

**YURIY KVACH, VENIAMIN ZAMOROV,
MIHAILS PUPINS**

**REVIEW OF INVASIVE
PONTO-CASPIAN GOBIIDS:
*CURRENT RANGE AND
HISTORY OF EXPANSION***



**Daugavpils University
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2021**



**INSTITUTE OF MARINE BIOLOGY OF
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Cover photo: *The toad goby (Mesogobius batrachocephalus), a Ponto-Caspian species which spread the range in the Dniester and Dnieper rivers. Photograph by Yuriy Kvach.*

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Summary

The monograph consists of the comprehensive overview of the history of expansion of the Ponto-Caspian gobiids (Gobiiformes: Gobiidae) in Eurasian and North America, both in fresh and brackish waters.

The detailed review of the Ponto-Caspian gobiids showing invasions consists the information concerning the expansion of 7 fish species: monkey goby (*Neogobius fluviatilis*), round goby (*Neogobius melanostomus*), gorlap goby (*Ponticola gorlap*), bighead goby (*Ponticola kessleri*), racer goby (*Babka gymnotrachelus*), western tubenose goby (*Proterorhinus semilunaris*), and Caspian tubenose goby (*Proterorhinus semipellucidus*).

The data are supported by range maps and the annex table, where first findings are documented for each particular water basin.

The information presented in the monograph oriented on ichthyologists who study the Ponto-Caspian gobiids, on experts in aquatic invasions, also on aquaculture and nature conservation specialists.

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ROUTES OF AQUATIC INVASIONS IN EUROPE



The range expansion is one of the mechanisms of evolutionary diversification and biodiversity safety (Parmesan & Yohe 2003). This process was natural in past therefore the species spread on large distances took a long time (Alimov & Bogutskaya 2004; Alexandrov et al. 2007; Polačik et al. 2008). The development of the transport infrastructure has facilitated the translocation of live organisms to different parts of the World, which has broken natural barriers to the spread and distribution of species (Bij de Vaate et al. 2002; García-Berthou et al. 2005; Hirsch et al. 2016). The alien species expansion harms the natural safety, representing one of the greatest threats to global biodiversity (Leppäkoski et al. 2002; Hirsch et al. 2016).

The artificial water routes and irrigation canals lead the expansion of the Ponto-Caspian invertebrates into the European water bodies (Bij de Vaate et al. 2002). Except for the invertebrates, the numerous aquatic organisms spread their ranges in Europe via rivers and the other inland waters (Copp et al. 2005a). Thus, three main routes of aquatic invasions, so-called corridors of invasions, were described for the European continent (Fig. 1):

- 1) Northern Corridor of Aquatic Invasions (NCAI). It connects the Caspian Sea with the Baltic Sea via the drainages of the rivers Volga and Neva. Also, via the Volga-Don canal, it connects the Sea of Azov with the Volga basin, thus joining the Black Sea basin with the Caspian and the Baltic seas. In the north, the Volga basin connects to the White Sea basin via the White Sea-Baltic Canal.
- 2) Central Corridor of Aquatic Invasions (CCAI). It connects the Black Sea with the Baltic Sea via the Dnieper and Pripyat drainages, the Kanal Królewski (Dnieper-Bug Canal), and the Vistula and Bug drainages. Then, it connects the Baltic Sea with the North Sea via the Kiel Canal and the system of the other inland canals.
- 3) Southern Corridor of Aquatic Invasions (SCAI). Starting from the Black Sea, it connects the Danube drainage with the Rhine

drainage via the Maine-Rhine Canal, and then with the North Sea. The system of inland canals connects the Rhine basin with the Meuse basin, and then to the west.

Panov et al. (2009) developed the concept, describing the corridors or routes of spread of not only the Ponto-Caspian invertebrate to west and north but also all the other non-indigenous species, also in revert direction. In addition, they proposed the fourth corridor, so-called the Western Corridor of Invasions, which connects the Mediterranean Sea with the North Sea via the drainages of the rivers Rhône, Rhine, and Seine.

