

THREATS TO THE PONTOCASPIAN FAUNA



Matteo Lattuada, Doctoral Thesis



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PONTOCASPIAN FAUNA

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by

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Dreissena bugensis

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ABSTRACT



Oil glistens on the Caspian Sea surface. © Getty Images

ABSTRACT

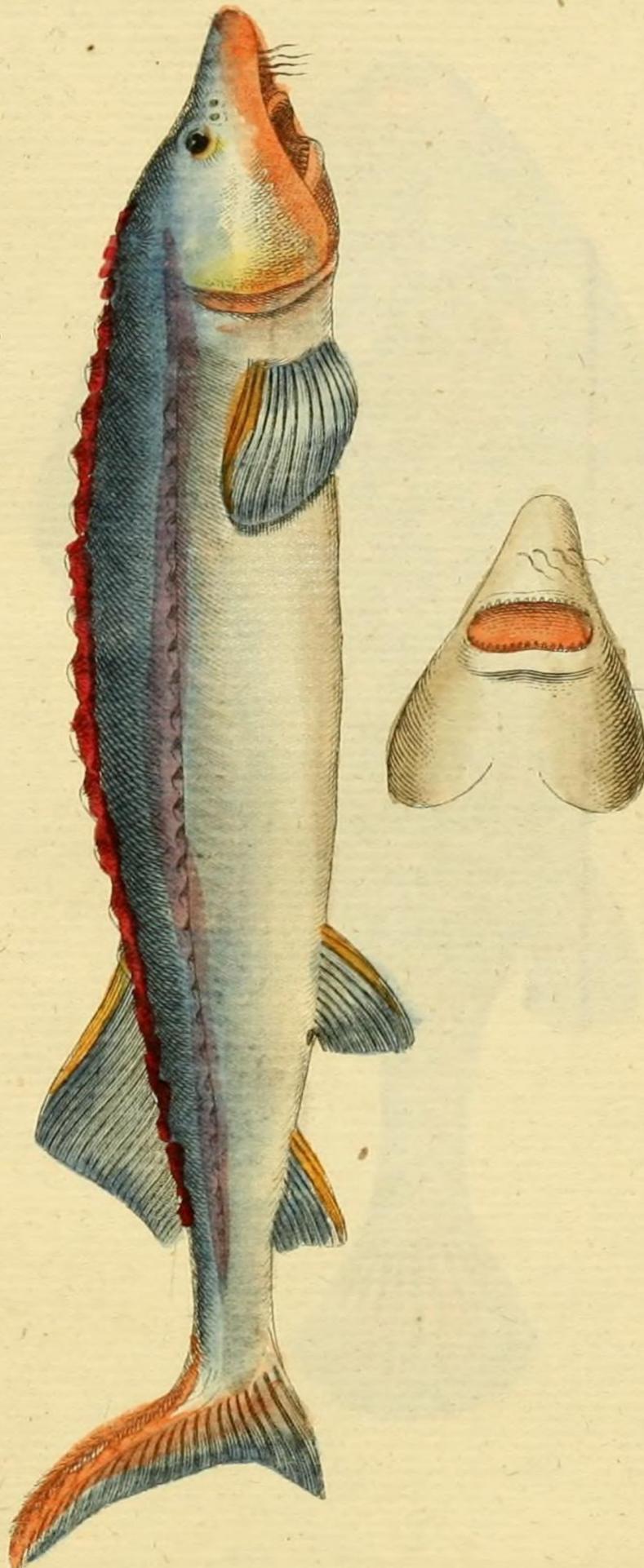
The Pontocaspian region is a unique system of connected and independent basins constantly transformed by major geo-climatic events. The intermittent connections of basins with different water salinity drove the evolution of an atypical brackish water biodiversity, best represented by fish, crustaceans and mollusks. During the Anthropocene, human activities started to exert strong pressure on the Pontocaspian region biota, becoming a relevant threat to its biodiversity. In this context, in my PhD I used the endemic mollusks of the Caspian Sea to evaluate the current anthropogenic threats to the Pontocaspian region. I used geospatial modeling to map nine anthropogenic pressures, finding that chemical pollution, invasive species, poaching and streamflow regulations have the highest impact score on the Caspian Sea mollusks. However, the intensity and the relative contribution of these anthropogenic pressures varied along vertical and horizontal dimensions. For example, poaching and streamflow regulation resulted in a higher pressure score in the northern part of the Caspian Sea, whereas pressure from chemical pollution and invasive species increases in the middle and southern parts of the basin. To evaluate how endemic species are affected by the anthropogenic threats, I used ecological and morphological data to review the taxonomy of the Pontocaspian endemic mollusks and to estimate hotspots of endemic mollusk diversity in the Caspian Sea. Subsequently, I evaluated the spatial overlap between anthropogenic pressures and mollusk hotspots, finding that invasive species and chemical pollution are the major anthropogenic threats to likely impact mollusks. Finally, I generated 28 spatially explicit environmental variables to facilitate the development of ecological models to investigate the combined influence of anthropogenic and environmental factors in driving spatial patterns of biodiversity. As the new variables match the world ocean data set Bio-ORACLE, they can be used to extend marine ecological models to the Caspian Sea. This allows for the first time the inclusion of the Caspian in cross-system models relevant for conservation management and planning.

ZUSAMMENFASSUNG

Die pontokaspische Region ist ein einzigartiges System von miteinander verbundenen als auch unabhängiger Becken, die durch wichtige geoklimatische Ereignisse ständig verändert wurden. Die intermittierenden Verbindungen von Becken mit unterschiedlichem Salzgehalt des Wassers bedingten die Entwicklung einer atypischen Brackwasser-Biodiversität voran, die am besten durch Fische, Krebs- und Weichtiere repräsentiert werden. Während des Anthropozäns begannen menschliche Aktivitäten einen starken Druck auf die Biota der pontokaspischen Region auszuüben und wurden zu einer relevanten Bedrohung für die Biodiversität in diesem Gebiet. Die vorliegende Doktorarbeit evaluiert in diesem Zusammenhang die gegenwärtigen anthropogenen Bedrohungen für die pontokaspische Region, wobei das Kaspische Meer als Modellsystem und die Mollusken als Modeltaxon verwendet werden. Dafür wurde eine georäumliche Modellierung genutzt, um die neun wichtigsten anthropogenen Belastungen im Kaspischen Meer zu kartieren. Die Analyse zeigte, dass chemische Verschmutzung, invasive Arten, Wilderei und Flussregulierungen den größten Einfluss auf die Mollusken im Kaspischen Meer haben. Um zu beurteilen, wie endemische Arten von den anthropogenen Bedrohungen betroffen sind, wurden ökologische und morphologische Daten verwendet, um die Nomenklatur und den Artstatus der endemischen, pontokaspischen Mollusken zu überprüfen und Hotspots der endemischen Molluskendiversität im Kaspischen Meer zu identifizieren. Im Anschluss an diese Analyse wird die räumliche Überlappung zwischen anthropogener Belastung und Mollusken-Hotspots bewertet, aus der resultiert, dass invasive Arten und chemische Verschmutzung die wahrscheinlich größte anthropogene Bedrohung für Mollusken sind. Es wurden 28 räumlich explizite Umweltvariablen generiert, um die Entwicklung ökologischer Modelle zur Untersuchung des kombinierten Einflusses von anthropogenen und Umweltfaktoren auf die räumlichen Biodiversitätsmuster zu ermöglichen. Da diese neuen Variablen mit dem globalen Ozeandatensatz *Bio-ORACLE* übereinstimmen, können sie verwendet werden, um die auf meeresökologische, modelbasierende Forschung auf das Kaspische Meer auszuweiten. Damit wird zum ersten Mal auch die Einbeziehung des Kaspischen Meeres in systemübergreifende Modelle ermöglicht, die für Naturschutzmanagement und -planung relevant sind.

I. SYNTHESIS

129.
ACIPENSER HUSO.
Der Hausen.
Le grand Esturgeon.
The great Sturgeon.



P. H. H. sc.

Illustration of Beluga sturgeon (*Huso huso*) by Marc Éliésér Bloch for the book "Ichthyologie; ou, Histoire naturelle des poissons: En six parties avec 216 planches dessinées et enluminées d'après nature", 1796.

1 | INTRODUCTION

Global climate and environmental changes have a large impact on biodiversity and natural ecosystems^{1,2}. In the Anthropocene era, human activities profoundly amplified the effects of natural changes in both terrestrial and aquatic ecosystems and their biota²⁻⁵. Major anthropogenic threats to flora and fauna include agricultural-related land surface transformation such as fire application, long-term overexploitation of wild species, habitat fragmentation, and anthropogenic climate change^{6,7}. How organisms respond to these new conditions is hard to predict, but a growing body of evidence indicates a rapid biodiversity loss that could lead to a sixth mass extinction^{5,6}. However, taxon-specific effects of anthropogenic pressures depend on the plasticity to adapt to novel environmental conditions and/or on dispersal capabilities to emigrate in more favorable habitats⁸⁻¹⁰.

While all ecosystems are exposed to anthropogenic pressures^{3,6}, inland waters and coastal wetlands show a higher rate of local extinction in comparison with terrestrial and marine habitats¹¹. This is particularly critical as inland waters and coastal wetlands are hotspots of biodiversity and provide essential services to the human society^{12,13}. Thus, the cumulative anthropogenic pressures on these aquatic ecosystems have a disproportional effect on global biodiversity and water security and availability¹²⁻¹⁴.

Ancient lakes can be hundreds of thousands to even several millions of years old and home to impressive species richness and endemism^{13,15-18}. This diversified biota is the result of a combination of *in situ* evolutionary processes, the survival of ancient populations that have become extinct elsewhere and past migrations of species from other systems¹⁹⁻²¹. A large proportion of this biota is often found nowhere else in the world and it can be particularly vulnerable to environmental changes and threats, given its unusual and distinctive adaptation to ancient lake environments²²⁻²⁶. Before the Anthropocene, climatic and geological events largely affected lake communities¹⁵. However, in the Anthropocene, the exceptional biota of these ecosystems have been severely threatened by long term unsustainable human practices leading to a potential mass extinction^{14,15,17,22,26,27}. See in Fig. 1 an example of the long term overexploitation of the Caspian Sea's sturgeons.

While major efforts have been made to protect the unique biotic communities in these critical habitats^{15,26}, the Pontocaspian basins have been largely neglected. This resulted in a vague

assessment of their species diversity and in an incomplete overview of potential threats to the ecosystem^{28,29}. Previous studies have been focused on commercially important species like sturgeons, but very little attention has been given on the spatial distribution of anthropogenic pressures and their impact on the overall biodiversity, which appear to be facing a dramatic decrease³⁰⁻³².



Figure 1: Long term overexploitation of sturgeons in the Caspian Sea basin led to the collapse of all the five sturgeon species. The beluga (*Huso huso*, Linnaeus 1758, in photo) population recorded the major drop in the number and size of individuals³³. Large fish like the ones in the photo from the 19th century are not caught anymore in the Caspian Sea, indicating a young and unviable population³⁴. Image from историческая-самара.рф.

In this context, the PRIDE (drivers of Pontocaspian Rise and DEmise) project was initiated to shed more light on the evolutionary and ecological processes underpinning the autecological variations of the Pontocaspian fauna in space and time. The results were then used to inform policymakers and facilitate conservation practices in the region, for example in the context of the Tehran Convention, a treaty aimed to ensure the sustainable development of the Caspian Sea³⁵.

THE PONTOCASPIAN REGION

The Pontocaspian region is an aquatic system of isolated and semi-isolated basins that include the Black, Azov, Caspian and Aral seas³⁶, see Fig. 2. These basins, across the border of Europe and Asia, formed 5–3 million years (Ma) ago with the final disintegration of the Paratethys Sea and regional tectonic activities³⁶. Throughout the last 5 Ma, irregular basin connections resulted from shallow tectonic gateways and climatic changes driving lake/sea-level variations^{37,38}. These dynamic conditions led to a history of alternating states of salinity, ranging from oligohaline (0.5–5 ppt) to mesohaline (5–18 ppt)^{36,39,40}. The fluctuation of salinity seems to be the key abiotic factor that defined Pontocaspian habitats, thereby shaping biogeographical patterns of the Pontocaspian biota in the past and present time^{41–43}.

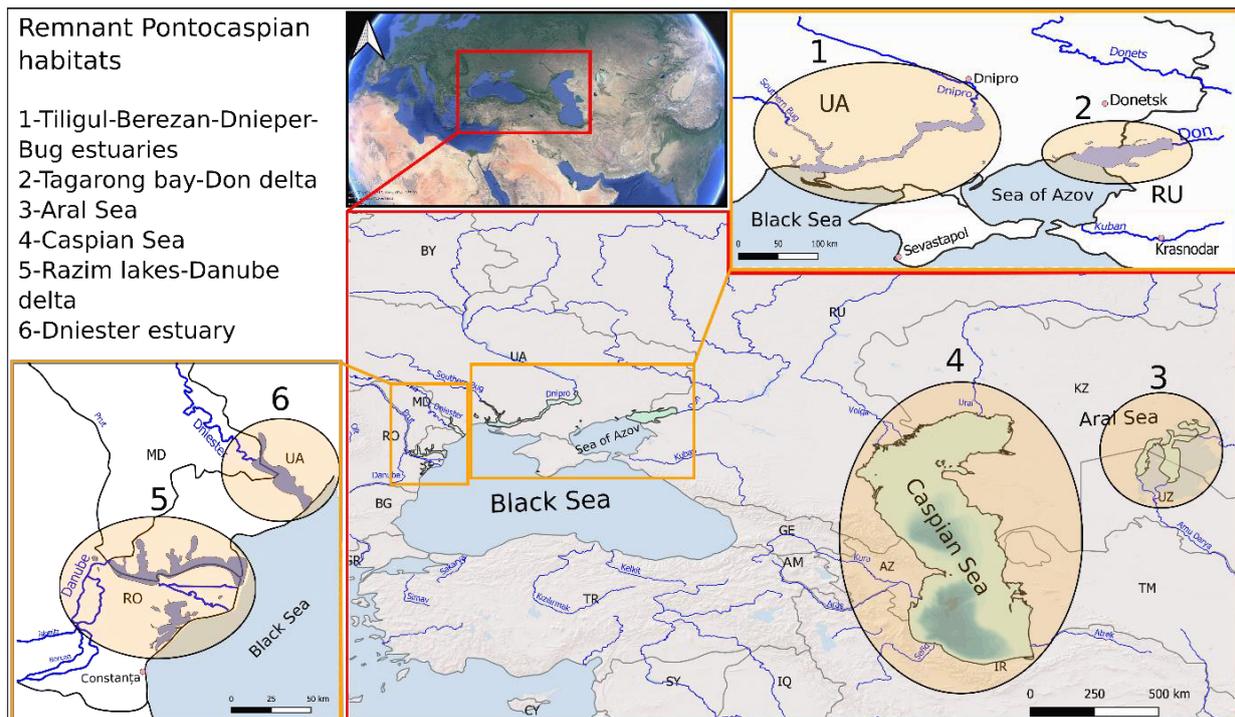


Figure 2: Map showing the current Pontocaspian habitats (yellow shaded ovals).

Given the frequent past connections with the Mediterranean Sea, the Black Sea salinity has often been the highest among the Pontocaspian basins. Hence, it functioned as an environmental filter limiting the distribution of typically oligohaline taxa, which have evolved in the Pontocaspian region and are referred to as Pontocaspian species^{44,45}. Similarly, salinity

has played a major role in shaping species composition and distribution in the Caspian Sea^{31,46}. Today, the Pontocaspian habitats are restricted to the estuaries of the northern Black Sea and Azov Sea, the North Aral Sea and the majority of the Caspian Sea³⁰ (see Fig. 2). The current salinity among these basins differs largely. The maximum salinity of the Azov Sea, the Caspian Sea and the Black Sea is 12 ppt, 14 ppt and 22 ppt, respectively³⁶. However, the salinity content in the Aral Sea has recently dramatically increased due to excessive water extraction, causing an almost complete disappearance of the lake and its biota⁴⁷. Only in 2005 the North Aral Sea was dammed to attempt a partial habitat restoration⁴⁷.

NATURAL AND ANTHROPOGENIC PRESSURES ON THE PONTOCASPIAN BIOTA

As a consequence of intermittent connectivity between the Pontocaspian basins, a rich array of aquatic taxa adapted and diversified across these dynamic habitats^{31,36}. Paleogeographic and phylogeographic studies tracked the origin of the endemic Pontocaspian species to the Parathethys fauna^{30,31,36,44,48}. Modern Pontocaspian taxa that directly evolved from the ancestral Parathethys fauna are fish, crustaceans and mollusks^{21,30,42,48}. The spatial heterogeneity in habitat conditions likely promoted *in situ* diversification and led to high species richness and endemism in these groups of organisms^{36,46,49}.

Paleogeographic reconstructions through the Quaternary Period suggest that major changes in water level and salinity content affected the composition and community dynamics of the Pontocaspian biota^{21,50–53}. Dated molecular phylogenies and fossil records suggested that during the transgression-regression cycles in the Pleistocene, multiple migrations occurred between the Caspian Sea and the Black Sea basins in fish⁵⁴, crustaceans^{42,21} and mollusks^{50,55,56}. The most recent natural connection among the two basins is dated back to 15 thousand years ago (ka), when the Mediterranean bivalve *Cerastoderma glaucum* (Bruguière, 1789) reached the Caspian Sea^{21,39}. These historical migrations affected the community composition and shaped the contemporary geographic distribution of the Pontocaspian species^{18,21,43,49}.

Today, the majority of Pontocaspian species occur in the Caspian Sea^{31,36}. This indicates that the species likely evolved in the Caspian Sea under relatively stable mesohaline conditions

that prevailed in the Pleistocene and are comparable to the modern Caspian environment^{30,36,40,49,57}. At the same time, the salinity level in the Black Sea largely fluctuated due to the inflow of Mediterranean water³⁷. This drove the decline in the diversity of typically brackish water Pontocaspian taxa in the majority of the Black Sea. However, some species survived in lagoons^{21,41,42,56,58}.

In the last two centuries, the Pontocaspian life forms started to be heavily exposed to intensifying negative effects of anthropogenic pressures^{32,34,59–62}. The impact of these activities is particularly strong in the enclosed Caspian Sea because pollutants cannot be diluted through water exchange and organisms cannot easily disperse to more favorable conditions^{61–63}. The nearshore habitats are even more sensitive to anthropogenic activities because of the high concentration of endemic biodiversity^{29,49,59,61}.

The consequences of these anthropogenic pressures have been increasingly evident for several decades^{29,32,64} and include the intensification of threats caused by chemical pollution^{65–69}, invasive species^{70–72}, poaching^{73–75} and streamflow regulations (see Box1 for a general description of the main threats)^{33,76}. Pollutants affect the whole aquatic biota through physiological impairments that vary among species^{62,77,78}. Taking mollusk as an example, high concentrations of lead decreases nutrient uptake in the Pontocaspian bivalve *Dreissena polymorpha* (Andrusov, 1897)⁷⁸, whereas pesticides function as endocrine-disrupting compounds^{79,80}. Introduced species appear to have negatively impacted native species. For example, the growth in the population of the Mediterranean bivalve *Mytilaster minimus* (Poli, 1795, Fig. 3b) seems to have displaced endemic bivalves in the central and southern basins of the Caspian Sea⁶⁴. Whereas the appearance of the comb jellyfish *Mnemiopsis leidyi* (Agassiz, 1865, in Fig. 3a) caused a decrease in survival rates and contraction of range size in the native benthic species⁸¹. *Mnemiopsis leidyi* induces these detrimental effects by direct predation on mollusk larval stages and by enriching the nutrients in the lakebed sediment as a consequence of a large amount of dead jellyfish deposition^{70,81,82}. Poaching and streamflow regulation mostly affected anadromous fish like sturgeons and the endemic Caspian seal (*Pusa caspica*, Gmelin, 1788)^{33,76}. As sturgeons and seals are the top predators in the ecosystem, the decline in their population has driven ecological changes in the whole trophic web⁸³.

The most dramatic period for the Caspian biota was likely at the peak of the Soviet Union industrial production in the late '80s, when the cumulative pressures exerted on the

environment led to acute deterioration of the Caspian Sea habitat and its biota^{32,61}. These effects were particularly noticeable in mollusks, as they are sensitive to minimal changes in the environment^{84,85}.

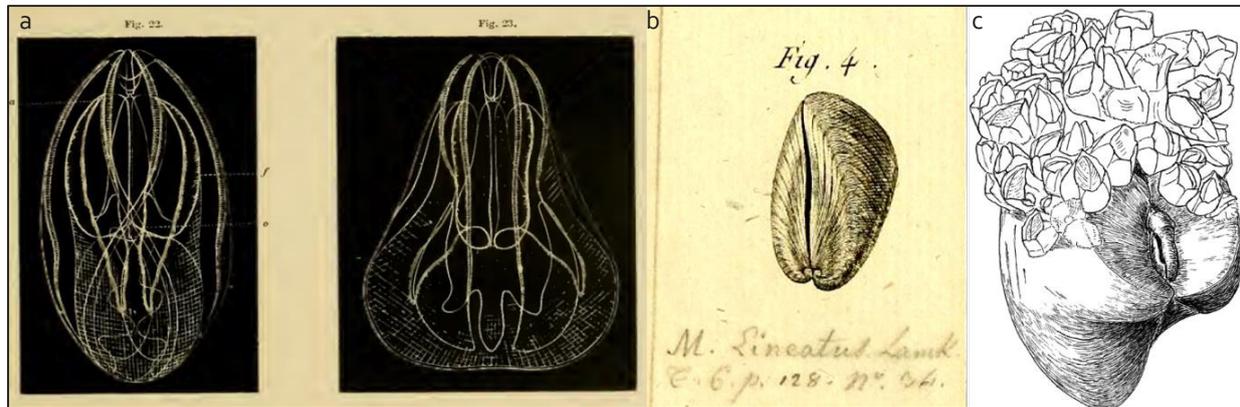


Figure 3: Three of the invasive species with considerable effects on the Pontocaspian fauna. a) the American comb jellyfish *Mnemiopsis leidyi* original drawings from Agassiz, 1865⁸⁶. b) *Mytilaster minimus* in an historical illustration from 1827⁸⁷. c) *Balanus improvisus* fouling on an individual of a *Didacna* species in the Caspian Sea⁸⁸.

THE CASPIAN SEA MOLLUSKS

Mollusks are one of the richest phyla in the Caspian Sea, represented by two classes: Gastropoda and Bivalvia³¹. According to Wesselingh et al.³⁰, there are at least 19 and 52 endemic bivalves and gastropods, which translate in a proportion of endemic species of 54% and 67%, respectively³⁰. Besides the high endemism, mollusks are also an essential functional group for the ecosystem, making up 90% of the total benthic biomass^{31,83}. This makes mollusks the main prey base for large fish, including juvenile stages of sturgeon species³⁴.

Mollusks are ubiquitous in the Caspian Sea, inhabiting the benthic layer up to about 400 m deep, with higher diversity in the bathymetric range between 25 and 75 m^{49,89}. This, together with their sensitivity to environmental changes, makes them suitable organisms for monitoring both anthropogenic and natural disturbances in the basin. For example, the fluctuations in their population sizes have been commonly used to evaluate anthropogenic effects of pollutants^{78,90}, invasive species^{70,91} and perturbations in the benthic sediment⁹². As

another example, in the northern part of the Caspian Sea the mollusk benthic assemblages were altered by recent natural water level changes of about three meters^{93–95}.

Invasive species are of particular concern to the endemic Caspian mollusks. At least two endemic bivalves, *Dreissena elata* (Andrusov 1897, *species dubium*, Fig. 4a) and *Dreissena caspia* (Eichwald, 1855), seem to be in immediate danger of extinction or already extinct after the rapid range expansion of the invasive mussel *Mytilaster minimus*³⁰. The bivalve family of Lymnocardiiids experienced also range contractions due to the resource competition with *Mytilaster minimus* and to the unfavorable associations the invasive crustacean *Balanus improvisus* (Darwin, 1854, Fig. 3c), which fouls on their shells^{88,96}. Concerning the gastropods, the situation is unclear given their naturally scattered and scarce distribution^{97,98}. In general, the dominance of invasive species introduced in the 20th century is considered to be a leading cause of the decline of native species in the Caspian Sea^{89,93,95,99–101}.

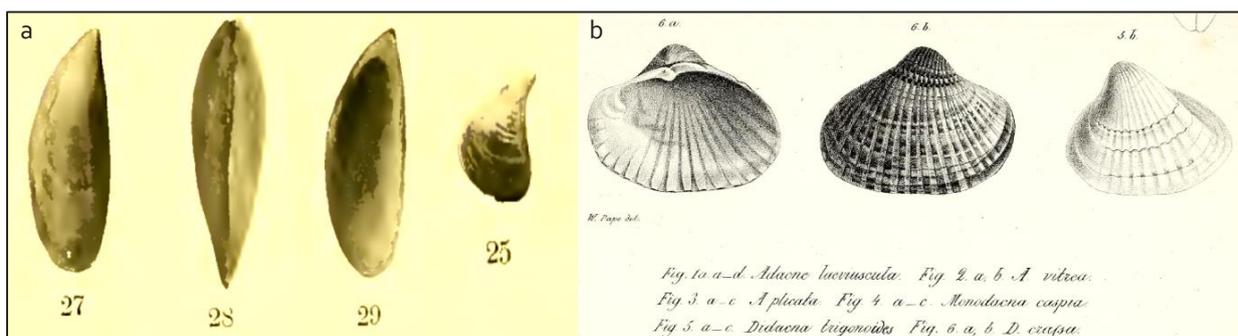


Figure 4: Example of native pontocaspian bivalves. a) Forms of *Dreissena polymorpha* (Pallas, 1771), in a drawing by Andrusov. Andrusov's book "Fossile und lebende Dreissenidae Eurasiens" contains the original descriptions of the potential species *Dreissena elata* (*nomen dubium*), identified by the number 25¹⁰². b) Illustration of the Caspian endemic *Didacna eichwaldi* (Krynicky, 1837). In the readable original caption from "Fauna Caspio-Caucasia nonnullis observationibus novis", Eichwald, in 1841, identified this species as *Didacna crassa*¹⁰³.

The sensitivity of mollusks to habitat variations enables also reconstruction of past environmental changes, through the identification of shell remains preserved as fossils in the basin sediments. Using morphological and autecological analogies between extant and fossil species, it is possible to infer past community structures and hindcast climatic conditions^{18,104}. Paleontological studies can be used also to determine more recent changes related to anthropogenic pressures. Van de Velde et al.¹⁰⁵, for example, found that about 2000 – 2500 years ago the mollusk richness in the northwestern Caspian Sea was three times higher than the same location today, which is dominated by invasive species¹⁰⁵. This type of studies

highlights the importance of paleontological studies in providing baseline information to disentangle the pressures from natural and human-induced disturbances on today community composition^{105,106}. Further studies in the PRIDE project, in addition to recent literature, highlighted the fact that it is currently more difficult to find endemic mollusks in the Caspian Sea in comparison to past expeditions^{30,61,64,97}.

2 | LACK OF KNOWLEDGE AND OBJECTIVES

Anthropogenic pressures in the Caspian Sea have been known to affect the ecosystem for many years^{32,61,101}. However, a systematic and spatially explicit cumulative assessment of these threats does not exist. This lack hampers the evaluation of the impact of anthropogenic pressures on the Caspian Sea biodiversity.

In this context, spatial-explicit analyses to map environmental and anthropogenic pressures in the Caspian Sea are fundamental to identify areas of high interest for ecosystem management. Examples are hotspots of biodiversity or localities threatened by specific human activities. Therefore, in this thesis, several techniques to model and map diverse types of anthropogenic and environmental data are presented. These results are aimed to facilitate the implementation of sustainable management plans, in line with the objectives of the Caspian Sea littoral countries ratified in the Tehran Convention³⁵.

In addition to the poorly known distribution of anthropogenic pressures, also the taxonomical classification and the range of the Caspian species is not satisfactorily resolved³⁰. The spatial gradients of environmental variables such as salinity and temperature, fundamental to identify species ecological requirements, are also poorly documented⁴⁶. The Caspian is not included in standard data sets available for the world oceans, as it is not connected to them^{107,108}. All these issues prevent an accurate spatial evaluation of species traits describing biodiversity trends, such as the Essential Biodiversity Variables¹⁰⁹. As a consequence, the regional conservation status of the Caspian species is uncertain. Given the future economic development of the Caspian Sea, it is essential to provide information to ensure the conservation, restoration and sustainable use of the unique Caspian fauna^{35,110} in line with obligations under international agreements.

Thus, in this thesis the spatial magnitude of anthropogenic pressure, species geographical ranges and environmental variable gradients in the Caspian Sea were assessed through the following objectives:

Objective 1 (O1): Assessing the spatial distribution of anthropogenic pressures in the Caspian Sea;

Objective 2 (O2): Evaluation of spatial relations between anthropogenic pressures and hotspots of the Caspian Sea endemic mollusks;

Objective 3 (O3): Compilation of a tool to advance ecological modeling within and beyond the Caspian Sea basin.

To allow the maximum benefit from the results of my thesis, all the outcomes are openly accessible and employable by anybody interested in using them, according to the FAIR principles stating that data should be findable, accessible, interoperable and reusable¹¹¹.

3 | PAPER OUTLINES

This dissertation comprises four peer-reviewed articles separated according to the three objectives as follows:

Objective 1 (O1): For this objective I present a paper providing a spatial-explicit assessment of the anthropogenic pressures in the Caspian Sea (Paper 1):

Paper 1 (O1)

Lattuada, M., Albrecht, C., Wilke, T., 2019. Differential impact of anthropogenic pressures on Caspian Sea ecoregions. *Marine Pollution Bulletin* 142, 274–281.

doi: 10.1016/j.marpolbul.2019.03.046

Outline – This paper aims to compile a spatially-explicit cumulative environmental assessment (CEA) for the Caspian Sea. Individual and combined effects of the most critical anthropogenic pressures on the Caspian Sea ecoregions were evaluated. Pressure scores for nine anthropogenic stressors were quantified and summed to obtain a final CEA score. We also analyzed the spatial patterns of individual pressures for the whole Caspian Sea and compared the results among ecoregions. We found that anthropogenic pressures in the Caspian Sea are unevenly distributed and there are significant differences among the ecoregions. In general, the northern Caspian Sea accumulated higher anthropogenic pressures, whereas the middle and southern deeper sub-basins seem to be subjected to lower pressures. While the northern areas are mostly affected by poaching and streamflow regulation, the deeper waters in middle and southern sub-basins are exposed to invasive species and chemical pollution. These findings indicate that environmental management and conservation policies should focus on different anthropogenic pressures according to the target areas of intervention.

Contribution – Lead author, experimental design, data collection, and data analysis

Objective 2 (O2): For this objective I present a paper providing a taxonomical review of the Pontocaspian mollusks (paper 2) and an article linking the spatial analyses of anthropogenic pressures from paper 1 with the hotspots of endemic mollusk diversity in the Caspian Sea (paper 3):

Paper 2 (O2)

Wesselingh, F., Neubauer, T.A., Anistratenko, V., Vinarski, M.V., Yanina, T., ter Poorten, J.J., Kijashko, P., Albrecht, C., Anistratenko, O., D'Hont, A., Frolov, P., Martínez Gándara, A., Gittenberger, A., Gogaladze, A., Karpinsky, M., Lattuada, M., Popa, L., Sands, A., van de Velde, S., Vandendorpe, J., Wilke, T., 2019. Mollusk species from the Pontocaspian region – an expert opinion list. *ZooKeys* 827, 31–124. doi: 10.3897/zookeys.827.31365

Outline – This paper addresses the lack of taxonomical clarity for the Pontocaspian mollusks. The number of endemic Pontocaspian mollusk species is estimated to be between 55 and 99. This considerable variation is given by the fact that several species are cryptic and their differentiation should be resolved by combining morphological, ecological, anatomical, and molecular traits. However, fresh material from live specimens is limited, given the difficulties of finding organisms and the insufficient sampling efforts. Hence, data to apply a comprehensive approach for species identification are currently not available. In this context, Pontocaspian mollusk experts gathered existing information to more accurately: (1) document Pontocaspian mollusk species, (2) estimate their richness, and (3) identify and discuss taxonomic uncertainties. The obtained results, which are not a definitive taxonomical classification of the Pontocaspian mollusks, pointed out to a general decrease of Pontocaspian mollusks over space and time, which should be taken into account for conservation purposes, given the uniqueness of this fauna.

Contribution – Analytical support, revision and final approval of the article.

Paper 3 (O2)

Lattuada, M., Albrecht, C., Wesselingh, F.P., Klinkenbuß, D., Vinarski, M.V., Kijashko, P., Raes, N., Wilke, T., 2020. Endemic Caspian Sea mollusks in hotspot and non-hotspot areas differentially affected by anthropogenic pressures. *Journal of Great Lakes Research. Advance online publication*. doi: 10.1016/j.jglr.2019.12.007.

Outline – This paper aggregates the results of paper 1 and 2, with the aim of mapping potential anthropogenic threats to the endemic Caspian Sea mollusks of the Caspian Sea. We selected 71 endemic Caspian Sea mollusks, 19 bivalves and 52 gastropods, according to the results of paper 2. We then used the Caspian Sea bathymetry and the ecoregions produced by Fendereski et al.⁴⁶ to infer the species distribution ranges based on occurrences collected in literature. Finally, we summed all the distribution ranges to obtain diversity hotspots for all the mollusks together and for bivalves and gastropods separately. These hotspots were used to compare cumulative and individual pressure scores among them and with non-hotspot areas. The pressure scores were selected as the most relevant estimated in paper 1. Our results showed that gastropod hotspots are exposed to lower cumulative pressure scores compared to bivalve hotspots and non-hotspot areas. Individual pressures also differ significantly among all the tested areas. This is likely because most of the gastropods are distributed in deeper waters, which are less exposed to anthropogenic pressures. Nonetheless, chemical pollution and invasive species were the highest contributors to the average cumulative pressure score for both gastropods and bivalves. Hence, from a management perspective, concentrating resources to reduce these two anthropogenic pressures will greatly benefit the Caspian Sea mollusks and, as a consequence, the overall ecosystem.

Contribution – Lead author, experimental design, data collection, and data analysis

Objective 3 (O3): For this objective I introduce a data paper containing a novel data set of spatially explicit environmental variables that is relevant to implement ecological modeling across the Caspian Sea and the world oceans (Paper 4):

Paper 4 (O3)

Lattuada, M., Wilke, T., Raes, N., 2020 Caspian Sea environmental variables: an extension of the Bio-ORACLE ocean data set. *Ecology* 0, 3076. doi: 10.1002/ecy.3076

Outline – The objective of this research is to extend the Bio-ORACLE data set with 28 environmental variables from the Caspian Sea. To compile the new variables, we used the complete World Ocean Database point data collected in the Caspian Sea from 1914 to 2011 (NOAA, 2018), and modeled maximum, mean, minimum and range of temperature, salinity, and dissolved oxygen at the sea surface and the bottom. Besides, we used raster statistics to create surface layers of maximum, mean, minimum and range of chlorophyll-a, using remotely sensed data collected by the MODIS instrument installed on the Terra and Aqua satellites (NASA, 2017). The compiled raster layers of Caspian Sea environmental variables were then resampled to match the spatial grid of the Bio-ORACLE data set to allow seamless integration among the two data sets. With these extensions, it is possible to extend marine ecological studies from the world's oceans into the Caspian Sea based on spatially-explicit environmental variables. Therefore, the data set presented in this paper contributes to policies addressing, for example, invasive species management targets and will facilitate novel research and the development of the Essential Biodiversity Variables (EBV) aiming at the conservation of the unique and endemic biota of the Caspian Sea.

Contribution – Lead author, experimental design, data collection, and data analysis

4 | RESULTS AND DISCUSSION

The here assembled studies focus on the provision of novel spatial-explicit information concerning anthropogenic pressures, environmental variable gradients and species distribution in the Caspian Sea. The results of these papers present also an exploratory investigation into the spatial associations between hotspots of endemic mollusks and anthropogenic pressures.

SPATIAL DISTRIBUTION OF ANTHROPOGENIC PRESSURES IN THE CASPIAN SEA (O1)

Nine major environmental threats to the Caspian Sea habitats have been identified based on literature research (see Box 1). With this data I compiled a Cumulative Environmental Assessment (CEA) balancing local habitat vulnerabilities to individual anthropogenic pressures using two weighting methods. The first is based on a semi-quantitative estimation of pressure scores based on specific responses of ecoregions to the individual anthropogenic pressures, whereas the second considers expert opinions of local stakeholders, which focus on specific anthropogenic pressures effects in each country.

Areas with the highest anthropogenic pressure scores were located in the waters around Baku and in the vicinity of the Volga Delta (Fig. 5a). However, the anthropogenic pressures contributing to the high CEA scores in the two locations were different: in the Baku area the major anthropogenic pressure was chemical pollution, whereas in the Volga Delta was poaching^{73,74}. This follows a general north to south pattern along latitude. The northern ecoregions recorded a higher contribution in the overall pressure scores from poaching. In contrast, poaching is relatively low in the central and southern ecoregions, where chemical pollution is the most relevant threat, together with the introduction of invasive species (Fig. 5a).

Box 1: Major anthropogenic pressures in the Caspian Sea *



Unsustainable fishing

Fishing is an important activity in the Caspian Sea. Traditionally, the coastal countries use diverse methods to target different fish species. The most commercially relevant species are sturgeons (*Acipenser* spp. and *Huso huso*), Caspian kutum (*Rutilus kutum*) and sprats (*Clupeonella* spp.). In the last decades, the landing of these species decreased (photo on the left: Iranian fishermen).



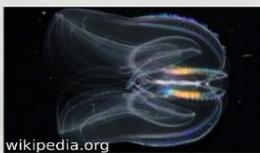
Chemical pollution

Chemical pollution is a great concern in the Caspian Sea, as many industrial sectors released chemicals in the environment, especially during the peak production at the end of the 80's. The industrial sector collapsed at the beginning of the 90's together with the Soviet Union. Since then, the release of pollutants diminished (photo on the left: Oil glistens in the Caspian Sea).



Streamflow regulation

Dams interrupt the river continuity. Therefore, they are an insurmountable obstacle for anadromous fish, such as sturgeons. In fact, the decrease of sturgeons in the Caspian Sea seems to be strongly related to the inaccessibility of spawning ground (photo on the left: Volgograd dam).



Invasive species

Invasive species are a well-known problem in the Caspian Sea. Most of them originated in the world oceans and reached the Caspian Sea through the Volga-Don Canal. The most relevant in terms of impact on the ecosystem is the comb jellyfish *Mnemiopsis leidyi*, which contributed to the decrease of endemic species (photo on the left: *Mnemiopsis leidyi*).



Oil industry disturbances

The Caspian Sea hosted the first offshore oil well in 1946, the first in the world. Since then, the oil and gas industry has been the most important activity for the Caspian coastal countries. Connected to that, there is a big impact due to well construction, fuel transportation and leaking events (photo on the left: Oil Rocks in Azerbaijan).



Coastal development

Coastal development is higher where there is a high concentration of human population. Along the Caspian Sea coast, this impact is rather limited given the fact that the Caspian Sea level is fluctuating extensively (photo on the left: Ramsar, Iran).



Agriculture by-product discharge

Residual of fertilizers from farming may be discharged in water basins by rivers, creating an excessive nutrient enrichment in the water, which can cause several problems to the other organisms. In the Caspian Sea, the majority of these nutrients come from the Volga river (photo on the left: Algae in the North Caspian Sea).



Eutrophication

Chlorophyll *a* is generally considered an indicator of eutrophication of waters. When algae abundance in water is high, it causes a decrease in dissolved Oxygen and many organisms cannot survive. In the Caspian Sea eutrophication is more evident offshore the Volga delta (photo on the left: North Caspian Sea).



