubenov (2015); Vidinova et al. (2016)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Drensky 1947; Wohlberedt 1911
BG	NA	Kamchiya River Mouth and backwaters	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Valkanov 1957a); TT (2010, 2011, 2014, PO)
BG	NA	Lake Burgas (Vaya)	- Angelov (2000); Drensky (1947); Valkanov (1957a)	- Angelov (2000); Drensky (1947); Valkanov (1957a)	- Pandourski (2001); Vidinova et al. (2016)	- Pandourski (2001); Vidinova et al. (2016)	PC taxa (*Theodoxus*) present (Angelov 2000; Valkanov 1957a)
BG	NA	Lake Mandra	- Drensky (1947); Mihailova-Neikova (1961)	+ Drensky (1947, L. lincta live, June 1944); Mihailova-Neikova (1961)	- Hubenov (2015); Vidinova et al. (2016)	- Pandourski (2001); Vidinova et al. (2016)	PC taxa (*Dreissena*, *Theodoxus*) present (Angelov 2000; Valkanov 1957a); TT (2010, 2011, 2014, PO)
BG	NA	Ropotamo River Mouth	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	PC taxa (*Theodoxus*) present (Angelov 2000; Valkanov 1957a)
BG	NA	Dyavolsko Blato Marsh	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	
BG	NA	Karaagach River Mouth and Marsh	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	PC taxa (*Theodoxus*) present (Valkanov 1957a)
BG	NA	Veleka River Mouth	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	PC taxa (*Theodoxus*) present (Valkanov 1957a)
BG	NA	Silistar River Mouth	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	PC taxa (*Theodoxus*) present (Valkanov 1957a)
BG	NA	Rezovska Reka River Mouth	- Angelov (2000); Valkanov (1957a)	- Angelov (2000); Valkanov (1957a)	- Hubenov (2015)	- Hubenov (2015)	PC taxa (*Theodoxus*) present (Valkanov 1957a)

Table A2.2.2. Sub-areas within the Dniester Liman. ID numbers of the sub-areas are used in Figures A2.2.1-4 for display (see below). + indicates the presence and – the absence of the relevant PC mollusc target taxa in 20th and 21st centuries. C stands for century. PO stands for personal observation. PC habitat map of the Dniester Liman (Fig. 2.7 in the manuscript) and the Dniester Liman shapefile (Appendix 2.3) are based on the data in this table.

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
UA	1	Outer Dniester Liman	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ MOS, OYA, VVA (PO)	- MOS, OYA, VVA (PO)	PC taxa (*Theodoxus*) present
UA	2	Middle-Inner Dniester Liman	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ Munasypova-Motyash (2006); MOS, OYA, VVA (PO)	+ MOS, OYA, VVA (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
UA	3	Lower Dniester Floodplain	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ Grinbart (1953a); Son (2007a)	- MOS, OYA, VVA (PO)	- MOS, OYA, VVA (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
UA, MD	4	Kuchurgan Liman	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ Grinbart (1953a); Markovsky (1953); Son (2007a)	+ Filipenko (2011), MOS, VVA (PO)	- Filipenko (2011), MOS, VVA (PO)	
MD	5	Dniester River from Cioburciu to Dubasari	+ Cartea Roșie a Republicii Moldova (2015); Munjiu (2012)	- Balashov et al. (2013)	- Cartea Roșie a Republicii Moldova (2015)	- Balashov et al. (2013)	PC taxa (*Dreissena*, *Theodoxus*) present

Table A2.2.3. Sub-areas within the Dnieper-Bug Estuary. ID numbers of the sub-areas are used in Figures A2.2.1-4 for display (see below). + indicates the presence and – the absence of the relevant PC mollusc target taxa in 20th and 21st centuries. C stands for century. PO stands for personal observation. PC habitat map of the Dnieper-Bug Estuary (Fig. 2.8 in the manuscript) and the Dnieper-Bug Estuary shapefile (Appendix 2.3) are based on the data in this table.