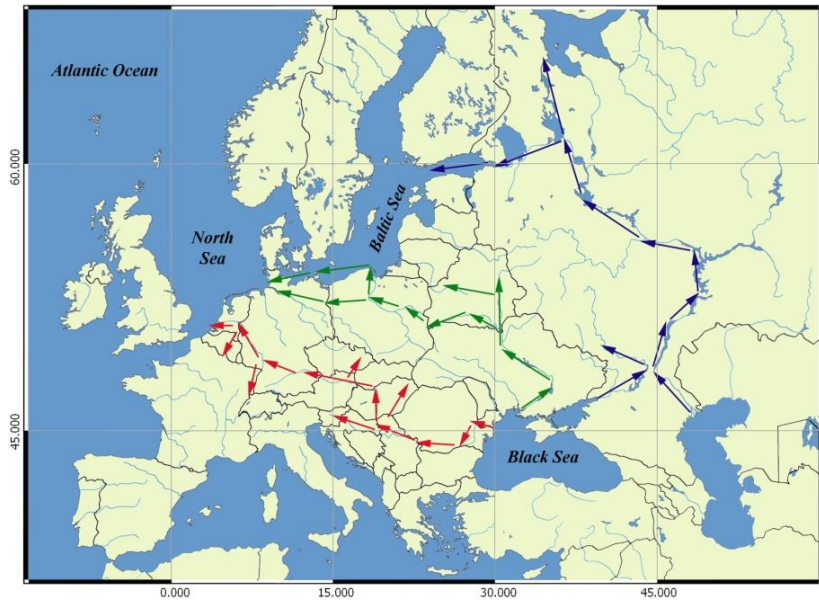


Fig. 1. Corridors of Aquatic Invasions in Europe (modified due to *Bij de Vaate et al. 2002*). Blue – Northern Corridor; Green – Central Corridor; Red – Southern Corridors.

Although the expansion of some species has been facilitated after the connection of previously divided drainages, many water invasions have not occurred as a result of independent active expansion, but as a result of the artificial transfer by humans (e.g. amateur fishermen), as hitchhikers of aquaculture facilities, or with ballast water of vessels (Aleksandrov 2004; Copp et al. 2005a). The distribution of alien species is usually not limited by political boundaries (Copp et al. 2005a). Moreover, the geopolitical changes that have taken place in Europe over the last 50 years have contributed to the development of traffic flow from east to west, which in turn has provoked new biological invasions (Roche et al. 2013). Under communist regimes, trade took place mainly between the countries of the so-called socialism camp, but the traffic to the Upper Danube (Austria, Germany) was limited. After 1991 the main invasion localities in the Danube River were ports of Bratislava and Vienna, which are placed on the border between two camps. After the fall of the communist regimes, the volume of container traffic from the Port of Sulina (Romania) upstream of the Danube River significantly increased between 1992 and 2001. It is accordingly facilitated the expansion upstream the Danube drainage of many Ponto-Caspian species, among them are the Ponto-Caspian gobiids and their introduction into the North Sea basin.

Transcontinental transport promotes penetration with ballast water of European (particularly mainly Ponto-Caspian) species into North America, where at least 43 alien invasive species were recorded since 1959 (Grigorovich et al. 2003). The main place of the invasive alien species registration in North America is the basin of the Great Lakes, which started to be a place of introduction of many Ponto-Caspian species, such as the representatives of the gobiid family (Gobiiformes: Gobiidae) (Corkum et al. 2004; Stepien et al. 2005).