Poaching

Poaching is a great threat for the sturgeons and the Caspian seal (*Pusa caspica*). As it is an illegal activity, it is difficult to quantify its impact. The literature report that poaching is mostly carried out in shallow water when sturgeons are migrating. This is more efficient, because sturgeons are in high density and they swim slow (photo on the left: *Huso huso*).

* The references for the anthropogenic pressure descriptions can be found in Table 1 of paper 1

The validation of anthropogenic pressure scores in terms of quantitative impact on the biota or habitat quality could not be assessed due to the general scarcity of data. However, independent publications reported similar findings, indicating that the Azerbaijani section of the Caspian Sea is largely polluted with chemical compounds derived from oil and gas industry^{112,113} and invaded by dense populations of alien species^{64,96}. Additional literature points out the consequences of water management issues and poaching in the low Volga Delta, which caused a severe depletion of habitat quality and biodiversity^{73,74,94,114}.

Similar anthropogenic pressures have been detected in the other ancient lakes^{22,24,26,115–117}. In comparison to the Caspian Sea, invasive species had a larger effect on the Lake Victoria, where the introduction of the Nile perch in the '50s had considerably increased the predation pressure on the endemic cichlid fishes, driving the loss of about half of the species once present¹¹⁸. The development of mining threatens the African Rift Valley lakes¹¹⁷ and, more recently, Lake Titicaca¹¹⁹. Likewise, ancient lakes in the former Soviet Union, including the Caspian Sea, share similar threats, given the comparable industrial development based on mineral resource exploitation^{22,120}. Poaching is a widely spread illegal activity targeting commercially valuable species such as sturgeons in several basins^{121,122}. However, as the Caspian Sea sturgeon population is the largest in the world^{34,75}, ecosystemic effects of its collapse in the Caspian Sea are likely more pronounced than in other basins⁸³.

The first objective of this thesis illustrates the current conditions of the Caspian Sea to improve its management with a modern spatially explicit approach comparable to the methods developed for the Mediterranean and Baltic seas^{123,124}. Thus, the CEA can be used to facilitate management decisions towards the sustainable development of the Caspian Sea to fulfill objectives stated in the regional Framework Convention for the Protection of the Marine Environment of the Caspian Sea³⁵.

SPATIAL RELATIONS BETWEEN ANTHROPOGENIC PRESSURES AND HOTSPOTS OF THE CASPIAN SEA ENDEMIC MOLLUSKS (O2)

We compiled a review of Pontocaspian mollusks, for which regional taxonomists contributed with their knowledge to identify previously unused modern and fossil material found in

several collections and fresh malacological samples collected during the PRIDE project. Unfortunately, live specimens that could enable molecular analyses were not found. Thus, the overall assessment is based on morphological traits. In this context, I tested whether two dreissenids with significant intraspecific variation could be better distinguished by autecological characteristics⁵⁶. I modeled the ecological niche of *Dreissena elata* in comparison to the ecological niche of *Dreissena polymorpha*. The model revealed a suitable habitat for *Dreissena elata* in the middle and southern basins of the Caspian Sea with salinity higher than 5 ppt. In contrast, the strictly freshwater *Dreissena polymorpha* is limited only to the northern part of the Caspian Sea, where the salinity is greatly reduced by river inflows. This autecological difference implies that the two dreissenids *D. polymorpha* and *D. elata* are likely separated species.

Moreover, the ecological information of the endemic species previously collected was used to project the location of mollusk diversity hotspots for: 1) gastropods, 2) bivalves and 3) gastropods + bivalves. Hotspots, which were defined as the 2.5% of the area with the highest number of species, pointed out a higher richness of gastropods than bivalves, with 38 and 14 species, respectively, see Fig. 5b and 5c¹²⁵. The estimation of the anthropogenic pressure scores in the three hotspots showed that gastropods are exposed to a lower CEA score than bivalves. This is because gastropods diversity peaked at a higher depth than bivalves, where anthropogenic pressure scores are reduced⁵⁹.

Despite the cumulative difference in pressure scores, for both gastropods and bivalves the anthropogenic pressures with the highest contribution in the hotspots were chemical pollutants and invasive species. This is concerning because mollusks accumulate pollutants in their tissues through feeding, which can impair their physiological activities and decrease their abundance in contaminated areas^{78,84,85,126}. The considerable effects of alien species in the Caspian Sea are well documented and reflect a global problem, especially in the littoral zones that host higher diversity^{13,17,25}.

The high anthropogenic pressures in shallower areas may have important consequences for the conservation of the Caspian Sea ecosystem since bivalves largely occur in areas with high anthropogenic pressure scores (Fig. 5c). As they are essential for ecosystem functionality³¹, with a contribution up to 90% of the benthic biomass³¹, a decrease in their abundance and the potential replacement by alien species could cause a profound disruption in the Caspian Sea food web leading to a risk of ecosystem collapse^{34,64,83}.

The causes underpinning the different bathymetric distribution for bivalve and gastropod hotspots in the Caspian Sea are not fully understood. A possible reason could be related to the mechanisms controlling the distribution of these species¹²⁷. For example, the gastropod and bivalve richness seem to be primarily driven by habitat heterogeneity^{128,129}. However, previous studies suggest that specific environmental factors related to temperature and nutrients may have a stronger influence in bivalve dynamics^{94,127,128}, whereas the low dispersal ability is a strong driver in limiting the horizontal range of gastropod distribution^{127,130–132}. Nonetheless, higher specialization to diverse substrata contributed to a richer gastropod diversity along the bathymetric gradient^{130,133,134}. This is opposite for bivalves as they are largely restricted to the littoral zone⁹⁶. Besides the Caspian Sea, this pattern is also confirmed in other ancient lakes such as Baikal¹³³, Ohrid¹³², Lanao¹³⁵ and the African Rift lakes²³.

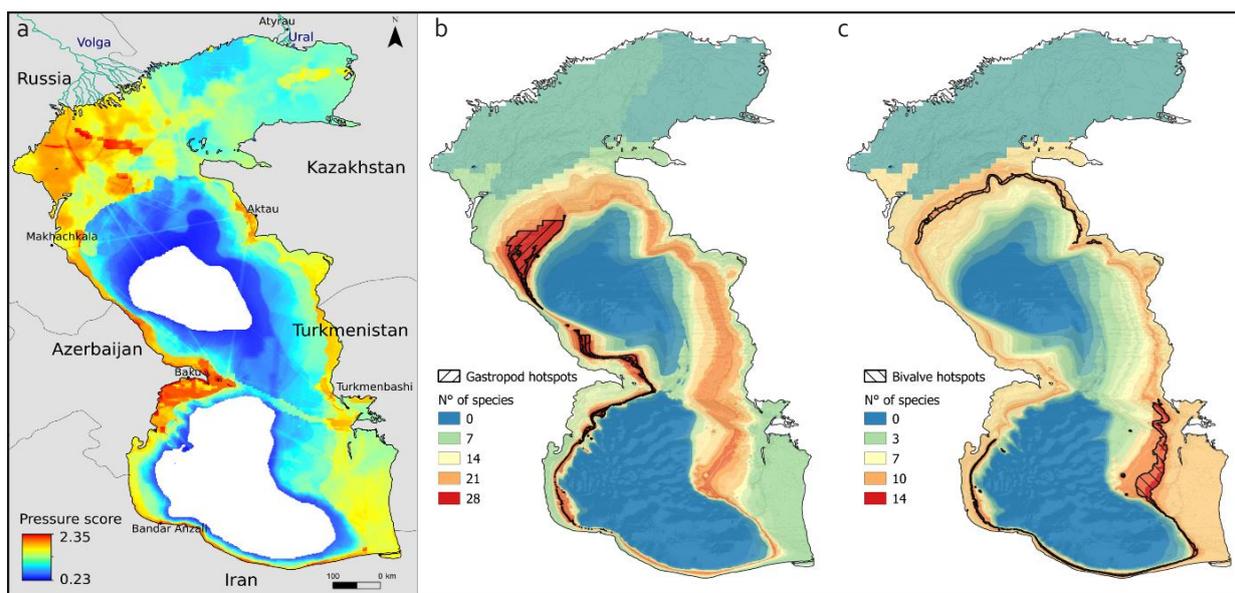


Figure 5: Main results from paper 1 and 3 a) Visualization of cumulative pressure score values, paper 1⁵⁹. b) gastropod and c) bivalve hotspots highlighted with oblique lines. The remaining colors describe species richness, paper 3¹²⁵.

The new insights into the mollusk distribution would help to plan cost-effective solutions addressing specific threats to greatly reduce human pressures on the Caspian Sea endemic benthic species. Therefore, the research in this thesis provides valuable results for the planning and application of targeted biodiversity restoration programs to achieve the Tehran Convention aims and protect the Caspian Sea's unique endemic biodiversity³⁵.

A TOOL TO ADVANCE ECOLOGICAL MODELING WITHIN AND BEYOND THE CASPIAN SEA BASIN (O3)

For the last objective of this thesis I developed a new spatially explicit data set of environmental variables that can be integrated with the existing ocean data set Bio-ORACLE¹⁰⁷. These variables were selected according to their relevance for the ecoregion classification of the Caspian Sea, according to Fendereski et al.⁴⁶, and their representation in Bio-ORACLE data set¹⁰⁷. The variables identified by Fendereski et al.⁴⁶ are of crucial importance to understand the biogeography of the Caspian Sea biota. However, in their study they lack an accurate spatially explicit component. For example, salinity was simply digitized from an image of isohaline contours⁴⁶. For this reason, I produced 28 spatially explicit new layers at 5 ArcMin resolution including maximum, minimum, mean and range of the four most relevant variables: temperature, salinity, dissolved oxygen at both surface and benthos and chlorophyll *a* concentration in the sea surface, in Table 1.

The compilation of these variables allows ecological modeling across the Caspian Sea and the world oceans. Together with anthropogenic pressures detected in paper 1 of this thesis, the new data set provides a spatial framework to investigate species responses to the combination of environmental and anthropogenic pressures. This is a crucial achievement for modern environmental modeling based on spatially explicit methods. Thus, state-of-the-art ecological research can be now implemented also in the Caspian Sea, a region that has so far been relatively neglected. New research in the Caspian Sea should highlight trends in biodiversity and ecosystem integrity¹³⁶, which could be compared with results from studies in similar regions, like the Baltic and Black Seas^{123,124}.

Finally, the data set presented in this paper contributes to policies addressing various topics, such as the sustainable development of the Caspian Sea³⁵ and invasive species management targets¹³⁷. Moreover, it will facilitate novel research towards the development of Essential Biodiversity Variables aiming at the conservation of the unique biota of the Caspian Sea as a hotspot of endemism of global significance¹⁰⁹.

5 | CONCLUDING REMARKS AND OUTLOOK

This thesis addresses the spatial extent of the main threats to the Caspian Sea endemic biodiversity and produces novel data to identify the ecological requirements of Caspian Sea species aiming at its conservation.

A spatial-explicit assessment revealed that the potential impact of anthropogenic pressures in the Caspian Sea is strongly driven by local environmental characteristics and the type of exploitative activities. As a consequence, conservation and restoration planning should target specific anthropogenic pressures according to regional preconditions.

We identified the taxonomy and distribution of 71 endemic Caspian mollusks, discovering that gastropods are less exposed to anthropogenic pressures than bivalves, due to their occurrences in deeper waters where the anthropogenic pressures are reduced. Nonetheless, both gastropods and bivalves are affected by chemical pollution and invasive species. Therefore, future conservation planning aiming to tackle these two threats would result in an effective solution to greatly reduce pressures on endemic mollusks.

To discern the relative importance of anthropogenic pressures for the distribution of Caspian Sea species, I also modeled 28 gridded environmental variables to match the Bio-ORACLE data set for the global oceans. This novel data set could greatly improve the evaluation of Caspian species habitat suitability. In combination with anthropogenic pressures, this information sets out a positive outlook to realize future targeted and efficient conservation measures in the Caspian Sea and to manage invasive Caspian species outside their native range.

Finally, the applied focus of this thesis constitutes a fundamental framework to facilitate research and conservation of the poorly-known Pontocaspian species focusing on the Caspian Sea, the basin hosting the richest Pontocaspian fauna. Future investigations based on this work will focus on providing additional information in the regional context of sustainable development of the Caspian Sea and towards the global objectives of collecting information to monitor and forecast biodiversity changes. Given the ongoing global mass extinction and the specific sensitivity of the Pontocaspian fauna, this work could be used to early detect potential critical threats to biodiversity to minimize the impact of future natural and/or anthropogenic changes on the Pontocaspian species.

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II. PUBLICATIONS



Ctenophores illustration by Joseph E. Trumpey. **Mnemiopsis leidyi*, an invasive species in the Caspian Sea

DIFFERENTIAL IMPACT OF ANTHROPOGENIC PRESSURES ON CASPIAN SEA ECOREGIONS

2019 | *Marine Pollution Bulletin*

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Differential impact of anthropogenic pressures on Caspian Sea ecoregions

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ARTICLE INFO

Keywords:

Caspian Sea
Cumulative environmental assessment
Anthropogenic impact
Ecoregions
Endemic species

ABSTRACT

Over the past decades, overall ecological conditions in the Caspian Sea have deteriorated. However, a comprehensive understanding of lake-wide spatial differences in anthropogenic pressures is lacking and the biological consequences of human impacts are poorly understood. This paper therefore aims at assessing the individual and combined effects of critical anthropogenic pressures on the Caspian Sea ecoregions. First, cumulative pressure scores were calculated with a cumulative environmental assessment (CEA) analysis. Then, the individual contribution of anthropogenic pressures was quantified. Finally, ecoregion-specific differences were assessed. The analyses show that both cumulative and individual pressure scores are unevenly distributed across the Caspian Sea. The most important individual pressures are invasive species, chemical pollution and poaching. This uneven distribution of pressure scores across Caspian Sea ecoregions creates new challenges for future conservation strategies, as different ecoregions usually require different conservation measures.

1. Introduction

The Caspian Sea is a large lake renowned for its diverse aquatic fauna (Zenkevitch, 1963; Karpinsky, 2005). However, over the last decades, many of its unique species assemblages have increasingly suffered from environmental (e.g., water-level fluctuations, salinity changes) and anthropogenic pressures (e.g., oil extraction, overfishing, introduction of invasive species). As a consequence, the overall ecosystem health has deteriorated and many endemic species have become regionally or globally extinct (Dumont, 1995; Karpinsky, 2005; Zonn, 2005; Zarbaliyeva et al., 2016; Mammadov et al., 2016; Wesselingh et al., 2019).

Unfortunately, our knowledge about the impact of environmental and anthropogenic factors on the native biodiversity in the Caspian Sea is largely biased towards few key stressors related to natural water-level fluctuations and human activities, such as fishery and mineral extraction (Malinovskaja et al., 1998; Agah et al., 2007; Malinovskaya and Zinchenko, 2010, 2011; Khodorevskaya et al., 2014; Yanina, 2014; Latypov, 2015; Mammadov et al., 2016; Poorbagher et al., 2017). Moreover, most previous human impact studies in the Caspian Sea are restricted to coastal areas (Nasrabadi et al., 2011; Aliyeva et al., 2013; Bastami et al., 2014), individual countries (Aliyeva et al., 2013; Dmitrieva et al., 2013; Bastami et al., 2014; Yancheshmeh et al., 2014; Mashroofeh et al., 2015; Varnosfaderany et al., 2015) or selected target species (Bickham et al., 1998; Agah et al., 2007; Dmitrieva et al., 2013; Ermolin and Svolkina, 2016; Poorbagher et al., 2017). Therefore, a

comprehensive understanding of lake-wide spatial differences in combined and individual pressures is lacking and the biological consequences of human impacts are poorly understood.

A potential solution to this problem arises from the fact that the Caspian Sea has been divided into ten ecoregions based on ecologically relevant environmental variables (Fendereski et al., 2014). These ecoregions generally correspond to the distribution ranges of many endemic, native and invasive species (Fendereski et al., 2014), and they allow for a coarse latitudinal and vertical (bathymetrical) assessment of anthropogenic pressures. Thus, ecoregion-specific environmental analyses might be a suitable approach to obtain a basic understanding of the spatially-explicit impact of anthropogenic pressures on Caspian Sea biota.

In this paper, we therefore estimated cumulative and individual pressure scores of critical anthropogenic pressures for the ten Caspian Sea ecoregions by using a cumulative environmental assessment (CEA) analysis.

Our specific goals were to:

1) infer the spatial distribution of cumulative pressure scores, i.e. the sum of individual pressure score intensities multiplied by specified weighting variables (see formula in Section 2.2.),

2) assess spatial differences in individual pressure scores, i.e. the contribution of single anthropogenic pressures to the cumulative pressure scores and

3) investigate ecoregion-specific differences in pressure scores.

This spatially-explicit study is, to our best knowledge, the first

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attempt to quantify ecoregion-specific impacts of anthropogenic pressures in the Caspian Sea. It might thus provide important baseline data for subsequent management decisions and conservation strategies, for example in the frame of the Tehran Convention ([Caspian Sea littoral countries, 2003](#)).

2. Methods

2.1. Study system

The Caspian Sea is the largest enclosed water body in the world, with a surface area of about 370,000 km². Located between Asia and Europe, it is bordered by five countries: Russia, Kazakhstan, Turkmenistan, Iran and Azerbaijan. It is limnologically divided into three parts (sub-basins) based on geophysical characteristics: the northern, middle and southern Caspian Sea ([Rodionov, 1994](#)).

The northern Caspian Sea has a maximum depth of 30 m and salinities below 10. Water-level, water current and salinity are strongly influenced by wind and river input, creating a highly dynamic environment. In contrast, the limnological conditions in the middle and southern Caspian Sea are more stable, with relatively constant salinities around 13. Water depths approach 800 m in the middle and exceed 1000 m in the southern Caspian Sea ([Kosarev, 2005](#)). Recently, the Caspian Sea has been divided into ten ecoregions ([Fig. 1](#)) based on ecologically relevant environmental variables ([Fendereski et al., 2014](#)).

2.2. Cumulative environmental assessment analysis

The cumulative environmental assessment (CEA) analysis, used in the current study to evaluate the impact of anthropogenic pressures in the Caspian Sea, is based on the method of [Halpern et al. \(2008\)](#). Accordingly, a spatial grid of the study area was created with a grid cell resolution of 1 ArcMin, and cumulative pressure scores (C_t , in the formula below) were calculated for each cell. As a specific pressure may have different impacts in different ecoregions, the impact of the pressures was weighted ([Halpern et al., 2007](#); [Halpern and Fujita, 2013](#)). For doing so, the original equation for calculating cumulative pressure scores was modified as follows:

$$C_t = \sum_{i=1}^n P_i * \mu_i$$

whereby n is the number of the anthropogenic pressure layers, P_i is the standardized intensity for each pressure layer and μ_i is the weighting variable in each grid cell i . Note that C_t was not calculated for areas with water depths of > 400 m due to the limited data available.

2.3. Quantification of the contribution of individual anthropogenic pressures

In the C_t equation, P_i represents the respective individual intensity of the key anthropogenic pressure proxies listed in the GIWA regional assessment ([Stolberg et al., 2006](#), in [Table 1](#)). To construct specific proxies in space, data were taken from the literature and converted to raster layers (for details see Supplementary Data). For standardization purposes, some proxy layers were log [X]-transformed according to the distribution of their intensity values, and all were max-min linearly rescaled ($[x_i - x_{min}] / [x_{max} - x_{min}]$). The resulting values are unitless and range from 0 to 1.

The second element of the C_t equation is the weighting variable μ_i . It was calculated by multiplying the stressor score of the respective anthropogenic pressure for the entire basin with the local stressor score. The former stressor score was estimated from literature data, following the method of [Halpern et al. \(2007\)](#), who developed a ranking system to evaluate the vulnerability of habitats to anthropogenic pressures. The vulnerability measures include scale, frequency and functional impact of the threats as well as resistance and recovery time of the ecosystem.

It also includes the certainty of the evaluation to prioritize better known anthropogenic pressures. The local stressor score was taken from expert assessments ([Stolberg et al., 2006](#)). As the latter authors performed an expert evaluation to rank the anthropogenic pressures for each Caspian Sea littoral country, the results were transferred to the ecoregion level by applying a weighted average according to the shared surface between countries and ecoregion (see Supplementary Data).

2.4. Ecoregion-specific differences in cumulative pressure scores

For inferring ecoregion-specific (and thus spatially- and bathymetrically-specific) differences in cumulative pressure scores, a Principal Component Analysis (PCA) was conducted. The PCA was run using the function *princomp* in the base package *stats* for the statistical environment R ([R Core Team, 2016](#)). Additionally, a similarity matrix based on the Euclidean distance between the contributions of individual pressure effects was calculated for the ecoregions. This similarity matrix was then used to cluster the ecoregions with the Partitioning Around Medoids (PAM) method, a more robust version of K-means ([Reynolds et al., 1992](#)). These analyses were done with the functions *daisy* and *pam* of the R package *cluster* ([Maechler et al., 2016](#)). Visual plots were created with the package *ggplot2* ([Wickham, 2009](#)) and maps were generated in ArcGIS 10.5 (ESRI).

3. Results

3.1. Cumulative and individual pressure scores in the Caspian Sea

Cumulative pressure scores in the Caspian Sea ranged from 0.23 to 2.35 (theoretical values 0 to 4; [Fig. 2a](#)). The highest scores were estimated for the Baku area and in the west of the Volga Delta. Lowest scores were detected in the deeper parts (below 120 m) of the middle Caspian Sea sub-basin ([Fig. 2a](#)).

The three northwestern ecoregions of the Caspian Sea showed the highest average cumulative pressure scores (NCB-T = 1.46, NCB-RO = 1.31, NCB-WS = 1.30) of all Caspian Sea ecoregions, with the most relevant individual pressure being poaching ([Fig. 2b](#), [Table 2](#)).

Lowest average cumulative pressure scores were calculated for the open water ecoregions MCB-OS and SCB-OS with scores of 0.47 and 0.69, respectively. For the latter ecoregions, the strongest individual pressure was chemical pollution ([Table 2](#)).

Overall, three anthropogenic pressures (invasive species, chemical pollution and poaching) were the highest individual contributors to the cumulative pressure scores ([Table 2](#), for a full list of all anthropogenic pressure contributions see Supplementary Data). Each of them was responsible for at least 10% of the scores in more than half of the Caspian Sea grid cells ([Fig. 3](#)).

3.2. Ecoregion-specific differences in individual pressure scores

The PCA, which was conducted to infer ecoregion-specific differences in individual pressures, showed three clusters ([Fig. 4](#)). The two dominant factors are poaching and chemical pollution (78% of the summative variance; $\sigma^2 = 0.11$; [Fig. 4](#)). They have loadings on the first PC of -0.757 and 0.617 , respectively.

The dissimilarity of individual pressure contributions across paired ecoregions, measured as Euclidean distance, is visualized in [Fig. 5](#). The two offshore ecoregions, MCB-OS and SCB-OS, showed the highest difference to the northern Caspian ecoregions (for detailed values see Supplementary Data).

The PAM analysis of ecoregions yielded two clusters ([Fig. 2](#) in Supplementary Data). The first contained the five northern ecoregions and MCB-T (maximum and average Euclidean distance between elements 0.24 and 0.11, respectively), the second included MCB-C, MCB-OS and SCB (maximum and average Euclidean distances between elements 0.35 and 0.19, respectively; see Supplementary Data).

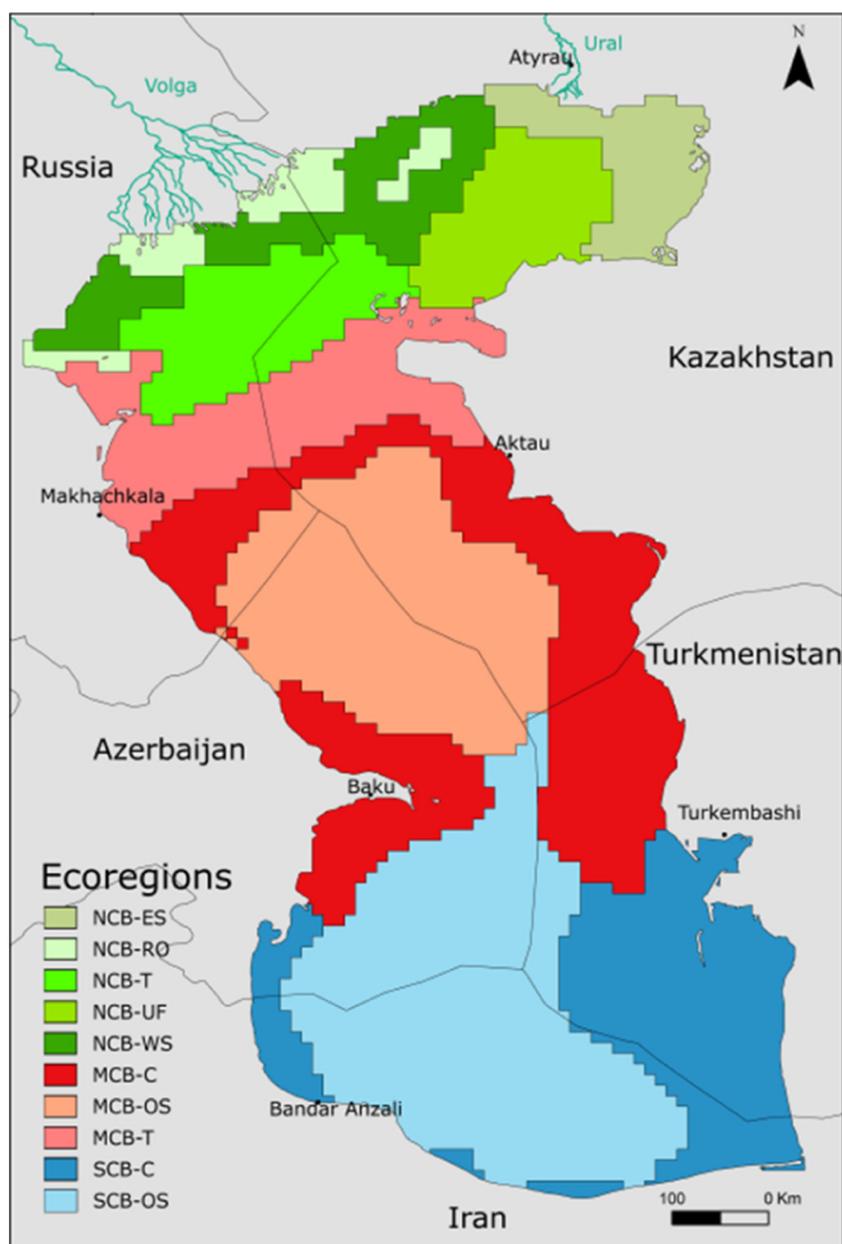


Fig. 1. Ecoregions of the Caspian Sea (modified from Fendereski et al., 2014). The principal colors green, red and blue refer to the northern (NCB), middle (MCB) and southern (SCB) Caspian Sea sub-basins, respectively. Abbreviations: -ES: eastern shelf, -RO: river outflows, -WS: western shelf, -UF: Ural furrow, -C: coastal, -T: transition, -OS: offshore. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Major anthropogenic activities/pressures in the Caspian Sea (following Stolberg et al., 2006) and respective proxies used for the CEA analysis. Note that anthropogenic pressure proxies are not mutually exclusive. For methodological details see Supplementary Data.

Anthropogenic pressure/activity	Proxy used in this study	Reference
Unsustainable fishing	Rate of annual fish catch	FAO (2018)
Chemical pollution	Concentration of chemical pollutants in sediment	de Mora et al. (2004), Tolosa et al. (2004)
Streamflow regulation	Sturgeon abundance	Lagutov (2008), Khodorevskaya et al. (2009)
Invasive species	Occurrence of invasive species	Karpinsky (2002)
Oil industry disturbances	Oil infrastructure and transportation	Anonymous (2012), AIS Marine Traffic (2016)
Coastal development	Human population densities along coastline	CIESIN (2016)
Agriculture by-product discharge	Total nitrogen content in river catchment	Potter et al. (2011), Lehner and Grill (2013)
Eutrophication	Chlorophyll <i>a</i> content	NASA, OceanColor Data (2017)
Poaching	Areas with poaching activities	Dmitrieva et al. (2013), Strukova et al. (2016)

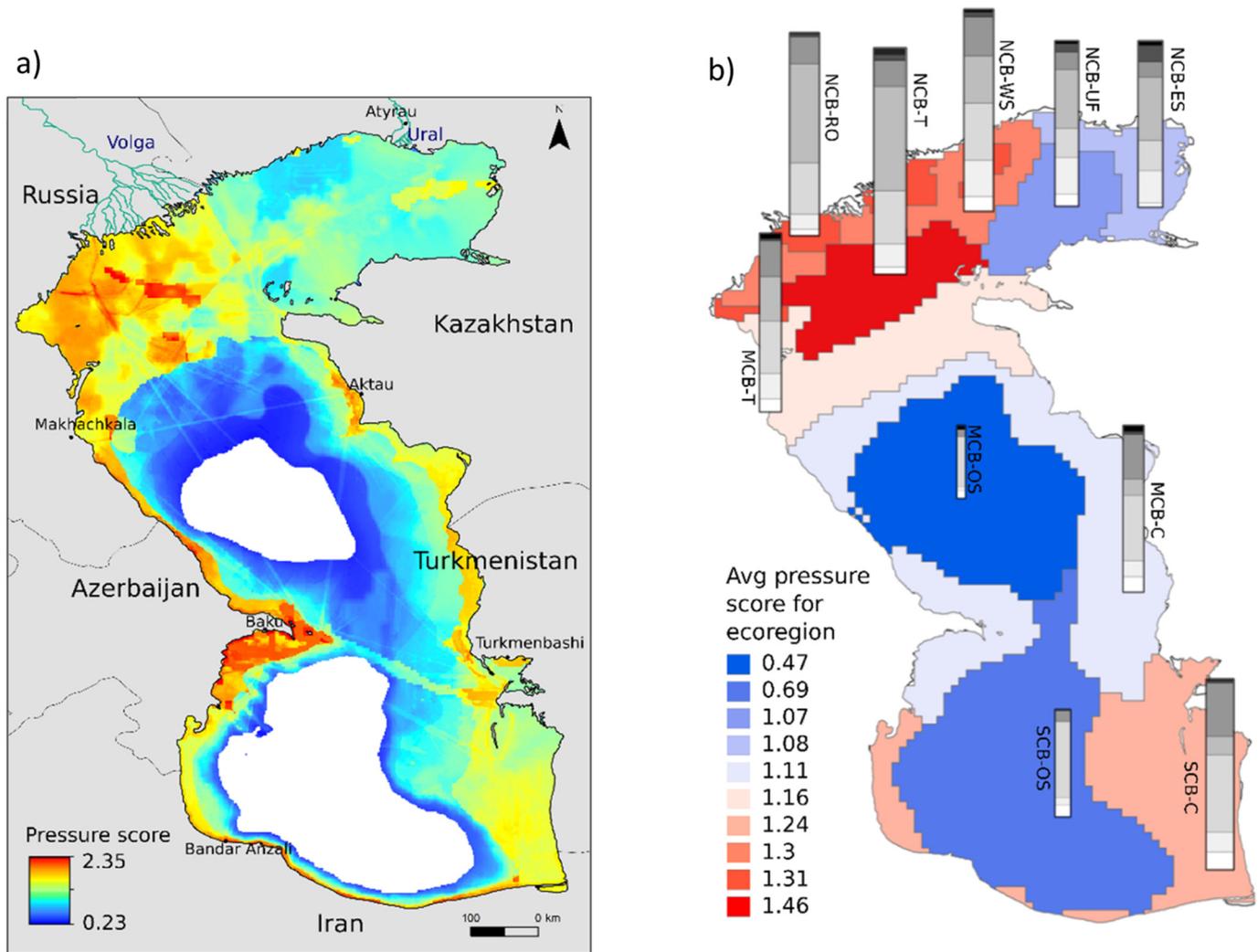


Fig. 2. a) Map showing the spatial distribution of cumulative pressure scores for each grid cell of the Caspian Sea at a resolution of 1 ArcMin (~2.2 km²). Areas with water depths > 400 m were excluded from the analysis. b) Map showing the spatial distribution of average cumulative pressure scores in each ecoregion. The gradient bars indicate the anthropogenic pressure contribution for each ecoregion. For detailed values see Table 2.

4. Discussion

Our results show that cumulative pressure scores are not equally distributed across the study area. Highest scores were found in Azerbaijani waters, near major oil fields and near the entrance of the Volga Delta. In contrast, offshore areas, in particular with water

depths > 120 m, had comparably low scores. We also found that both cumulative and individual pressure scores vary greatly among ecoregions. In the following sections, we discuss i) the socio-political and economic factors causing these spatial differences in anthropogenic pressure and ii) ecoregion-specific differences in anthropogenic pressure contributions.

Table 2

Average individual pressure scores for ecoregions as indicated in Fig. 2b. The color of the squares refers to the color coding of the gradient bars in Fig. 2b. The three highest individual pressure scores for each ecoregion are indicated in bold.

Ecoregion	Eutrophication	Agriculture by-product discharge	Unsustainable fishing	Coastal development	Invasive species	Poaching	Chemical pollution	Streamflow regulation	Oil industry disturbances
	■	■	■	■	■	■	■	■	■
MCB-C	0.04	0.01	0.01	0	0.27	0.1	0.4	0.08	0.09
MCB-OS	0.05	0	0	0	0.09	0.01	0.72	0.03	0.1
MCB-T	0.03	0.01	0.01	0	0.2	0.25	0.29	0.14	0.07
NCB-ES	0	0.03	0	0	0.13	0.51	0.25	0.05	0.03
NCB-RO	0.01	0.01	0	0	0.11	0.45	0.2	0.19	0.01
NCB-T	0.03	0	0	0	0.12	0.38	0.21	0.18	0.08
NCB-UF	0	0	0	0	0.14	0.51	0.26	0.06	0.03
NCB-WS	0.01	0.01	0	0	0.11	0.45	0.21	0.19	0.02
SCB-C	0.02	0.04	0	0.02	0.32	0.12	0.4	0.03	0.04
SCB-OS	0.05	0.02	0	0	0.14	0.01	0.68	0	0.1

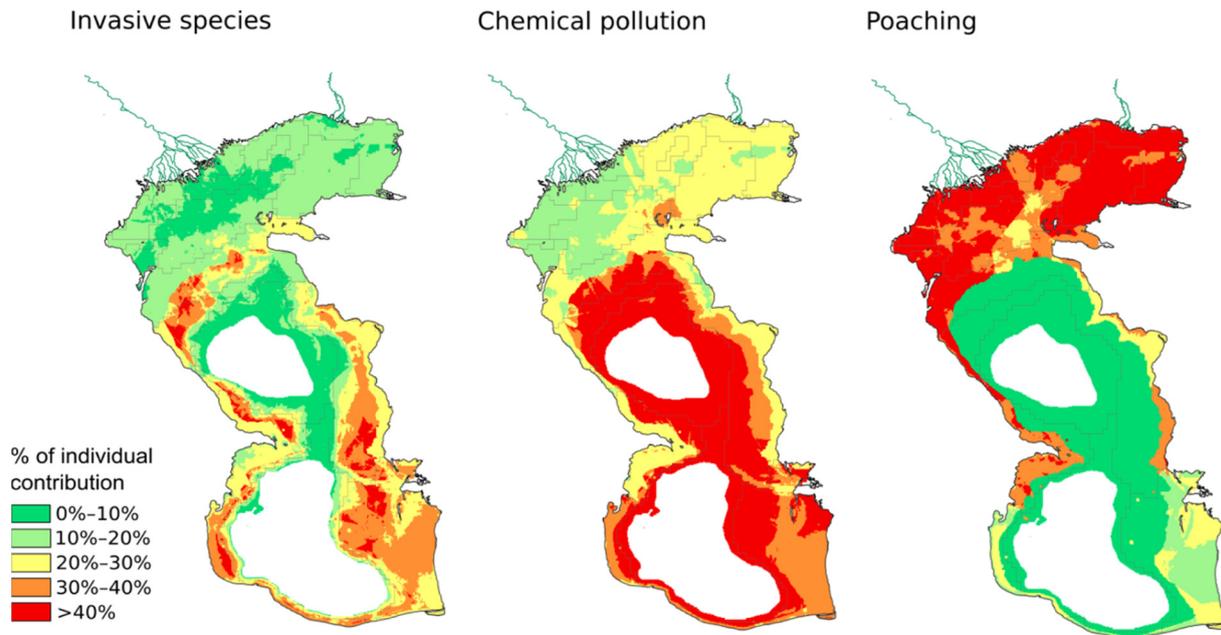


Fig. 3. Maps showing the contribution of the three major individual pressures contributing to the cumulative pressure scores in the Caspian Sea. Areas with water depths > 400 m were excluded from the analysis.

4.1. Contribution of individual pressures to the cumulative pressure scores

The anthropogenic pressures with the highest individual contributions are poaching, chemical pollution and invasive species. The former pressure has a higher impact in the northern Caspian Sea sub-basin; the latter two in the middle and southern sub-basins (Fig. 3). These findings indicate that similar cumulative pressure scores in different parts of the Caspian Sea (e.g., near the entrance to the Volga Delta and around Baku; Fig. 2a) may be caused by locally or regionally different individual pressures. The spatial differences are largely driven by socio-political and economic factors, mostly related to the collapse of the industrial sector of the former Soviet Union (Kosarev and Yablonskaya, 1994; Dumont, 1995; Zonn, 2005). For example, registered sturgeon catches peaked in the late 1980's. A few years later, the fishing fleet was largely dismantled and anglers started to harvest sturgeons without

formal regulation (Khodorevskaya et al., 2014; Mammadov et al., 2016; Strukova et al., 2016). Our results indicate that poaching is still a major concern (Fig. 3) and that the effectiveness of the different national anti-poaching approaches may vary (Ermolin and Svolkinas, 2016).

The spatial pattern of chemical pollution is also linked to the socio-economic development of oil exploration in the Caspian Sea (Kosarev and Yablonskaya, 1994). In 1950, the first oil wells were drilled off the coast of Azerbaijan, while land-based oil production already started a century earlier (Zhiltsov et al., 2016). Given the poor environmental standards at that time and the subsequent abandonment of wells, a persistent leaking of oil compounds and heavy metals into the water has been evident (Bickham et al., 1998; de Mora et al., 2004). Pollutant concentrations were at alarming levels in the 1980's and 1990's, when heavy metal residuals from mining activities increased chemical pollution (de Mora et al., 2004). Recently, hazardous chemicals are

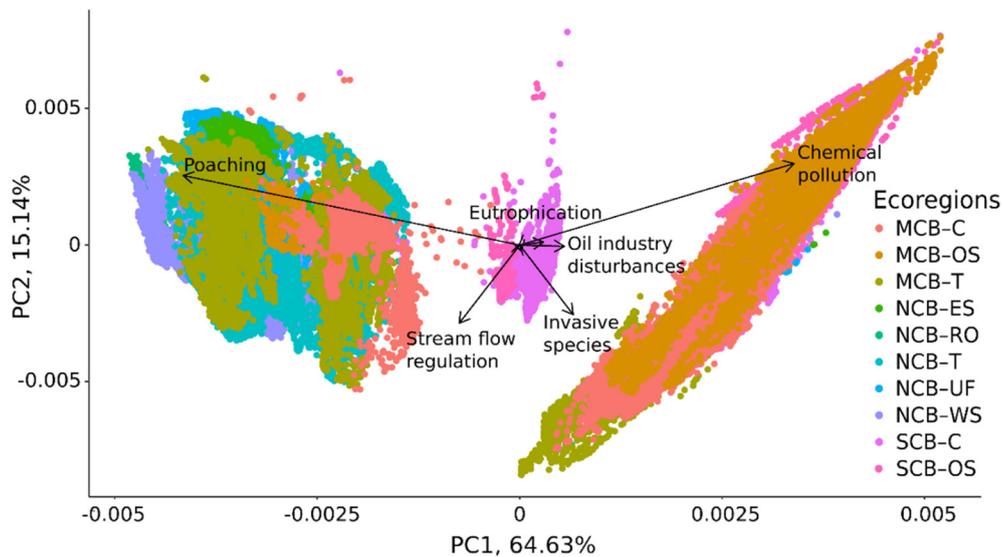


Fig. 4. PCA showing ecoregion-specific differences in individual pressures. Black arrows indicate factor loadings of pressures. Pressures not labeled in the plot had a minimal contribution. For abbreviations of ecoregions see Fig. 1.