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
UA	1	Tiligul Liman	+ Grinbart (1953b)	- Grinbart (1953b)	- Son (2007a)	- MOS (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
UA	2	Berezan Liman	+ Grinbart (1953b)		- Son (2007a)	- MOS (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
UA	3	Bug River upstream from Mykolaiv	+ Markovsky (1954a)	+ Markovsky (1954a)	- MOS (PO)	- MOS (PO)	PC taxa (*Dreissena*, *Theodoxus*) present
UA	4	Dnieper - South Bug Estuary	+ Markovsky (1954a); Zhadin (1931)	+ Markovsky (1954a)	+ Alexenko (2004); Munasypova-Motyash (2006); MOS, OYA, VVA (PO)	+ Alexenko (2004); MOS, OYA, VVA (PO)	
UA	5	Lower Dnieper -downstream from Inhulets	+ Markovsky (1954a)	+ Markovsky (1954a)	+ Alexenko (2004); OYA, VVA (PO)	+ Alexenko (2004); Wilke et al. (2007); MOS, OYA, VVA (PO)	
UA	6	Lower Dnieper – from Inhulets to Kakhovka Reservoir	+ Markovsky (1954a); TA (PO)	+ Markovsky (1954a); TA, VVA (PO)	+ TA, VVA (PO)	+ TA, VVA (PO)	Common 20st century occurrence of hydrobiids, only sporadic 21st century occurrence of hydrobiids (TA, PO)
UA	7	Dnieper upstream from Kakhovka Reservoir	+ Munasypova-Motyash (2006); VVA (PO)	Data deficient	+ Munasypova-Motyash (2006); Semenchenko et al. (2016)	Data deficient	PC taxa (*Dreissena*, *Theodoxus*) present 21st C
UA	8	Yagorlyk Bay	Data deficient	+ Anistratenko (1996)	Data deficient	Data deficient	PC taxa (*Dreissena*, *Theodoxus*) present 21st C

Table A2.2.4. Sub-areas within the Taganrog Bay-Don Delta. ID numbers of the sub-areas are used in Figures A2.2.1-4 for display (see below). + indicates the presence and – the absence of the relevant PC mollusc target taxa in 20th and 21st centuries. C stands for century. PO stands for personal observation. PC habitat map of the Taganrog Bay-Don Delta (Fig. 2.9 in the manuscript) and the Taganrog Bay-Don Delta shapefile (Appendix 2.3) are based on the data in this table and Table A2.2.5 below.

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
UA, RU	1	Taganrog Bay/ outer Don Delta	+ Mordukhay-Boltovskoy (1960); Scarlato and Starobogatov (1972b); Stark (1960); Vorobyev (1949); Nekrasova (1972)	+ Anistratenko (2007a); Golikov and Starobogatov (1972); Mordukhay-Boltovskoy (1960)	+ Nabozhenko (2005); Nabozhenko (2008); Shokhin et al. (2006)	+ Kovalenko (2009) ¥	¥ highly abundant in the Don River Delta, Kalancha channel, deep pit in 2 km upstream from mouth
RU	2	Mius Liman	+ Mordukhay-Boltovskoy (1960)	Data deficient, but given abundant records in 200 (TW, PO) likely present	+ VLS, 2003, 2006 (PO)	+ Wilke et al. (2007); Frank Riedel (PO), 2016	Likely presence of PC taxa in 20th C given the common occurrence in observations in 2000
RU	3	Lower Don up to Manych confluence	+ Mordukhay-Boltovskoy (1960)	Data deficient	+ Nabozhenko (2008)	Data deficient	PC taxa (*Dreissena*, *Theodoxus*) present 20-21st C (Zhivoglyadova and Frolenko 2017); VLS, 2017-2019 (PO)
RU	4	Tsimlyansk Reservoir	+ Scarlato and Starobogatov (1972b)	- Son et al. (2020)	+ Son et al. (2020)	- Son et al. (2020)	PC taxa (*Dreissena*, *Theodoxus*) present 21st Century (Bulysheva et al. 2019); VLS, 2018-2019 (PO)

Table A2.2.5. Sub-areas within the SE Azov Sea coast. ID numbers of the sub-areas are used in Figures A2.2.1-4 for display (see below). + indicates the presence of the relevant PC mollusc target taxa in 20th and 21st centuries. C stands for century. PC habitat map of the Taganrog Bay-Don Delta (Fig. 2.9 in the manuscript) and the Taganrog Bay-Don Delta shapefile (Appendix 2.3) are based on the data in this table and Table A2.2.4 above.