Fish is an important component of the economies of many states, but the risk management measures (e.g. quarantine control) are generally less stringent for fish than for other animals (Copp et al. 2005b). A significant increase in the introduction of freshwater

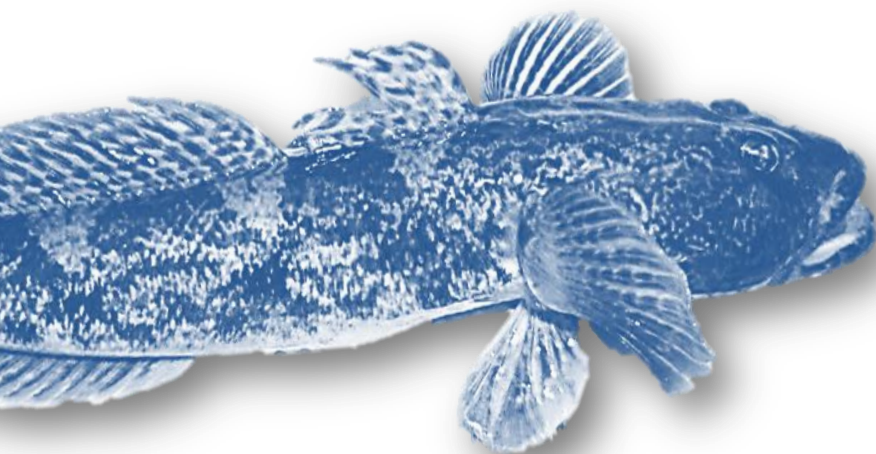
fish, due to the negative socio-economic, environmental, and evolutionary impact of globalization on local biodiversity has been observed in the last few decades (Hulme 2009; Vitule et al. 2009; Gozlan et al. 2010; Cucherousset & Olden 2011). The negative impact of alien species on local ecosystems includes predation, forage and spatial competition with native species, hybridization, the spread of parasites and pathogens, modification of trophic relationships, and modification of biochemical cycles (Leunda 2010; Cucherousset & Olden 2011). A case of hidden threat is so-called cryptic invasion when genes that are not peculiar to a local population are introduced into this (Morais & Reichard 2018). As a result of hybridization of native and introduced lines of the same species, new, more expandable populations are formed, which increase their numbers within the range, disturbing the balance in biodiversity. Thus, so-called native invaders may spread, when an outbreak and disbalance in the ecosystem is caused not by an alien species, but by an indigenous one (Carey et al. 2012).

The group of fish with the common name 'gobies' is related to the order of goby-like fish (Actinopterygii: Gobiiformes), which includes the family Gobiidae (Betancur-R et al. 2017). The order consists of several species, considered aggressive invaders. The introduction of them leads to the degradation of communities of the local fish species, which recorded in the different parts of the World, such as Australia, California, Latvia, the Netherlands, Poland, etc. (Brittan et al. 1970; Vaas et al. 1975; Middleton 1982; Matern & Fleming 1995; Kutsokon et al. 2021).

Particular attention should be paid to Ponto-Caspian gobiids (Gobiidae: Benthophilinae), which are some of the most successful invaders in the past several decades (Copp et al. 2005a). Many of the representatives of this subfamily belong to the so-called neolimnetics, i.e. species that are originally brackish-water but inhabited freshwaters as a result of competition with the other species (mostly of Mediterranean and Atlantic origin) on the Black Sea coastal near-shore, its deltaic zones, coastal lakes, lagoons and estuaries (Kvach & Kutsokon 2017). At least five species among the