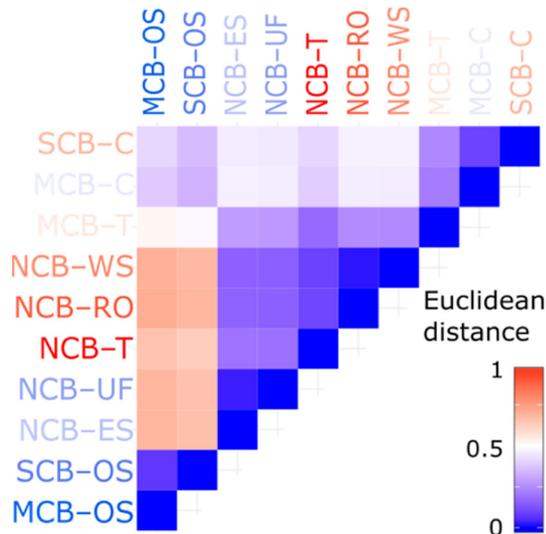


Fig. 5. Similarity matrix based on Euclidean distances between ecoregions. Colors of ecoregion labels indicate average cumulative pressure scores according to Fig. 2b. For abbreviations see Fig. 1.

decreasing along the coasts of the Caspian Sea (Nemirovskaya, 2016). However, pollutants are increasingly accumulated in the deepest parts of the basin due to water cycles (Tolosa et al., 2004; Korshenko and Gul, 2005; Nemirovskaya, 2016).

The continued introduction of invasive species, too, is directly linked to the economic development of the region. This concerns both the intended and unintended introduction. In the early 20th century, several invertebrate species, such as the annelid worm *Nereis diversicolor* and the bivalve *Abra segmentum*, were intentionally introduced in the Caspian Sea to increase feed biomass for sturgeon stock (Shiganova, 2010). Unintentional introductions were largely fostered by the construction of the Volga-Don Canal in 1952. It connects the Caspian Sea with the Black Sea and thus with the world's ocean (Shiganova, 2010). This, in turn, promotes the active and passive colonization of the Caspian Sea by invasive species. An example is *Mnemiopsis leidyi*, a comb jellyfish that originated in the Atlantic Ocean and reached the Caspian Sea in 1998 (Shiganova, 2010). This species caused the sharp decline of fish catches in Iran, as it competes with commercially used fish for food resources and preys on their eggs (Roohi et al., 2010, 2016; Pourang et al., 2016). The highest impact of invasive species can be seen in the middle and southern Caspian Sea, which are ecologically more similar to the native marine ecosystems of many introduced species (Shiganova, 2010).

Our results also show that cumulative pressure scores are an important mean for identifying spatial differences in overall human impacts on Caspian Sea ecoregions (Fig. 2a). However, different combinations of individual stressors (Fig. 3) may result in similar cumulative pressure scores. Therefore, the utilization of individual pressure scores might be more straightforward for implementing targeted (i.e., species- and area-specific) conservation and remediation practices.

4.2. Ecoregion-specific differences in anthropogenic pressure contribution

The ecoregions most affected by anthropogenic pressures are those in the continental shelf of the northwestern (NCB-T, NCB-RO, NCB-WS) and southern Caspian Sea (SCB-C). Ecoregions least affected are those in coastal areas of the northeastern Caspian Sea (NCB-UF, NCB-ES) as well as in the analyzed deepest parts of the basin (MCB-OS, SCB-OS) (Figs. 2b, 5). Moreover, our PCA analysis shows ecoregion-specific differences in the spatial distribution of individual anthropogenic pressures. Besides the main pressures discussed under 4.1. (i.e. poaching, chemical pollution and invasive species), other factors such

as eutrophication, stream flow regulation and oil industry disturbance also play a role, although the effects remain rather localized (Fig. 4 and Table 2). These patterns indicate strong bathymetrical and latitudinal divergences of cumulative and individual anthropogenic pressures among ecoregions. However, as shown by the similarity matrix in Fig. 5, similar ecoregions may also be affected by similar individual pressures.

The northern sub-basin, which lacks deep-water habitats and is nutrient-rich, favors the biomass growth of the main prey of young sturgeons (Guseinov, 2005; Malinovskaya and Zinchenko, 2010, 2011). As a consequence, the respective ecoregions are subject to a high impact from poaching (Dmitrieva et al., 2013). In contrast, they face relatively low impact from chemical pollution due to a geochemical barrier at the transition between fresh and brackish water, and the rich vegetation of the Volga Delta (Nemirovskaya, 2016). Invasive marine species also remain scarce in these ecoregions likely due to low salinities (Shiganova, 2010).

The ecoregions of the middle and southern Caspian Sea also show similar distributions of cumulative and individual anthropogenic pressures, with coastal ecoregions being more affected than offshore ones. Here, main individual pressures are invasive species (see Section 4.1.) and poaching. The latter may be explained by the fact that sturgeons migrate along the coastlines of the Caspian Sea, feeding on the rich benthos (Karpinsky, 2010).

Deep-water ecoregions of the middle and southern Caspian Sea are less affected by invasive species and poaching, but suffer from chemical pollution. This is due to the fact that these parts function as a sink for fine particles, as strong wind in the northern Caspian Sea move water and sediments southwards (Tolosa et al., 2004). In addition, deep-water ecoregions represent natural oil seeps (Nemirovskaya, 2016). Some of the respective compounds might be biologically magnified along the food chain, causing physiological impairments (Bickham et al., 1998; Moore et al., 2003; Wilson et al., 2014). Thus, chemical pollution may be of particular concern for endemic species in the deeper parts of the Caspian Sea (Parr et al., 2007; Tait et al., 2016) and could, for example, explain the strong decline of mollusks species in the profundal zone (Wesselingh et al., 2019).

Our ecoregion-specific analyses of anthropogenic pressure contributions show clear differences in cumulative and individual pressures among dissimilar ecoregions. As the respective ecoregions also harbor different native and endemic species, we may experience further shifts in community-assemblages in the future. This might, in particular, concern endemic species both in shallow and deeper waters, as well as native (including commercially-important) species in coastal ecoregions. These findings, in turn, substantiate the need for ecoregion-specific conservation efforts.

5. Conclusions

Cumulative pressure scores in the Caspian Sea are unevenly distributed, with coastal areas, particularly near major oil fields and the Volga Delta, showing higher values than deep-water areas. As the ten ecoregions in the Caspian Sea are, in part, defined by latitude and water depth, cumulative pressure scores also vary among ecoregions. However, analyses of individual anthropogenic pressures provide a more differentiated picture. Accordingly, the most important pressures are invasive species, chemical pollution and poaching. Invasive species are of particularly concern in the shelf areas of the middle and southern Caspian Sea sub-basins, i.e. in regions where the ecological conditions may allow introduced marine species to survive. In the shelf areas of the northern Caspian Sea sub-basin, poaching is the most severe anthropogenic pressure, hinting to region-specific differences in poaching intensities and regional problems in the implementation of anti-poaching strategies. Finally, the deep-water areas of the Caspian Sea are particularly affected by chemical pollution as they may serve as sinks for pollutants. This uneven distribution of cumulative and individual

pressure scores also concerns the individual ecoregions of the Caspian Sea, and their native and endemic species. This finding is of particular interest for future conservation strategies as species in dissimilar ecoregions might be affected by different anthropogenic pressures. We also show that cumulative pressure scores are an important mean for identifying spatial differences in overall human impacts. However, for implementing targeted conservation and remediation practices, a consideration of the underlying individual pressure scores might be more expedient.

This paper provided the first ecoregion-specific CEA analysis for the Caspian Sea. As such, our results might serve as a base line for future impact studies and for the prioritization of remediation plans, for example in the context of the Tehran Convention.

Declarations of interest

None.

Acknowledgments

This research was supported by the project PRIDE (Pontocaspian Rise and DEMise), which has received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No 642973. Many thanks go to Elena Jovanovska, Torsten Hauffe and Arthur F. Sands for the helpful discussions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2019.03.046>.

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MOLLUSK SPECIES FROM THE PONTOCASPIAN REGION – AN EXPERT OPINION LIST

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et al.

Mollusc species from the Pontocaspian region – an expert opinion list

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Academic editor: E. Neubert | Received 5 November 2018 | Accepted 20 December 2018 | Published 5 March 2019

<http://zoobank.org/10B66389-5E42-4E52-87D8-F49E2405D651>

Citation: Wesselingh FP, Neubauer TA, Anistratenko VV, Vinarski MV, Yanina T, ter Poorten JJ, Kijashko P, Albrecht C, Anistratenko OYu, D'Hont A, Frolov P, Gándara AM, Gittenberger A, Gogaladze A, Karpinsky M, Lattuada M, Popa L, Sands AF, van de Velde S, Vandendorpe J, Wilke T (2019) Mollusc species from the Pontocaspian region – an expert opinion list. ZooKeys 827: 31–124. <https://doi.org/10.3897/zookeys.827.31365>

Abstract

Defining and recording the loss of species diversity is a daunting task, especially if identities of species under threat are not fully resolved. An example is the Pontocaspian biota. The mostly endemic invertebrate faunas that evolved in the Black Sea – Caspian Sea – Aral Sea region and live under variable salinity conditions are undergoing strong change, yet within several groups species boundaries are not well established. Collection efforts in the past decade have failed to produce living material of various species groups whose taxonomic status is unclear. This lack of data precludes an integrated taxonomic assessment to clarify species identities and estimate species richness of Pontocaspian biota combining morphological, ecological, genetic, and distribution data. In this paper, we present an expert-working list of Pontocaspian and invasive mollusc species associated to Pontocaspian habitats. This list is based on published and unpublished data on morphology, ecology, anatomy, and molecular biology. It allows us to (1) document Pontocaspian mollusc species, (2) make species richness estimates, and (3) identify and discuss taxonomic uncertainties. The endemic Pontocaspian mollusc species richness is estimated between 55 and 99 species, but there are several groups that may harbour cryptic species. Even though the conservation status of most of the species is not assessed or data deficient, our observations point to deterioration for many of the Pontocaspian species.

Keywords

Aral Sea, bivalves, Black Sea, Caspian Sea, conservation, gastropods, nomenclature, taxonomy

Introduction

The aquatic Pontocaspian (or Ponto-Caspian) biota is constituted by taxa that evolved in saline water bodies in the Caspian Sea – Black Sea – Aral Sea region and surrounding rivers in the past few million years. They include diverse groups such as diatoms, dinoflagellates, foraminiferans, crustaceans, molluscs, as well as fish and the Caspian seal. Major Pontocaspian habitats are located in the northern coastal zone of the Black Sea (mostly confined to the Romanian and Ukrainian coasts) and the Sea of Azov (mostly in the Taganrog Bay), cover the entire Caspian Sea and, until recently, the Aral Sea (Fig. 1). However, Pontocaspian habitats are impacted by human activities such as pollution, habitat modification and introduction of invasive species (Bologna et al. 1995, Zolotarev 1996, Zaitsev and Mamaev 1997, Gomoiu et al. 2002, Grigorovich et al. 2003, Occhipinti-Ambrogi and Savini 2003, Barannik et al. 2004, Shalovenkov 2005, UNEP 2006, Stolberg et al. 2006, Selifonova 2008a, b, Popa et al. 2009), as well as the entire obliteration of environments in the case of the Aral Sea in the second half of the 20th century (Mainguet and Létolle 1997, Andreeva and Andreev 2003, Plotnikov et al. 2016).

Faunas in the Pontocaspian region have strongly changed in the past century. Pontocaspian species that were abundant only a century ago, such as *Dreissena elata* and *D. caspia* in the Caspian Sea, have vanished in the mid-20th century (Kosarev and Yablonskaya 1994). For the Aral Sea, the faunas appear to have largely disappeared with the demise of the lake system since the 1950s (Andreeva and Andreev 2003). Abundances of several other species in the Caspian Sea and Black Sea Basin have severely declined (Bologna et al. 1995, Zaitsev and Mamaev 1997, Barannik et al. 2004, Popa et al. 2012).

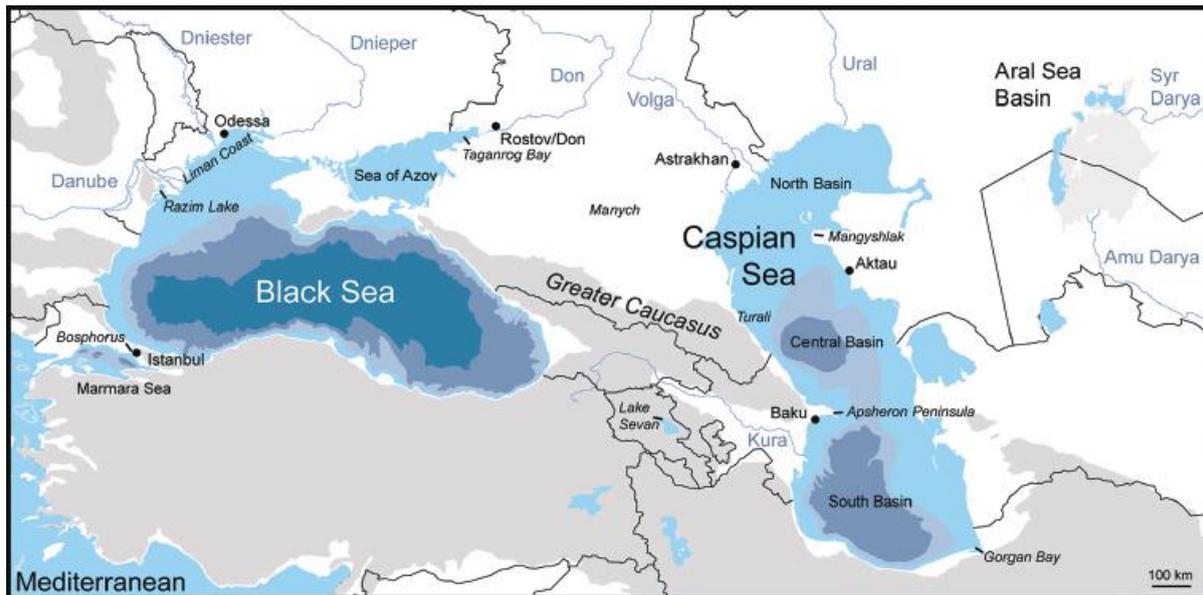


Figure 1. Map of the Pontocaspian region with the indication of major basins, rivers, regions, and cities referred to in the text.

However, we cannot evaluate the extent or nature of biodiversity loss as there is no general agreement on the species that it might concern. Much of the diversity in Pontocaspian mollusc groups is contained within a limited number of genera. Changing taxonomic approaches through time (e.g., Zhadin 1952, Logvinenko and Starobogatov 1969, Alexenko and Starobogatov 1987, Sitnikova and Starobogatov 1999, Munasyova-Motyash 2006a, b, Anistratenko 2007b, Kijashko in Bogutskaya et al. 2013, Vinarski and Kantor 2016, Neubauer et al. 2018) combined with large morphological variability and few diagnostic characters in certain groups, as well as the paucity of living material and partial disappearance of type material, has precluded critical reassessment of species boundaries and thus species richness. For the Caspian Sea, multiple efforts to collect fresh material in the past decade failed to produce sufficient living material to elucidate these taxonomic matters for most of the groups. Sampling efforts include coastal sampling around Turali, Russia (FW, 2003); northern Azerbaijan (FW, 2016), middle and southern Azerbaijan (VA, ML, AFS, TW, 2017); Mangyshlak region coastal areas, Kazakhstan (OA, VA, 2016, 2017); the transition of the northern to middle Caspian Sea Basin in Kazakhstan (PRIDE expedition, 2017); and the Gorgan Bay in Iran (AFS, 2018). A faunal inventory of the deep-water southern Caspian Sea Basin (> 200 m water depth) of southern Azerbaijan was published lately by Mirzoev and Alekperov (2017). We are uncertain whether it concerns living material nor can we assess the species identities. Their records are mentioned below but require further confirmation. We did find some living endemic species ourselves, and from coastal areas low numbers of such species have been reported elsewhere (e.g., Latypov 2015). Yet, many species and even groups of species (e.g., *Turricaspia* species) have not been encountered alive despite our attempts. Our inability to collect life specimens for several groups has made

a combined molecular-morphological approach to delineate species impossible. As a result, a reliable estimate of the number of species involved is lacking, and therefore the potential magnitude of the biodiversity decline is speculative. Hence, we need an alternative approach to outline the species boundaries and estimate the numbers affected.

By pooling all insights, data (published and unpublished) and expert opinions on the Pontocaspian mollusc species through taxonomists we aim to provide a list of Pontocaspian mollusc species that can serve as a base for further research. We use molluscs as a model group since they are (1) an important, representative and well-known part of the Pontocaspian fauna, (2) have a number of taxonomic specialists available, and (3) can often be identified based on their shell characters even when living populations have vanished. The Pontocaspian aquatic mollusc species list will highlight uncertainties in species complexes as to give guidance to further research in resolving taxonomic matters. The aim of this work is to compile a list of Pontocaspian mollusc species with the underlying arguments why we consider these species as (likely) valid species, to outline taxonomic uncertainties and to provide an updated estimate of species richness.

Materials and methods

A preliminary Pontocaspian mollusc species list was assembled during a PRIDE program workshop in Giessen, Germany, in May 2018. The PRIDE (“Drivers of Pontocaspian Rise and biodiversity Demise”) program is an EU funded Innovative Training Network that studies the drivers of the rise and demise of Pontocaspian faunas. Using listings in Vinarski and Kantor (2016) supplemented with further information from the participants, this initial list was then circulated among a wider community of taxonomic workers for further updates and comments. Data on distribution and type material were derived from Vinarski and Kantor (2016) and further completed and amended. The systematic order above the species level follows Bouchet et al. (2017) and MolluscaBase (2018a). In cases where we deviate from the supraspecific classification, arguments are discussed below.

The list comprises aquatic Holocene Pontocaspian mollusc faunas. A substantial number of Pontocaspian species has been described from empty shells from beach material or derive from grab samples. Such samples typically are dominated by time-averaged Holocene shell assemblages, which may or may not yield living specimens and in very rare occasions also contain older (Pleistocene) material (see, e.g., Leroy et al. 2018). For the Black Sea Basin, the Holocene time interval largely coincides with the date of the marine flooding through the Bosphorus and subsequent marginalisation of Pontocaspian species to the NW coastal zone (Danube Delta to Dnieper Estuary) and the Sea of Azov (Mordukhay-Boltovskoy 1960). For the Caspian Sea, the time interval corresponds to the so-called Novocaspian period that started after the very deep Mangyshlak regression 8 ka (Fedorov 1953, Neveeskaja 1958, 2007, Yanina 2005). The time interval contains the earliest impact of humans on native faunas, such as the introduction of *Cerastoderma glaucum* in the Caspian Basin during the early Holocene (Fedorov 1957, Yanina 2009). It also contains the large faunal changes of the 20th century related to pollution, invasive species, and obliteration of habitats (Kosarev and Yablonskaya 1994).

Table 1. Definitions we use to characterise the status of species.

Pontocaspian	Centre of evolutionary history in Pontocaspian lakes
Native	Present in the Pontocaspian region today and in the Quaternary (not introduced by man) but centre of evolution not necessarily in that region: e.g., planorbid species with a Palearctic distribution, <i>Cerastoderma glaucum</i> .
Introduced	Species introduced in the Pontocaspian from elsewhere, usually anthropogenic: some Pontocaspian species have migrated between Pontocaspian basins and their status is explained in detail there (e.g., <i>Monodacna colorata</i> / <i>Dreissena bugensis</i> : introduced in Caspian from natural ranges in Black Sea Basin).
Invasive	Species that have become disruptive in the ecosystem after introduction.

One of the greatest difficulties is to establish the identities of taxa reported as geographic subspecies. Many species have forms, varieties, and subspecies described from the Aral Sea, the Caspian Sea Basin, and the Black Sea Basin (including the Azov Sea). Often, such distinctions are made based on the geographical isolation alone or on a range of morphological characters whose variation seems to be overlapping in geographical subpopulations. In order to assess whether the geographical populations are indeed species, we need combined morphological, ecological, and molecular data, but only few studies produced this information to date (e.g., Popa et al. 2012 for Black Sea Basin *Monodacna*). For the Aral Sea, we expect difficulties to obtain fresh material of almost all species for molecular analyses due to the obliteration of most of the lake and its fauna in the 20th century (Andreeva and Andreev 2003, Plotnikov et al. 2016). To date, hardly any molecular data on closely related species that are (potentially) shared between the Caspian and Black Sea have been published with the exceptions of *Dreissena grimmi*/*D. bugensis* (e.g., Therriault et al. 2004, Stepien et al. 2013) and *Ecrobia maritima*/*E. grimmi* (Haase et al. 2010). For several potentially shared species, ecological tolerances and preferences between Caspian and Black Sea Basin populations are overlapping, but in some cases (like for *D. grimmi*/*D. bugensis*) they are not. We have adopted a conservative approach, and as long as no additional arguments (morphological, ecological, or genetic differences) were found, we consider the Aral, Caspian and Black Sea varieties/subspecies synonyms. Another difficulty in especially Caspian taxa is the erection of so-called “bathymetric” subspecies, which seem to be distinguished mostly based on their depths of occurrence. As long as no other (morphological, genetic) arguments are available, we synonymise such bathymetrical forms.

A listing of synonyms and important past misidentifications from the literature is given. The list is not exhaustive and intended to show major shifts in taxonomic thinking about Pontocaspian and invasive species. The format of synonymy lists follows mostly suggestions of Matthews (1973). Asterisks in front of a record indicate valid first descriptions, a superscript “o” a prior yet invalidly introduced synonym. The status of each species is defined according to criteria outlined in Table 1.

As for the conservation status we have indicated the IUCN Red List status as of July 2018 from [www.iucnredlist.org] and added our own observations. For updated stratigraphic terminology and age estimates we refer to Krijgsman et al. (2019).

Abbreviations used are:

- ZIN** Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.
RGM Naturalis Biodiversity Center, collections of fossil Mollusca, Leiden, The Netherlands.

For personal observations of the various authors we used the following abbreviations:

- | | | | |
|-----------|--------------------------|------------|--------------------|
| FW | Frank P. Wesselingh, | AFS | Arthur F. Sands, |
| TN | Thomas A. Neubauer, | MV | Maxim V. Vinarski, |
| VA | Vitaliy V. Anistratenko, | TW | Thomas Wilke. |
| OA | Olga Anistratenko, | | |

Finally, with the long literature record and various languages involved we came across some problems in spellings of geographical names and authors that we could not always resolve. Often, the transliteration of Russian names into French, German, and English literature resulted in different spellings, for example Ostroumoff/Ostroumov, Andrussoff/Andrussow/Andrusoff/Andrusov, and Apsheron/Absheron. We have followed the translations that are used by most the Russian-language authors of this paper but in some cases denote the different available spellings.

Systematic catalogue

Bivalvia

Remarks. Within the endemic bivalve species groups, a general lack of combined molecular, morphological, and ecological approaches has led to partially unresolved taxonomy, especially within the genera *Monodacna* and *Dreissena*. Much of the bivalve taxonomy follows the latest review of Caspian bivalves by Kijashko in Bogutskaya et al. (2013), and we discuss deviations from his schedule. The list of Aral bivalves published by Vinarski and Kantor (2016) is based chiefly on Andreeva and Andreev (2003), and it is used here as a base with appropriate changes in nomenclature.

Family Mytilidae Rafinesque, 1815

Mytilaster minimus (Poli, 1795)

*1795 *Mytilus minimus* Poli: 209–210, pl. 32, fig. 1.

1932 *Mytilaster lineatus* (Gmelin, 1790). – Bogachev: 38, pl. 1, figs 5–11 [**non** *Mytilus lineatus* Gmelin, 1791].

1952 *Mytilaster lineatus* (Gmelin, 1789). – Zhadin: 285, fig. 248 [**non** Gmelin, 1791].

- 1969 *Mytilaster lineatus* (Gmel.). – Logvinenko and Starobogatov: 311–312, figs 339a, b, pl. 5, figs 1, 2 [non Gmelin, 1791].
- 1969 *Mytilaster lineatus* (Gmelin, 1790). – Vekilov: 155–157, pl. 35, figs 1–25 [non Gmelin, 1791].
- 2013 *Mytilaster lineatus* (Gmelin, 1791). – Kijashko in Bogutskaya et al.: 316, fig. 104 [non Gmelin, 1791].

Status. Native to Black Sea Basin, invasive in Caspian Sea, introduced in Aral Sea but extinct there.

Type locality. Sicily, Italy.

Distribution. Native to the Mediterranean and Black Sea. Introduced in the Caspian Sea between 1917 and 1919 (Grigorovich et al. 2003).

Taxonomic notes. This species has commonly been mentioned as *Mytilaster lineatus* (Gmelin, 1791), but the Caspian-Aral species lacks the ribbing typical for that species. The attribution to *M. minimus* is based on shell morphology but confirmation from molecular analyses is required.

Remarks. *Mytilaster minimus* has successfully replaced *Dreissena caspia* and *D. elata* between 1938 and 1957 (Kostianoy and Kosarev 2005) in the Caspian Sea. Logvinenko and Starobogatov (1969) reported this species from the southern areas of the northern Caspian Sea, in the middle and the southern Caspian Sea down to 35–50 m water depth. Rarely, small individuals were found at depths down to 100 m. The species does not tolerate salinities below 7–8‰. This species was mentioned from depths between 200 and 600 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *M. lineatus*). These deep records are unusual given other records and will require confirmation.

Conservation status. Not assessed.

Family Cardiidae Lamarck, 1809

Remarks. For the genus *Cerastoderma*, the species status of Pontocaspian material is subject of debate where morphological and increasingly molecular arguments show the possibility of sibling species occurrences (Sromek et al. 2016). The genus *Didacna* is relatively well established, however much uncertainty exists over distinction between the genera *Monodacna*, *Adacna*, and *Hypanis*. The generic concepts have shifted through time. Only lately, Kijashko in Bogutskaya et al. (2013) treated *Monodacna* as a subgenus of *Adacna*. Büyükmeriç and Wesselingh (2018) discussed the distinction between the three genera and considered *Monodacna*, *Adacna*, and *Hypanis* as valid.

Adacna laeviuscula (Eichwald, 1829)

- *1829 *G.[lycymeris] laeviuscula* Eichwald: 279, pl. 5, fig. 1a, b.
- 1838 *Adacna Laeviuscula* m. – Eichwald: 170–171.
- 1841 *Adacna laeviuscula*. – Eichwald: 281–282, pl. 39, fig. 1a–d.

- 1905 *Adacna laeviuscula* (Eichwald, 1829). – Ostroumov: pl. 2, fig. E.
 1907 *Adacna laeviuscula*. – Ostroumov: 25, text fig., pl. 4, figs 6–8.
 1952 *Adacna (Adacna) laeviuscula* (Eichwald, 1829). – Zhadin: 353–354, pl. 9, fig. 331.
 1958 *Adacna (Adacna) laeviuscula* (Eichwald, 1829). – Nevesskaja: 49–50, pl. 9, figs 15–18.
 1969 *Hypanis laeviuscula laeviuscula* (Eichw.). – Logvinenko and Starobogatov: 337, fig. 353(5).
 1973 *Hypanis laeviuscula laeviuscula* Eichwald, 1829. – Grossu: 144–145, text fig. 29.
 2013 *Adacna laeviuscula* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 377, fig. 154, photo 48.
 2016 *Adacna (Adacna) laeviuscula* (Eichwald, 1829). – Vinarski and Kantor: 64.

Status. Pontocaspian species, endemic to Caspian Sea and possibly Black Sea Basin.

Type locality. Azerbaijan, Caspian Sea, Gulf of Baku is the type locality given by Vinarski and Kantor (2016) and this is written on the label of the type material. However, the type description reads “Hab. australem ripam maris caspii, in sinu Astrabadensi” [southern border of the Caspian Sea, in bight of Astrabad (= Gorgan, Iran)]. Further research on the labels and documentation is required to assess whether a new lectotype or even neotype must be assigned for *Adacna laeviuscula*.

Distribution. Caspian Sea; limans, coastal lakes, and Danube Delta in Black Sea Basin (in case *A. fragilis* will be shown to be a synonym of *A. laeviuscula*).

Taxonomic notes. See discussion under *A. fragilis*.

Remarks. Kijashko in Bogutskaya et al. (2013) list the presence of this species at 30–60 m water depth in the Caspian Sea from muddy, sandy-mud, and rarely sandy bottoms. Logvinenko and Starobogatov (1969) reported the species from the northern, middle, and southern Caspian Sea basins down to 80–85 m water depth. In the Caspian Sea, the species has not been found in areas with salinities below 4‰. However, the common occurrence of fresh (paired) specimens on beaches seen at Turali (Dagestan, Russia) and northern Azerbaijan indicates this species maintains viable populations in foreshore and possibly even shoreface habitats.

Conservation status. Not assessed.

Adacna fragilis Milaschewitsch, 1908

- *1908 *Adacna fragilis* Milaschewitch: 992–993.
 1973 *Hypanis laeviuscula fragilis* Milashevitsch, 1916. – Grossu: 145.
 ?2006b *Hypanis (Adacna) laeviuscula fragilis* (Milachevitch, 1908). – Munasyypova-Motyash: 522.
 2009 *Adacna (Adacna) fragilis* Milashevich, 1908. – Popa et al.: 13, fig. 5.
 2016 *Adacna (Adacna) fragilis* Milaschewitsch, 1908. – Vinarski and Kantor: 64.

Status. Pontocaspian species, Black Sea Basin, status uncertain.

Type locality. Odessa region, Dniester liman and Katlabhuk Lake (Ukraine: Vinarski and Kantor 2016).

Distribution. Danube Delta region and NW Black Sea Basin coastal areas of Ukraine.

Taxonomic notes. We are uncertain about the status of *Adacna fragilis* Milaschewitch, 1908. The Black Sea Basin material has a wide variety of shapes and often is thinner and sometimes more elliptical than the Caspian *A. laeviuscula*. Both forms were synonymised by Graf and Cummings (2018) and indicated as a possible synonym in MolluscaBase (2018b). However, the Black Sea Basin occurrences are recorded from (coastal) lakes and small rivers suggesting little or only partial overlap in the ecological (and especially salinity) preferences of *A. laeviuscula* (e.g., Munasypova-Motyash 2006a, b, Popa et al. 2009). We are uncertain if *A. fragilis* might constitute a geographical subspecies (a status advocated by Grossu 1973), and further molecular analyses are needed to clarify the status of the Black Sea taxon.

Remarks. The species has been reported alive by Popa et al. (2009) from the Razim Lake complex on the Romanian Black Sea coast.

Conservation status. Not assessed.

Adacna minima Ostroumov, 1907

*1907 *Adacna minima* Ostroumov: 23, text fig., pl. 4, figs 1–5.

1952 *Adacna (Adacna) vitrea* var. *minima* (Ostroumoff, 1907). – Zhadin: 353.

1967 *Hypanis minima ostroumovi* Logvinenko and Starobogatov: 233.

1969 *Hypanis minima ostroumovi* Logv. et Star. – Logvinenko and Starobogatov: 338, fig. 354(3).

1973 *Hypanis minima ostroumovi* Logvinenko et Starobogatov, 1968. – Grossu: 146, text fig. 31.

?1974 *Hypanis minima sidorovi* Starobogatov: 246, fig. 213.

2003 *Hypanis minima minima* (Ostroumov, 1907). – Andreeva and Andreev: 88, fig. 5.1(3, 4).

?2009 *Hypania* [sic] *minima* (Ostroumoff, 1907). – Filippov and Riedel: 75, fig. 4s, t.

2013 *Adacna minima ostroumovi* (Logvinenko et Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 378, fig. 146.

2016 *Adacna (Adacna) minima minima* (Ostroumov, 1907). – Vinarski and Kantor: 64.

2016 *Adacna (Adacna) minima ostroumovi* Logvinenko et Starobogatov, 1967. – Vinarski and Kantor: 64.

Status. Pontocaspian species, endemic to Caspian Sea and Aral Sea; likely disappeared from the latter.

Type locality. The northern Caspian Sea and the Aral Sea (Vinarski and Kantor 2016).

Distribution. Aral Sea (probably extinct there; Andreeva and Andreev 2003), Caspian Sea.

Taxonomic notes. Graf and Cummings (2018) consider this species as a synonym of *A. vitrea*, but Kijashko in Bogutskaya et al. (2013) regards it as a valid species. The latter considers *A. minima minima* from the Aral Sea and *A. minima ostroumovi* syn. n. from the Caspian Sea as distinct geographical subspecies. The likely disappear-

ance of the species from the Aral Sea makes a molecular assessment of their distinctness very difficult and given the lack of other arguments we synonymise both. Furthermore, we are uncertain about the status of the subspecies *Hypanis minima sidorovi* Starobogatov, 1974 from the western Aral Sea. Without further data we assume it concerns a form that falls within the wide morphological variation of *A. minima*. We moreover are very uncertain as to the status of *Hypanis minima* from Holocene deposits of Aral Sea as illustrated by Filippov and Riedel (2009, fig. 4s, t). The juvenile specimen has relatively strong cardinal teeth, onset of clear ribs, and a general shape that more resembles *Monodacna caspia*.

Remarks. The species has been recorded mostly from the middle and southern Caspian Sea and more rarely from the eastern areas in the northern Caspian Sea down to 35 m water depth (Logvinenko and Starobogatov 1969) as well as from the Aral Sea from where it may have disappeared.

Conservation status. Not assessed.

Adacna vitrea (Eichwald, 1829)

- *1829 *G.[lycymeris] vitrea* Eichwald: 279, pl. 5, fig. 3.
- 1838 *Adacna vitrea* m. – Eichwald: 172–173.
- 1841 *Adacna vitrea*. – Eichwald: 282–283, pl. 39, fig. 2a, b.
- 1905 *Adacna glabra* Ostroumov: 18–19.
- 1932a *Adacna vitrea* (Eichwald, 1829). – Bogachev: pl. 1, figs 3, 4, 11.
- 1932b *Adacna vitrea* (Eichwald, 1829). – Bogachev: 33, pl. 3, figs 13–16, 28–29.
- 1952 *Adacna (Adacna) vitrea* (Eichwald, 1829). – Zhadin: 352–353, fig. 330.
- 1958 *Adacna (Adacna) vitrea* (Eichwald), 1838. – Neveeskaja: 47–48, pl. 9, figs 19–22.
- 1969 *Hypanis vitrea vitrea* (Eichw.). – Logvinenko and Starobogatov: 337, fig. 354(1), pl. 5, fig. 11.
- 1969 *Hypanis vitrea glabra* (Ostr.). – Logvinenko and Starobogatov: 338, fig. 354(2).
- 1973 *Hypanis vitrea vitrea* Eichwald, 1829. – Grossu: 145–146, text fig. 30A.
- 1973 *Hypanis vitrea glabra* Ostroumoff, 1905. – Grossu: 146, text fig. 30B.
- 2003 *Hypanis vitrea bergi* Starobogatov, 1974. – Andreeva and Andreev: 86, fig. 5.1(1, 2).
- 2013 *Adacna (Adacna) vitrea vitrea* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 378, fig. 148.
- 2013 *Adacna (Adacna) vitrea glabra* Ostroumoff, 1905. – Kijashko in Bogutskaya et al.: 379, fig. 149.
- 2016 *Adacna (Adacna) vitrea vitrea* (Eichwald, 1829). – Vinarski and Kantor: 65.
- 2016 *Adacna (Adacna) vitrea glabra* Ostroumov, 1905. – Vinarski and Kantor: 65.
- 2016 *Adacna (Adacna) vitrea bergi* (Starobogatov, 1974). – Vinarski and Kantor: 65.

Status. Pontocaspian species, endemic to Caspian Sea Basin, Black Sea Basin, and Aral Sea Basin.

Type locality. “Australem oram caspii maris, Astrabadensem” [southern coast of Caspian Sea, near Astrabad (= Gorgan, Iran)].

Distribution. Black Sea Basin (also in Azov Sea and adjacent lower Don River), Caspian Sea Basin, and Aral Sea (including delta of Amu-Darya River). The Aral populations may have gone extinct in the 1980s (Andreeva and Andreev 2003).

Taxonomic notes. The species has been subdivided into three geographical subspecies which were not recognised by Graf and Cummings (2018). It concerns a species with thin shells that yield very few diagnostic characters that show overlap. Here, we synonymise the subspecies pending molecular assessments of their status.

Conservation status. Not assessed.

***Cerastoderma glaucum* (Bruguière, 1789) s.l.**

*1789 *Cardium glaucum* Bruguière: 221–222.

1789 *Cardium Glaucum* Poiret: 13–15.

1869 *Cardium isthmicus* Issel: 74–76.

1952 *Cardium edule* L., 1758. – Zhadin: 344–345, fig. 318 [**non** *Cardium edule* Linnaeus, 1758].

2003 *Cerastoderma isthmicum* (Issel, 1869). – Andreeva & Andreev: 54, 62, figs 6.1(b), 6.7.

2013 *Cerastoderma glaucum* (Poiret, 1789). – Kijashko in Bogutskaya et al.: 342, fig. 126, photo 39.

2016 *Cerastoderma glaucum* (Bruguière, 1789). – Vinarski and Kantor: 69.

2016 *Cerastoderma isthmicus* (Issel, 1869). – Vinarski and Kantor: 70.

Status. Native Pontocaspian species (Black Sea Basin), Holocene invasive in Caspian Sea and Aral Sea.

Type locality. French Mediterranean.

Distribution. NE Atlantic, Baltic Sea, Mediterranean, Black Sea Basin, Caspian Sea Basin, Aral Sea, isolated Saharan lakes (Plaziat 1991).

Taxonomic notes. DNA studies have shown a strong structuring between Atlantic–western Mediterranean, Ionian, and Aegean–Pontocaspian populations of *C. glaucum* (Nikula and Väinölä 2003, Sromek et al. 2016). According to Sromek et al. (2016: 515), the “strong genetic differentiation and the occurrence of private alleles may hint at the presence of cryptic species within *C. glaucum*”. For a discussion on the authority of *C. glaucum*, see Vinarski and Kantor (2016: 69–70).

Remarks. The arrival of *Cerastoderma glaucum* in the Caspian Sea circa 8000 years ago has been linked to human settlement expansion through the Manych corridor (Fedorov 1957, Yanina 2009). It would be among the earliest human-mediated dispersal events for invertebrate species known to date.

Conservation status. Not assessed.

***Cerastoderma* sp. A [**non** *C. rhomboides* (Lamarck, 1819)]**

1916 *Cardium edule* var. *nuciformis* Milaschewitch: 257–259, pl. 7, figs 7, 8 [**non** *Cardium nuciforme* d’Orbigny, 1850].

2003 *Cerastoderma rhomboides rhomboides* (Lamarck, 1819). – Andreeva and Andreev: 93, fig. 6.1(A) [**non** *Cardium rhomboides* Lamarck, 1819].

2013 *Cerastoderma rhomboides* (Lamarck, 1819). – Kijashko in Bogutskaya et al.: 343, fig. 127, photo 40 [**non** Lamarck, 1819].

2016 *Cerastoderma rhomboides* (Lamarck, 1819). – Vinarski and Kantor: 70 [**non** Lamarck, 1819].

Status. Native Pontocaspian species (Black Sea Basin), introduced to Caspian Sea and Aral Sea.