Country	ID	Sub-area	PC Cardiidae 20th C	PC Hydrobiidae 20th C	PC Cardiidae 21st C	PC Hydrobiidae 21st C	Remarks
RU	5	Coastal limans Kuban delta incl. Akhtarsk Liman	+ Mordukhay-Boltovskoy (1960)	+ Golikov and Starobogatov (1972)	+ Korpakova et al. (2007); Korpakova et al. (2008)	Data deficient	*Dreissena* community present (Korpakova et al. 2010)

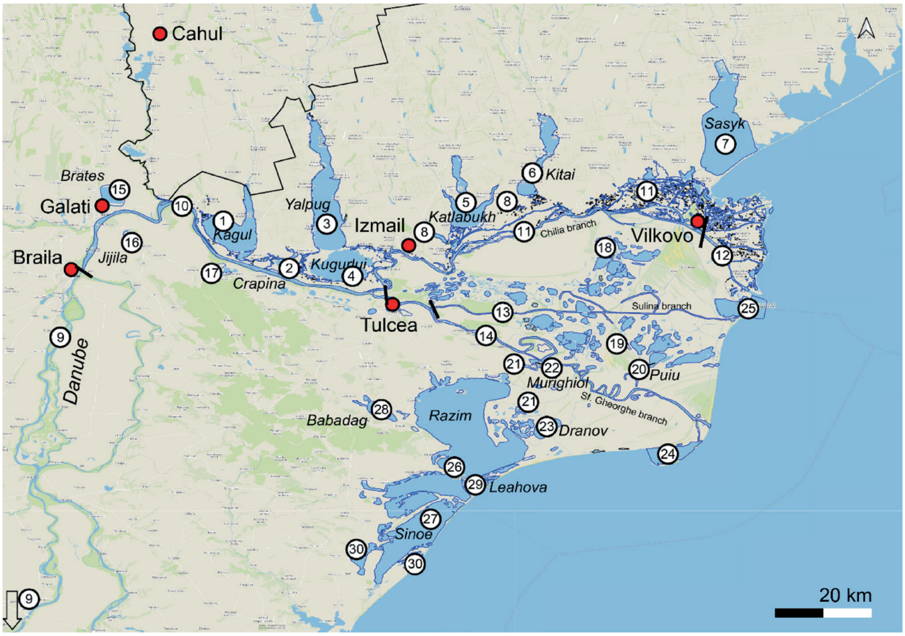

Figure A2.2.1. Danube-Razim and Bulgarian coastal wetlands. See IDs of the sub-areas in Table A2.2.1. Map is projected in EPSG Projection 4326 - WGS 84.