Ponto-Caspian gobiids are characterized as invasive species in Europe, showing a negative impact on ecosystems (Roche et al. 2013). These are such fish as the monkey goby (*Neogobius fluviatilis* (Pallas, 1814)), round goby (*Neogobius melanostomus* (Pallas, 1814)), bighead goby (*Ponticola kessleri* (Günther, 1861)), racer goby (*Babka gymnotrachelus* (Kessler, 1857)) and the western tubenose goby (*Proterorhinus semilunaris* Heckel, 1837). In addition, two species of the Caspian origin spread their ranges via the Volga riverine basin: gorlap (or Caspian bighead) goby (*Ponticola gorlap* (Iljin, 1949)) and the Caspian tubenose goby (*Proterorhinus semipellucidus* Kessler, 1863) (Sokolov et al. 1989; Slynko et al. 2001). The intensive spread of the Ponto-Caspian gobies observed in all three main corridors of invasions in Europe. Also, the Transatlantic invasion is observed, e.g. two species of the Ponto-Caspian gobiids, the round goby, and the western tubenose goby are registered in the North-American Great Lakes (Corkum et al. 2004). Negative effects of alien gobiids on local ecosystems include food competition with native demersal fish, spatial competition (particularly for spawning space), and predation (Charlebois et al. 1997; Corkum et al. 2004; Copp et al. 2005a).

HISTORY OF EXPANSION OF THE PONTO-CASPIAN GOBIIDS



In general, there are 7 species of the Ponto-Caspian gobiid fish, which significantly spread their ranges and are considered invasive. The timetable of the main historical stages of the gobiid expansion in the World is presented in the supplementary table.

The first data on the expansion of the Ponto-Caspian gobiid fish are related to 1914 when the monkey goby (*Neogobius fluviatilis*) was registered in the Middle Dnieper River near the City of Kyiv (Beling 1914). This begins the earlier stage of the Ponto-Caspian gobiid expansion. A little bit later, in the 1930s, the western tubenose goby (*Proterorhinus semilunaris*), mentioned that time as *Proterorhinus marmoratus* (Pallas, 1814), was recorded in some tributaries of the Middle Dnieper, Ukraine (Beling 1937).

The first case of the artificial introduction of the gobiid fish was in 1950s, when the round goby (*Neogobius melanostomus*) and the gorlap goby (*Ponticola gorlap*) were transferred from the Caspian Sea into the Sea of Aral as hitchhikers of the aquaculture grey mullet fries (Mordukhai-Boltovskoy 1972; Moskal'kova 1996; Plotnikov et al. 2012). Both goby fish were successfully acclimated. The construction of the Dubossary Hydroelectric Power Plant on the Dniester River in 1954, the round goby spread its range into the upper river reach (Khudyi 2002), which is another case of the invasion caused by human activity.

The start of the major expansion of the Ponto-Caspian gobiids in the water bodies of the World could be considered in 1970, when the monkey goby was recorded in Lake Balaton, Hungary (Bíró 1971). There are numerous small-river inflows into the lake, but the water body is connected with the Sió River (the tributary of the Danube River) via the Sió-csatorna Canal. This could be a route of the introduction of the fish into the lake. In 1984 this species occurred also in the Hungarian part of the Danube River (Pintér 1989). In the same years, two goby species, the round goby and the gorlap goby (*Ponticola gorlap*) (mentioned as *Neogobius kessleri* Günther, 1861), were found in the middle reach of the Volga River (Gavlena 1970, 1977). In 1978, the racer goby (*Babka gymnotrachelus*) was registered in the Dnieper River near Kyiv

(Pinchuk et al. 1985). According to Pinchuk et al. (1985) this species was never registered in the ichthyological works, therefore the finding indicates the expansion of its range. Except for the racer goby, several other goby species were registered in the Middle Dnieper at the same time, e.g. the round goby occurred in 1980 for the first time (Pinchuk et al. 1985). During the 1980s this fish species spread the range not only in the Dnieper River but also in the Volga River basin, to be registered in the Moskva River in 1989 (Sokolov et al. 1989).

The next important stage of the gobiid expansion began in 1990, when non-indigenous gobies were registered outside the basins of the Black and Caspian seas. This year, the Ponto-Caspian round goby occurred in the Gulf of Gdańsk, the Baltic Sea, inside the marine port of the City of Hel, Poland (Skóra & Stolarski 1993). Almost at the same time, the same two Ponto-Caspian gobies, i.e. the round goby and the western tubenose goby (mentioned as *P. marmoratus*), were registered in the St. Clair River, inflowing into Lake St. Clair, one of the North-American Great Lakes (Jude et al. 1992). It has been suggested that in both cases the gobiids have entered the new environments with ballast water of vessels (Skóra & Stolarski 1993; Charlebois et al. 1997; Corkum et al. 2004).