Distribution. Black Sea (including Sea of Azov), Caspian Sea, Aral Sea, Aegean.

Taxonomic notes. This concerns a common rhomboid-shaped species in the Pontocaspian region whose name is uncertain. It has a short ligament in common with *C. glaucum* and the persistent occurrence of ribs on the posterior margin, the well-defined character of the ribs and the regular occurrence of scales in common with western European *C. edule*. This form has been often referred to as *C. rhomboides* (Lamarck, 1819) that has been described from the Italian Pliocene but that concerns a typical *glaucum* form (Fig. 2), not the rhomboid form of the Pontocaspian *Cerastoderma*. The species has been named *Cardium edule* var. *nuciformis* by Milaschewitch (1916), but that name is a junior primary homonym of *Cardium nuciforme* d’Orbigny, 1850. Even though some morphological features mentioned in the description of *C. lamarcki* (Reeve, 1845) may resemble those of the Pontocaspian species, the former has been traced to southern Great Britain from where molecular analyses only show the presence of *C. glaucum* (Nikula and Väinölä 2003).

Conservation status. Not assessed.

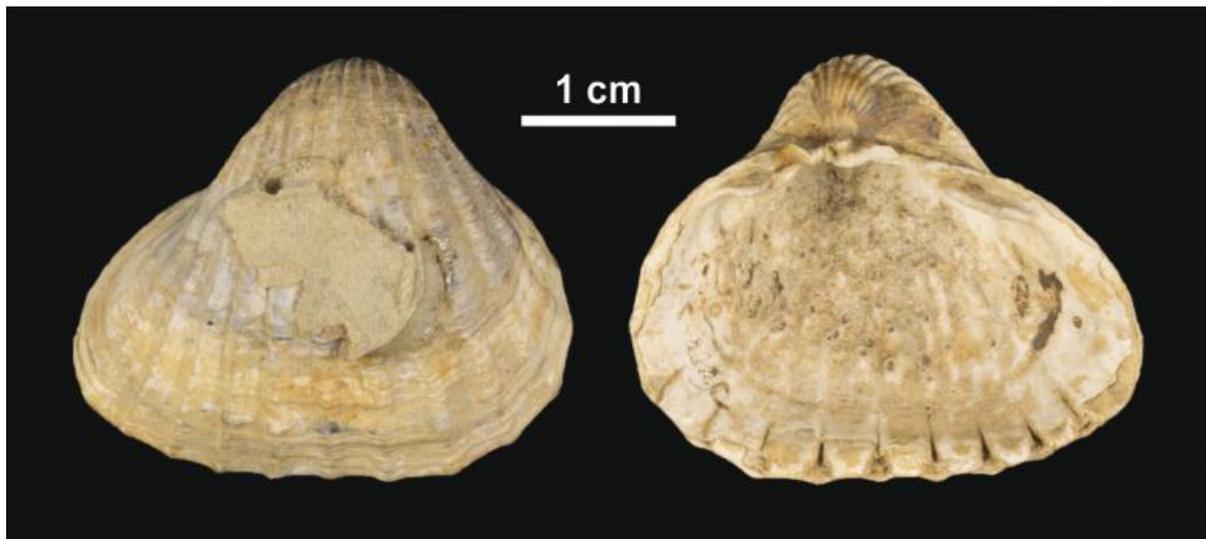


Figure 2. Syntype of *Cerastoderma rhomboides* (Lamarck, 1819), stored in the Muséum national d’Histoire naturelle Paris (MNHN.FA50142), Pliocene, Tuscany, Italy. Photograph by E Porez. https://science.mnhn.fr/institution/mnhn/collection/f/item/a50142?lang=fr_FR

***Didacna baeri* (Grimm, 1877)**

Fig. 3a

- *1877 *Cardium Baeri* Grimm: 51–54, pl. 8, figs 2, 3.
 1914 *Didacna Baeri* (Grimm, 1877). – Nalivkin & Anisimov: 4, pl. 1, figs 4, 5.
 1932 *Didacna Baeri* (Grimm, 1877). – Bogachev: 29, pl. 3, figs 1–7.
 1933 *Didacna Baeri* (Grimm, 1877). – Zhizhchenko: 34, pl. 2, figs 5–8.
 1952 *Didacna baeri* (Grimm, 1877). – Zhadin: 347–348, figs 321, 322.
 1953 *Didacna baeri* (Grimm, 1877). – Fedorov: 129, pl. 20, figs 10, 11.
 1968 *Didacna baeri* (Grimm, 1877). – Gadzhiev: 76–77, pl. 1, figs 1, 2.
 1969 *Didacna baeri* (Grimm). – Logvinenko & Starobogatov: 324, fig. 344(2).
 1969 *Didacna baeri* (Grimm, 1877). – Vekilov: 139–144, pl. 25, figs 1–8.
 1973 *Didacna baeri* Grimm, 1877. – Grossu: 131, text fig. 7.
 1983 *Didacna baeri* (Grimm, 1877). – Popov: 180, pl. 16, figs 20–23.
 1988 *Didacna baeri* (Grimm, 1877). – Yanina & Svitoch: 129, pl. 3, figs 7–13.
 2005 *Didacna baeri* (Grimm, 1877). – Yanina: 242–244, pl. 14, figs 12–15.
 2007 *Didacna baeri* (Grimm, 1877). – Neveeskaja: 940–941, pl. 23, figs 11–17.
 2013 *Didacna baeri* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 352, fig. 136, photo 41 [pars, excluding synonymy of *Didacna crassa*].
 2016 *Didacna baeri* (Grimm, 1877). – Vinarski & Kantor: 71 [pars, excluding synonymy of *Didacna crassa*].

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, offshore Turkmenistan, station 132, 40°32'N, 52°23'E.

Distribution. Logvinenko and Starobogatov (1969) reported *Didacna baeri* from the southern basin (mostly on the eastern side) and from the middle basin down to 60 m water depth.

Taxonomic notes. In recent works (e.g., Kijashko in Bogutskaya et al. 2013), the species *Didacna crassa* (Eichwald, 1829) [= *D. eichwaldi* (Krynicky, 1837)] has been considered a synonym of *D. baeri*. However, both species can be distinguished. *Didacna baeri* has a less extended, more roundish shell, a less developed keel, and a low top with less projecting beak and in general more ribs than *D. eichwaldi* (Fig. 3). *Didacna baeri* occurred for the first time in the Novocaspian transgressive deposits whereas *D. crassa* already occurred in the late Khvalynian (Late Pleistocene). Both became very common during the Novocaspian.

Conservation status. Not assessed.

***Didacna barbotdemarnii* (Grimm, 1877)**

- *1877 *Cardium Barbot-de-Marnii* Grimm: 56–58, pl. 8, figs 5, 6.
 1952 *Didacna barbot-de-marnyi* [sic] (Grimm, 1877). – Zhadin: 348, fig. 323.
 1969 *Didacna barbotdemarnyi* [sic] (Grimm). – Logvinenko and Starobogatov: 326–327, fig. 346, pl. 5, fig. 8.

- 1973 *Didacna barbotdemarnyi* [sic] Grimm, 1877. – Grossu: 133, text fig. 10.
 2007 *Didacna barbotdemarnyi* [sic] (Grimm, 1877). – Neveeskaja: 941–943, pl. 24, figs 10–14.
 2013 *Didacna barbotdemarnii* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 353, fig. 139, photo 42.
 2016 *Didacna barbotdemarnii* (Grimm, 1877). – Vinarski and Kantor: 71.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, station 116, 44°17'N, 50°22'E.

Distribution. Southern, middle, and southern part of the northern Caspian Sea down to 40 m water depth, preferentially on sandy sediments (Logvinenko and Starobogatov 1969).

Conservation status. Not assessed.

Didacna eichwaldi (Krynicky, 1837)

Fig. 3b

- °1829 *C.[ardium] crassum* Eichwald: 283 [**non** *Cardium crassum* Gmelin, 1791].
 *1837 *Cardium Eichwaldi* Krynicky: 61 [**nom. nov.** pro *C. crassum* Eichwald, 1829, **non** Gmelin, 1791].
 1841 *Didacna crassa*. – Eichwald: 273, pl. 39, fig. 6a, b.
 1876 *Cardium crassum* Eichwald, 1829. – Grimm: 136–138, pl. 6, fig. 3.
 1905 *Didacna crassa* (Eichwald, 1829). – Ostroumov: 15, 69, pl. 2(A).
 1932 *Didacna* aff. *crassa* (Eichwald, 1829). – Bogachev: 27, pl. 2, figs 11–14.
 1952 *Didacna crassa* Eichwald, 1841. – Zhadin: 349, fig. 325.
 1953 *Didacna crassa* (Eichwald, 1829). – Fedorov: 130, pl. 20, figs 8, 9, 12, 13.
 1958 *Didacna crassa crassa* Eichwald, 1829. – Neveeskaja: 39–40, pl. 7, figs 8, 9.
 1969 *Didacna crassa* (Eichwald, 1829). – Vekilov: 134–139, pl. 24, figs 1–6, pl. 27, figs 1, 2.
 1988 *Didacna crassa crassa* (Eichwald, 1829). – Yanina and Svitoch: pl. 12, figs 8, 9, pl. 13, figs 1–5.
 2005 *Didacna crassa* (Eichwald, 1829). – Yanina: 242, pl. 14, figs 3–6.
 2007 *Didacna crassa* (Eichwald, 1829). – Neveeskaja: 939–940, pl. 23, figs 1–5.
 2013 *Didacna baeri* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 352 [pars, non fig. 136, photo 41, **non** *Cardium baeri* Grimm, 1877].
 2016 *Didacna baeri* (Grimm, 1877). – Vinarski and Kantor: 71 [pars, **non** Grimm, 1877].

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. “Caspium mare” (Caspian Sea) (for *C. crassum* Eichwald, 1829).

Distribution. Caspian Sea. *Didacna eichwaldi* is known from the middle and southern Caspian Sea basins down to 35 m water depth and cannot tolerate lowered salinities.



Figure 3. *Didacna baeri* versus *D. eichwaldi* from Holocene (Novocaspian) deposits of Turali Lagoon (Dagestan, Russia). **a** RGM.961899, *Didacna baeri* (Grimm, 1877) **b** RGM.961900, *Didacna eichwaldi* (Krynicky, 1837), same locality. Scale bar: 1 cm.

Taxonomic notes. In recent works (Kijashko in Bogutskaya et al. 2013), the species *Didacna crassa* (Eichwald, 1829) [= *D. eichwaldi* (Krynicky, 1837)] has been considered a synonym of *D. baeri*. However, we see morphological discontinuities in our extensive material from the northern Caspian Sea Basin that implies that *D. eichwaldi* with its protruding umbo and shouldered appearance is distinct from *D. baeri* that is characterised by a rounded umbo (see discussion above under *D. baeri*). Despite being in common usage, the name *Didacna crassa* is invalid as it is a junior homonym of *Cardium crassum* Gmelin, 1791; Krynicky (1837) introduced *Cardium eichwaldi* as replacement name.

Conservation status. Not assessed.

***Didacna longipes* (Grimm, 1877)**

*1877 *Cardium longipes* Grimm: 54–56, pl. 8, fig. 4a–c.

1952 *Didacna longipes* (Grimm, 1877). – Zhadin: 349–350, fig. 326.

1969 *Didacna longipes* (Grimm). – Logvinenko and Starobogatov: 326, fig. 345.

- 1973 *Didacna longipes* Grimm, 1877. – Grossu: 132, text fig. 9, pl. 1, fig. 2.
 ?2007 *Didacna carinata* Neveeskaja: 943, pl. 24, figs 15–19.
 2013 *Didacna longipes* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 354, fig. 137, photo 43.
 2016 *Didacna longipes* (Grimm, 1877). – Vinarski and Kantor: 71.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, offshore Azerbaijan, approximately 40°39'N, 50°26'E.

Distribution. Southern and middle Caspian Sea basins and southern part of the northern Caspian Sea down to 30–40 m water depth. The species often co-occurs with *D. barbotdemarnii*.

Remarks. We are uncertain about the status of *Didacna carinata* Neveeskaja, 2007. The overall outline resembles that of *D. barbotdemarnii*, but the former species appears smaller and thinner. Kijashko in Bogutskaya et al. (2013) considered *D. carinata* as a synonym of *D. longipes*.

Conservation status. Not assessed.

Didacna parallela Bogachev, 1932

- *1932a *Didacna parallela* Bogachev: pl. 2, figs 2, 3.
 1932b *Didacna parallela* Bogachev: 44, pl. 5, figs 1–7, 9.
 1953 *Didacna parallella* [sic] Bogachev, 1932. – Fedorov: 126, pl. 17, figs 1–11.
 1969 *Didacna parallella* [sic] Bog. – Logvinenko and Starobogatov: 324–325, fig. 344(3).
 1969 *Didacna parallella* [sic] Bogachev, 1932. – Vekilov: 117–120, pl. 21, figs 1–8.
 1973 *Didacna parallella* [sic] Bogachev, 1922 [sic]. – Grossu: 131, text fig. 8, pl. 1, fig. 4.
 2005 *Didacna parallella* [sic] Bogachev, 1932. – Yanina: 237–238, pl. 12, figs 1–8.
 2007 *Didacna parallella* [sic] Bogachev, 1932. – Neveeskaja: 933–935, pl. 21, figs 1–5.
 2013 *Didacna parallela* Bogachev, 1932. – Kijashko in Bogutskaya et al.: 355–356, fig. 138.
 2016 *Didacna parallela* Bogachev, 1932. – Vinarski and Kantor: 72.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Khala, Apsheron Peninsula, Azerbaijan (early Khvalynian, Late Pleistocene).

Distribution. Caspian Sea, southern basin and western part of middle basin between 50–85 m water depth (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017), but we are not certain whether it concerns living specimens.

Remarks. *Didacna parallela* has been considered as extinct by Neveeskaja (2007) but was nevertheless treated in Kijashko in Bogutskaya et al. (2013). Live records are known at least until 1986 and we have no particular reason to assume it is extinct.

Conservation status. Not assessed.

***Didacna praetrigonoides* Nalivkin & Anisimov, 1914**

- *1914 *Didacna praetrigonoides* Nalivkin & Anisimov: 5–6, 16–17, pl. 1, figs 1, 2.
 1932a *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Bogachev: pl. 2, fig. 1.
 1932b *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Bogachev: 42, pl. 4, figs 1–8, pl. 5, fig. 8.
 1948 *Didacna praetrigonoides* Nal. – Fedorov: pl. 2, figs 10–13.
 1953 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Fedorov: 128, pl. 18, figs 1–6, pl. 19, figs 1–6.
 1958 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Neveeskaja: 17–20, pl. 1, figs 1–14.
 1969 *Didacna trigonoides praetrigonoides* Nal. & Anis. – Logvinenko and Starobogatov: 324, fig. 343(2).
 1969 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Vekilov: 120–128, pl. 22, figs 1–9.
 1973 *Didacna trigonoides praetrigonoides* Nalivkin & Anisimov, 1915. – Grossu: 129, text fig. 5.
 1983 *Didacna praetrigonoides praetrigonoides* Nalivkin & Anisimov, 1914. – Popov: 195, pl. 15, figs 1, 2.
 1988 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Yanina and Svitoch: pl. 8, figs 4–7.
 2005 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Yanina: 241, pl. 14, figs 1, 2.
 2007 *Didacna praetrigonoides praetrigonoides* Nalivkin & Anisimov, 1914. – Neveeskaja: 927, pl. 19, figs 9, 10.

Status. Pontocaspian species, endemic to Caspian Sea. Possibly extinct.

Type locality. Apsheron Peninsula, Azerbaijan, Quaternary.

Distribution. Caspian Sea. Logvinenko and Starobogatov (1969) reported the species from the southern Caspian Sea Basin and the southern part of the middle Caspian Sea Basin down to 60 m water depth. The species has been collected from Holocene deposits and beach occurrences the western part of the middle Caspian Sea Basin as well (FW, pers. obs.). The species is reportedly extinct, not mentioned in Kijashko in Bogutskaya et al. (2013).

Remarks. The first appearance of *Didacna praetrigonoides* is in lower Khvalynian deposits, it became widespread during the late Khvalynian and was rare during the Novocaspian.

Conservation status. Not assessed. *Didacna praetrigonoides* has been reported to occur ‘rarely in the modern Caspian Sea’ (Neveeskaja 2007: 927), but material from recent assemblages has not been found.

***Didacna profundicola* Logvinenko & Starobogatov, 1966**

- *1966a *Didacna profundicola* Logvinenko & Starobogatov: 13–14, fig. 1.
 1969 *Didacna profundicola* Logv. & Star. – Logvinenko and Starobogatov: 328–329, fig. 349.

- 1973 *Didacna profundicola* Logvinenko & Starobogatov, 1966. – Grossu: 134, text fig. 13.
 2007 *Didacna profundicola* Logvinenko & Starobogatov, 1966. – Nevesskaja: 944, pl. 20, fig. 28a–c.
 2013 *Didacna profundicola* Logvinenko & Starobogatov. – Kijashko in Bogutskaya et al.: 356, fig. 140, photo 45.
 2016 *Didacna profundicola* Logvinenko & Starobogatov. – Vinarski and Kantor: 72.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Central part of the Caspian Sea, 39°38'N, 52°02'E (offshore Turkmenistan).

Distribution. Middle and southern basins of Caspian Sea between 75 and 409 m water depth (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 600 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Conservation status. Not assessed.

Didacna protracta (Eichwald, 1841)

- *1841 *Adacna protracta* Eichwald: 280, pl. 40, figs 10, 11 [non figs 9, 10 as indicated in the text].
 1877 *Cardium catillus* Eichw. – Grimm: 58, pl. 8, figs 7, 8 [**non** *Monodacna catillus* Eichwald, 1841].
 1910 *Didacna protracta* (Eichwald, 1841). – Andrusov: 67, pl. 8, figs 22, 33, pl. 9, figs 1–9.
 1952 *Didacna protracta* (Eichwald, 1841). – Zhadin: 348–349, fig. 324.
 1953 *Didacna protracta* (Eichwald, 1829). – Fedorov: 127, pl. 14, figs 12–15, pl. 15, figs 1–16.
 1967 *Didacna protracta* Eichwald, 1841. – Svitoch: 42–43, pl. 6, figs 6–9, pl. 7, figs 1, 2.
 1969 *Didacna protracta protracta* (Eichw.). – Logvinenko and Starobogatov: 327, fig. 347.
 1973 *Didacna protracta protracta* Eichwald, 1841. – Grossu: 133, text fig. 11.
 1973 *Didacna protracta submedia* Andrusov, 1911. – Grossu: 133–134, text fig. 12.
 1999 *Didacna protracta* (Eichwald, 1829). – Fedorov: pl. 12, figs 4–7.
 2005 *Didacna protracta* (Eichwald, 1829). – Yanina: 238–239, pl. 12, figs 9–19.
 2007 *Didacna protracta protracta* (Eichwald, 1829). – Nevesskaja: 938–939, pl. 22, figs 4–13.
 2013 *Didacna protracta* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 356, fig. 141.
 2013 *Didacna protracta submedia* Andrusov, 1910. – Kijashko in Bogutskaya et al.: 356, fig. 142.
 2016 *Didacna protracta* (Eichwald, 1841). – Vinarski and Kantor: 72.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. The type series (?Recent, Caspian Sea) was reported as lost by Nevesskaja (2007) who introduced a neotype from the Elton Lake surroundings in the northern Caspian plains, Russia (early Khvalynian, Late Pleistocene).

Distribution. Middle and southern Caspian Sea basins; it is most common in the middle basin at 25–85 m water depth (Logvinenko and Starobogatov 1969).

Taxonomic notes. According to Logvinenko and Starobogatov (1969), two subspecies occur in the Caspian Sea at different depth ranges: *D. protracta protracta* at 25–50 m and *D. protracta submedia* Andrusov, 1910 at 50–85 m. The latter differs from *D. p. protracta* by the relative posterior location of the umbo that is furthermore subdued. Both forms of *Didacna protracta* are widespread in the Khvalynian deposits of the Caspian Sea and Manych depression. According to Kijashko in Bogutskaya et al. (2013) morphological differences characteristic for the subspecies of *Didacna protracta* are due to allometric growth. The mere difference in depth distribution, with overlapping depths and intermediate forms, does not provide any argument to maintain these subspecies. *Didacna protracta* is the type species of the subgenus *Protodidacna* Logvinenko & Starobogatov, 1966.

Remarks. The authorship attribution of this species to Eichwald (1829) as proposed by several authors was rejected in Vinarski and Kantor (2016). According to them, *Cardium protractum* Eichwald, 1829, described from the western Ukraine, probably refers to a different species.

Conservation status. Not assessed.

Didacna pyramidata (Grimm, 1877)

*1877 *Cardium pyramidatum* Grimm: 46–49, pl. 8, fig. 1a–d.

1932 *Didacna pyramidata* (Grimm, 1877). – Bogachev: 28–29, pl. 2, figs 15, 16.

1952 *Didacna pyramidata* (Grimm, 1877). – Zhadin: 347, fig. 320.

1969 *Didacna pyramidata* (Grimm). – Logvinenko and Starobogatov: 324, fig. 344(1).

1969 *Didacna pyramidata* (Grimm, 1877). – Vekilov: 144–147, pl. 26, figs 1–5.

1973 *Didacna pyramidata* Grimm, 1877. – Grossu: 130, text fig. 6, pl. 1, fig. 1.

2007 *Didacna pyramidata* (Grimm, 1877). – Neveeskaja: 940, pl. 23, figs 6–10.

2013 *Didacna pyramidata* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 357, fig. 135, photo 47.

2016 *Didacna pyramidata* (Grimm, 1877). – Vinarski and Kantor: 73.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, offshore Azerbaijan, 39°47'N, 49°59'30"E (Kijashko in Bogutskaya et al. 2013).

Distribution. Caspian Sea: southern basin and southern part of the middle basin at depths between 30–100 m (Logvinenko and Starobogatov 1969).

Conservation status. Not assessed.

Didacna trigonoides (Pallas, 1771)

*1771 *Cardium trigonoides* Pallas: 478.

1831 *Cardium trigonoides* (Pallas, 1771). – Eichwald: 282.

- 1838 *Didacna trigonoides* n. – Eichwald: 166–167.
 1841 *Didacna trigonoides*. – Eichwald: 271–272, pl. 39, fig. 5a–c.
 1876 *Cardium trigonoides*, Pall. – Grimm: 138–140, pl. 6, fig. 2.
 1914 *Didacna trigonoides* (Pallas, 1771). – Kalitskiy: pl. 3, figs 1, 2.
 1914 *Didacna trigonoides* (Pallas, 1771). – Nalivkin and Anisimov: 6, pl. 1, fig. 3.
 1932a *Didacna trigonoides* (Pallas, 1771). – Bogachev: pl. 1, figs 5, 6.
 1932b *Didacna trigonoides* (Pallas, 1771). – Bogachev: 25, pl. 2, figs 1–9.
 1933 *Didacna trigonoides* (Pallas, 1771). – Zhizhchenko: 35–36, pl. 2, figs 9, 10.
 1950 *Didacna trigonoides* (Pallas, 1771). – Pravoslavlev: 21–22, figs 1–4.
 1952 *Didacna trigonoides* (Pallas, 1771). – Zhadin: 346, fig. 319.
 1953 *Didacna trigonoides* (Pallas, 1771). – Fedorov: 129, pl. 20, figs 7–9.
 1969 *Didacna trigonoides trigonoides* (Pall.). – Logvinenko and Starobogatov: 323, fig. 343(1), pl. 5, fig. 7.
 1969 *Didacna trigonoides* (Pallas, 1771). – Vekilov: 128–134, pl. 23, figs 1–9, pl. 27, fig. 6.
 1973 *Didacna trigonoides trigonoides* Pallas, 1771. – Grossu: 129, text fig. 4, pl. 1, fig. 3.
 1977 *Didacna trigonoides tuzetae* Tadjalli-Pour: 97, pl. 1, fig. 3.
 1983 *Didacna trigonoides* (Pallas, 1771). – Popov: 204, pl. 16, fig. 19.
 1986 *Didacna trigonoides* (Pallas, 1771). – Yakhimovich et al.: 79, pl. 10, fig. 1.
 1988 *Didacna trigonoides* (Pallas, 1771). – Yanina and Svitoch: pl. 9, figs 7–12.
 2005 *Didacna trigonoides* (Pallas, 1771). – Yanina: 244–245, pl. 14, figs 7–11.
 2007 *Didacna trigonoides* (Pallas, 1771). – Neveeskaja: 941, pl. 24, figs 1–9.
 2013 *Didacna trigonoides* (Pallas, 1771). – Kijashko in Bogutskaya et al.: 358, fig. 134.
 2016 *Didacna trigonoides* (Pallas, 1771). – Vinarski and Kantor: 70.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, a neotype has been designated based on a specimen from Chechen Island by Neveeskaja (2007, pl. 24, fig. 4).

Distribution. Caspian Sea, mostly eastern part of northern Caspian Sea Basin (Logvinenko and Starobogatov 1969). Furthermore found in living position in Novocaspian deposits near Turali, Dagestan (western part middle basin; FW).

Remark. Genetic data are available through Albrecht et al. (2014).

Conservation status. Not assessed.

Hypanis plicata (Eichwald, 1829)

- *1829 *G.[lycymeris] plicata* Eichwald: 279, pl. 5, fig. 2a, b.
 1838 *Adacne* [sic] *plicata* m. – Eichwald: 171–172.
 1916 *Adacna relictata* Milaschewitch: 274–276, pl. 8, figs 10–13 [non figs 10–12 as indicated in the text].
 1926 *Adacna relictata* var. *dolosmiana* Borcea: 468–469, pl. 18, figs 156–158, pl. 21, fig. 2.
 1952 *Adacna (Hypanis) plicata* (Eichwald, 1829). – Zhadin: 354–355, fig. 332.
 1958 *Adacna (Hypanis) plicata* (Eichwald), 1829. – Neveeskaja: 50–51, pl. 9, figs 9–14.
 1969 *Hypanis plicata plicata* (Eichw.). – Logvinenko and Starobogatov: 331–332, fig. 350.

- 1973 *Hypanis plicata plicata* Eichwald, 1829. – Grossu: 136, text fig. 14, pl. 1, fig. 5.
 1973 *Hypanis plicata relicta* Milashevitsch, 1916. – Grossu: 136, text fig. 15, pl. 1, figs. 6, 20–23.
 1973 *Hypanis dolosmaniana* [sic] Borcea, 1826. – Grossu: 136, text fig. 16, pl. 1, figs. 16–19.
 1977 *Hypanis plicata golbarga* Tadjalli-Pour: 99, pl. 1, fig. 5.
 2006a *Hypanis plicata relicta* (Milachevitch, 1916). – Munasyypova-Motyash: 45–46.
 2009 *Adacna (Hypanis) plicata relicta* Milashevich, 1916. – Popa et al. 12, fig. 4.
 2013 *Hypanis plicata* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 387, fig. 164, photo 56.
 2016 *Hypanis plicata plicata* (Eichwald, 1829). – Vinarski and Kantor: 73.
 2016 *Hypanis plicata relicta* (Milashevitsch, 1916). – Vinarski and Kantor: 74.

Status. Pontocaspian species, endemic to Caspian Sea Basin and Black Sea Basin.

Type locality. “Sinum Astrabadensem” [Caspian Sea near Astrabad (= Gorgan, Iran)].

Distribution. Caspian Sea, western liman coast Black Sea Basin.

Taxonomic notes. The Black Sea populations of *H. plicata* show a large range of morphological variation with elongated specimens that cannot be distinguished from Caspian *H. plicata* to severely stunted and irregularly shaped specimens that have been considered as a subspecies (*H. plicata relicta*) or as distinct species (*H. dolosmiana*) (e.g., Munasyypova-Motyash 2006a). These forms have intermediates indicating that the Black Sea Basin specimens are a single species that should be attributed to *H. plicata* even though the latter appear to have lived under lower salinities than their Caspian counterparts. Molecular studies are required to elucidate the status of the Black Sea Basin material.

Conservation status. Not assessed. Fresh shells (including paired specimens) have been found at several beaches around the Caspian Sea (Turali, Dagestan, Russia; Şuraabad, Azerbaijan; FW). The species has been reported alive from the Razim lake complex of the Romanian Black Sea coast by Popa et al. (2009).

***Monodacna acuticosta* (Logvinenko & Starobogatov, 1967)**

- *1967 *Hypanis acuticosta* Logvinenko & Starobogatov: 232.
 1969 *Hypanis angusticostata acuticosta* Logvinenko & Starobogatov: 334, fig. 353(1).
 1973 *Hypanis angusticostata acuticosta* Logvinenko et Starobogatov, 1967. – Grossu: 141, fig. 23.
 2013 *Adacna (Monodacna) acuticosta* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 379, fig. 160, photo 50.
 2016 *Adacna (Monodacna) acuticosta* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 66.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. “Northern Caspian Sea on the central part of the slope” (Vinarski and Kantor 2016: 66), which likely refers to northern slope of the middle Caspian Sea Basin.

Distribution. Caspian Sea (middle Caspian Sea Basin).

Conservation status. Not assessed.

***Monodacna albida* (Logvinenko & Starobogatov, 1967)**

*1967 *Hypanis albida* Logvinenko & Starobogatov: 232.

1969 *Hypanis albida* Logv. & Star. – Logvinenko and Starobogatov: 336, fig. 353(3).

1973 *Hypanis albida* Logvinenko & Starobogatov, 1967. – Grossu: 144, text fig. 28.

2013 *Adacna (Monodacna) albida* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 380, fig. 162, photo 51.

2016 *Adacna (Monodacna) albida* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 66.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. “Western Caspian Sea southeastwards from Derbent” (Vinarski and Kantor 2016: 66).

Distribution. Caspian Sea (middle and southern Caspian Sea Basin). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Hypanis albida*).

Taxonomic notes. This species is part of a group of Caspian *Monodacna* with relative flat and wedge-shaped shells with low and sometimes poorly defined ribs (*M. albida*, *M. polymorpha*). Like for the *Monodacna caspia* group (see below), we are in need of studies to assess whether these taxa might form ecomorphs of a single species.

Conservation status. Not assessed.

***Monodacna caspia* (Eichwald, 1829)**

*1829 *C.[orbula] caspia* Eichwald: 281, pl. 5, fig. 6a, b.

1841 *Monodacna caspia*. – Eichwald: 274, pl. 39, fig. 4a–c.

1905 *Monodacna caspia* (Eichwald, 1829). – Ostroumov: pl. 3, fig. C.

1932a *Monodacna caspia* (Eichwald, 1829). – Bogachev: pl. 1, figs 10, 13.

1932b *Monodacna caspia* (Eichwald, 1829). – Bogachev: 30, pl. 3, figs 21–27.

1952 *Monodacna edentula* (Pallas, 1771) var. *caspia* Eichwald, 1841. – Zhadin: 350, fig. 327B.

1958 *Monodacna caspia* (Eichwald), 1829. – Nevesskaja: 44–46, pl. 9, figs 1–8.

1963 *Monodacna caspia caspia* (Eichwald, 1829). – Nevesskaja: 66, pl. 8, figs 1–4.

1965 *Monodacna caspia caspia* (Eichwald). – Nevesskaja: 187–198, pl. 9, figs 6–15, 17–19, 23–26, 29.

1969 *Monodacna caspia* (Eichwald, 1829). – Vekilov: 147–150, pl. 31, figs 9–11.

1973 *Hypanis caspia caspia* Eichwald, 1829. – Grossu: 139, text fig. 19B.

1977 *Hypanis caspia assalae* Tadjalli-Pour: 99, pl. 1, fig. 4.

1977 *Hypanis caspia nahali* Tadjalli-Pour: 99, pl. 1, fig. 6.

2013 *Adacna (Monodacna) caspia caspia* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 380, fig. 154.

2016 *Adacna (Monodacna) caspia caspia* (Eichwald, 1829). – Vinarski and Kantor: 67.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. “Caspium mare” [Caspian Sea].

Distribution. Caspian Sea.

Taxonomic notes. The *Monodacna caspia* group (*M. caspia*, *M. filatovae*, and *M. knipowitschi*) comprises three (sub-) species that all share the relatively convex and rounded shell and well-defined ribbing. These species have been described from different areas and habitats in the Caspian Sea and have been morphologically characterised by Kijashko in Bogutskaya et al. (2013). However, neither morphological analyses of intermediate populations nor genetic analyses have been performed to clarify if the three taxa are distinct or ecomorphs of a single species. We are therefore uncertain whether *M. filatovae* and *M. knipowitschi* should be maintained.

Conservation status. Not assessed.

Monodacna colorata (Eichwald, 1829)

*1829 *G.[lycymeris] colorata* Eichwald: 279–280, pl. 5, fig. 4a, b.

1838 *Adacna colorata* m. – Eichwald: 169–170.

?1838 *Monodacna pontica* Eichwald: 168–169.

1926 *Monodacna colorata* var. *ialpugensis* Borcea: 452, pl. 15, fig. 16.

1926 *Monodacna colorata* var. *angusticostata* Borcea: 452–453, pl. 15, figs 27, 28, pl. 16, figs 90, 91, pl. 18, figs 143, 169, 173, pl. 21, fig. 7.

1926 *Adacna Luciae* Borcea: 469–471, pl. 18, figs 146, 148–149, 151–153, pl. 21, figs 8, 9.

1952 *Monodacna colorata* (Eichwald, 1829). – Zhadin: 351, fig. 328.

?1972 *Hypanis caspia grossui* Scarlato and Starobogatov: 214, pl. 4, fig. 1a, b.

1973 *Hypanis caspia grossui* Scarlato & Starobogatov, 1971. – Grossu: 140, text fig. 21, pl. 1, fig. 8.

1973 *Hypanis angusticostata angusticostata* Borcea, 1926. – Grossu: 141, pl. 1, fig. 12.

1973 *Hypanis luciae* Borcea, 1926. – Grossu: 138, text fig. 18.

1973 *Hypanis ialpugensis* Borcea, 1926. – Grossu: 142, fig. 24, pl. 1, figs 9, 10.

1973 *Hypanis colorata* Eichwald, 1829. – Grossu: 142–143, fig. 25, pl. 1, figs 13–15.

1973 *Hypanis pontica* Eichwald, 1838. – Grossu: 143, fig. 26, pl. 1, fig. 11.

2006a *Hypanis colorata* (Eichwald, 1829). – Munasyypova-Motyash: 42–43.

?2006a *Hypanis pontica* (Eichwald, 1838). – Munasyypova-Motyash: 43–44.

?2006a *Hypanis angusticostata angusticostata* (Borcea, 1926). – Munasyypova-Motyash: 44.

2009 *Monodacna pontica* Eichwald, 1838. – Popa et al.: 10, text fig. 2.

2009 *Monodacna colorata* Eichwald, 1829. – Popa et al.: 10–11, text fig. 3.

2012 *Hypanis colorata* (Eichwald, 1829). – Popa et al.: 153, 154.

2012 *Hypanis angusticostata* (Borcea, 1926). – Popa et al.: 153, 154.

2013 *Adacna* (*Monodacna*) *colorata* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 383, fig. 158.

2016 *Adacna* (*Monodacna*) *angusticostata* (Borcea, 1926). – Vinarski and Kantor: 66.

2016 *Adacna* (*Monodacna*) *grossui* (Scarlato et Starobogatov, 1972). – Vinarski and Kantor: 67.

2016 *Adacna* (*Monodacna*) *ialpugensis* (Borcea, 1926). – Vinarski and Kantor: 68.

Status. Pontocaspian species, native to Black Sea Basin (including lower Danube River), invasive in Caspian Sea and Volga River.

Type locality. “Hypanin fluvium, ad nigrum usque mare” [Lower course of the Yuzhnyi Bug River, all the way to the Black Sea, Ukraine].

Distribution. Native to all Black Sea Basin Pontocaspian habitats and lower courses of adjacent rivers such as the Danube, Dnieper, and Dniester; invasive in Caspian Sea Basin and lower Volga, as well as Lake Balkhash (Kazakhstan). Occurs hundreds of kilometres upstream in major tributaries (Danube: Popa et al. 2009; recent observations in Volga River upstream Volgograd by MV and AFS).

Taxonomic notes. *Monodacna colorata* appears to be a morphologically very variable species. Here, we propose to synonymise several local Black Sea species with this taxon. Given the difficulty to distinguish relatively flat shells typically associated with *M. colorata* from the more convex shells typically associated with *M. pontica* in, e.g., Lake Razim (Romania) and the apparent lack of genetic differentiation of convex specimens from *M. colorata* we assume that *M. pontica* is a synonym of *M. colorata*. Shell differences have been attributed to substrate differences. Further investigations to confirm the synonymy are required. *Monodacna angusticostata* was synonymised by Popa et al. (2012) based on molecular evidence, even though some morphological distinction was reported from *M. colorata*, which they attributed to differential habitat preference (sediment type).

Conservation status. Not assessed.

***Monodacna filatovae* (Logvinenko & Starobogatov, 1967)**

1876 *Cardium caspium*, Eichw. – Grimm: 134–136 [pars].

*1967 *Hypanis caspia filatovae* Logvinenko and Starobogatov: 231.

1973 *Hypanis caspia filatovae* Logvinenko & Starobogatov, 1967. – Grossu: 139, text fig. 19a.

2013 *Adacna* (*Monodacna*) *caspia filatovae* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 381, fig. 155, photo 52.

2016 *Adacna* (*Monodacna*) *caspia filatovae* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 67.

Status. Pontocaspian species, endemic to Caspian Sea. Uncertain whether it concerns a morph of *M. caspia*.

Type locality. Gulf of Baku, Caspian Sea, Azerbaijan.

Distribution. Southern Caspian Sea Basin.

Taxonomic notes. See remarks under *Monodacna caspia* above for uncertain status of *M. filatovae*.

Conservation status. Not assessed.

***Monodacna knipowitschi* (Logvinenko & Starobogatov, 1966)**

*1966a *Hypanis caspia knipowitschi* Logvinenko & Starobogatov: 15, fig. 2.

1973 *Hypanis caspia knipowitschi* Logvinenko & Starobogatov, 1967. – Grossu: 140, text fig. 20.

2013 *Adacna (Monodacna) caspia knipowitschi* (Logvinenko & Starobogatov, 1966). – Kijashko in Bogutskaya et al.: 381–382, figs 152, 153, photo 53.

2016 *Adacna (Monodacna) caspia knipowitschi* (Logvinenko & Starobogatov, 1966). – Vinarski and Kantor: 67.

Status. Pontocaspian species, endemic to Caspian Sea. Uncertain whether it concerns a morph of *M. caspia*.

Type locality. Middle Caspian Sea Basin.

Distribution. Caspian Sea (middle and southern basins). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Hypanis caspia knipowitchi*).

Taxonomic notes. See remarks under *Monodacna caspia* above for uncertain status of *M. knipowitschi*.

Conservation status. Not assessed.

***Monodacna polymorpha* (Logvinenko & Starobogatov, 1967)**

*1967 *Hypanis angusticostata polymorpha* Logvinenko & Starobogatov, 1967: 232.

1973 *Hypanis angusticostata polymorpha* Logvinenko & Starobogatov, 1967. – Grossu: 141, fig. 22, pl. 1, fig. 7.

2013 *Adacna (Monodacna) polymorpha* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 383–384, fig. 159, photo 54.

2016 *Adacna (Monodacna) polymorpha* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 68.

Status. Pontocaspian species, endemic to Caspian Sea. Status uncertain.

Type locality. Central part of northern Caspian Sea.

Distribution. Northern Caspian Sea.

Taxonomic notes. See remarks under *M. albida* for uncertain species status.

Conservation status. Not assessed.

***Monodacna semipellucida* (Logvinenko & Starobogatov, 1967)**

*1967 *Hypanis semipellucida* Logvinenko & Starobogatov: 232–233.