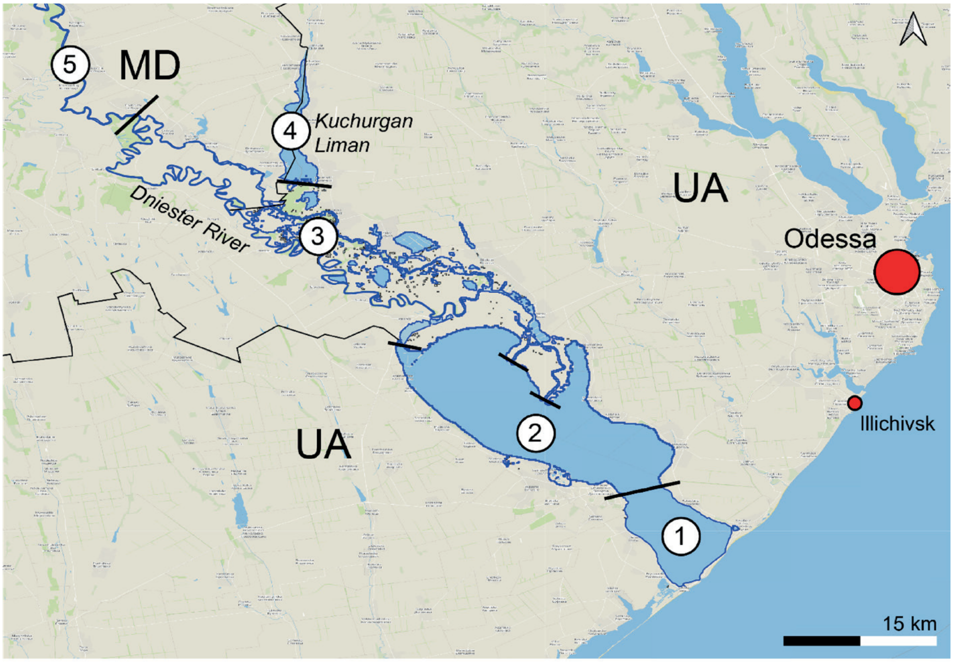

Figure A2.2.2. Dniester Liman. See IDs of the sub-areas in Table A2.2.1. Map is projected in EPSG Projection 4326 - WGS 84.

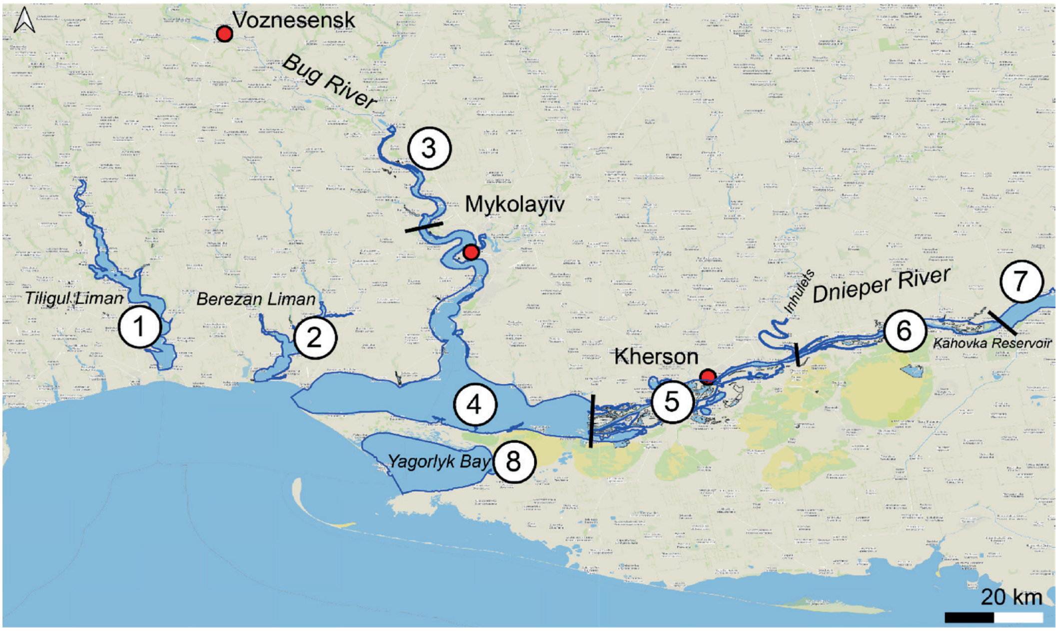

Figure A2.2.3. Dnieper-Bug Estuary. See IDs of the sub-areas in Table A2.2.1. Map is projected in EPSG Projection 4326 - WGS 84.

Figure A2.2.4. Taganrog Bay-Don Delta and SE Azov Sea coast. See IDs of the sub-areas in Table A2.2.1. Map is projected in EPSG Projection 4326 - WGS 84.

Appendix 2.3. Pontocaspian habitat polygon shapefiles

Available at https://datadryad.org/stash/share/cMhMU-zTUUULuZM1XjtQKZNwN5M-L6cwKiKP4kaf6go.