The further history of expansion in North America is different for the round goby and the western tubenose goby. The western tubenose goby invaded Lake St. Clair, Detroit River, western Lake Erie, and also Lake Superior near the Port of Duluth, Minnesota, USA (Vanderploeg et al. 2002). During the next ten years, the round goby invaded all the Great Lakes and almost all rivers of their basins (Jude 2001; Stepien & Tumeo 2006). In 1993 this fish occurred in the Calumet River (Illinois, USA), which inflows into Lake Michigan, also in the Detroit River (Ohio, USA). Then, in 1994, it occurred in Lake Huron (Ontario, Canada) and southern Lake Michigan (Hammond Marina, Indiana, USA), in 1995 – in western Lake Superior and eastern Lake Erie, in 1996 – in the Shiawassee River near the Argentine City, Michigan, USA (Charlebois et al. 1997). In 2001, the round goby started to be the most important component of the

Lake Ontario ecosystem (Vélez-Espino et al. 2010). In the Saint Lawrence River, which connects the Great Lakes basin with the Atlantic Ocean, the round goby first occurred in 1997 near the Quebec City (riverine mouth), but in 2005 it is found more western, near the City of Cornwall, Ontario, Canada (Hickey & Fowlie 2005).

In the Baltic Sea, during the next 10 years after the first registration, the round goby significantly spread their range in the Gulf of Gdańsk, and became a numerous common species in the Puck Bay and the Vistula Lagoon (Sapota 2004; Sapota & Skóra 2005). In the next several years the range spread of this fish had western vector, along the whole Polish coasts, where it was registered near the cities of Władysławowo and Świnoujście, also in the Szczecin Lagoon (Czugała & Woźniczka 2010). In Germany, the round goby was first registered in 1998 near the Rügen Island (Winkler 2006), then spread the range along the German Baltic coasts to the west (Wolter & Rohr 2010). Later, the expansion of this fish moved to the east and north from the Gulf of Gdańsk, where it was found in Lithuania near all its sea coasts and in the Curonian Lagoon, also in Estonia, in the Gulf of Riga and Gulf of Finland (Bacevičius 2003, 2008; Ojaveer 2006; Rakauskas et al. 2008).

In the 1990s, the introduction of two other gobiid species, the monkey goby and the racer goby, took place in the Baltic basin, e.g. both species were registered in the Bug River, the eastern tributary of the Vistula River (Danilkiewicz 1996, 1998). Later, both species were registered in the main flow of the Vistula River from the mouth of the Bug River to the Vistula delta in the north (Kostrzewa & Grabowski 2001, 2002; Kostrzewa et al. 2004). In 2008, one more Ponto-Caspian goby species, the western tubenose goby (mentioned as *P. marmoratus*), was registered in the Baltic basin (Grabowska et al. 2008). The molecular analysis of nine mtDNA cytochrome b gene haplotypes of the racer goby confirmed the origin of the Vistula population from the Dnieper ones, which probably penetrated the Baltic basin via the Dnieper-Bug Canal (Ohayon & Stepien 2007).