- 1973 *Hypanis semipellucida* Logvinenko & Starobogatov, 1967. – Grossu: 144, text fig. 27.
 2013 *Adacna (Monodacna) semipellucida* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 384, fig. 161, photo 55.
 2016 *Adacna (Monodacna) semipellucida* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 68–69.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Off Tokmak Cape (also as Toqmaq Müyis), southern Kazakhstan, Caspian Sea.

Distribution. Middle Caspian Sea.

Conservation status. Not assessed.

Family Semelidae Stoliczka, 1870

Abra segmentum (Récluz, 1843)

°1836 *Erycina ovata* Philippi: 13, pl. 1 fig. 13 [**non** *Erycina ovata* Gray, 1825].

*1843 *Syndosmya segmentum* Récluz: 365–366.

1969 *Abra ovata* (Phil.). – Logvinenko and Starobogatov: 339, fig. 355, pl. 5, fig. 12.

2013 *Abra segmenta* (Récluz, 1843). – Kijashko in Bogutskaya et al.: 391, fig. 165.

2015 *Abra ovata* (Philippi, 1836). – Latypov: 240.

Status. Invasive Pontocaspian species.

Type locality. Mediterranean coast near Taranto (Italy).

Distribution. Mediterranean, Black Sea coastal regions, Sea of Azov, Caspian Sea, Aral Sea.

Taxonomic notes. This species has been reported in much of the 20th century literature as *Abra ovata* (Philippi, 1836), which is invalid since the original name (*Erycina ovata* Philippi, 1836) represents a junior primary homonym of *Erycina ovata* Gray, 1825.

Remarks. The first transfer of *Abra segmentum* into the Caspian Sea occurred in 1947–1948, and the species has not been detected since 1955 (Latypov, 2015).

Conservation status. Not assessed.

Family Cyrenidae Gray, 1840

Corbicula fluminalis (Müller, 1774)

*1774 *Tellina fluminalis* Müller: 205–206.

1952 *Corbicula fluminalis* (Müller, 1774). – Zhadin: 317, fig. 283.

2012 *Corbicula fluminalis* (Müller, 1774). – Welter-Schultes: 15, unnumbered text figures.

2016 *Corbicula fluminalis* (O.F. Müller, 1774). – Nabozhenko and Nabozhenko: 62, text fig. 1(3, 4).

2016 *Corbicula fluminalis* (O.F. Müller, 1774). – Vinarski and Kantor: 80.

Status. Native/Invasive Pontocaspian species.

Type locality. Euphrates River.

Distribution. Native to large parts of western Asia (including southern Caspian river systems) and northern Africa, introduced in 1939 to southern North America and in 1980 from there to Europe (Seddon and Van Damme 2016). The species has been recently recorded from the Caspian Dagestan coast (Nabozhenko and Nabozhenko 2016).

Remarks. This species has been native to south Caspian rivers including the Kura river system (Zhadin 1952) and has expanded several times in the Late Pleistocene into the Caspian Sea, where in time intervals it survived in proximal lacustrine habitats. A recent introduction and expansion of the species has been recorded in the Kizlyarsky Gulf in Dagestan (Nabozhenko and Nabozhenko 2016) and the strong increase in fresh material found around the gulf in subsequent years, including whole specimens (AS Gasanova, Makhachkala, pers. comm.) suggests the species may have established there.

Conservation status. Least Concern (Seddon and Van Damme 2016).

Family Dreissenidae Gray, 1840

Remarks. Pontocaspian dreissenid taxonomy suffers from a lack of coordinated shell and DNA analyses. A large part of our considerations relies on the work of Rosenberg & Ludyanskiy (1994) who examined and illustrated all type material of Pontocaspian *Dreissena*.

Dreissena bugensis Andrusov, 1897

*1897 *Dreissensia bugensis* Andrusov: 285–286, pl. 15, figs 31–37.

1972 *Dreissena rostriformis bugensis* (Andrusov, 1897). – Scarlato and Starobogatov: 232–233, pl. 6, fig. 16.

1994 *Dreissena bugensis* (Andrusov, 1897). – Rosenberg and Ludyanskiy: 1479–1480, fig. 1a–e.

2013 *Dreissena bugensis* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 331, fig. 119.

2016 *Dreissena bugensis* (Andrusov, 1897). – Vinarski and Kantor: 78.

Status. Until mid-20th century endemic to northern Black Sea liman coast, since then invasive elsewhere in Black Sea Basin, Volga catchment, western Europe, and North America.

Type locality. Bug Liman near Nikolaev, Ukraine.

Distribution. Endemic to western Ukrainian liman coast, introduced in Danube Delta, Azov Sea, Volga catchment, western and central Europe, and North America (Orlova et al. 2005, Coughlan et al. 2017).

Taxonomic notes. This species has been considered as a subspecies of *D. rostriformis* (Deshayes, 1838) by some authors (e.g., Orlova et al. 2005), yet we follow the argumentation of Kijashko in Bogutskaya et al. (2013) to consider it as a distinct species. The proposed synonymy of Caspian *D. rostriformis* (= *D. grimmi*) and Black Sea *D. bugensis* by Stepien et al. (2013) is discussed below under *D. grimmi*.

Conservation status. Least Concern (von Rintelen and Van Damme 2011a).

***Dreissena caspia* Eichwald, 1855**

*1855 *Dreissena caspia* Eichwald: 311–312, pl. 10, figs 19–21.

1969 *Dreissena caspia* (Eichw.). – Logvinenko and Starobogatov: 316–318, fig. 341(2).

1994 *Dreissena caspia* Eichwald, 1855. – Rosenberg and Ludyanskiy: 1482, fig. 3e, f.

2013 *Dreissena caspia* Eichwald, 1855. – Kijashko in Bogutskaya et al.: fig. 109.

2016 *Dreissena (Dreissena) caspia caspia* Eichwald, 1855. – Vinarski and Kantor: 76.

Status. Caspian endemic, probably extinct.

Type locality. Chistyi Bank and Cheleken Island, Caspian Sea, Russia.

Distribution. Caspian Sea and Aral Sea, probably extinct.

Taxonomic notes. The species is commonly subdivided into a Caspian subspecies (*D. caspia caspia*) and an Aral Sea subspecies (*D. caspia pallasi* Andrusov, 1897). However, syntypes of the latter illustrated in Rosenberg and Ludyanskiy (1994, fig. 3f) show a broad and keeled *Dreissena* that has major morphological characters in common with *D. polymorpha/elata* rather than *D. caspia*. Filippov and Riedel (2009) reported *Dreissena caspia* from Holocene core deposits of Aral Sea, but given the juvenile status of their material they noted they were uncertain whether it might comprise *D. polymorpha*. *Dreissena caspia* was reported alive from the remaining “small Aral Sea” by Plotnikov et al. (2016). However, this latter record concerns more likely *D. polymorpha* and needs confirmation. Andreeva and Andreev (2003) mentioned that this subspecies has not been found in the Aral Sea since 1989.

Conservation status. Critically endangered, possibly extinct (von Rintelen and Van Damme 2011b).

***Dreissena elata* Andrusov, 1897**

*1897 *Dreissensia polymorpha* var. *elata* Andrusov: 353, pl. 20, fig. 25.

1969 *Dreissena elata* (Andr.). – Logvinenko and Starobogatov: 316, fig. 341(1).

1994 *Dreissena elata* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1482, fig. 3g.

2013 *Dreissena elata* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: fig. 108.

2016 *Dreissena (Dreissena) elata* (Andrusov, 1897). – Vinarski and Kantor: 76.

Status. Pontocaspian species, endemic to the Caspian Sea, probably extinct. Species status uncertain.

Type locality. Kuuli Cape, Dazmyk, Apsheron Peninsula, Azerbaijan (Vinarski and Kantor 2016).

Distribution. Caspian Sea. Probably extinct.

Taxonomic notes. *Dreissena elata* has morphological features in common with *D. polymorpha*, including a relatively wide shell and a well-pronounced keel located close to the ventral margin. However, the *D. elata* shell is in general wider, flatter, and has a more rounded abapical margin even though shell characters are highly variable. *Dreissena elata* has been reported from areas in the Caspian Sea with salinities well above 5 ‰, which is unusual for *D. polymorpha* elsewhere. We are uncertain whether *D. elata* might be a sibling species. Its apparently distinct morphology and autecological preferences suggest it is different from *D. polymorpha*, but it will require molecular comparison to investigate whether it concerns a mere morph that has undergone “ecological release” (Kohn 1972) or is a different species. However, no living specimens of *D. elata* have been recorded since 1957 (Kostianoy and Kosarev 2005) when its Caspian habitats were invaded by *Mytilaster minimus*.

Conservation status. Not assessed. It was reported as extinct by Kostianoy and Kosarev (2005, and references therein). If *D. elata* is accepted as a valid species, it might qualify for the same conservation status as *D. caspia* (critically endangered, possibly extinct; von Rintelen and Van Damme 2011b).

Dreissena grimmi (Andrusov, 1890)

Fig. 4b

- 1877 *Dreissena Brardii* var. *caspia* Grimm: 74–75 [**non** *Dreissena caspia* Eichwald, 1855].
 *1890 *Dr.[eissena] Grimmi* Andrusov: 233 [**nom. nov.** pro *Dreissena caspia* Grimm, 1877, **non** Eichwald, 1855].
 1897 *Dreissensia Grimmi* Andrus. – Andrusov: 279–282, pl. 16, figs 16–18.
 1897 *Dreissensia rostriformis* var. *distincta* Andrusov: 273–278, pl. 14, figs 18–24.
 1897 *Dreissensia Tschaudae* var. *pontocaspica* Andrusov: 294–297, pl. 9, figs 27–32, pl. 15, figs 29, 30.
 1966a *Dreissena rostriformis compressa* Logvinenko and Starobogatov: 15–16, fig. 3.
 1969 *Dreissena rostriformis grimmi* Andr. – Logvinenko and Starobogatov: 318, fig. 341(3).
 1969 *Dreissena rostriformis pontocaspica* (Andr.). – Logvinenko and Starobogatov: 319, fig. 341(6).
 1994 *Dreissena rostriformis* (Deshayes, 1838). – Rosenberg and Ludyanskiy: 1477–1479, figs 1f, 2a–j [**non** *Mytilus rostriformis* Deshayes, 1838].
 2013 *Dreissena rostriformis* (Deshayes, 1838). – Kijashko in Bogutskaya et al.: 330 [**non** Deshayes, 1838].
 2013 *D.[reissena] rostriformis compressa* Logvinenko & Starobogatov, 1966. – Kijashko in Bogutskaya et al.: 331, fig. 117a, photo 38.
 2013 *D.[reissena] rostriformis distincta* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 331, fig. 117c.
 2013 *D.[reissena] rostriformis grimmi* (Andrusov, 1890). – Kijashko in Bogutskaya et al.: 331, fig. 117b.
 2013 *D.[reissena] rostriformis pontocaspica* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 331, fig. 117d.



Figure 4. Lectotype *Dreissena rostriformis* versus *D. grimmi*. **a** *D. rostriformis* Deshayes, 1838. Lectotype. Pliocene, Crimea. Reproduced from Archambault-Guezou (1976, pl. 6, fig 2a-2c) **b** RGM.961901, *D. grimmi* (Andrusov, 1890). Caspian Sea offshore Aktau, Kazakhstan, sample KAZ17-21, depth 44.3 m. Scale bar: 1 cm.

Status. Caspian Sea endemic.

Type locality. Caspian Sea.

Distribution. Middle to southern Caspian Sea basins. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *D. rostriformis compressa*) and found living offshore Aktau (Kazakhstan) in 2017 below 20 m water depth.

Taxonomic notes. This Caspian species is very often cited as *Dreissena rostriformis*. Rosenberg and Ludyanskiy (1994: 1497) discuss the uncertainties of this attribution but state that “*D. pontocaspica*, *D. distincta*, *D. compressa*, and *D. grimmi* are synonyms of *D. rostriformis*” even though they find “some justification for maintaining a distinction between an extinct subspecies, *D. rostriformis rostriformis* and a living one, for which *D. rostriformis grimmi* is the oldest name”. Their figure of the lectotype of *D. rostriformis* (Rosenberg and Ludyanskiy 1994: fig. 2a), which derives from Pliocene deposits of the Black Sea Basin, concerns a relative small, thick-shelled, and low *Dreissena* with a pointed beak and lacking a keel. On interior view, the shell area outside the pallial line is thick. Deshayes’s lectotype has several characters in common with modern Caspian *D. rostriformis* and the closely related Black Sea Basin *D. bugensis*. Yet, the Pliocene form has a broader umbonal area that results in a more subquadrangular shape, which is different from the modern Caspian *Dreissena* that have tear-drop to pear-shaped shells. The subquadrangular shape of Deshayes’s material is even more pronounced in the pallial line on the shell’s interior, a feature not seen in any modern Caspian material. The Pliocene Black Sea *D. rostriformis* has its general shape in common with Apsheronian (Early Pleistocene) Caspian dreissenids referred to as *D. carinatocurvata* as illustrated in Kolesnikov (1950, pl. 14, figs 14–16). Hence, we conclude

that the recent Caspian species should be treated different from Pliocene *D. rostriformis* and the name *D. grimmi* should be applied instead.

Various subspecies have been attributed to Caspian *Dreissena rostriformis* (see, e.g., Kijashko in Bogutskaya et al. 2013 for a synonymy list). Even though morphological differences appear to be large, intermediates are known between the morphs. Stepien et al. (2013) reviewed molecular evidence for species boundaries within *Dreissena*. They concluded that (1) all Caspian Sea forms that have been mentioned in literature as (sub-) species of *D. rostriformis* (= *D. grimmi*) are one and the same species and (2) there is not enough molecular evidence and great difficulty in morphology to separate the Caspian species from the Black Sea Basin *D. bugensis*. We agree with the first point made by Stepien et al. (2013); all forms reported from the middle and southern Caspian Sea basins appear to be mere morphs of a single species, a feature also noted by Rosenberg and Ludyanskiy (1994). However, we disagree with their second proposal. *Dreissena bugensis* and *D. grimmi* have non-overlapping ecological tolerances and are separated geographically (Rosenberg and Ludyanskiy 1994). This fact together with the very limited but consistent genetic differentiation suggests that it may concern very recently evolved sister species. In the early 1980s, *D. bugensis* was introduced in the Volga (Zhulidov et al. 2005) and since then spread from there to central and western Europe and North America. So far, *Dreissena bugensis* has only been reported from the Volga itself and its delta but not from the northern Caspian Sea Basin. If it would be conspecific with the middle-southern Caspian species, which lives at higher salinities and deeper habitats, we would expect that the invasive populations in the north would have been blended with the Caspian population in the south. With no such intermediate populations found so far we consider both taxa as viable species.

Conservation status. Least Concern (for *Dreissena rostriformis*; von Rintelen and Van Damme 2011c).

Dreissena polymorpha (Pallas, 1771) s.l.

*1771 *Mytilus polymorphus* Pallas: 368, 435, 478.

1897 *Dreissensia Andrusovi* Andrusov: 374–376 pl. 18, figs 21–23.

1897 *Dreissensia Pallasii* Andrusov: 671–672, pl. 20, figs 33–35.

1897 *Dreissensia polymorpha* var. *aralensis* Andrusov: 354–355.

1897 *Dreissensia polymorpha* var. *obtuscarinata* Andrusov: 354.

1994 *Dreissena polymorpha* (Pallas, 1771). – Rosenberg and Ludyanskiy: 1480–1482, fig. 3a, b.

1994 *Dreissena polymorpha aralensis* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1480, fig. 3c.

1994 *Dreissena polymorpha obtuscarinata* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1481, fig. 3d.

1994 *Dreissena caspia pallasii* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1482, fig. 3f.

2003 *Dreissena caspia pallasii* (Andrusov, 1897). – Andreeva and Andreev: 80, fig. 4.1(7–9).

2003 *Dreissena polymorpha aralensis* (Andrusov, 1897). – Andreeva and Andreev: 79, fig. 4.1(1–3).

- 2003 *Dreissena obtusecarinata* (Andrusov, 1897). – Andreeva and Andreev: 80, fig. 4.1(4–6).
- 2013 *Dreissena (Dreissena) polymorpha* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 328, fig 118a [pars, status fig. 118b uncertain].
- 2016 *Dreissena (Dreissena) polymorpha polymorpha* (Andrusov, 1897). – Vinarski and Kantor: 75.
- ?2016 *Dreissena (Dreissena) polymorpha andrusovi* (Brusina in Andrusov, 1897). – Vinarski and Kantor: 75.
- ?2016 *Dreissena (Dreissena) polymorpha aralensis* (Andrusov, 1897). – Vinarski and Kantor: 75.
- ?2016 *Dreissena (Dreissena) polymorpha obtusecarinata* (Andrusov, 1897). – Vinarski and Kantor: 76.
- ?2016 *Dreissena (Dreissena) caspia pallasi* (Andrusov, 1897). – Vinarski and Kantor: 7.

Status. Native Pontocaspian species.

Type locality. Volga and Yaik (Ural) rivers, Caspian Sea.

Distribution. Eurasian (native and invasive), North America (invasive) rivers, lakes, estuaries, deltas (Rosenberg and Ludyanskiy 1994, Cummings and Graf 2015, Coughlan et al. 2017). Several unique forms/species within this group reported from the Pontocaspian region.

Taxonomic notes. *Dreissena polymorpha* has been subject of intense DNA and ecological studies, but rarely were Caspian communities involved. Combined insights into the shell morphology, ecology, and molecular biology has to date not fully resolved several aspects of Pontocaspian records of this species. Occurrences in rivers and deltas of the Pontocaspian region are consistently attributed to *Dreissena polymorpha*. However, slightly deviating morphs exist(ed) in salinities typically not favoured by *D. polymorpha* elsewhere in the Caspian and Aral seas. A particular form of *Dreissena polymorpha*, documented by Kijashko in Bogutskaya et al. (2013), viz. *D. polymorpha andrusovi* (his figure 118b) will need further study as it has many morphological similarities with *D. caspia* (including general shape, location of semidiameter, and broad flat shape of hinge platform).

Conservation status. Least Concern (Van Damme 2014).

Mytilopsis leucophaeata (Conrad, 1831)

*1831 *Mytilus leucophaeatus* Conrad: 263–264, pl. 11, fig. 13.

2013 *Mytilopsis leucophaeata* (Conrad, 1831). – Kijashko in Bogutskaya et al.: 320, fig. 107.

Status. Invasive Pontocaspian species.

Type locality. Southern coast of eastern United States.

Distribution. Black Sea Basin, Caspian Sea, coasts of western Europe, Caribbean, and northern South America.

Remarks. The species, native to the southern coast of North America, was first introduced in Europe in 1835 (Heiler et al. 2010). In the Pontocaspian region, it first

appeared in the northern Black Sea Basin in 2002 and was first collected in the Caspian Sea in 2009 (Heiler et al. 2010). It is easily distinguished from Pontocaspian dreissenids by the presence of an aphophysis near the hinge.

Conservation status. Least Concern (Cummings 2011).

Gastropoda

Family Neritidae Rafinesque, 1815

Theodoxus danubialis (Pfeiffer, 1828)

*1828 *Nerita danubialis* Pfeiffer: 48, pl. 8, figs 17, 18.

2009 *Theodoxus danubialis* (C. Pfeiffer, 1828). – Fehér et al.: figs 2a–k, 4a–c, 5a–c.

2012 *Theodoxus danubialis* (Pfeiffer, 1828). – Welter-Schultes: 27, unnumbered text figures.

2016 *Theodoxus* (*Theodoxus*) *danubialis* (Pfeiffer, 1828). – Vinarski and Kantor: 156 [and synonyms therein].

Status. Accepted native species.

Type locality. Danube River, Vienna, Austria.

Distribution. Danube River catchment, central to south-eastern Europe, as well as northern Italy (Fehér et al. 2009).

Taxonomic notes. The latest phylogenetic data supports a sister relationship between *Theodoxus danubialis* and the clade containing *T. fluviatilis* and *T. velox* (AFS, unpublished data). Some authors believe *T. danubialis* and *T. prevostianus* may represent different species given some level of genetic, ecological, and morphological differentiation (Fehér et al. 2009, Welter-Schultes 2012; but see also Bandel 2001). More recent unpublished results may suggest that the genetic level of differentiation between these species is more indicative of intraspecific diversity within a single species (AFS, unpublished data).

Conservation status. Least Concern (Tomovic et al. 2010).

Theodoxus fluviatilis (Linnaeus, 1758)

*1758 *Nerita fluviatilis* Linnaeus: 777.

1865 *Theodoxus fluviatilis* var. *subthermalis* Issel: 22–23.

1886 *Neritina euxina* Clessin: 55.

1908 *Neritina danubialis* var. *danasteri* Lindholm: 214–215.

?1972 *Theodoxus dniestrovienensis* Put': 80–82, text fig. 5.

?1999 *Th. dniestrovienensis* Put', 1972. – Anistratenko et al.: 19, figs 4, 8.

1999 *Th. fluviatilis* (Linnaeus, 1758). – Anistratenko et al.: 13–15, figs 3, 4.

2005 *Theodoxus fluviatilis* (Linnaeus, 1758). – Anistratenko: 7–8, text figs 3, 4.

2012 *Theodoxus euxinus* (Clessin, 1886). – Welter-Schultes: 27, unnumbered text figures.

2012 *Theodoxus fluviatilis* (Linnaeus, 1758). – Welter-Schultes: 28, unnumbered text figures.

- 2015 *Theodoxus fluviatilis* (Linnaeus, 1758). – Glöer and Pešić: 88–91, figs 1, 3–5, 9, 13–34.
 2016 *Theodoxus* (*Theodoxus*) *fluviatilis* (Linnaeus, 1758). – Vinarski and Kantor: 154–155 [pars, excluding synonyms *sarmatica* and *velox*].
 2016 *Theodoxus* (*Theodoxus*) *euxinus* (Clessin, 1886). – Vinarski and Kantor: 155.
 2016 *Theodoxus* (*Theodoxus*) *subthermalis* (Bourguignat in Issel, 1865). – Vinarski and Kantor: 157–158.

Status. Accepted native species.

Type locality. Near Uppsala, Sweden. The lectotype was designated by Anistratenko (2005).

Distribution. Widely distributed all over Europe, Anatolia, and north-western Africa. Within the Pontocaspian region, it is a common component of the lower reaches of Black and Azov Sea drainages (specifically in Bulgaria, Romania, and Ukraine). Towards the east, the species extends at least as far as the Don River system in Russia and the coastal rivers of Georgia, but it is absent from the Caspian system. Records of this species from Iran and western Asia are likely misidentifications (AFS, unpublished data).

Taxonomic notes. *Theodoxus fluviatilis* exhibits considerable variation in shell colouration and shape (Glöer and Pešić 2015). Unpublished molecular data confirm the synonymy of a number of taxa such as *Theodoxus euxinus* syn. n., *T. danasteri*, and *T. subthermalis* syn. n., and further suggest the inclusion of *T. saulcyi* and *T. heldreichi* (AFS, unpublished data). A final decision concerning the status of *T. dniestrovien-sis* Put', 1972 described from the Dniester River (Rukhotyn village, Khotyn district, Chernivtsi region, Ukraine) is not possible at the moment. Despite appropriate efforts, we were unable to trace the type specimens of this species. Based on the original description and illustration (Put' 1972) it was considered as a junior synonym of *T. fluviatilis* by Anistratenko et al. (1999) having an unusual colour pattern. *Theodoxus milachevichi* was described as a subfossil from the Crimean coast. It closely resembles morphotypes of both *T. fluviatilis* and *T. velox* V. Anistratenko in O. Anistratenko et al., 1999 and might be synonym of either species (compare type material illustrated in Kantor and Sysoev 2006). However, the morphological variability of the taxa involved, as well as the lacking possibility of acquiring genetic data for *T. milachevichi*, complicates a decision on the independence or synonymy of this species.

Conservation status. Least Concern (Kebapçı and Van Damme 2012).

Theodoxus pallasii Lindholm, 1924

- °1838 *Neritina liturata* Eichwald: 156–157 [**non** *Neritina liturata* Schultze, 1826].
 *1924 *Theodoxus pallasii* Lindholm: 33, 34 [**nom. nov.** pro *Neritina liturata* Eichwald, 1838, **non** Schultze, 1826].
 1947 *Theodoxus* (*Theodoxus*) *pallasii* var. *naliwkini* Kolesnikov: 106, 110.
 1976 *Theodoxus pallasii* Lindholm, 1924. – Akramovskiy: 88, text fig. 23, pl. 1, figs 1, 2.
 1994 *Theodoxus astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova and Pirogov: 8–9, fig. 1(1, 2).
 1994 *Theodoxus astrachanicus* Starobogatov et al.: 8–9, fig. 1(1, 2).

- 2009 *Theodoxus pallasii* Lindholm, 1924. – Filippov and Riedel: 70, 72, 74, 76, fig. 4g–i.
- 2011 *Theodoxus astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova & Pirogov, 1994. – Anistratenko et al.: 54–55, fig. 1(6).
- 2012 *Theodoxus pallasii* Lindholm, 1924. – Welter-Schultes: 29, unnumbered text figures.
- 2016 *Theodoxus (Theodoxus) astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova & Pirogov, 1994. – Vinarski and Kantor: 155–156.
- 2016 *Theodoxus (Theodoxus) pallasii* (Lindholm, 1924). – Vinarski and Kantor: 156–157 [and synonyms therein].
- 2017 *Theodoxus pallasii* Lindholm, 1924. – Anistratenko et al.: 221, figs 4, 7, 10, 11.
- 2018 *Theodoxus pallasii* Lindholm, 1924. – Neubauer et al.: 48–51, fig. 4A–F.

Status. Accepted Pontocaspian species, name uncertain.

Type locality. “Inter Fucos littoris Derbendensis viva” (living among algae on the shores of Derbent), Dagestan, Russia.

Distribution. Present along the Caspian Sea shores, in the Volga River, and the Sea of Azov. Lived until the late 1980s in the Aral Sea but is possibly extinct there now (Andreev et al. 1992, Aladin et al. 1998, Micklin et al. 2014).

Taxonomic notes. Eichwald (1838) introduced the species *Neritina liturata* based on material from the shores of Derbent (Dagestan, Russia, northwestern Caspian Sea). That name is invalid as it is a junior primary homonym of *N. liturata* Schultze, 1826; it was replaced by Lindholm (1924) with *Theodoxus pallasii* (see also Anistratenko et al. 2017). *Theodoxus pallasii* is a widely used name, but a major nomenclatural change might be due. Unpublished molecular data suggest that all *Theodoxus* from the Caspian Sea, Azov Sea, and Armenian lakes Sevan and Yerevan, as well as several mineral springs and streams in the Khorasan provinces of Iran, belong to a single species (AFS, unpublished results). The oldest name available for that group is *Theodoxus major* Issel, 1865, described from Lake Sevan in Armenia (originally as variety of the unavailable name *T. schirazensis*). Akramovskiy (1976) noted the similarity of *T. pallasii* and *T. major* and considered the latter as a morphotype of the former. Although he did not explicitly state it, he thereby suggested the two taxa to be synonymous. This view was adopted by Vinarski and Kantor (2016), who listed *major* in synonymy of *pallasii*, although Issel’s (1865) name has priority. The potential synonymy also involves *T. schultzei*. Despite the characteristic appearance of the syntypes, the presence of intermediate morphologies in samples taken on shores of Azerbaijan and Kazakhstan in 2016 and 2017 (pers. obs. OA, VA, FW) indicates a close relationship with *T. pallasii*. The radulae of these two species differ in the relative width of the central and marginal teeth (see Zettler 2007 and compare Anistratenko et al. 2017).

Unfortunately, the types of *T. major*, supposed to be in the Museo Regionale di Scienze Naturali, Torino, are inaccessible at the moment due to museum renovation (E Gavetti, pers. comm., Oct 2018). We refrain from a final conclusion on the synonymy of the species involved until information on the types of all taxa as well as published molecular data are available. For details on the taxonomic relationship between *T. pallasii* and *T. astrachanicus*, see discussion in Anistratenko et al. (2017).

Conservation status. Data Deficient (Van Damme and Kebapçı 2014).

***Theodoxus schultzii* (Grimm, 1877)**

- *1877 *Neritina Schultzii* Grimm: 77–78, pl. 7, fig. 5, pl. 8, fig. 16.
 1909 *Neritina (Ninnia) Schultzei* [sic] Grimm. – Andrusov: 106–107, pl. 6, fig. 38.
 ?1947 *Theodoxus (Ninnia) schultzi* [sic] var. *jukovi* Kolesnikov: 106, 110.
 1950 *Theodoxus (Ninnia) schultzei* [sic] (Grimm). – Kolesnikov: 215–216, pl. 26, figs 12, 13.
 1969 *Theodoxus schultzi* [sic] (Grimm, 1877). – Logvinenko and Starobogatov: 344, fig. 357.
 ?1974 *Theodoxus zhukovi* [sic] Kolesnikov, 1947. – Starobogatov: 255, text fig. 223.
 2007 *Theodoxus (Theodoxus) schultzii* (Grimm, 1877). – Zettler: 249, figs 2–5.
 2016 *Theodoxus (Theodoxus) schultzii* (Grimm, 1877). – Vinarski and Kantor: 157.

Status. Pontocaspian species, status uncertain.

Type locality. Caspian Sea, in two localities, given by Grimm (1877) as 43°17'N, 01°03'E, 40 fathoms, and 42°48'N, 01°22'E, 48 fathoms. Since the longitude was calculated relative to the geographic position of Baku, situated approximately at 50E, the correct longitude should be about 51°00'E (Vinarski and Kantor 2016).

Distribution. Middle and southern Caspian Sea basins, between 15 and 100 m (Logvinenko and Starobogatov 1969).

Taxonomic notes. See discussion of *T. pallasi* for notes on the potential synonymy with *T. major* Issel, 1865. The status of *T. jukovi* still requires confirmation (Vinarski and Kantor 2016).

Conservation status. Not assessed.

***Theodoxus velox* V. Anistratenko in O. Anistratenko et al., 1999**

- *1999 *Th.[eodoxus] velox* V. Anistratenko in O. Anistratenko et al.: 17–18, fig. 4(7).

Status. Pontocaspian species, name uncertain.

Type locality. Dnieper Delta, Zbur'ivka liman, Ukraine.

Distribution. This species was believed to be restricted to drainage systems of the northern Black Sea coast (even though the Oskol River lies far from the Black Sea coast), but unpublished molecular data suggest it may be distributed as far north as the eastern part of the Baltic Sea and as far south as Anatolia (AFS, unpublished data).

Taxonomic notes. The species was listed as junior synonym of *T. fluviatilis* by Vinarski & Kantor (2016). *Theodoxus velox* is indeed challenging to differentiate from some regional morphotypes of that species given the overlap in shell patterns. Unpublished molecular data indicate however that *T. velox* belongs to a different molecular clade (AFS, unpublished data). The distribution range of that clade overlaps with the range of *T. sarmaticus* (Lindholm, 1901), which is widely accepted as a junior synonym of *T. fluviatilis* in the literature (e.g., Vinarski and Kantor 2016). A revision of the taxa involved and study of the type material is required to solve the synonymy issues.

Conservation status. Not assessed.

Family Cochliopidae Tryon, 1866***Eupaludestrina stagnorum* (Gmelin, 1791)**

*1791 *Helix stagnorum* Gmelin: 3653.

1975 *Falsihydrobia streletzkiensis* Chukhchin: 121.

2012 *Heleobia stagnorum* (Gmelin, 1791). – Welter-Schultes: 39, unnumbered text figures.

2012 *Semisalsa stagnorum* (Gmelin, 1791). – Kroll et al.: 1520.

Status. Accepted, native Pontocaspian or immigrant species.

Type locality. Kaasjeswater, Zierikzee, the Netherlands.

Distribution. Coastal areas of Europe and the Mediterranean region, extending to North Africa and east to Iran (Glöer 2002). Occurrence in Black Sea according to, e.g., Chukhchin (1975) and in the Caspian Sea (TW, unpublished data).

Taxonomic notes. We find the attribution of this species to the genus *Eupaludestrina* unsatisfactory, yet a further revision is required to establish and stabilise the generic attribution as there is considerable confusion. It is commonly classified in the South American genus *Heleobia* (e.g., Prié 2011), whereas Kroll et al. (2012) suggested that this species belongs to the genus *Semisalsa*, a group of European Cochliopidae distinct from *Heleobia*. However, *Semisalsa* is currently listed as junior synonym of *Eupaludestrina* Mabille, 1877 (type species: *Hydrobia macei* Paladilhe, 1867, by subsequent designation by Kadolsky 2008). Following Kadolsky (2008), *Eupaludestrina* is currently ranked as subgenus of *Heleobia* in MolluscaBase (2018), but both the phylogenetic and geographic distinction of the European and American species suggest separation on the genus level.

Remarks. It is unclear whether the species is native to the Pontocaspian area or a recent immigrant.

Conservation status. Least Concern (Prié 2011).

Family Hydrobiidae Stimpson, 1865

Remarks. The Hydrobiidae form the most species-rich mollusc group in the Pontocaspian region. However, in general, useful shell characters are few and highly variable (Wilke and Delicado in press). Descriptions in the past have often been very general, and illustrations of types are notably poor for several of the endemic taxa. A strong tendency of naming large numbers of species has developed throughout the 20th century (e.g., Logvinenko and Starobogatov 1969), but for some groups where morphological and genetic analyses could be performed (e.g., *Caspihydrobia* spp.) it has been demonstrated that actual species numbers were much lower than the number of species described (Haase et al. 2010). For many of the endemic species, especially in the genus *Turricaspia*, the apparent loss of types, combined with the lack of living material makes it impossible to assess their taxonomic status. Currently, a number of taxonomic works is in progress on the endemic Pontocaspian hydrobiid groups, and some different insights on the genus-level classifications exist. Here, we adopt a conservative approach, mostly based on Neubauer et al. (2018).

Subfamily Caspiinae Dybowski, 1913

Remarks. The distinction of the genera *Caspia*, *Ulskia*, and *Clathrocaspia* follows Neubauer et al. (2018). The three taxa are differentiated based on details of the protoconch and the expression of teleoconch sculpture. *Caspia* s. s. is characterised by a single distinct but fine spiral keel below the suture. It is usually smooth, yet within the type species some reticulate ornament can be found. Species of *Clathrocaspia* expose a distinctive, reticulate pattern on the teleoconch and a malleate protoconch with faint spiral threads. The aperture of *Clathrocaspia* often develops a distinct flat base. The distinction of the two genera is subject of current research. *Ulskia* also has a malleate protoconch but with more distinct spiral threads; teleoconch sculpture is occasionally present as minute elongate nodules.

Caspia baerii Clessin & Dybowski in Dybowski, 1887

*1887 *Caspia Baerii* Clessin & Dybowski in Dybowski: 36–37.

1888 [*Caspia*] *Baerii* n. sp. – Dybowski: 79, pl. 3, fig. 4a, b.

1969 *Pyrgula (Caspia) baerii* (Cless. & Dyb.). – Logvinenko and Starobogatov: 377, fig. 367(3).

2016 *Caspia baerii* Clessin & W. Dybowski in W. Dybowski, 1888. – Vinarski and Kantor: 224.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea and possibly Danube Delta (Romania). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia baerii*).

Taxonomic notes. The type material is stored in the von Baer collection of Caspian Sea molluscs in the Zoological Museum of Lviv University (Ukraine) and comprises more than a hundred syntypes (Anistratenko et al. 2018). The slender shell, the presence of a fine spiral keel below the suture, and the occasionally weakly reticulated surface distinguish this species from congeners.

Conservation status. Not assessed.

Caspia valkanovi (Golikov & Starobogatov, 1966)

*1966 *P[yr]gula* [*Caspia*] *baeri* [sic] *valkanovi* Golikov & Starobogatov: 354–355, fig. 1(9).

2006 *Caspia valkanovi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 88, pl. 41, fig. N.

Status. Pontocaspian species, identity uncertain.

Type locality. Off Crimea, station 18, sample 173.

Distribution. Endemic to the Black Sea Basin.

Taxonomic notes. The identity and status of this subfossil taxon, described from phaseoline silt, are somewhat uncertain. The holotype illustrated in Kantor and Sysoev (2006) is poorly preserved and does not allow a proper assessment of its validity. The general shape and size are indicative of the genus *Caspia* and it looks like a variety that might even be a synonym of *C. baerii*. Furthermore, we are not entirely certain as to the stratigraphic age of the stratigraphic origin of this species. The phaseoline silt is a marine Holocene unit, yet it contains reworked Late Pleistocene Neoeuxinian (Pontocaspian) species (FW, pers. obs.).

Conservation status. Not assessed.

***Clathrocaspia brotzkajae* (Starobogatov in Anistratenko & Prisjazhnjuk, 1992)**

*1992 *Caspia* (*Clathrocaspia*) *brotzkajae* Starobogatov in Anistratenko & Prisjazhnjuk: 18–19, fig. 2a.

2016 *Caspia brotzkajae* Starobogatov in Anistratenko & Prisjazhnjuk, 1992. – Vinarski and Kantor: 224.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea shores of Dagestan, Russia, at ca. 60 m.

Distribution. Presently endemic to the Caspian Sea. The species was also recorded from the Holocene of Danube Delta, Ukraine (Anistratenko and Prisjazhnjuk 1992).

Taxonomic notes. The species differs from its congeners in the bulbous shape, with a ratio of body whorl height/shell height of approx. 3/4, as well as regarding the expanded aperture.

Conservation status. Not assessed.

***Clathrocaspia gmelinii* (Clessin & Dybowski in Dybowski, 1887)**

*1887 *Caspia Gmelinii* Clessin & Dybowski in Dybowski: 37–38.

1888 [*Caspia*] *Gmelini* [sic] n. sp. – Dybowski: 79, pl. 3, fig. 7a, b.

1969 *Pyrgula* (*Caspia*) *gmelinii* (Cless. & W. Dyb.). – Logvinenko and Starobogatov: 378, fig. 367(7).

?1969 *Pyrgula* (*Caspia*) *sowinskyi* Logvinenko and Starobogatov: 378, fig. 367(4).

?1977 *Pyrgula* (*Caspia*) *gaillardi* Tadjalli-Pour: 107, pl. 2, fig. 8.

2015 *Caspia gmelinii* Clessin & W. Dybowski, 1887. – Boeters et al.: 178, figs 1–6.

2016 *Caspia gmelinii* Clessin & W. Dybowski in W. Dybowski, 1888. – Vinarski and Kantor: 224.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea, recorded from the middle and southern parts. This species was mentioned from depths between 200 and 300 m in the

South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia gmelinii*).

Taxonomic notes. The broad shell and the heavily reticulated surface distinguish this species from congeners. *Pyrgula sowinskyi*, from the middle and southern Caspian Sea, and *P. gaillardi*, from the Caspian Sea shore between Astara and Hashtpar (= Talesh), Iran, closely resemble *C. gmelinii* in terms of shell shape, the shape of the aperture, and the distinct reticulate teleoconch sculpture. Very likely, the two species are synonyms of *C. gmelini*. Since the type material of Logvinenko and Starobogatov (1969) has not been found, and the whereabouts of the material of Tadjalli-Pour (1977) is unknown, a re-examination of these species has to be postponed. Here, we suggest to treat them as nomina dubia until more information becomes available.

Conservation status. Data Deficient (same for *P. sowinskyi*; Son 2011a, Vinarski 2011o).

Clathrocaspia isseli (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Caspia*) *isseli* Logvinenko & Starobogatov: 378, fig. 367(6).

2016 *Pyrgula isseli* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 239.

Status. Pontocaspian species, identity uncertain.

Type locality. Southern Caspian Sea (no details), between 40–75 m water depth.

Distribution. Endemic to the Caspian Sea.

Taxonomic notes. This species hardly differs from *C. pallasii* and might be a junior synonym. Observations on Holocene material from the southern and northern Caspian Sea shores (VA, TN, FW) suggest that the minor differences range within intraspecific variability but further studies (preferentially involving DNA) are required to solve the identity of this taxon. The classification in *Clathrocaspia* is based on the reticulate sculpture typical of that genus.

Conservation status. Data Deficient (Vinarski 2011j).

Clathrocaspia knipowitschii (Makarov, 1938)

*1938 *Caspia gmelini* [sic] var. *Knipowitschii* Makarov: 1058.

?1966 *P[yr]gula* (*Caspia*) *gmelini* [sic] *aluschtensis* Golikov and Starobogatov: 354, fig. 1(8).

1966 *P[yr]gula* (*Caspia*) *makarovi* Golikov and Starobogatov: 353–354, fig. 1(5).

?1987 *Caspia gmelinii stanislavi* Alexenko and Starobogatov: 33, fig. 1.

1992 *Caspia* (*Clathrocaspia*) *knipowitchi* Makarov, 1938. – Anistratenko and Prisjahnjuk: 19, fig. 2b.

2006 *Caspia knipowitchi* [sic] Makarov, 1938. – Kantor and Sysoev: 87–88, pl. 41, fig. J.

2006 *Caspia makarovi* (Golikov et Starobogatov, 1966). – Kantor and Sysoev: 88, pl. 41, fig. L.

2013 *Caspia knipowitchii* [sic] Makarov, 1938. – Anistratenko: 53–55, figs 1A–I, 3A–D, 5A–D.

2013 *Caspia makarovi* (Golikov & Starobogatov, 1966). – Anistratenko: 56–59, figs 2A–E, 3E.

2016 *Caspia knipowitchi* [sic] Makarov, 1938. – Vinarski and Kantor: 224.

2016 *Caspia makarovi* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 225.

?2016 *Caspia stanislavi* Alexenko & Starobogatov, 1987. – Vinarski and Kantor: 225.

Status. Accepted Pontocaspian species.

Type locality. Ukraine, in the Dniester River (exact locality not specified).

Distribution. Azov Sea and northern Black Sea Basin. Known from the Holocene of Danube Delta, Ukraine (Anistratenko and Prisjzhnjuk 1992).

Taxonomic notes. *Clathrocaspia knipowitschii*, *C. makarovi*, *C. gmelini aluschtensis*, and *C. stanislavi* were all described from the northern margin of the Black Sea. After detailed morphological comparison of *C. knipowitschii* and *C. makarovi* syn. n. and preliminary genetic analyses (TW, unpublished data), we conclude that both taxa should be considered synonyms. Very likely, also *C. gmelini aluschtensis* and *C. stanislavi* are synonyms of *C. knipowitschii*, but a final decision on that matter requires investigation of the type material.

Conservation status. Least Concern (same for *C. makarovi*; Son 2011b, c).

***Clathrocaspia logvinenkoi* (Golikov & Starobogatov, 1966)**

*1966 *P.[yrgula]* (*Caspia*) *logvinenkoi* Golikov & Starobogatov: 354, fig. 1(7).

2006 *Caspia logvinenkoi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 88, pl. 41, fig. I.

2007a *Caspia* (*Clathrocaspia*) *logvinenkoi* (Golikov & Starobogatov, 1966). – Anistratenko: 25–26, fig. 2.

2016 *Caspia logvinenkoi* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 224–225.

Status. Accepted Pontocaspian species.

Type locality. Don Delta, Russia.

Distribution. Known only from the type locality.

Taxonomic notes. The species has distinctive shell characters: broad conical shape with a weak subsutural bulge and apically thickened peristome.

Remarks. The type material was collected by Mordukhay-Boltovskoy in 1937 and comprises two specimens, the holotype and the paratype. Three additional specimens were collected from the same region in 2006 (Anistratenko 2007a). The salinity at the type locality fluctuates between freshwater and ca. 1‰.

Conservation status. Not assessed. In the fifty years since the description of this species five specimens have been collected; this is likely evidence of its rarity. Known only from two close localities, *C. logvinenkoi* appears to have an extremely narrow distributional range in the Azov–Black Sea Basin, being endemic to the Taganrog province (e.g., Anistratenko 2007a).

***Clathrocaspia milae* (Boeters, Glöer & Georgiev, 2015)**

*2015 *Caspia milae* Boeters, Glöer & Georgiev in Boeters et al.: 180–183, figs 9–21.

Status. Pontocaspian species, identity uncertain.

Type locality. Bulgaria, Danube Island Vardim (43°37'N, 25°28'E).

Distribution. Only known from type locality.

Taxonomic notes. This species closely resembles *C. knipowitschii* concerning shape, size, and sculpture. According to Boeters et al. (2015), the two species differ in the degree of cover of the umbilicus, the shape of the peristome and the size and number of whorls of the protoconch. Molecular and/or more in-depth morphological and anatomical studies are required to confirm that these apparently minor differences are sufficient to separate the species.

Remarks. If the species would be confirmed, it concerns a Pontocaspian species whose distribution currently is outside prime Pontocaspian habitat, yet Boeters et al. (2015) implied they would expect that several of the *Caspia* records from the lower Danube and Razim Lake complex might be attributed to *C. milae* as well. The Razim Lake complex is Pontocaspian habitat.

Conservation status. Not assessed.

***Clathrocaspia pallasii* (Clessin & Dybowski in Dybowski, 1887)**

*1887 *Caspia Pallasii* Clessin & Dybowski in Dybowski: 37.

1888 *Caspia Pallasii* n. sp. – Dybowski: 79, pl. 3, fig. 3a, b.

1969 *Pyrgula (Caspia) pallasii* (Cless. & W. Dyb.). – Logvinenko and Starobogatov: 378, fig. 367(5).

2016 *Pyrgula pallasii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 241.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea.

Taxonomic notes. This species differs from the other Caspian species *C. gmelinii* in its very slender shape.

Conservation status. Not assessed.

***Ulskia behningi* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula (Ulskia) behningi* Logvinenko & Starobogatov: 380, fig. 367(13).

2016 *Pyrgula behningi* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 236.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the southern Caspian Sea, in the vicinity of the Kura River mouth, 39°05'N, 49°48'E, 120 m.

Distribution. Type locality only.

Taxonomic notes. The drawings provided by Logvinenko and Starobogatov (1969) sketch a broad and conical shell. As such, it differs from the more elongate and ovoid *Ulския ulskii* (Neubauer et al. 2018). A revision is required to clarify its taxonomic status.

Conservation status. Data Deficient (Vinarski 2011f).

?*Ulския derzhavini* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Ulския*) *derzhavini* Logvinenko & Starobogatov: 379, fig. 367(9).

2016 *Pyrgula derzhavini* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 237.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle and southern Caspian Sea, 45–81 m.

Distribution. Type locality only.

Taxonomic notes. The species differs from *U. ulskii* and *U. behningi* in the very slender elongate shape and the presence of a subsutural band; this suggests *P. derzhavini* might be likely a member of *Caspia* s.s. A revision is required to clarify its taxonomic status and generic placement.

Conservation status. Not assessed.

Ulския ulskii (Clessin & Dybowski in Dybowski, 1887)

*1887 *Caspia Ulския* Clessin & Dybowski in Dybowski: 38–39.

1888 [*Caspia*] *Ulския* n. sp. – Dybowski: 79, pl. 3, fig. 8a, b.

1969 *Pyrgula* (*Ulския*) *nana* Logvinenko and Starobogatov: 379–380, fig. 367(12).

1969 *Pyrgula* (*Ulския*) *schorygini* Logvinenko and Starobogatov: 379, fig. 367(11).

2016 *Pyrgula ulskii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 244.

2018 *Ulския ulskii* (Clessin & W. Dybowski in W. Dybowski, 1887). – Neubauer et al.: 52–54, fig. 5A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Western part of the Caspian Sea. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia ulskii*, *T. schorygini*, and *T. nana*).

Taxonomic notes. This species was recently studied by Neubauer et al. (2018), who considered *P. nana* and *P. schorygini* as its junior synonyms.

Conservation status. Not assessed.

Subfamily Hydrobiinae Stimpson, 1865

Remarks. In addition to the taxa discussed below, the following species of Hydrobiinae have been mentioned from the Black Sea basin (updated statuses after MolluscaBase 2018a): *Hydrobia aciculina* (Bourguignat, 1876), *H. acuta* (Draparnaud, 1805), *H. euryomphala* (Bourguignat, 1876), *H. mabilli* (Bourguignat, 1876) [currently accepted as *Peringia mabilli*], *H. macei* Paladilhe, 1867 [currently accepted as *Heleobia macei*], *H. procerula* (Paladilhe, 1869) [currently considered a synonym of *H. acuta*] (Anistratenko et al. 2011). These species were described from the Western Mediterranean and their occurrence in the Black Sea region requires re-investigation; partly the records might be misidentifications of the species of *Ecrobia* listed below or *Eupaludestrina* (Cochliopidae) listed above.

Ecrobia grimmi (Clessin in Dybowski, 1887)

*1887 *Hydrobia grimmi* Clessin in Dybowski: 55–56.

1888 [*Hydrobia*] *grimmi* Clessin. – Dybowski: 79, pl. 3, fig. 2.

2009 *Caspiohydrobia grimmi* (Clessin & Dybowski, 1888). – Filippov and Riedel: 70–72, 74–76, fig. 4a–d.

Status. Accepted native Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea; Aral Sea; salt lakes near Chelyabinsk, Russia (Shishkoeva 2010); Lake Sawa, Iraq (Haase et al. 2010); Arabian (Persian) Gulf (Glöer and Pešić 2012); possibly also northern and central Kazakhstan and Tajikistan (Vinarski and Kantor 2016), however, no molecular data are known to confirm the identity of the Central Asian snails. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Caspiohydrobia curta* and *C. gemma*).

Taxonomic notes. Most of the species that have been assigned to the genus *Caspiohydrobia* Starobogatov, 1970, including its type species, *Pyrgohydrobia eichwaldiana* Golikov & Starobogatov, 1966, range within the morphological variability of *E. grimmi*. Previous examination of some *Caspiohydrobia* juvenile shells (Filippov and Riedel 2009, Anistratenko 2013, fig. 4A–C) as well as reproductive systems and radula did not find any criteria to support differentiation. Probably, all of the thirty *Caspiohydrobia* species listed by Kantor and Sysoev (2006) and Vinarski and Kantor (2016) for the Caspian Sea are morphotypes of a single species. Preliminary genetic analyses of *Caspiohydrobia* spp. from salt lakes near Chelyabinsk, Russia (TW, unpublished data) support this assumption.

Conservation status. Data Deficient (Vinarski 2011b).

Ecrobia maritima (Milaschewitch, 1916)

*1916 *Hydrobia maritima* Milaschewitch: 60–61, pl. 2, fig. 34.

1973 *Hydrobia pontieuxini* Radoman: 15–16.

- 1977 *Ventrosia pontieuxini* (Radoman, 1973). – Radoman: 210, pl. 21, figs 19, 20.
 1992 *Pseudopaludinella cygnea* Anistratenko in Anistratenko and Prisjazhnjuk: 17, fig. 1a.
 1992 *Pseudopaludinella inflata* Anistratenko in Anistratenko and Prisjazhnjuk: 17–18, fig. 1b.
 1992 *Pseudopaludinella ismailensis* Anistratenko in Anistratenko and Prisjazhnjuk: 18, fig. 1c.
 2011 *Pseudopaludinella pontieuxini* (Radoman, 1973). – Anistratenko et al.: 78, pl. 3, fig. 4.
 2015 *Graecoanatolica yildirimi* Glöer and Pešić: 49–50, figs 10–14.

Status. Accepted, Pontocaspian species.

Type locality. Black Sea, at Feodosiya and Adler (Crimea, Ukraine).

Distribution. Black Sea Basin; northern Aegean Sea; Lake Sarikum, Turkey; northern Adriatic Sea.

Taxonomic notes. *Hydrobia pontieuxini*, described from the Black Sea coast in Mangalia, Romania, has been considered a synonym of *E. maritima* based on molecular data (Kevrekidis et al. 2005). Herein, we also consider the *Pseudopaludinella* species introduced by Anistratenko and Prisjazhnjuk (1992) as junior synonyms of *E. maritima* based on morphological similarities. A proper revision is still pending.

Conservation status. Not assessed.

Ecrobia ventrosa (Montagu, 1803)

- *1803 *Turbo ventrosus* Montagu: 317, pl. 12, fig. 13.
 2012 *Ecrobia ventrosa* (Montagu, 1803). – Kadolsky: 69–70.
 2012 *Hydrobia ventrosa* (Montagu, 1803). – Welter-Schultes: 40, unnumbered text figures.

Status. Accepted, immigrant species.

Type locality. On the Kent coast (United Kingdom), at Folkstone and Sandwich.

Distribution. Widespread along the coastal zones of northern and western Europe, the Mediterranean Sea, the Russia White Sea; introduced into the western Black Sea.

Taxonomic notes. Unpublished genetic data (TW) suggest that most previous records of *E. ventrosa* in the Black Sea are likely misidentifications of *E. grimmi*. A notable exception is a recent, genetically confirmed record from Constanța, Romania (Osikowski et al. 2016). Probably, the French species *Paludestrina arenarum* Bourguignat, 1876, *P. leneumicra* Bourguignat, 1876, *P. paludinelliformis* Bourguignat, 1876, and *Ventrosia cissana* Radoman, 1977, which have been listed for the Black Sea Basin (Anistratenko 1991, Anistratenko and Prisjazhnjuk 1992, Anistratenko et al. 2011), are junior synonyms or misidentifications of this species.

Conservation status. Least Concern (Van Damme 2011a).

Subfamily Pyrgulinae Brusina, 1882

Remarks. The genus concepts of Pontocaspian Pyrgulinae follow the revision of Neubauer et al. (2018). Further change is expected in several of the keeled species here

listed under ?*Turricaspia* (?*T. aenigma*, ?*T. basalis*, ?*T. dimidiata*, ?*T. pseudobacuana*, and ?*T. pseudodimidiata*) that may be grouped in their own genus for which the name *Trachycaspia* Dybowski & Grochmalicki, 1917 (type species: *Rissoa dimidiata* Eichwald, 1838) is available. However, such a decision will require further documentation.

***Clessiniola variabilis* (Eichwald, 1838)**

- *1838 *Paludina variabilis* Eichwald: 151–152.
- 1838 *Paludina Triton* Eichwald: 152.
- 1874 *Bithynia? Eichwaldi* Martens: 81.
- ?1887 *Caspia Grimmi* Clessin and Dybowski in Dybowski: 39
- ?1888 [*Caspia*] *Grimmi* n. sp. – Dybowski: 79, pl. 3, fig. 5a, b.
- 1887 *Clessinia Martensii* Clessin and Dybowski in Dybowski: 43.
- 1888 *Clessinia Martensii* n. sp. – Dybowski: 79, pl. 2, fig. 5.
- 1902a *Clessinia ahngeri* Westerlund: 45–46.
- 1966 *P[yrigula] (Clessiniola) pseudotriton* Golikov and Starobogatov: 356–357, fig. 2(3)
- ?1969 *Pyrgula (Casiella) derbentina* Logvinenko and Starobogatov: 374, fig. 366(8).
- 1969 *Pyrgula (Casiella) ovum* Logvinenko and Starobogatov: 374, fig. 366(9).
- 1969 *Pyrgula (Casiella) trivialis* Logvinenko and Starobogatov: 374–375, fig. 366(10).
- 1987 *Turricaspia (Clessiniola) variabilis* (Eichwald, 1838). – Alexenko and Starobogatov: 34, text fig. 5.
- 1987 *Turricaspia (Clessiniola) triton* (Eichwald, 1838). – Alexenko and Starobogatov: 34, text fig. 3.
- 1987 *Turricaspia (Clessiniola) martensii* (Clessin & Dybowski in Dybowski, 1888). – Alexenko and Starobogatov: 34, text fig. 4.
- 1987 *Turricaspia (Clessiniola) bogensis* (Küster, 1852). – Alexenko and Starobogatov: 34.
- 2006 *Turricaspia variabilis* (Eichwald, 1838). – Kantor and Sysoev: 111, pl. 49, fig. J.
- 2011 *Turricaspia martensii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Anistratenko et al.: 86, fig. 3(17).
- 2011 *Turricaspia triton* (Eichwald, 1838). – Anistratenko et al.: 85–86, fig. 3(16).
- 2011 *Turricaspia variabilis* (Eichwald, 1838). – Anistratenko et al.: 85, fig. 3(15).
- 2014 *Turricaspia variabilis*. – Taviani et al.: 4, fig. 3b.
- ?2016 *Turricaspia derbentina* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 247.
- 2016 *Turricaspia martensii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 248.
- 2016 *Turricaspia ovum* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 248–249.
- 2016 *Turricaspia pseudotriton* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 249.
- 2016 *Turricaspia triton* (Eichwald, 1838). – Vinarski and Kantor: 250.
- 2016 *Turricaspia trivialis* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 250–251.
- 2016 *Turricaspia variabilis* (Eichwald, 1838). – Vinarski and Kantor: 251.
- 2018 *Clessiniola variabilis* (Eichwald, 1838). – Neubauer et al.: 60–63, fig. 7A–I.

Status. Accepted Pontocaspian species.

Type locality. At the Volga River mouth near Astrakhan, and towards the Caspian Sea; also in recently lithified fossil limestone at the shores of Dagestan, Russia.

Distribution. Caspian Sea, Azov Sea, and northern Black Sea region. This species was mentioned in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia variabilis*, *T. derbentica*, and *T. trivialis*).

Taxonomic notes. Neubauer et al. (2018) recently demonstrated the high variability of this species. Comparison of available illustrations and descriptions of the species listed in the synonymy list indicates that all of them range within this species' variability. Consequently, we consider all of them as junior synonyms of *C. variabilis*. A more in-depth review of the type material of the species involved is required to confirm this approach.

The status of *Paludina bogensis* Dubois in Küster, 1852, which was listed as a valid species of *Turricaspia* by Anistratenko and Stadnichenko (1995), is still unclear. That species was described from the Zapadniy Bug River in Poland and closely resembles *C. variabilis*. It is, however, unlikely that a Pontocaspian species typical of oligohaline conditions occurs so far away in a pure freshwater environment. “*Paludina eichwaldi* Krynicki, 1837” found in the literature is a nomen nudum. Martens (1874) provided measurements and made the name available, but he listed *Paludina variabilis* Eichwald, 1838 in synonymy, which has priority. Dybowski (1887) obviously overlooked this and considered *Nematurella eichwaldi* Krynicki a valid species. We follow Vinarski and Kantor (2016) and consider the species as a junior synonym of *Clessiniola variabilis*.

Conservation status. Least Concern (Cioboiu et al. 2011).

***Laevicaspia abichi* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Caspiella*) *abichi* Logvinenko & Starobogatov: 372, fig. 366(3).

2016 *Pyrgula abichi* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 235.

Status. Accepted Pontocaspian species.

Type locality. Southern and western parts of the Middle Caspian Sea, 36–120 m.

Distribution. Middle and South Caspian Basin. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia abichi*).

Taxonomic notes. The species differs from the *L. cincta* in its much larger size, the conical shape, the narrower subsutural band, and the larger aperture (compare Neubauer et al. 2018).

Conservation status. Data Deficient (Vinarski 2011e).

***Laevicaspia caspia* (Eichwald, 1838)**

*1838 *Rissoa caspia* Eichwald: 154–155.

non 1888 *Micr.[omelania] caspia* Eichw. sp. – Dybowski: 78, pl. 1, fig. 1.

- ?1896 *B.[uliminus]* (*Napaeus?*) *goebeli* Westerlund: 188.
 1915 *Micromelania* (?) *curta* Nalivkin: 21–22, 31, pl. 6, figs 1, 2 [pars, non figs 3, 4, 7, 9–14].
 1915 [*Micromelania* (?) *curta*] var. *plano-convexa* Nalivkin: 22, 31, pl. 6, figs 15–18.
 non 1915 *Micromelania caspia* Eichw. – Nalivkin: 22, 31, pl. 6, figs 5, 6 [pars, non fig. 8].
 non 1917 *Micromelania* (*Turricaspia*, *Laevicaspia*) *caspia* Eichw. – Dybowski and Grochmalicki: 5–8, 36–38, pl. 1, figs 1–3.
 non 1969 *Pyrgula caspia* (Eichw.). – Logvinenko and Starobogatov: 369–370, fig. 364(1).
 2006 *Turricaspia caspia* (Eichwald, 1838). – Kantor and Sysoev: 106, pl. 49, fig. M.
 2016 *Turricaspia caspia* (Eichwald, 1838). – Vinarski and Kantor: 246.
 2018 *Laevicaspia caspia* (Eichwald, 1838). – Neubauer et al.: 63–66, fig. 8A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. In fossil limestone of Dagestan, Russia.

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia caspia* and *T. curta*).

Taxonomic notes. For a detailed discussion about the identity of this species, its synonyms and former misidentifications, see Neubauer et al. (2018).

Conservation status. IUCN indicates “Least Concern” (Vinarski 2012), but the true status of this species is highly uncertain.

Laevicaspia cincta (Abich, 1859)

- *1859 *Rissoa cincta* Abich: 57, pl. 2, fig. 6.
 ?1887 *Caspia Orthii* Clessin & Dybowski in Dybowski: 40.
 ?1888 [*Caspia*] *Orthii* n. sp. – Dybowski: 79, pl. 3, fig. 6.
 1969 *Pyrgula* (*Caspiella*) *cincta* (Abich). – Logvinenko and Starobogatov: 372, fig. 366(4).
 2006 *Pyrgula cincta* (Abich, 1859). – Kantor and Sysoev: 98, pl. 47, fig. L.
 2016 *Pyrgula cincta* (Abich, 1859). – Vinarski and Kantor: 236–237.
 2018 *Laevicaspia cincta* (Abich, 1859). – Neubauer et al.: 66–68, fig. 9A–H.

Status. Accepted Pontocaspian species.

Type locality. Gulf of Baku, Azerbaijan.

Distribution. Southern Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. For a detailed discussion about the identity of this species and its synonym, see Neubauer et al. (2018).

Conservation status. Data Deficient (Vinarski 2011g).

Laevicaspia conus (Eichwald, 1838)

- *1838 *Rissoa Conus* Eichwald: 155.

- non 1876 *Eulima conus*, Eichw?. – Grimm: 154–156, pl. 6, fig. 14.
 non 2006 *Turricaspia conus conus* (Eichwald, 1838). – Kantor and Sysoev: 106, pl. 48, fig. J.
 2016 *Turricaspia conus conus* (Eichwald, 1838). – Vinarski and Kantor: 246–247.
 2018 *Laevicaspia conus* (Eichwald, 1838). – Neubauer et al.: 69–71, fig. 9I–P [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. In fossil limestone of Dagestan, Russia.

Distribution. Endemic to the Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia conus*).

Taxonomic notes. For a detailed discussion about the identity of this polymorphic species and previous misidentifications, see Neubauer et al. (2018).

Conservation status. Data Deficient (Vinarski 2011p).

?*Laevicaspia ebersini* (Logvinenko & Starobogatov, 1969)

- *1969 *Pyrgula* (*Oxyprygula*) *ebersini* Logvinenko & Starobogatov: 368, fig. 363(7).
 2016 *Pyrgula ebersini* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 238.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the middle Caspian Sea, 0–50 m water depth.

Distribution. Type locality only.

Taxonomic notes. We cannot verify the status of this species given the inadequate descriptions and illustrations and its general resemblance to other species that were described earlier.

Conservation status. Data Deficient (Vinarski 2011h).

?*Laevicaspia ismailensis* (Golikov & Starobogatov, 1966)

- *1966 *P[yr]gula* *ismailensis* Golikov & Starobogatov: 358, fig. 2(11).
 2006 *Turricaspia ismailensis* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 108, pl. 50, fig. A.
 2016 *Turricaspia ismailensis* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 248.

Status. Accepted Pontocaspian species.

Type locality. Ukraine, Danube Delta, lakes Yalpug and Kugurlui.

Distribution. North-western Black Sea Basin (Anistratenko and Stadnichenko 1995).

Taxonomic notes. Based on the illustration of the holotype in Kantor and Sysoev (2006), we tentatively place the species in the genus *Laevicaspia*. A more detailed study is necessary to clarify its systematic position.

Conservation status. Vulnerable (Son and Cioboiu 2011).

***Laevicaspia kolesnikoviana* (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966)**

- *1966 *P[yrghula]* (*Caspiella*) *kolesnikoviana* Golikov & Starobogatov: 357–358, fig. 2(8–9).
 1969 *Pyrgula* [(*Caspiella*)] *kolesnikoviana* Logv. & Star. – Logvinenko and Starobogatov: 372, fig. 366(1).
 2006 *Pyrgula kolesnikoviana* Logvinenko & Starobogatov in Golikov & Starobogatov, 1966. – Kantor and Sysoev: 100, pl. 47, fig. N.
 2016 *Pyrgula kolesnikoviana* Logvinenko & Starobogatov in Golikov & Starobogatov, 1966. – Vinarski and Kantor: 239.
 2018 *Laevicaspia kolesnikoviana* (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966). – Neubauer et al.: 71–73, fig. 10A–E, K, N.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea, northward of Apsheron Peninsula, north-westward from Kamni Dva Brata Island, 40°47'N, 49°42'E, 30 m water depth.

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia kolesnikoviana*).

Taxonomic notes. For a detailed discussion about the identity of this species, see Neubauer et al. (2018).

Conservation status. Data Deficient (Vinarski 2011k).

***Laevicaspia kowalewskii* (Clessin & Dybowski in Dybowski, 1887)**

- *1887 *Caspia Kowalewskii* Clessin & Dybowski in Dybowski: 40–41.
 1888 [*Caspia*] *Kowalewskii* n. sp. – Dybowski: 79, pl. 3, fig. 9a–c.
 2006 *Pyrgula kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 100, pl. 47, fig. M.
 2016 *Pyrgula kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 239–240.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea, recorded from southern basin (Logvinenko and Starobogatov 1969) and middle basin (personal observation based on material from Dagestan region, TAN, FW). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia kowalewskii*).

Taxonomic notes. This species differs from *L. kolesnikoviana* in its bigger size, broader shape, and thinner peristome. *Laevicaspia cincta* can be distinguished based on the stouter shape and the presence of a narrow subsutural band.

Conservation status. Not assessed.

***Laevicaspia lencoranica* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Eurycaspia*) *lencoranica* Logvinenko & Starobogatov: 357, fig. 358(14).
2016 *Pyrgula lencoranica* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 240.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. Based on the illustrations provided in Kantor and Sysoev (2006), this species differs from *L. cincta* and *L. kowalewskii* in the conical shape and large body whorl. A revision is required to assure its status as distinct species.

Conservation status. Not assessed.

***Laevicaspia lincta* (Milaschewitch, 1908)**

*1908 *Micromelania lincta* Milaschewitch: 991.

?1966 *P.[yrgula]* (*Caspiella*) *azovica* Golikov and Starobogatov: 357, fig. 2(7).

?1966 *P.[yrgula]* (*Caspiella*) *boltovskoji* Golikov and Starobogatov: 357, fig. 2(4).

?1966 *P.[yrgula]* (*Caspiella*) *crimeana* Golikov and Starobogatov: 358, fig. 2(10).

?1966 *P.[yrgula]* (*Caspiella*) *limanica* Golikov and Starobogatov: 357, fig. 2(6).

?1966 *P.[yrgula]* (*Caspiella*) *lindholmiana* Golikov and Starobogatov: 357, fig. 2(5).

?1966 *P.[yrgula]* (*Laevicaspia*) *iljinae* Golikov and Starobogatov: 358–359, fig. 2(14).

?1966 *P.[yrgula]* (*Laevicaspia*) *milachevitchi* Golikov and Starobogatov: 359, fig. 2(15).

?1966 *P.[yrgula]* (*Laevicaspia*) *ostroumovi* Golikov and Starobogatov: 358, fig. 2(13).

?1966 *P.[yrgula]* (*Turricaspia*) *borceana* Golikov and Starobogatov: 359, fig. 2(16).

?1966 *P.[yrgula]* (*Turricaspia*) *neveskae* Golikov and Starobogatov: 359, fig. 2(17).

?1987 *Turricaspia abichi phaseolinica* Alexenko and Starobogatov: 33.

?1987 *Turricaspia* (*Caspiella*) *derbentina borysthenica* Alexenko and Starobogatov: 34–35, fig. 6.

?1987 *Turricaspia* (*Laevicaspia*) *grigorievi* Alexenko and Starobogatov: 35, fig. 7.

?1987 *Turricaspia* (*Laevicaspia*) *meneghiniana ukrainica* Alexenko and Starobogatov: 35, fig. 9.

?2006 *Euxinipyrgula azovica* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 95, pl. 44, fig. K.

?2006 *Euxinipyrgula borysthenica* (Alexenko & Starobogatov, 1987). – Kantor and Sysoev: 95, pl. 44, fig. J.

?2006 *Euxinipyrgula grigorievi* (Alexenko & Starobogatov, 1987). – Kantor and Sysoev: 95, pl. 44, fig. I.

?2006 *Euxinipyrgula limanica* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 95, pl. 44, fig. H.

2006 *Euxinipyrgula lincta* (Milaschewitsch, 1908). – Kantor and Sysoev: 95–96, pl. 45, fig. D.

?2006 *Euxinipyrgula milachevitchi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 96, pl. 45, fig. C.

?2006 *Euxinipyrgula ostroumovi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 96, pl. 45, fig. B.

- ?2006 *Euxinipyrgula ukrainica* (Alexenko & Starobogatov, 1987). – Kantor and Sysoev: 95, pl. 45, fig. A.
- ?2006 *Turricaspia boltovskoji* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 105–106, pl. 48, fig. K.
- ?2006 *Turricaspia borceana* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 106, pl. 49, fig. B.
- ?2006 *Turricaspia conus lindholmiana* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 107, pl. 48, fig. L.
- ?2006 *Turricaspia crimeana* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 107, pl. 48, fig. C.
- ?2006 *Turricaspia iljinae* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 108, pl. 49, fig. D.
- ?2006 *Turricaspia neveskiae* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 109, pl. 49, fig. L.

Status. Accepted Pontocaspian species.

Type locality. Kotlabukh Lake, Odessa Region, Ukraine (approximately 45°25'35"N, 28°59'41"E).

Distribution. Limans and lower reaches of rivers Don, Dnieper, Dniester, and Southern Bug entering the northern Black Sea Basin and the Azov Sea (Taganrog Bay), as well as in coastal lakes Kotlabukh and Yalpug (Vinarski and Kantor 2016). The record of an undescribed subspecies of *T. boltovskoji* from the Caspian Sea mentioned by Anistratenko and Stadnichenko (1995) is probably based on a misidentification.

Taxonomic notes. Golikov and Starobogatov (1966) and Alexenko and Starobogatov (1987) introduced a plethora of names for morphologically similar species from the northern Black Sea Basin, partly deriving from subfossil horizons. They differ from *Laevicaspia lincta* slightly in the number of whorls and outline shape, but overall range within its morphological variability. Here, we consider them tentatively all junior synonyms of *L. lincta*. Since Starobogatov's type material is unknown, support for this approach requires collection of new material from the type localities of these taxa. Molecular data confirmed the conspecificity of *L. lincta* and *L. milachevitchi* (Wilke et al. 2007).

Conservation status. Least Concern (Son 2011e).

?*Laevicaspia marginata* (Westerlund, 1902)

*1902a *Nematurella marginata* Westerlund: 45.

2013 *Pyrgula marginata* (Westerlund, 1902). – Vinarski et al.: 85, fig. 2F.

2016 *Pyrgula marginata* (Westerlund, 1902). – Vinarski and Kantor: 240.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea, “near Krasnojarsk” (Westerlund 1902a). This statement is clearly erroneous since Krasnojarsk is situated in Siberia. Most probably, Westerlund meant Krasnovodsk (nowadays Turkmenbashi) in Turkmenistan (Vinarski et al. 2013).

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia marginata*).

Taxonomic notes. The status of this species is uncertain. The illustrations of the type material by Vinarski et al. (2013) suggest a tentative placement in the genus *Laevicaspia*. It shows close similarities with *L. sieversii* (Clessin in Dybowski, 1887). A careful revision of the species is required to clarify its taxonomic status and systematic placement.

Conservation status. Not assessed.

Laevicaspia sieversii (Clessin in Dybowski, 1887)

*1887 *Nematurella Sieversii* Clessin in Dybowski: 45–46.

1888 *Nematurella Sieversi* [sic] n. sp. – Dybowski: 78, pl. 2, fig. 1.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea.

Taxonomic notes. This species has not been found since its first description, its identity is unclear (Vinarski and Kantor 2016). Judging from the description and drawing in Dybowski (1887), we suggest a systematic placement in *Laevicaspia*. It might be related to *L. conus* (Eichwald, 1838).

Conservation status. Not assessed.

?*Turricaspia aenigma* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula (Celekenia) aenigma* Logvinenko & Starobogatov: 375, fig. 366(12).

2016 *Pyrgula aenigma* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 235.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea, northward of Apsheron Peninsula, 75 m.

Distribution. Type locality only.

Taxonomic notes. The identity of this species is unclear. The illustrations of the holotype in Kantor and Sysoev (2006) show a small shell with four whorls, of which the latter two bear a distinct keel. The small size and the relatively large protoconch suggest that the type specimen is a juvenile shell. More specimens (including adult material) are required to shed light on this species' identity.

Conservation status. Not assessed.

Turricaspia andrussowi (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania (Turricaspia) andrussowi* Dybowski & Grochmalicki: 125–126, pl. 3, fig. 31a, b.

?1969 *Pyrgula (Oxyppyrgula) dubia* Logvinenko and Starobogatov: 368, fig. 363(5).

- ?1969 *Pyrgula (Oxypyrgula) turkmenica* Logvinenko and Starobogatov: 368, fig. 363(6).
 2006 *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 104–105, pl. 48, fig. A [pars, excluding synonymy].
 2016 *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 245 [pars, excluding synonymy].
 2018 *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 74–76, fig. 11A, BB.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea. The two tentative synonyms were recorded from the western part of the middle Caspian Sea and the eastern part of the southern Caspian Sea, respectively. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *T. turkmenica*, *T. dubia*, and *T. andrussowi*).

Taxonomic notes. The species was recently investigated by Neubauer et al. (2018). *Pyrgula dubia* and *P. turkmenica* are tentatively considered juveniles and thus junior synonyms of this species.

Conservation status. Not assessed.

?*Turricaspia basalis* (Dybowski & Grochmalicki, 1915)

- *1915 *Micromelania dimidiata* var. *basalis* Dybowski & Grochmalicki: 131, pl. 3, fig. 36a, b.
 1969 *Pyrgula (Trachycaspia) laticarinata* Logvinenko and Starobogatov: 359, fig. 359(3).
 2006 *Pyrgula basalis basalis* (B. Dybowski & J. Grochmalicki, 1915). – Kantor and Sysoev: 97, pl. 46, fig. A.
 2006 *Pyrgula basalis laticarinata* Logvinenko & Starobogatov, 1968. – Kantor and Sysoev: 97, pl. 46, fig. B.
 2016 *Pyrgula basalis basalis* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 236.
 2016 *Pyrgula basalis laticarinata* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 236.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *T. laticarinata*).

Taxonomic notes. The species is characterised by a massive keel near the lower suture. ?*Turricaspia dimidiata* is distinguished based on its more centrally placed keel. This distinction is tentative and only based on comparison of available illustrations; we are aware of the possibility that these differences might not be diagnostic. Moreover, the keel seems to become stronger with increasing water depth (Starobogatov 1968).

Pyrgula laticarinata Logvinenko & Starobogatov, 1969, which differs from *T. basalis* only in the strength of the keels, was considered a junior synonym by Neubauer et al. (2018).

Conservation status. Not assessed.

?*Turricaspia bogatscheviana* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxyprygula*) *bogatscheviana* Logvinenko & Starobogatov: 367, fig. 363(2).

2016 *Turricaspia bogatscheviana* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 245.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. The description and drawing of this species provided by Logvinenko and Starobogatov (1969) do not allow an evaluation whether it is a distinct species or synonym of a previously species.

Conservation status. Not assessed.

***Turricaspia chersonica* Alexenko & Starobogatov, 1987**

*1987 *Turricaspia* (*Oxyprygula*) *chersonica* Alexenko & Starobogatov: 35–36, fig. 10.

2016 *Turricaspia chersonica* Alexenko & Starobogatov, 1987. – Vinarski and Kantor: 246.

Status. Pontocaspian species, identity uncertain.

Type locality. Ukraine, in the Dnieper Delta.

Distribution. Type locality only.

Taxonomic notes. The status of this species is highly uncertain. The slender conical shell illustrated by Alexenko and Starobogatov (1987) suggest classification in the genus *Turricaspia*, which is otherwise only known from the Caspian Sea.

Conservation status. Data Deficient (Son 2011d).

***Turricaspia columna* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Oxyprygula*) *columna* Logvinenko & Starobogatov: 368, fig. 363(8).

2016 *Pyrgula columna* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 237.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the southern Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. The species has not been found since its first description, and the whereabouts of the type material is unknown. Logvinenko and Starobogatov (1969) illustrate a small slender shell with convex whorls. It might well be a juvenile of another species.

Conservation status. Not assessed.

***Turricaspia concinna* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *concinna* Logvinenko & Starobogatov: 365, fig. 362(3).
 2016 *Pyrgula concinna* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 237.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle Caspian Sea, 25–80 m.

Distribution. Type locality only.

Taxonomic notes. The illustrations provided by Logvinenko and Starobogatov (1969) indicate a large conical shell with nine convex whorls and a large, slightly inflated last whorl. These features are reminiscent of *T. meneghiniana* (Issel, 1865). However, *T. concinna* has not been found since its first description. The type material has been very recently detected in the collections of ZIN and awaits further study.

Conservation status. Not assessed.

***Turricaspia dagestanica* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *dagestanica* Logvinenko & Starobogatov: 361, fig. 360(3).
 2016 *Turricaspia dagestanica* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 247.

Status. Pontocaspian species, identity uncertain.

Type locality. Western shore of the middle Caspian Sea.

Distribution. Middle and south Basin of Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The status of this species is highly uncertain. The illustrations of Logvinenko and Starobogatov (1969) show a slightly distorted shell with weakly convex whorls and a thin line below the suture. We are uncertain whether it might concern a growth aberration of a more common species.

Conservation status. Data Deficient (Vinarski 2011r).

***Turricaspia dimidiata* (Eichwald, 1838)**

*1838 *Rissoa dimidiata* Eichwald: 156.

?1947 *Turricaspia bakuana* Kolesnikov: 108, 112.

2006 *Pyrgula dimidiata* (Eichwald, 1838). – Kantor and Sysoev: 99, pl. 46, fig. K.

?2006 *Pyrgula bakuana* (Kolesnikov, 1947). – Kantor and Sysoev: 97, pl. 47, fig. C.

2016 *Pyrgula dimidiata* (Eichwald, 1838). – Vinarski and Kantor: 238.

2016 *Pyrgula bakuana* (Kolesnikov, 1947). – Vinarski and Kantor: 236–237.

Status. Accepted Pontocaspian species.

Type locality. In fossil limestone of Dagestan, Russia.

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. Although there is little doubt about the validity of this species, its true identity and possible synonyms are unclear. Eichwald's (1838) description clearly indicates a slender shell with median keel. His type material is unfortunately unknown. The high number of keeled species complicates an evaluation what is the "true" *T. dimidiata* and what are synonyms. We tentatively consider *Turricaspia bakuana* Koleznikov, 1947 a junior synonym of this species, based on its slender shell with median keel matching Eichwald's description as well as the prevailing concept of *T. dimidiata* (compare Kantor and Sysoev 2006). More data are required to support this view.

Conservation status. Not assessed.

Turricaspia eburnea (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Laevicaspia*) *eburnea* Logvinenko & Starobogatov: 370, fig. 365(1).
2016 *Turricaspia eburnea* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 247.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the southern Caspian Sea.

Distribution. South Caspian Basin. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The identity of this species is unclear. Its shell resembles *T. lyrata* (Dybowski & Grochmalicki, 1915) in terms of general shape and the large, flat protoconch; it differs from that species in the large size. The type material has been very recently found in the collection of ZIN and awaits further study. Until then, we refrain from a final decision on the species' status, but we have severe doubt that *Pyrgula eburnea* is a distinct species.

Conservation status. Not assessed.

Turricaspia elegantula (Clessin & Dybowski in Dybowski, 1887)

*1887 *Micromelania elegantula* Clessin & Dybowski in Dybowski: 33.
1888 [*Micromelania*] *elegantula* n. sp. – Dybowski: 78, pl. 1, fig. 7a–c.
2016 *Turricaspia elegantula* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 247–248.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. There is considerable confusion about the identity of this species. Dybowski (1887) described and illustrated a very slender shell with a distinct

whorl profile showing a straight-sided upper half and a convex lower half. In contrast, the illustrations in Logvinenko and Starobogatov (1969) suggest a similarly slender yet distorted shell with near almost sided whorls and expanded aperture. A restudy of the type material of *T. elegantula* show close similarities to *T. spica*. It differs from that species in the more slender outline and flattened whorls.

Conservation status. Not assessed.

***Turricaspia eulimellula* (Dybowski & Grochmalicki, 1915)**

*1915 *Micromelania* (*Turricaspia*) *eulimellula* Dybowski & Grochmalicki: 123–125, pl. 3, fig. 27a, b.

2006 *Pyrgula eulimellula* (B. Dybowski & J. Grochmalicki, 1915). – Kantor and Sysoev: 99–100, pl. 46, fig. L.

2016 *Pyrgula eulimellula* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 238–239.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle Caspian Sea Basin (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The nearly straight-sided, strongly attached whorls easily distinguish this species from most other *Turricaspia* species. Only *Turricaspia grimmi* (Clessin & Dybowski in Dybowski, 1887) has a similar whorl arrangement, but its shell is slightly wider and the whorls are weakly stepped and bear a thin subsutural band.

Conservation status. Not assessed.

***Turricaspia fedorovi* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *fedorovi* Logvinenko & Starobogatov: 362, fig. 360(2).

2016 *Pyrgula fedorovi* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 239.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the middle Caspian Sea, 80 m.

Distribution. Middle and South Caspian Basin. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The slender elongate shell with whorls slowly increasing in height distinguishes this species from its congeners. However, a proper assessment of the species' status requires investigation. The whereabouts of the type material is unknown and no other records of this species are known, so we are not able to verify the status of this species.

Conservation status. Not assessed.

***Turricaspia grimmi* (Clessin & Dybowski in Dybowski, 1887)**

- *1887 *Micromelania Grimmi* Clessin & Dybowski in Dybowski: 27–29.
1888 [*Micromelania*] *Grimmi* n. sp. – Dybowski: 78, pl. 1, fig. 2a–c.
2006 *Pyrgula grimmi* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 100, pl. 46, fig. L.
2016 *Pyrgula grimmi* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 239.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Southern Caspian Sea Basin (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The peculiar morphology with straight-sided, weakly stepped whorls with a thin subsutural band is unique among Caspian Pyrgulinae. See above for a comparison with *T. eulimellula*.

Conservation status. Data Deficient (Vinarski 2011i).

***Turricaspia lyrata* (Dybowski & Grochmalicki, 1915)**

- *1915 *Micromelania (Turricaspia) spica* var. *lyrata* Dybowski & Grochmalicki: 117, pl. 2, fig. 18.
2006 *Pyrgula lirata* [sic] (B. Dybowski & J. Grochmalicki, 1915). – Kantor and Sysoev: 101, pl. 46, fig. E.
2016 *Pyrgula lirata* [sic] (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 240.
2018 *Turricaspia lyrata* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 77–79, fig. 12A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea (after Logvinenko and Starobogatov 1969); it occurs in the western part of the middle and southern Caspian Sea basins, but these authors used a slightly different concept of the species. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia lirata*).

Taxonomic notes. See Neubauer et al. (2018) for a detailed discussion of the species and its synonyms.

Conservation status. Not assessed.

***Turricaspia marisnigri* Starobogatov in Alexenko & Starobogatov, 1987**

*1987 *Turricaspia lirata marisnigri* Starobogatov in Alexenko & Starobogatov: 33.

Status. Pontocaspian species, identity uncertain.

Type locality. “Meotida” station 24, sample 229, near the coast of Crimea, in phaseoline silt (Holocene).

Distribution. Type locality only.

Taxonomic notes. The species can be distinguished based on its extremely slender shell with whorls slowly increasing in size. Still, clarification of its identity as well as its generic classification requires investigation of additional material.

Conservation status. So far only known from Holocene deposits of the type locality; species might be extinct. Within Holocene deposits in the Black Sea small amounts of reworked Late Pleistocene “Neoeuxinian” faunas are found (FW, pers. obs.), and therefore the stratigraphic origin of such Pontocaspian species is uncertain.

***Turricaspia meneghiniana* (Issel, 1865)**

*1865 *Bythinia Meneghiniana* Issel: 21, pl. 1, figs 12, 13.

1902a *Micromelania subulata* Westerlund: 47.

?1969 *Pyrgula caspia* (Eichw). – Logvinenko and Starobogatov: 369–370, fig. 364(1)

[**non** *Rissoa caspia* Eichwald, 1838].

non 1987 *T.[urricaspia] meneghiniana meneghiniana* (Iss.). – Alexenko and Starobogatov: 35, fig. 8.

2006 *Turricaspia meneghiniana* (Issel, 1865). – Kantor and Sysoev: 109, pl. 49, fig. E.

2016 *Turricaspia meneghiniana* (Issel, 1865). – Vinarski and Kantor: 248.

2018 *Turricaspia meneghiniana* (Issel, 1865). – Neubauer et al.: 79–81, fig. 13A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. Baku, Azerbaijan; (sub?)fossil.

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. The species was recently discussed in detail by Neubauer et al. (2018), who also discussed previous misidentifications.

Conservation status. Not assessed.

***Turricaspia nossovi* Kolesnikov, 1947**

*1947 *Turricaspia nossovi* Kolesnikov: 108, 111.

2006 *Pyrgula nossovi* (Kolesnikov, 1947). – Kantor and Sysoev: 101, pl. 45, fig. G.

2016 *Pyrgula nossovi* (Kolesnikov, 1947). – Vinarski and Kantor: 241.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The very slender shape and the characteristic, highly convex whorls that slowly and regularly increase in height distinguish the species from most congeners. *Pyrgula vinogradovi* Logvinenko & Starobogatov, 1969 and *P. astrachanica* Pirogov, 1971, which show very similar traits, might be junior synonyms. A more in-depth study is required to solve their statuses.

Conservation status. Data Deficient (Vinarski 2011l).

?*Turricaspia obventicia* (Anistratenko in Anistratenko & Prisjazhnjuk, 1992)

*1992 *Caspia (Clathrocaspia) obventicia* Anistratenko in Anistratenko & Prisjazhnjuk: 19–20, fig. 2b.

Status. Uncertain Pontocaspian species.

Type locality. Well 37 near Kiliya, Izmail district, Odessa region, Ukraine (from Holocene sediments).

Distribution. Type locality only.

Taxonomic notes. This species was originally attributed to the genus *Caspia* due to its small shell. A study of the holotype of this species, specifically its protoconch characteristics, suggest placement in the genus *Turricaspia*. Further studies are required to assure its validity.

Remarks. The species is known only from the holotype. The occurrence of *Turricaspia* in the Black Sea Basin is unusual, as almost all other pyrguline Black Sea species are assigned to the genus *Laevicaspia* (but see remark at *T. spica* for another unusual occurrence).

Conservation status. So far only known from Holocene deposits of the type locality; species might be extinct.

?*Turricaspia pseudobacuana* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula (Eurycaspia) pseudobacuana* Logvinenko & Starobogatov: 358, fig. 358(16).

2016 *Pyrgula pseudobacuana* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 241.

Status. Pontocaspian species, probably junior synonym.

Type locality. Southern Caspian Sea, 50–80 m.

Distribution. South Caspian Basin. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The slender shell with a keel near the lower suture is reminiscent of *T. basalis* (Dybowski & Grochmalicki, 1915). The short description and

poor drawing precluded the verification of its status. The type material has been very recently detected in the collection of ZIN and awaits further study.

Conservation status. Not assessed.

?*Turricaspia pseudodimidiata* (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania* (*Turricaspia*) *pseudodimidiata* Dybowski & Grochmalicki: 126–128, pl. 3, fig. 32a, b.

?1969 *Pyrgula* (*Eurycaspia*) *pseudodimidiata* (Dyb. et Gr.). – Logvinenko and Starobogatov: 357, fig. 358(15).

?2006 *Pyrgula pseudodimidiata* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 102, pl. 47, fig. G.

2016 *Pyrgula pseudodimidiata* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 241.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The identity of this species is uncertain. Dybowski and Grochmalicki (1915) describe and illustrate a shell with eight convex whorls bearing a weak, hardly protruding, irregular shaped keel near the lower suture. According to these authors, the keel varies considerably between a thin thread, a blunt bulge, or a weak thickening at the suture. In contrast, the drawings provided by Logvinenko and Starobogatov (1969) and reproduced by Kantor and Sysoev (2006) suggest a shell with straight-sided whorls and a distinct keel. Inspection of the type material is required to clarify the status of this species.

Conservation status. Not assessed.

Turricaspia pseudospica (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxyppyrgula*) *pseudospica* Logvinenko & Starobogatov: 366, fig. 363(1).

2016 *Pyrgula pseudospica* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 241–242.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle and southern Caspian Sea, 15–75 m.

Distribution. Type locality only.

Taxonomic notes. The identity of this species is unclear. Judging from the drawing by Logvinenko and Starobogatov (1969), showing a small slender shell with ca. 6.5 convex whorls, the species might be based on a juvenile specimen. Moreover, it could be a junior synonym of the similarly shaped *T. spica* (Eichwald, 1855).

Conservation status. Not assessed.

***Turricaspia pulla* (Dybowski & Grochmalicki, 1915)**

- *1915 *Micromelania* (*Turricaspia*) *caspia* var. *pulla* Dybowski & Grochmalicki: 111, pl. 1, fig. 6a.
 1969 *Pyrgula* [(*Turricaspia*)] *pulla* (Dyb. et Gr.). – Logvinenko and Starobogatov: 361–362, fig. 360(8).
 2006 *Pyrgula pulla* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 102, pl. 46, fig. C.
 2016 *Pyrgula pulla* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 242.
 2018 *Turricaspia pulla* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 81–82, fig. 14A–J.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea, reported from the middle and southern Caspian Sea basins (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The species can be easily distinguished from other *Turricaspia* species based on its relatively broad shell, the low-convex whorls, and its small size (Neubauer et al. 2018).

Conservation status. Data Deficient (Vinarski 2011m).

***Turricaspia pullula* (Dybowski & Grochmalicki, 1915)**

- *1915 *Micromelania* (*Turricaspia*) *caspia* var. *pullula* Dybowski & Grochmalicki: 111–112, pl. 1, fig. 7.
 1969 *Pyrgula* [(*Turricaspia*)] *pullula* (Dyb. et Gr.). – Logvinenko and Starobogatov: 366–367, fig. 363(3).
 2006 *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 109, pl. 50, fig. B.
 2016 *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 249.
 2018 *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 82–84, fig. 14K–L.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea, reported from the western part of the middle Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. The very characteristic tripartite whorl profile allows an easy identification and discrimination from other Pontocaspian Pyrgulinae (Neubauer et al. 2018).

Conservation status. Data Deficient (Vinarski 2011s).

***Turricaspia rudis* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *rudis* Logvinenko & Starobogatov: 362, fig. 360(5).

2016 *Pyrgula rudis* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 242.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle and southern Caspian Sea, 50–100 m.

Distribution. Type locality only.

Taxonomic notes. The status of this species is unclear. The drawing provided by Logvinenko and Starobogatov (1969) shows strong similarities to *T. grimmi* in terms of the nearly straight-sided whorls and the large aperture. Since the whereabouts of the type material is unknown, we refrain from a final conclusion on the potential synonymy.

Conservation status. Data Deficient (Vinarski 2011n).

***Turricaspia sajenkova* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *sajenkova* Logvinenko & Starobogatov: 361, fig. 360(4).

2016 *Turricaspia sajenkova* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 249–250.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. The available drawing of this species suggests a very slender shell with highly convex whorls bearing a subsutural band. The type material has not been found, and the identity of this species remains unclear.

Conservation status. Data Deficient (Vinarski 2011t).

***Turricaspia similis* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Caspiella*) *similis* Logvinenko & Starobogatov: 375, fig. 366(11).

2016 *Pyrgula similis* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 243.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the middle Caspian Sea, 20–50 m.

Distribution. Middle and southern Caspian Basin. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. Judging from the drawing in Logvinenko and Starobogatov (1969), presenting a small slender shell with ca. 5.5 highly convex whorls, the species might be based on a juvenile specimen. It might be a junior synonym of the similarly shaped *T. meneghiniana* (Issel, 1865). Without investigating the type material, which has not been found in the ZIN collection, the identity of this species remains unclear.

Conservation status. Not assessed.

***Turricaspia simplex* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Oxyppyrgula*) *simplex* Logvinenko & Starobogatov: 367–368, fig. 363(4).
2016 *Pyrgula simplex* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 243.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle Caspian Sea, 40–120 m.

Distribution. Middle and southern Caspian Sea. This species was mentioned from depths between 200 and 900 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. As for the previous species, it is highly uncertain whether this taxon is a distinct species. It might also be based on a juvenile and could be a synonym of an earlier described species, perhaps *T. pulla* or *T. lyrata*.

Conservation status. Not assessed.

***Turricaspia spasskii* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *spasskii* Logvinenko & Starobogatov: 361, fig. 360(7).
2016 *Turricaspia spasskii* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 250.

Status. Accepted Pontocaspian species.

Type locality. Western part of the middle Caspian Sea.

Distribution. Middle and southern Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The fast growing whorls terminating in a large body whorl with expanded aperture are characteristic for this species and facilitate discrimination from other *Turricaspia* species.

Conservation status. Data Deficient (Vinarski 2011u).

***Turricaspia spica* (Eichwald, 1855)**

*1855 *Paludina spica* Eichwald: 303–304, pl. 10, figs 8, 9.
?1992 *Turricaspia spica* (Eichw.). – Anistratenko and Prisjazhnyuk: 18, fig. 2d.
2006 *Turricaspia spica* (Eichwald, 1855). – Kantor and Sysoev: 110, pl. 49, fig. F.
2009 *Turricaspia* cf. *spica* (Eichwald, 1855). – Filippov and Riedel: 70, 72, 74, 76, fig. 4e, f.
2016 *Turricaspia spica* (Eichwald, 1855). – Vinarski and Kantor: 250.

Status. Accepted Pontocaspian species.

Type locality. Ostrov Chechen' (island in NW Caspian Sea), Dagestan, Russia.

Distribution. Endemic to the Caspian Sea. Occurred also in the Aral Sea during the Holocene (Filippov and Riedel 2009) but now extinct there. It has been reported from the Holocene of Danube Delta (Anistratenko and Prisjazhnyuk 1992) (see below).

Taxonomic notes. As the oldest described species presently attributed to *Turricaspia*, the validity of this species is without doubt. Its identity, however, is poorly known, given the limited information and poor drawing provided by Eichwald (1855), as well as the largely diverging concepts applied by later authors (see Neubauer et al. 2018 for a detailed discussion of the matter). We have a geographic record (Anistratenko and Prisjazhnjuk 1992) that is outside the Caspian–Aral distribution range of this genus. Comparison of the Danube material with Caspian specimens suggests the identification might be correct, yet further detail study is required to assess whether the Danube record might actually not be an unusual form of *Laevicaspia lincta*.

Conservation status. Not assessed.

***Turricaspia turricula* (Clessin & Dybowski in Dybowski, 1887)**

*1887 *Micromelania turricula* Clessin & Dybowski in Dybowski: 34.

1888 [*Micromelania*] *turricula* n. sp. – Dybowski: 78, pl. 1, fig. 3a–c.

2006 *Turricaspia turricula* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 111, pl. 49, fig. I.

2016 *Turricaspia turricula* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 244.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The species is characterised by a slender conical shell with weakly convex whorls with weak subsutural swelling and a slightly inflated body whorl with large aperture.

Conservation status. Not assessed.

***Turricaspia uralensis* (Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Turricaspia*) *uralensis* Logvinenko & Starobogatov: 359, fig. 360(1).

2016 *Pyrgula uralensis* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 244.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the northern Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. Logvinenko and Starobogatov (1969) illustrated a comparably small shell with eight highly convex whorls, large body whorl, and large aperture. Reliable assessment of the species' status requires investigation of the type material, which has only been discovered in ZIN in June 2018 and awaits further study.

Conservation status. Not assessed.

***Turricaspia vinogradovi* (Logvinenko & Starobogatov, 1969)**

- *1969 *Pyrgula* (*Oxypyrghula*) *vinogradovi* Logvinenko & Starobogatov: 368, fig. 363(9).
 ?1971 *Pyrgula astrachanica* Pirogov: 249–251, fig. 1.
 ?2006 *Turricaspia astrachanica* (Pirogov, 1971). – Kantor and Sysoev: 105, pl. 48, fig. B.
 2006 *Turricaspia vinogradovi* (Logvinenko & Starobogatov, 1968). – Kantor and Sysoev: 111, pl. 50, fig. C.
 2016 *Turricaspia vinogradovi* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 251.

Status. Pontocaspian species, identity uncertain.

Type locality. Northern Caspian Sea.

Distribution. Northern Caspian Sea and Volga Delta (Logvinenko and Starobogatov 1969).

Taxonomic notes. The species as illustrated by Logvinenko and Starobogatov (1969) is based on a slender shell with highly convex whorls. The same traits are also typical for *Pyrgula astrachanica*; in fact, the type of *T. vinogradovi* could be a juvenile of that species. Moreover, both of them might be synonyms of *Turricaspia nossovi* Kolesnikov, 1947. Since a part of the type material of the species involved is lacking and some of the taxa are based on incomplete or presumably juvenile specimens, the identities of *Pyrgula astrachanica* and *Turricaspia vinogradovi* remain unresolved.

Conservation status. *Turricaspia vinogradovi* has not been assessed by the IUCN, *T. astrachanica* is marked as “Data Deficient” (Vinarski 2011q).

Hydrobiidae incertae sedis***Abeskunus brusinianus* (Clessin & Dybowski in Dybowski, 1887)**

- *1887 *Zagrabica Brusiniana* Clessin & Dybowski in Dybowski: 52–53.
 1888 *Zagrabica Brusiniana* n. sp. – Dybowski: 79, pl. 2, fig. 7.
 2006 *Pseudamnicola brusiniana* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 114, pl. 51, fig. J.
 2016 *Pseudamnicola brusiniana* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 222.
 2018 *Abeskunus brusinianus* (Clessin & W. Dybowski in W. Dybowski, 1887). – Neubauer et al.: 87–88, fig. 16A–I.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969, Parr et al. 2007). Mirzoev and Alekperov (2017) mention *Pseudamnicola brusinianus* from depths between 200 and 400 m in the South Caspian Basin of

Azerbaijan but we are not entirely certain whether these records might include other *Abeskunus* species as well.

Taxonomic notes. For a detailed description and discussion, see Neubauer et al. (2018).

Conservation status. Least Concern (Vinarski 2011c).

Abeskunus depressispira (Logvinenko & Starobogatov, 1969)

*1969 *Pseudamnicola* (*Abeskunus*) *depressispira* Logvinenko & Starobogatov: 381, fig. 367(14).

2016 *Pseudamnicola depressispira* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 222–223.

Status. Accepted Pontocaspian species.

Type locality. Western part of the southern Caspian Sea, northward of Kuraginsky Kamen' [= Kür Daşı] Island (approximately 39°01'05"N, 49°20'02"E), 81 m water depth.

Distribution. In addition to the type locality, specimens have been found in Holocene material retrieved near the Kura Delta, a few kilometres north of the type locality.

Taxonomic notes. Current investigations on recently collected Holocene material from the south-western Caspian Sea confirm that this species belongs to the genus *Abeskunus*. The finely ribbed, low trochiform shell facilitates distinction from its congeners. The species epithet is based on the Latin noun *spira*, spire, and is to be considered a noun in apposition (ICZN 1999, Art. 31.2.1.).

Conservation status. Data Deficient (Vinarski 2011d).

Abeskunus exiguus (Eichwald, 1838)

°1837 *Lithoclypus* [sic] *Caspicus* m. – Krynicki: 58 (nomen nudum).

*1838 *Paludina exigua* Eichwald: 152–153.

1863 *Bithinia sphaerion* Mousson: 409–410.

1874 *Lithoglyphus?* *Caspicus* Krynicki. – Martens: 80.

1877 *Lithoglyphus caspius* Grimm: 82–84, pl. 9, fig. 8.

1977 *Pseudamnicola* (*Abeskunus*) *brusiniana michelae* Tadjalli-Pour: 108, pl. 2, fig. 9.

2016 *Pseudamnicola exigua* (Eichwald, 1838). – Vinarski and Kantor: 223.

2016 *Pseudamnicola sphaerion* (Mousson, 1863). – Vinarski and Kantor: 223.

Status. Accepted Pontocaspian species.

Type locality. In fossil (likely Pleistocene) limestone of Dagestan, Russia.

Distribution. Western Caspian Sea, known from northern and southern parts. Records from the eastern Caspian Sea by Logvinenko and Starobogatov (1969) could not be confirmed.

Taxonomic notes. An in-depth study of the literature suggests that the names *Paludina exigua*, *Bithinia sphaerion* syn. n., and *Lithoglyphus caspius* all refer to the

same species. The name *Lithoglyphus caspius* was made available by Martens (1874) by referring to the description and illustration of Eichwald's species, rendering *L. caspius* a junior objective synonym of *Abeskunus exiguus*. All three taxa share the globular shape, short spire, and inflated last whorl. The subspecies *Pseudamnicola brusiniana michelae* syn. n. from Iranian coasts of the Caspian Sea closely resembles *A. exiguus* and is herein considered a synonym as well. *Abeskunus exiguus* differs from *A. brusinianus* in the highly globular shell with small spire. A revision of the species is currently being prepared.

Conservation status. Not assessed.

***Andrusovia andrusovi* Starobogatov, 2000**

*2000 *Andrusovia andrusovi* Starobogatov: 39–41, fig. 1B.

2016 *Andrusovia andrusovi* Starobogatov, 2000. – Vinarski and Kantor: 214.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the South Caspian Sea (39°05'N, 52°35'E).

Distribution. Middle and southern Caspian Sea (Starobogatov 2000).

Taxonomic notes. The species is very similar to the type species of *Andrusovia*, *A. dybowskii*, regarding the low spire. Investigation of the type material is required to clarify whether both taxa are distinct.

Remarks. Only recently, paratypes of this species were detected at the Zoological Museum of Moscow University. A study of the taxonomy of *Andrusovia* is currently under way.

Conservation status. Not assessed.

***Andrusovia brusinai* Starobogatov, 2000**

*2000 *Andrusovia brusinai* Starobogatov: 41, fig. 1C.

2016 *Andrusovia brusinai* Starobogatov, 2000. – Vinarski and Kantor: 214.

2018 *Andrusovia brusinai* Starobogatov, 2000. – Neubauer et al.: 54–56, fig. 6F–K, M–N.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the middle Caspian Sea (42°42.5'N, 51°32.5'E), at 80 m water depth.

Distribution. Northern, middle, and southern Caspian Sea (Starobogatov 2000, Neubauer et al. 2018).

Taxonomic notes. The species was recently described in detail by Neubauer et al. (2018). The species was distinguished from *A. dybowskii* and *A. andrusovi* by the higher spire, but this is a variable character. Currently, the taxonomy of *Andrusovia* species is the subject of further study.

Remarks. Starobogatov (2000) mentioned that the type material is housed in the ZIN collection, but we were unable to find the holotype and it is presumed lost. Only

recently, paratypes of this species were detected at the Zoological Museum of Moscow University and are currently being studied.

Conservation status. Not assessed.

Andrusovia dybowskii Brusina in Westerlund, 1902b

*1902b *Andrusovia Dybowskii* Westerlund: 133.

? 2000 *Andrusovia dybowskii* Brusina in Westerlund, 1903. – Starobogatov: 39, fig. 1A.

2016 *Andrusovia dybowskii* Brusina in Westerlund, 1903. – Vinarski and Kantor: 214.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Starobogatov 2000).

Taxonomic notes. Apparently, Brusina considered both the more conical and flatter shells (“conoidea vel discoidea”) to belong to a single species. Starobogatov (2000) in turn referred only the flat type to as *Andrusovia dybowskii* and considered the conical ones to belong to separate species (*A. brusinai* and *A. marina*). The recently rediscovered type material represents the conico-globular type and is currently subject of study by V. Anistratenko and colleagues.

Conservation status. Not assessed.

Andrusovia marina (Logvinenko & Starobogatov, 1969)

*1969 *Horatia (Caspiohoratia) marina* Logvinenko & Starobogatov: 382, fig. 367(18).

2000 *Andrusovia marina* (Logvinenko & Starobogatov, 1969). – Starobogatov: 41–42, fig. 1D.

2016 *Andrusovia marina* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 214–215.

Status. Pontocaspian species, identity uncertain.

Type locality. Northern slope of the middle Caspian Sea Basin, 43°32.5'N, 49°17.5'E, 60 m water depth.

Distribution. Middle and southern Caspian Sea (Starobogatov 2000). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Horatia marina*).

Taxonomic notes. According to Neubauer et al. (2018), this species might be a senior synonym of *A. brusinai* Starobogatov, 2000. Inspection of recently discovered type material appears to support that view, but more in-depth studies are required to evaluate the status of this species.

Remarks. The holotype is not traced and presumed lost. Only recently, paratypes of this species were detected at the Zoological Museum of Moscow University and are currently being studied.

Conservation status. Not assessed.

Family Lithoglyphidae Tryon, 1866***Lithoglyphus naticoides* (Pfeiffer, 1828)**

*1828 *Paludina naticoides* Pfeiffer: 45–46, pl. 8, figs 1, 2, 4.

2012 *Lithoglyphus naticoides* (Pfeiffer, 1828). – Welter-Schultes: 41, unnumbered text figures.

2016 *Lithoglyphus naticoides* (C. Pfeiffer, 1828). – Vinarski and Kantor: 253.

Status. Accepted native species.

Type locality. In the Danube at Vienna, Austria, and at Pesth (today part of Budapest), Hungary.

Distribution. Originally only in rivers entering the Black Sea, in the Danube up to Regensburg (Germany). After 1800, also introduced to Elbe and Rhine regions by artificial canals; after 1900 in France (Welter-Schultes 2012). Very common in the Volga Delta (Vinarski et al. 2018).

Conservation status. Least Concern (Van Damme 2011b).

Family Tateidae Thiele, 1925***Potamopyrgus antipodarum* (Gray, 1843)**

*1843 *Amnicola antipodarum* Gray: 241.

1951 *Potamopyrgus jenkinsi* E. A. Smith 1889. – Grossu: 693–695, fig. 1a–d.

1966 *P.[yrgula] (Trachycaspia?) grossui* Golikov and Starobogatov: 359.

1991 *Potamopyrgus polistchuki* Anistratenko: 75, fig. 1(2).

1995 *Potamopyrgus alexenkoae* Anistratenko in Anistratenko and Stadnichenko: 92–93, fig. 69.

2012 *Potamopyrgus antipodarum* (Gray, 1843). – Welter-Schultes: 40, unnumbered text figures.

Status. Accepted species, invasive.

Type locality. New Zealand (no details).

Distribution. Originally from New Zealand, probably introduced in 1859 to England, in 1872 to Tasmania, in 1895 to mainland Australia, in ca. 1900 to European mainland (Ponder 1988), and in 1987 to North America (Zaranko et al. 1997).

Taxonomic notes. The two Black Sea species *P. polistchuki* syn. n. and *P. alexenkoae* syn. n. are here considered as junior synonyms of *P. antipodarum*, differing only very weakly in outline. Vinarski and Kantor (2016) listed *Pyrgula (Trachycaspia?) grossui* syn. n. Golikov & Starobogatov in the synonymy of *T. dimidiata* (Eichwald, 1838). Golikov and Starobogatov (1966) introduced this species as new name for the supposedly misidentified *Potamopyrgus jenkinsi* sensu Grossu (1951) from Razim Lake

in Romania. The shell they later illustrated (Golikov and Starobogatov 1972) indeed shows similarities with *T. dimidiata*. The shell illustrated in Grossu (1951), however, is completely different and shows a keeled form of *P. antipodarum*.

Conservation status. Least Concern (Van Damme 2013).

Family Planorbidae Rafinesque, 1815

Gyraulus eichwaldi (Clessin & Dybowski in Dybowski, 1887)

°1876 *Pl.[anorbis] Eichwaldi*. – Grimm: 157 (nomen nudum).

*1887 *Planorbis Eichwaldi* Clessin & Dybowski in Dybowski: 49–52.

1888 *Planorbis Eichwaldi* Grimm. – Dybowski: 79, pl. 2, fig. 11a–c, pl. 3, fig. 10a–c.

?1966b *Anisus (Andrusowia) [sic] eichwaldi infundibularis* Logvinenko and Starobogatov: 1472, fig. 4.

?1977 *Anisus djalali* Tadjalli-Pour: 109, pl. 2, fig. 10.

2016 *Gyraulus (Gyraulus) eichwaldi* (Grimm in W. Dybowski, 1888). – Vinarski and Kantor, 2016: 378.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 900 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Anisus eichwaldi*).

Taxonomic notes. The species is characterised by a relatively large, asymmetrical shell. *Anisus eichwaldi infundibularis* is probably a morphotype of *G. eichwaldi*. We are uncertain about the status of *Anisus djalali* Tadjalli-Pour, 1977 as the description is very brief and the photographs are not very clear. It may be within the range of the morphological variability of *G. eichwaldi*.

Conservation status. Not assessed.

Gyraulus dybowskii (Kolesnikov, 1947)

*1947 *Planorbis eichwaldi* var. *dybowskii* Kolesnikov: 109, 112, fig. in tab. 1.

1966b *Anisus (Andrusowia) [sic] kolesnikovi* Logvinenko and Starobogatov: 1473, fig. 5.

1966b *Anisus (Andrusowia) [sic] kolesnikovi sublittoralis* Logvinenko and Starobogatov: 1472–1473, fig. 6.

2016 *Gyraulus (Gyraulus) kolesnikovi* (Logvinenko & Starobogatov, 1966). – Vinarski and Kantor, 2016: 379.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea, 40°37'N, 50°52'E, 115 m.

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South

Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Anisus colesnikovi* [sic]).

Taxonomic notes. Logvinenko and Starobogatov (1966b) considered this species and *Andrusovia dybowskii* Brusina in Westerlund, 1902b to belong in the same genus, *Anisus* (*Andrusovia*), rendering *P. dybowskii* Kolesnikov, 1947 a junior homonym. Therefore, they introduced *A. kolesnikovi* as replacement name. Since both taxa do clearly not belong to the same genus or even the same family, the replacement name is to be discarded.

The species resembles *G. eichwaldi* regarding the general habitus; it differs in the more pronounced angle at the transition between whorl flank and apical plane. A revision is required to investigate if the Caspian *Gyraulus* species are distinct species or morphotypes of *G. eichwaldi*. The generic placement follows Vinarski and Kantor (2016). Note that those authors listed the earlier described *P. eichwaldi dybowskii* Kolesnikov, 1947 as a synonym of *G. kolesnikovi*.

Conservation status. Least Concern (for *Anisus kolesnikovi*; Vinarski 2011a).

***Gyraulus sulcatus* (Logvinenko & Starobogatov, 1966, non Hilgendorf, 1867)**

*1966b *Anisus* (*Andrusowia*) [sic] *sulcatus* Logvinenko & Starobogatov: 1474, fig. 7.
2016 *Gyraulus* (*Gyraulus*) *sulcatus* (Logvinenko & Starobogatov, 1966). – Vinarski and Kantor, 2016: 382.

Status. Pontocaspian species, identity uncertain, name invalid.

Type locality. Caspian Sea, 42°45'N, 48°29'E, 79 m.

Distribution. Middle Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. The species in its present combination as *Gyraulus sulcatus* (following Vinarski and Kantor 2016) is invalid as it is a secondary homonym of the Miocene *Gyraulus sulcatus* (Hilgendorf, 1867). We refrain here from introducing a replacement name as the species' status is uncertain. It resembles *G. eichwaldi* and *G. kolesnikovi* in outline shape and differs only in the more pronounced angle between whorl flank and apical plane and the shallow furrow on the apical side. An in-depth revision is required to clarify if *Gyraulus sulcatus* is a distinct species or a mere morphotype of *G. eichwaldi* (Clessin & Dybowski in Dybowski, 1887).

Conservation status. Not assessed.

Discussion and conclusions

The annotated check-list presented here is a first attempt to assess the species diversity of the Pontocaspian molluscs by experts working in different countries and fields (neontology, palaeontology, biogeography, phylogenetics). Hitherto, progress has been limited by a number of factors: (1) fresh material for genetic studies is available only for few nominal species, and (2) the type series of many species are lost or at least have not yet been found. This concerns not only the species described by Eichwald or Grimm in the

19th century; the type specimens of many species established by Starobogatov and his co-workers in the 1960–2000s could not be traced in ZIN (Kantor and Sysoev 2006, Vinarski and Kantor 2016). Furthermore, progress has been limited by (3) a lack of representative shell samples to undertake quantitative statistical analyses of conchological variation, and (4) insufficient ecological and distribution data for many of the species.

Three species that have been reported from the Pontocaspian region are not included in this list. The bithyniid gastropod *Alocinma caspica* (Westerlund, 1902) has been described from the east side of the Caspian Sea (Beriozkina et al. 1995 indicated this record is probably from the vicinity of Krasnovodsk, Turkmenistan). However, Starobogatov et al. (2004) argued the species lives in waterbodies of Bol'shoy Balkhan (Turkmenistan) and probably not in the Caspian Sea itself (Vinarski et al. 2013, Vinarski and Kantor 2016). Furthermore, two *Pseudamnicola* species have been described from Lake Razim in Romania (*P. leontina* Grossu, 1986 and *P. razelmiana* Grossu, 1986) that is prime Pontocaspian habitat. Like bithyniids, *Pseudamnicola* has not been reported as a Pontocaspian group elsewhere, and probably they are freshwater species that live in the surrounding streams or in springs. For now, we have excluded these species from the Pontocaspian species list.

This list contains 55 accepted and a further 44 uncertain endemic Pontocaspian mollusc species (Table 2), here defined as species that are considered to be endemic for at least one of the Pontocaspian basins. There are 14 native and three immigrant species (at least in one of the Pontocaspian basins), even though some species may be native or endemic in one of the basins and have become invasive in another of the Pontocaspian Basins. All species that have an uncertain status belong to the Pontocaspian category. The Caspian Sea Basin has the highest number of accepted endemic Pontocaspian species (48) but also poses the greatest taxonomic challenges, with a further 37 species whose status are unclear.

The species richness estimate reflects the current shift of molluscan systematics from morphology-based to integrated studies, with increasing contributions of molecular and statistical species delineation approaches (Vinarski 2018). It has recently been shown that many nominal taxa of fresh- and brackish-water snails and mussels described on the basis of their shell characters (the Pontocaspian molluscs rarely were described on the base of anatomical studies) lack a genetic support (with few exceptions such as e.g., Popa et al. 2012, Stepien et al. 2013) and thus do not represent evolutionary meaningful units. On the other hand, cryptic speciation is known within many taxa of molluscs in long-lived lakes (Albrecht et al. 2006), and the Pontocaspian biota may include some previously unrecognised species. Thus, we consider our check-list rather as a starting point for further integrated research, not a definitive and fixed inventorisation of the Pontocaspian molluscs.

Anyone who reads this list or works such as Logvinenko and Starobogatov (1969) or Vinarski and Kantor (2016) may think that the Caspian Sea still maintains its unique and species-rich mollusc fauna. However, the actual state of affairs is problematic as many species thought to be endemic to this large saline lake have not been found since their description, and recent attempts to obtain fresh material for genetic studies mostly failed. Clearly, the conservation status of Pontocaspian species is insufficiently known. With our working list we aim to assist in the necessary follow-up conservation assessments.

Table 2. Pontocaspian mollusc species list. Abbreviations: Status: A – accepted, U – uncertain. Basins: AS – Aral Sea, BSB – Black Sea Basin, CSB – Caspian Sea Basin. Species are E – endemic, EX – extinct, IM – immigrant, IN – invasive, N – native (definitions in Table 1); *species encountered alive during the PRIDE program expeditions by participants; †very fresh material of species encountered, but not living specimens.

Species	Status	BSB	CSB	AS
<i>Mytilaster minimus</i> (Poli, 1795)*	A	N	IN	IM/EX
<i>Adacna laeviuscula</i> (Eichwald, 1829)	A	?	E	
<i>Adacna fragilis</i> Milaschewitsch, 1908	U	E		
<i>Adacna minima</i> Ostroumov, 1907	A		E	E/EX?
<i>Adacna minima ostroumovi</i> (Logvinenko & Starobogatov, 1967)	U		E	
<i>Adacna vitrea</i> (Eichwald, 1829)	A	E	E	E/EX?
<i>Adacna vitrea glabra</i> Ostroumov, 1905	U	E	E	
<i>Adacna vitrea bergi</i> (Starobogatov, 1974)	U			E/EX?
<i>Cerastoderma glaucum</i> (Bruguère, 1789) s.l.*	A	N	IN	IN?
<i>Cerastoderma</i> sp. A [non <i>C. rhomboides</i> (Lamarck, 1819)]*	A	N	IN	IN?
<i>Didacna baeri</i> (Grimm, 1877)	A		E	
<i>Didacna barbotdemarnii</i> (Grimm, 1877)*	A		E	
<i>Didacna eichwaldi</i> (Krynicky, 1837)	A		E	
<i>Didacna longipes</i> (Grimm, 1877)*	A		E	
<i>Didacna parallela</i> Bogachev, 1932	A		E	
<i>Didacna praetrigonoides</i> Nalivkin & Anisimov, 1914	A		E/EX	
<i>Didacna profundicola</i> Logvinenko & Starobogatov, 1966†	A		E	
<i>Didacna protracta</i> (Eichwald, 1841)	A		E	
<i>Didacna pyramidata</i> (Grimm, 1877)	A		E	
<i>Didacna trigonoides</i> (Pallas, 1771)*	A		E	
<i>Hypanis plicata</i> (Eichwald, 1829)	A	E	E	
<i>Monodacna acuticosta</i> (Logvinenko & Starobogatov, 1967)	A		E	
<i>Monodacna albida</i> (Logvinenko & Starobogatov, 1967)	A		E	
<i>Monodacna caspia</i> (Eichwald, 1829)	A		E	?
<i>Monodacna colorata</i> (Eichwald, 1829)*	A	E	IM	
<i>Monodacna filatovae</i> (Logvinenko & Starobogatov, 1967)	U		E	
<i>Monodacna knipowitschi</i> (Logvinenko & Starobogatov, 1966)	U		E	
<i>Monodacna polymorpha</i> (Logvinenko & Starobogatov, 1967)	U		E	
<i>Monodacna semipellucida</i> (Logvinenko & Starobogatov, 1967)	A		E	
<i>Abra segmentum</i> (Récluz, 1843)*	A	N	IN	IN
<i>Corbicula fluminalis</i> (Müller, 1774)	A		N/IN	
<i>Dreissena bugensis</i> Andrussov, 1897†	A	E/IN	IN	
<i>Dreissena caspia</i> Eichwald, 1855	A		E/EX	E/EX
<i>Dreissena elata</i> Andrusov, 1897	U		E/EX	
<i>Dreissena grimmi</i> (Andrusov, 1890)*	A		E	
<i>Dreissena polymorpha</i> (Pallas, 1771) s.l.*	A	N	N	N
<i>Mytilopsis leucophaeata</i> (Conrad, 1831)*	A	IN	IN	
<i>Theodoxus danubialis</i> (Pfeiffer, 1828)*	A	N		
<i>Theodoxus fluviatilis</i> (Linnaeus, 1758)	A	N		
<i>Theodoxus pallasi</i> Lindholm, 1924*	A	N	N	N/EX?
<i>Theodoxus schultzei</i> (Grimm, 1877)*	U		E	
<i>Theodoxus velox</i> V. Anistratenko in O. Anistratenko et al., 1999	A	N		
<i>Eupaludestrina stagnorum</i> (Gmelin, 1791)	A	N/IM	N/IM	
<i>Caspia baerii</i> Clessin & Dybowski in Dybowski, 1887	A	E?	E	
? <i>Caspia valkanovi</i> (Golikov & Starobogatov, 1966)	U	E		
<i>Clathrocaspia brotzkajae</i> (Starobogatov in Anistratenko & Prisjazhnyuk, 1992)	A	?E	E	
<i>Clathrocaspia gmelinii</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	
<i>Clathrocaspia isseli</i> (Logvinenko & Starobogatov, 1969)	U		E	

Species	Status	BSB	CSB	AS
<i>Clathrocaspia knipowitschii</i> (Makarov, 1938)	A	E		
<i>Clathrocaspia logvinenkoi</i> (Golikov & Starobogatov, 1966)	A	E		
<i>Clathrocaspia milae</i> Boeters, Glöer & Georgiev, 2015	U	E		
<i>Clathrocaspia pallasii</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	
<i>Ulskia behningi</i> (Logvinenko & Starobogatov, 1969)	U		E	
? <i>Ulskia derzhavini</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Ulskia ulskii</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	
<i>Ecrobia grimmi</i> (Clessin in Dybowski, 1887)*	A		N	N
<i>Ecrobia maritima</i> (Milaschewitsch, 1916)*	A	N		
<i>Ecrobia ventrosa</i> (Montagu, 1803)	A	IM		
<i>Clessiniola variabilis</i> (Eichwald, 1838)	A	E	E	
<i>Laevicaspia abichi</i> (Logvinenko & Starobogatov, 1969)	A		E	
<i>Laevicaspia caspia</i> (Eichwald, 1838)	A		E	
<i>Laevicaspia cincta</i> (Abich, 1859)	A		E	
<i>Laevicaspia conus</i> (Eichwald, 1838)	A		E	
? <i>Laevicaspia ebersini</i> (Logvinenko & Starobogatov, 1969)	U		E	
? <i>Laevicaspia ismailensis</i> (Golikov & Starobogatov, 1966)	A	E		
<i>Laevicaspia kolesnikoviana</i> (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966)	A		E	
<i>Laevicaspia kowalewskii</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	
<i>Laevicaspia lencoranica</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Laevicaspia lincta</i> (Milaschewitsch, 1908)	A	E		
? <i>Laevicaspia marginata</i> (Westerlund, 1902)	U		E	
<i>Laevicaspia sieversii</i> (Clessin in Dybowski, 1887)	U		E	
? <i>Turricaspia aenigma</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia andrussowi</i> (Dybowski & Grochmalicki, 1915)	A		E	
? <i>Turricaspia basalis</i> (Dybowski & Grochmalicki, 1915)	U		E	
? <i>Turricaspia bogatscheviana</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia chersonica</i> Alexenko & Starobogatov, 1987	U	E		
<i>Turricaspia columna</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia concinna</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia dagestanica</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia dimidiata</i> (Eichwald, 1838)	A		E	
<i>Turricaspia eburnea</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia elegantula</i> (Clessin & Dybowski in Dybowski, 1887)	U		E	
<i>Turricaspia eulimellula</i> (Dybowski & Grochmalicki, 1915)	A		E	
<i>Turricaspia fedorovi</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia grimmi</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	
<i>Turricaspia lyrata</i> (Dybowski & Grochmalicki, 1915)	A		E	
<i>Turricaspia marisnigri</i> Starobogatov in Alexenko & Starobogatov, 1987	U	E/EX?		
<i>Turricaspia meneghiniana</i> (Issel, 1865)	A		E	
<i>Turricaspia nossovi</i> Kolesnikov, 1947	A		E	
? <i>Turricaspia obventicia</i> (Anistratenko in Anistratenko & Prisjajhnjuk, 1992)	U	E		
? <i>Turricaspia pseudobacuana</i> (Logvinenko & Starobogatov, 1969)	U		E	
? <i>Turricaspia pseudodimidiata</i> (Dybowski & Grochmalicki, 1915)	U		E	
<i>Turricaspia pseudospica</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia pulla</i> (Dybowski & Grochmalicki, 1915)	A		E	
<i>Turricaspia pullula</i> (Dybowski & Grochmalicki, 1915)	A		E	
<i>Turricaspia rudis</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia sajenkovae</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia similis</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia simplex</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia spasskii</i> (Logvinenko & Starobogatov, 1969)	A		E	
<i>Turricaspia spica</i> (Eichwald, 1855)	A	?E	E	?E
<i>Turricaspia turricula</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	

Species	Status	BSB	CSB	AS
<i>Turricaspia uralensis</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Turricaspia vinogradovi</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Abeskunus brusinianus</i> (Clessin & Dybowski in Dybowski, 1887)	A		E	
<i>Abeskunus depressispira</i> (Logvinenko & Starobogatov, 1969)	A		E	
<i>Abeskunus exiguus</i> (Eichwald, 1838)	A		E	
<i>Andrusovia andrusovi</i> Starobogatov, 2000	U		E	
<i>Andrusovia brusinai</i> Starobogatov, 2000	U		E	
<i>Andrusovia dybowskii</i> Brusina in Westerlund, 1902	A		E	
<i>Andrusovia marina</i> (Logvinenko & Starobogatov, 1969)	U		E	
<i>Lithoglyphus naticoides</i> (Pfeiffer, 1828)*	A	N	IM?	
<i>Potamopyrgus antipodarum</i> (Gray, 1843)*	A	IM		
<i>Gyraulus eichwaldi</i> (Clessin & Dybowski in Dybowski, 1887)†	A		E	
<i>Gyraulus dybowskii</i> (Kolesnikov, 1947)	U		E	
<i>Gyraulus sulcatus</i> (Logvinenko & Starobogatov, 1966)	U		E	

Most taxonomic difficulties were encountered for the bivalve genera *Monodacna* and *Dreissena* and the Pyrgulinae gastropods (especially genera *Turricaspia* and *Laevicaspia*). Furthermore, there is an urgent need to assess whether representatives of species complexes in the three main Pontocaspian basins (Aral Sea, Caspian Sea, Black Sea) concern separate species as several of these regional populations are in immediate danger of extinction or already extinct (for example with the disappearance of the Aral Sea). Combined methodological efforts will enable us to estimate the extent and characterise the nature of Pontocaspian faunal turnover, and this species list is a first attempt in the required uniform taxonomic base.

Acknowledgments

The PRIDE program has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 642973. TAN was supported by an Alexander-von-Humboldt Scholarship. Further support came from the German Research Foundation (DFG, grant no. WI1902/14) to TW. MV has financial support from the Russian Ministry of Higher Education and Science (project no. 6.1352.2017/4.6). TY was supported by the Russian Science Foundation (grant no. 16-17-10103). We thank Ana Bianca Pavel (Geocomar, Constanța, Romania) and AS Gasanova (Makhachkala, Russia) for additional observations on living species occurrences. We are furthermore grateful to Dietrich Kadolsky and Mathias Harzhauser, as well as to the editor Eike Neubert and the technical editor Nathalie Yonow, for constructive comments.

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ENDEMIC CASPIAN SEA MOLLUSKS IN HOTSPOT AND NON-HOTSPOT
AREAS DIFFERENTIALLY AFFECTED BY ANTHROPOGENIC PRESSURES

2020 | *Journal of Great Lakes Research*

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Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijglr

Endemic Caspian Sea mollusks in hotspot and non-hotspot areas differentially affected by anthropogenic pressures

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ARTICLE INFO

Article history:

Received 1 August 2019

Accepted 12 December 2019

Available online xxxx

Communicated by Walter Salzburger

Keywords:

Caspian Sea

Endemism

Hotspots

Spatial data analysis

Aquatic invertebrates

Environmental degradation

ABSTRACT

The Caspian Sea is renowned for its endemic mollusk biodiversity. However, over the past decades, increasing anthropogenic pressures have caused decreases in abundances and even extinction of species. Both key pressures and endemic taxa are distributed spatially unevenly across the Caspian Sea, suggesting that ecologically different taxa such as gastropods and bivalves are also affected differentially. In addition, hotspot and non-hotspot areas for these taxa might differ quantitatively in pressure scores and qualitatively in key individual anthropogenic pressures. To test this working hypothesis, hotspot areas for endemic bivalve and gastropod species were identified using stacked species ranges. Cumulative and individual pressure scores were estimated for hotspot and non-hotspot areas of bivalves and gastropods. Differences in cumulative and individual pressure scores were tested for significance using non-parametric MANOVA and Wilcoxon rank sum tests, respectively. We identified various mollusk biodiversity hotspots across locations and depths, which are differentially affected both in terms of cumulative pressure scores and in the composition of the contributing individual pressures. Similarly, hotspot and non-hotspot areas for both bivalves and gastropods are differentially affected by anthropogenic pressures. By defining endemic hotspot areas and the respective anthropogenic pressures, this study provides an important baseline for mollusk-specific conservation strategies.

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Introduction

The Caspian Sea is the largest endorheic lake in the world and renowned for its diverse endemic faunas in many higher taxonomic groups (Karpinsky, 2005; Wesselingh et al., 2019; Zenkevitch, 1963). These endemic faunas have evolved under brackish water conditions in relative isolation and are therefore unique in the world (Karpinsky, 2005; Zenkevitch, 1963).

However, over the last decades, anthropogenic pressures, such as poaching, stream flow regulation, introduction of invasive species, oil extraction and chemical pollution (Karpinsky et al., 2005; Lattuada et al., 2019; Shiganova, 2010; Zonn, 2005), have become strong pressures acting on endemic Caspian Sea faunas (Dumont, 1995; Karpinsky, 2005; Mammadov et al., 2016; Zorbaliyeva et al., 2016; Zonn, 2005). As a consequence, many taxa have experienced

decreases in abundance and/or range reductions over the last decades. This is particularly evident in the Mollusca, one of the most species rich phyla in the Caspian Sea, represented in this water body by the two classes Gastropoda and Bivalvia. According to Wesselingh et al. (2019), there are at least 19 and 52 endemic bivalve and gastropod species, respectively. However, at least 5 of them are in immediate danger of extinction or already extinct (Wesselingh et al., 2019, see also Electronic Supplementary Material (ESM) Table S1 for the full list of endemic species).

Whereas the exact impacts of individual anthropogenic pressures on these endemic Caspian Sea mollusks are not well understood, a recent assessment indicated that key pressures are spatially unevenly distributed across the Caspian Sea and that coastal areas are generally more affected than deep-water regions (Lattuada et al., 2019). These findings have two important implications for conservation strategies. Firstly, ecologically different groups may be differentially affected by anthropogenic pressures. Endemic Caspian Sea bivalves, for example, which mainly occur

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<https://doi.org/10.1016/j.jglr.2019.12.007>

0380-1330/© 2019 Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.

in littoral and sublittoral zones, may be more affected by shallow-water pressures such as poaching and the introduction of invasive species. In contrast, endemic gastropod species, which predominantly inhabit the profundal zone, might be more affected by deep-water pressures such as chemical pollution. Second, the richness of endemic mollusk species is not evenly distributed across the Caspian Sea, and many endemic taxa were described from few 'hotspot' areas such as off the coasts of Azerbaijan and Russia (Karpinsky, 2002; Parr et al., 2007; see also Fig. 1). Thus, hotspot and non-hotspot areas might differ quantitatively in pressure scores and qualitatively in key individual anthropogenic pressures. The main goal of this paper is to test the working hypothesis that endemic bivalve and gastropod species in hotspot areas, and hotspot vs. non-hotspot areas within bivalves and gastropods, are differentially affected by major anthropogenic pressures.

In this paper we have three objectives. The first is to identify hotspot areas for three taxa: total mollusks, gastropods only and bivalves only, as the 2.5% of areas with the highest number of species (sensu Orme et al., 2005). To avoid a possible bias caused by the recent biodiversity crisis in the Caspian Sea, historical data for the spatial (horizontal) and bathymetric (depth) distribution of endemic species generated over the past 150 years were used for the analyses (summarized in Wesselingh et al., 2019). The second objective is to estimate spatially explicit anthropogenic pressure scores. Both for hotspot and non-hotspot areas of the three taxa, major individual and cumulative pressure scores were calculated based on the data assembled by Lattuada et al. (2019). The last objective is to test for significant differences in cumulative and individual pressure scores between hotspot and non-hotspot areas for all taxa.

Materials and methods

Study system

The Caspian Sea is located between Asia and Europe and bordered by five countries: Russia, Kazakhstan, Turkmenistan, Iran and Azerbaijan. It has a surface area of about 370,000 km² and is divided into three sub-basins based on geophysical characteristics (Fendereski et al., 2014; Rodionov, 1994). Maximum water depths range from 30 m in the northern Caspian Sea basin to >1000 m in the southern Caspian Sea basin. Likewise, salinities vary between <10 PSU in the northern Caspian Sea basin and around 13 PSU in the middle and southern Caspian Sea basins (Kosarev, 2005). Recently, the Caspian Sea has been divided into ten ecoregions

based on ecologically relevant environmental variables such as salinity, water temperature and total suspended matter (Fendereski et al., 2014).

Reconstruction of hotspot areas of endemic mollusk richness

In this study we used distribution data for 71 confirmed endemic mollusk species (19 bivalve and 52 gastropod species), as listed by Wesselingh et al. (2019), to calculate individual species ranges. If these data were not available in Wesselingh et al. (2019), we extracted additional bathymetrical data from the primary literature (see *ESM Table S1*). For three species for which no detailed information was obtainable, the Caspian Sea ecoregions matching the type locality were used as species ranges (*ESM Table S1*). This is justifiable as ecoregions are reliable habitat proxies (Fendereski et al., 2014). The full list of species is available in *ESM Table S1*.

We calculated species ranges by extracting spatial and bathymetric information from the raster file of the Caspian Sea bathymetry at 1 ArcMin resolution (Holt et al., 2009). Each range results in a binary raster where 1 is the range distribution and 0 is the area outside the range. Ranges were then summed to create a range stack, which represents the total number of endemic mollusk species for each 1 ArcMin raster cell (range information are freely available as GeoTIFF files at the PANGAEA data publisher, DOI: <https://doi.pangaea.de/10.1594/PANGAEA.908169>). To obtain hotspots of endemic species richness, the 2.5% of the range stack with the highest number of species were retained. This threshold was proposed to represent a broad range of studies (Orme et al., 2005). The non-hotspot areas are defined by the remaining 97.5% of cells. We did all analyses for each taxon separately with the *raster* package (Hijmans, 2018) in the R statistical environment, version 3.4.3.0097 (R Core Team, 2019).

Spatially explicit estimation of anthropogenic pressure scores

For this study, the five most relevant anthropogenic pressures in the Caspian Sea were used as identified by Lattuada et al. (2019). These are poaching, chemical pollution, invasive species, river stream flow regulation in the Caspian catchments and oil industry disturbances, which contributed >90% to the cumulative pressure score (Lattuada et al., 2019). Individual anthropogenic pressure layers and methodological details are available at the PANGAEA data publisher (<https://doi.org/10.1594/PANGAEA.900207>).

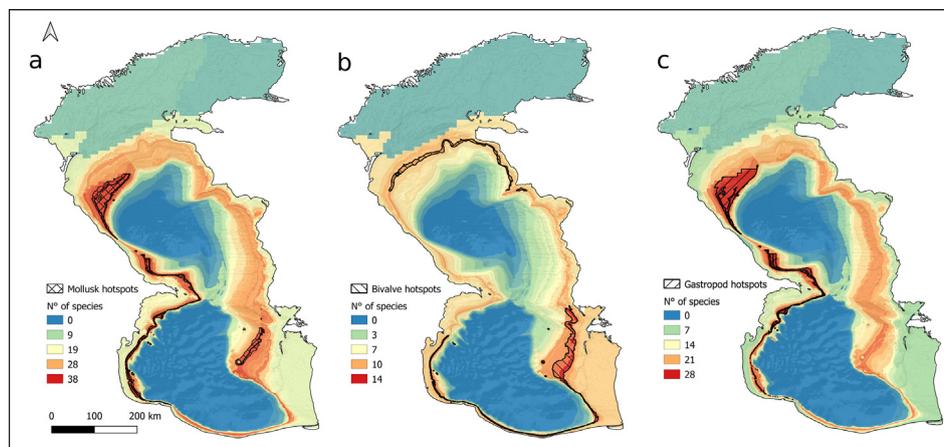


Fig 1. Visualization of hotspot areas and total endemic species richness for Caspian Sea mollusks. Hotspot areas represent the 2.5% of grid cells with the highest number of species for mollusks (a), bivalves (b) and gastropods (c).

Please cite this article as: M. Lattuada, C. Albrecht, F. P. Wesselingh et al., Endemic Caspian Sea mollusks in hotspot and non-hotspot areas differentially affected by anthropogenic pressures, *Journal of Great Lakes Research*, <https://doi.org/10.1016/j.jglr.2019.12.007>

These five anthropogenic pressure scores were extracted for the hotspot and non-hotspot areas of total mollusks, gastropods only and bivalves only. Then, the mean individual and cumulative pressure scores were computed averaging the pressure score values of the grid cells falling in the hotspot and non-hotspot areas of the three taxa. Furthermore, the individual pressure percentage contribution to the cumulative pressure scores was calculated as proportion of the mean cumulative pressure score for the hotspot and non-hotspot areas of the three taxa.

Test for significant differences in pressure scores

To test whether cumulative pressure scores were significantly different between hotspot and non-hotspot areas for total mollusks, bivalves only and gastropods only, we first used the Shapiro test to check for the normality of the cumulative pressure score distribution. As the results indicated a non-normal distribution, a non-parametric MANOVA test was employed with the function *rankMANOVA* from the R package of the same name (Dobler et al., 2019). The test was run with 10,000 resampling iterations, each based on a wild bootstrap approach with Rademacher weights (Dobler et al., 2019). As a Post Hoc test, individual anthropogenic pressure score differences within the three group hotspots and between hotspot and non-hotspot areas were tested for each taxon using a Wilcoxon rank sum test function contained in the R package *stats* (R Core Team, 2019). To address the multiple comparisons in individual pressure scores within the three hotspots, we used a Bonferroni correction.

Results

Endemic species richness hotspots

We identified hotspot regions for total mollusks, bivalves only and gastropods only in different locations with limited partial overlap. The highest numbers of endemic species in any 1 ArcMin raster cell were 38, 14, and 28 for mollusks, bivalves, and gastropods, respectively. Endemic mollusk hotspot areas contained 35–38 co-occurring species (representing 49.3%–53.5% of the total number of endemic species). These areas covered a total area of about 7230 km² (or around 2% of the total lake area) and were predominantly located in the western part of the middle and southern Caspian Sea basins and in the eastern part of the southern Caspian Sea basin (Fig. 1a) in water depths between 31 and 62 m.

Hotspot areas for endemic bivalves contained 11–14 species (57.9%–73.7% of total number of species). They were distributed over a total area of 7340 km² and could be found in the transitional zone between the northern and the middle Caspian Sea basin as well as in the western and eastern parts of the southern Caspian Sea basin (Fig. 1b) in depths between 31 and 39 m.

Gastropod hotspot areas contained 26–28 endemic species (50.0%–53.8% of total number of species), covered 7133 km² and were mainly located in the western parts of the middle and southern Caspian Sea basins between 41 and 74 m (Fig. 1c).

Anthropogenic pressure scores

Cumulative pressure scores in hotspot areas were significantly different ($Z = 1437.061$, $p < 0.001$) and the means corresponded to 0.81, 1.09 and 0.71 for total mollusks, bivalves only and gastropods only, respectively. Values for non-hotspot areas were 1.06 (mollusks), 1.06 (bivalves) and 1.07 (gastropods). Most hotspot areas were located outside areas with the highest cumulative pressure scores (Fig. 2).

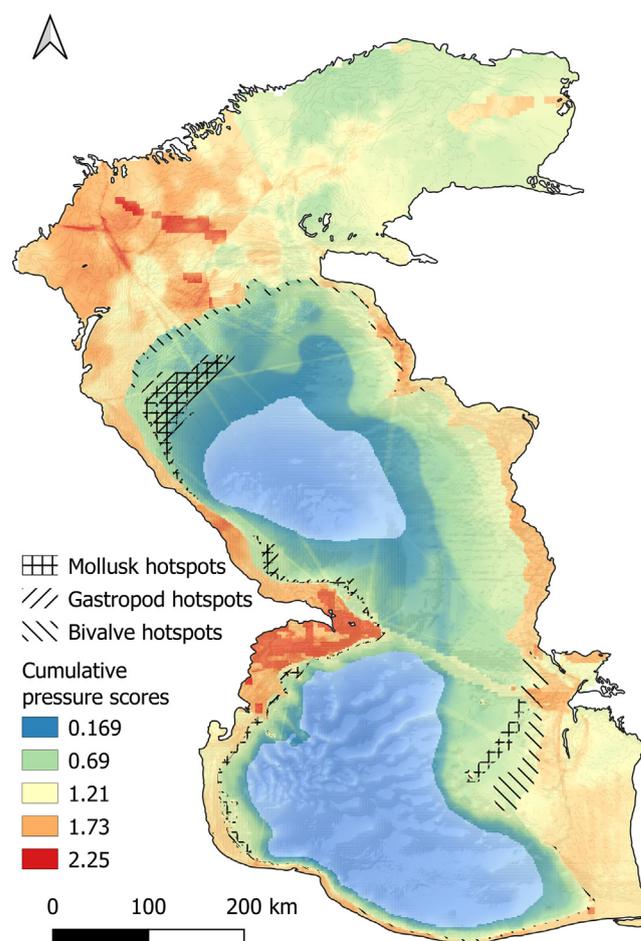


Fig 2. Locations of mollusk hotspot areas in the Caspian Sea in relation to the cumulative pressure scores for five major anthropogenic pressures. The maximum theoretical value for cumulative pressure scores is 4; the highest recorded score is 2.25. Pressure scores were only calculated for water depth <400 m depth, i.e. the threshold for mollusk occurrences.

Of the five major anthropogenic pressures analyzed, chemical pollution and invasive species dominated in hotspot areas for all taxa (Fig. 3). Both chemical pollution ($Z = 232.67$, $p < 0.001$) and invasive species ($Z = 370.78$, $p < 0.001$) resulted in significantly different pressure scores within hotspots. In non-hotspot areas, the largest contributions in cumulative pressure scores were related to chemical pollution and poaching (Fig. 3).

Differences in pressure scores between hotspot and non-hotspot areas

For all taxa, cumulative anthropogenic pressure scores were significantly different between hotspot and non-hotspot areas (total mollusks: $Z = 13969.47$, $p < 0.05$, bivalves only: $Z = 13726.57$, $p < 0.05$, gastropods only: $Z = 9683.636$, $p < 0.05$, Fig. 3). Whereas cumulative pressure scores for mollusks and gastropods were significantly lower in hotspot vs. non-hotspot areas, bivalves show a significant higher score in hotspot (1.09) compared to non-hotspot areas (1.06). As for the contribution of individual pressures, differences between hotspot and non-hotspot areas for each taxon were also significant (all $p < 0.05$, see Fig. 3 for differences in means and *ESM Table S2* for the summary statistics).

Discussion

The main goal of our study was to test the working hypothesis that both endemic bivalve vs. gastropod species and hotspot vs. non-hotspot areas are differentially affected by major anthro-

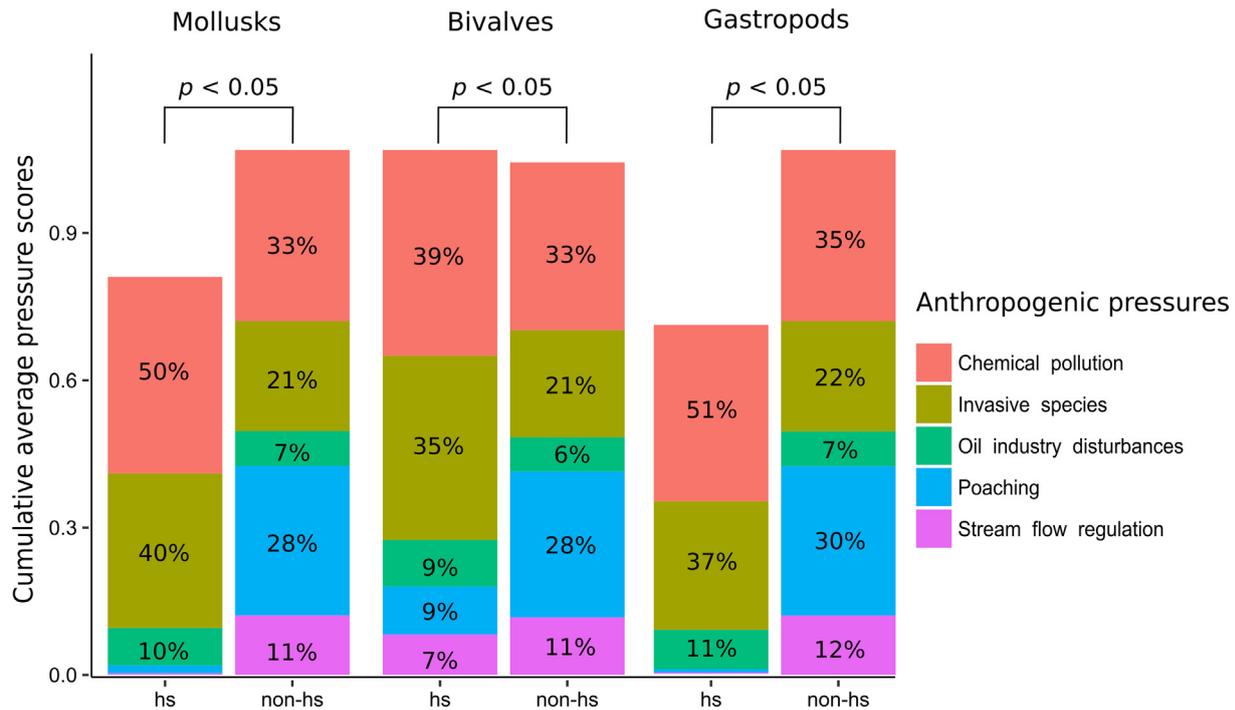


Fig 3. Barplots of cumulative and individual average pressure scores in Caspian Sea hotspot (hs) and non-hotspot (non-hs) areas for total mollusks, bivalves and gastropods. For all taxa, cumulative pressure scores are significantly different between hotspot and non-hotspot areas ($p < 0.05$). Likewise, the contributions of individual pressures are significantly different between hotspot and non-hotspot areas for all three taxa ($p < 0.05$). Percentages in the bars indicate the contribution of each individual pressure to the cumulative pressure score.

pogenic pressures in the Caspian Sea. This hypothesis will be discussed below in the context of: i) a differential spatial and bathymetric distribution of hotspots for bivalves and gastropods, ii) differences in anthropogenic pressures in bivalve vs. gastropod hotspot areas and iii) differences in anthropogenic pressures in hotspot vs. non-hotspot areas. Finally, we outline some implications for the conservation of endemic Caspian Sea mollusk.

Differential spatial and bathymetric distribution of endemic richness hotspots

Hotspot areas for bivalves and gastropods in the Caspian Sea are differentially distributed both spatially and bathymetrically. These patterns are likely driven by a complex interplay of community assembly processes such as environmental filtering and biotic interactions (Hauffe et al., 2016; van der Plas et al., 2015). In general, both endemic bivalve and gastropod richness in the northern Caspian Sea basin is low due to fluctuating environmental conditions, tolerable only by specialized groups, such as dreissenids and cardiid (Wesselingh, 2007). Moreover, shallow waters harbor only few endemic mollusk species due to: i) high predation pressures (e.g. Karpinsky, 2010, 1992), ii) high competition with native and non-native species (e.g. Colwell and Lees, 2000; Karpinsky, 1992; Malinovskaya and Zinchenko, 2010; Miyamoto et al., 2014) and iii) fluctuating limnological conditions (Guseinov, 2005; Malinovskaja et al., 1998; Malinovskaya and Zinchenko, 2010). Likewise, areas below 400 m water depth seems to be uninhabitable for most mollusk species (Parr et al., 2007).

These optima of endemic bivalve and gastropod richness in relatively narrow bathymetric zones in the middle and southern Caspian Sea basins might be reinforced by the mid-domain effect, i.e. an increased species richness in the center of a bounded area (Colwell and Lees, 2000; Miyamoto et al., 2014), which has previously been observed in other ancient lakes such as Lake Ohrid (Hauffe et al., 2011).

However, considering the distinct differences in the spatial and bathymetric distribution of bivalve and gastropod hotspots, the underlying drivers causing these dissimilarities remain largely unknown. Very likely, differential water-depth dependent, environmental filtering and species interactions might play a role. For example, bivalve species typically rely more on phytoplankton as food compared to gastropod species. As phytoplankton biomass is higher in shallower Caspian Sea waters (Nasrollahzadeh et al., 2014), this may explain why bivalve hotspot areas can be found in slightly shallower depths than gastropod hotspot areas. Moreover, the filter feeding bivalves are generally more abundant in shallower waters with more intense water movements (Cai et al., 2017).

Differences in anthropogenic pressures in bivalve vs. Gastropod hotspot areas

Besides significant quantitative differences in cumulative pressures scores between bivalve and gastropod hotspot areas, there are also significant qualitative differences in the composition of the contributing individual pressures. These might be related to functional traits such as body size, motility and feeding (Cai et al., 2017; Ellis et al., 2017), which may counteract or increase the effects of anthropogenic pressures in specific groups (Cai et al., 2017; Ellis et al., 2017). In the Caspian Sea, responses of endemic species are of particular interest for conservation, as several species are rare and/or spatially restricted. As a consequence, the accumulation of various pressures could have a synergistic effects, as indicated by ecosystem alterations following the invasion of *Mnemiopsis leidyi* (Pourang et al., 2016; Roohi et al., 2010).

Differences in anthropogenic pressures in hotspot vs. non-hotspot areas

Whereas gastropod hotspot areas were significantly less affected by anthropogenic pressures than non-hotspot areas, the

situation is reversed in bivalves, where hotspot areas were slightly more affected than non-hotspot areas. Besides differential water-depth dependent environmental filtering and species interactions, differential dispersal limitations in bivalve and gastropod species may play a role. Whereas bivalve species have a planktonic larval stage, facilitating rapid spread and large ranges, most endemic gastropod species in the region are direct developers (Anistratenko, 2013). This results in typically smaller ranges and/or patchy distributions (Grimm, 1877; Karpinsky, 2002; Parr et al., 2007). Thus, the gastropod hotspot areas identified (Fig. 1c) may well function as micro-refugia that are supported by locally favorable conditions. Such small refugia often play an important role in the maintenance of endemic gastropods in long-lived lakes (Clewing et al., 2016; Hauffe et al., 2011).

Implications for conservation of Caspian endemic mollusks

Conservation strategies for endemic mollusk species in the Caspian Sea suffer from a poor data base, mainly due to the lack of current monitoring information for endemic mollusks (for details see Wesselingh et al., 2019). New basin-wide surveys should be implemented as many endemic species (e.g., *Dreissena* spp. and *Adacna* spp.) have experienced decreases in abundances and ranges over the last decades (Kosarev and Yablonskaya, 1994). Some species like *Dreissena caspia* and *Dreissena elata* might have gone extinct (Wesselingh et al., 2019). Exact ranges remain unknown and reliable information on abundances are sparse for many mollusk species. Moreover, since the breakdown of the former Soviet Union, taxonomic efforts in the area have strongly decreased (Parr et al., 2007). This prevented the collection of fresh material to assist taxonomical classification with modern molecular techniques. Therefore, taxonomic uncertainties in many nominal species and subspecies remain an issue.

Pending the availability of such information, the results presented in the current study may provide some early important implications for management and conservation strategies: 1) the here identified hotspot areas for endemic gastropod and bivalve species might help in the identification of Key Biodiversity Areas (KBA); 2) the finding that both bivalve and gastropod hotspot areas are affected by the same key pressures (i.e. chemical pollution, invasive species and oil industry disturbances) implies that both taxa (and likely other invertebrate taxa as well) might benefit from similar conservation strategies; and 3) the potential presence of micro-refugia in the Caspian Sea might aid the efficient search for potentially extinct species. We strongly encourage conservation biologists and practitioners to use the mollusk hotspot areas identified in this study as target sites for monitoring and conservation efforts to protect the unique Caspian Sea mollusk fauna.

Conclusions

Our study demonstrated that hotspot areas for bivalve and gastropod species in the Caspian Sea are differentially distributed both spatially and bathymetrically. Bivalve hotspot areas mainly occur in water depths between 31 and 39 m in the transitional zone between the northern and the middle Caspian Sea basin, and in the western and eastern parts of the southern Caspian Sea basin. In contrast, gastropod hotspot areas can typically be found in water depths between 41 and 74 m in the western parts of the middle and southern Caspian Sea basins.

Spatially explicit estimations show different cumulative pressure scores for bivalve and gastropod hotspots areas (1.09 and 0.71 for bivalve and gastropod hotspot areas, respectively) and a different composition of the contributing individual pressures. However, the key anthropogenic pressures are similar. Moreover,

hotspot areas for gastropods have a significantly lower cumulative pressure score compared to non-hotspot areas. In contrast, the cumulative pressure score for bivalve hotspot areas is slightly larger than for on-hotspot areas.

Based on these findings, our working hypothesis that endemic bivalve and gastropod species, on the one hand, and hotspot and non-hotspot areas, on the other hand, are differentially affected by major anthropogenic pressures cannot be rejected.

This study has important implications for the protection and conservation of endemic mollusk species in the Caspian Sea. Total mollusk hotspot areas should become a major focus of conservation strategies; for now, there are no differential conservation measures necessary for bivalve and gastropod hotspot areas due to similar anthropogenic pressures and more ecological information is needed to enhance conservation measures.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was supported by the project PRIDE (Pontocaspian Rise and DEmise), which has received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No 642973. Partial financial support came also from the Russian Ministry of Higher Education and Science for financial support (project No. 6.1352.2017/4.6 to MV).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2019.12.007>.

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CASPIAN SEA ENVIRONMENTAL VARIABLES: AN EXTENSION OF THE BIO-ORACLE OCEAN DATA SET

2020 | *Ecology*

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Data Papers

Ecology, 0(0), 2020, e03076
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Caspian Sea environmental variables: an extension of the Bio-ORACLE ocean data set

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Citation: Lattuada, M., T. Wilke, and N. Raes. 2020. Caspian Sea environmental variables: an extension of the Bio-ORACLE ocean data set. *Ecology* 00(00):e03076. 10.1002/ecy.307610.1002/ecy.3076

Abstract. The Caspian Sea hosts unique native and endemic faunas. However, it is also a source and sink of invasive alien species (IAS), with some listed among the worst 100 invasive species by the IUCN. A common approach to study biodiversity and biogeographic patterns or to predict the invasive potential of species is the application of ecological niche models and species distribution models. These are statistical methods using spatially gridded environmental data and species occurrence information. As the Caspian Sea is not connected to the world's oceans, spatially gridded environmental data for the Caspian Sea are not available in the widely used Bio-ORACLE marine data set. To address this issue, we compiled 28 ecologically relevant spatially gridded environmental variables using Kriging interpolation of point data to model minimum, maximum, mean, and range of temperature, salinity, and dissolved oxygen for the surface and benthic zones of the Caspian Sea. Data were retrieved from the World Ocean Database. Additionally, we utilized raster statistics to create surface layers of maximum, mean, minimum, and range of chlorophyll *a* from remotely sensed data. We developed these environmental variables as they were previously confirmed to be relevant for the biogeographical classification of the Caspian Sea. To allow projections of models across the world's oceans into the Caspian Sea (and vice versa), we matched our raster dimensions with those of the Bio-ORACLE data set. Our extension of the Bio-ORACLE data set with data from the Caspian Sea provides an important basis for the monitoring and evaluation of suitable habitats for native species as well as predicting the invasive potential of Caspian Sea species into world oceans. Please cite this Data Paper and the associated Figshare data set if the data are used in publications.

Key words: *chlorophyll a; ecological modeling; invasive alien species; oxygen; salinity; sea surface temperature.*

The complete data sets corresponding to abstracts published in the Data Papers section in the journal are published electronically as Supporting Information in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3076/supinfo>.

DATA AVAILABILITY

The data set is also available on Figshare: <https://doi.org/10.6084/m9.figshare.9980954>

Manuscript received 9 November 2019; revised 25 February 2020; accepted 16 March 2020. Corresponding Editor: William K. Michener.

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III. APPENDIX



The map "Provinciarum Persicarum Kilaniae nempe Chirvaniae Dagestaniae" of the Caspian Sea territories, drawn by Johann Baptist Homann in 1720.

ACKNOWLEDGMENTS

I sincerely thank Prof. Thomas Wilke for involving me as an Early Stage Researcher in the PRIDE project. His support and contribution taught me a wide range of skills to become a better researcher. I especially want to thank him for the considerable effort he made to improve my writing and structuring scientific papers.

I also want to acknowledge the wonderful colleagues and friends in the Department of Animal Ecology & Systematics group, who supported, advised and encouraged me throughout my PhD. I especially want to thank, Dr. Christian Albrecht, Dr. Elena Jovanovska, Dr. Torsten Hauffe, Dr. Diana Delicado and Dr. Arthur Sands for the proactive and essential contribution to my PhD that goes far beyond my scientific outputs. Besides, I thank the personal support of the other member of the working group Catalina Ramirez-Portilla, Dr. Elena Quintanilla, Dr. Ivan Calixto-Botia and Dr. Sebastian Celis. Likewise, I want to thank the International Giessen Graduate Centre for the Life Sciences (GGL) network for the exciting discussions and for the grant which allowed me to stay one month at the Zoological Museum of the Zoological Institute of the Russian Academy of Sciences to collect valuable data for this thesis.

This PhD was in the frame of the PRIDE project, funded by the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No 642973. Thus, I am extremely grateful to the funds made available by the EU to carry out this awesome project, which greatly enhanced my scientific background and help to extend my professional and personal network through great experiences. I want to thank all the members and colleagues of the PRIDE science team, and particularly to Dr. Frank Wesselingh and Caroline van Impelen, who led PRIDE with their positive attitude and enthusiasm. Dr. Niels Raes strongly contributed to my research, giving me an essential hand in the development of the models I used in this PhD. Likewise, I thank all the other 14 Early Stage Researchers, who all became friends, especially Aleksandre Gogaladze, Lea Rausch, Manuel Sala-Perez and Alberto Martinez-Gandara. Prof. Maxim Vinarski and Dr. Pavel Kijashko helped with the logistic and scientific part of this project and supported me during my aforementioned stay in St. Petersburg. Könul Ahmadova and Dr. Elnara Cafarova generously assisted the Azerbaijani expeditions and Prof. Vitaliy Anistratenko for his support in several fieldwork activities.

Finally, I want to say a warm thank you to the people who supported me on a personal level. The most important is my partner Birke, who had to bear the major toll of my stress during the PhD. My mother, who was not physically close, gave me outstanding support through the PhD. Lastly, I want to thank the friends and basketball teammates with whom I shared nice and tough moments during these years.