The finding of a goby in the Neva River delta and the eastern Gulf of Finland described as *Proterorhinus marmoratus* (Antsulevich 2007), should be noted separately. At present, *Proterorhinus marmoratus* sensu lato is described as a complex of the cryptic species, including the marine tubenose goby (*P. marmoratus* sensu stricto), the eastern tubenose goby (*Proterorhinus nasalis* (Filippi, 1863)), the Caspian tubenose goby (*Proterorhinus semipellucidus*), the western tubenose goby (*P. semilunaris*), and the Chornaya tubenose goby (*Proterorhinus tataricus* Freyhof & Naseka, 2007) (Stepien & Tumeo 2006; Freyhof & Naseka 2007; Neilson & Stepien 2009b). In the Northern Corridor of Aquatic Invasions, which connects the Caspian Sea with the Baltic Sea via the Volga and Neva river basins, the expansion of the Caspian tubenose goby is registered. Therefore, we can consider that the goby found in the freshwater part of the Baltic Sea is related to the Caspian tubenose goby.

The spread of the Ponto-Caspian gobies in the Danube basin, which started in the 1980s with the registration of the monkey goby in Hungary, continued in the 1990s. First, the western tubenose goby (with the natural range up to Vienna) significantly extended its range in the Upper Danube in Austria (Ahnelt 1988; Harka 1990). At the end of the 1990s, the two other Ponto-Caspian goby species were registered in the middle reach of the Danube River (Wiesner 2005). It started from the finding of the bighead goby (*Ponticola kessleri* Günther, 1861) in the Hungarian part of the river (Erős & Guti 1997). Then, the monkey goby, the bighead goby, and the racer goby were registered in Slovakia and Austria (Stráňai 1997; Ahnelt et al. 2001; Kautman 2001; Stráňai & Andreji 2001; Holčík et al. 2003). Later, the round goby occurred in the Hungarian, then in the Austrian sectors of the Danube River (Guti et al. 2003; Erős et al. 2005; Wiesner 2005). Ahnelt et al. (1998) registered three species of the Ponto-Caspian gobiids, i.e. the monkey goby, the bighead goby, and the western tubenose goby, in the rivers of Tisza and Bodrog in Hungary. Since 2000, the bighead goby has been registered in the German part of the river (Seifert & Hartmann 2000). In 2004, the

round goby was registered in the Slovakian part of the Danube basin (Stráňai & Andreji 2004).

Since 1999, the Ponto-Caspian has been registered in the basin of the North Sea. The expansion started from the registration of the western tubenose goby in 1999 in the Main River, Germany (Reinartz et al. 2000; Schadt 2000). In 2002, this species invaded the Lower Rhine in the Netherlands (Dönni & Freyhof 2002). Between 2000 and 2002, this fish inhabited the whole the German span of the Rhine River (Freyhof 2003). In the same period, the western tubenose goby occurred in the left (western) tributary of the Rhine River, the Moselle River (von Landwüst 2006). In 2006, the round goby was registered in the Rhine delta in the Netherlands, in its branch, the Lek River (van Beek 2006). A year later, in 2007, the western tubenose goby was found in the French part of the Rhine River (Manné & Poulet 2008) and the bighead goby in the Waal River (a branch in the Rhine delta), the Netherlands (van Kessel et al. 2009). In 2009, the monkey goby joined the bighead goby in the Waal River (van Kessel et al. 2009). At the current time, four gobiid species spread their ranges in the whole German part of the Rhine basin (Borcherding et al. 2011).

In 2001, the information about the finding of this fish in the Aegean Sea near the Tenedos (Bozcaada) Island in Turkey was published (Eryilmaz 2002). But, further expansion of the species in this sea basin was not confirmed.

Several scientific works about the range expansion of the Ponto-Caspian gobiids in the Central Corridor of Aquatic Invasions (mainly in Belarus) were recently published. Thus, the four Ponto-Caspian goby species were registered in the Pripyat River and the Belarusian part of the Dnieper River, i.e. the monkey goby, the round goby, the racer goby, and the western tubenose goby (Rizevsky et al. 2007; Semenchenko et al. 2009). Two of these species, the monkey goby and the round goby, were also registered in the Dnieper-Bug Canal (Kanal Królewski) and in the Mukhavetz River, which is the eastern tributary of the Bug River, the Baltic Sea basin (Semenchenko et al. 2009, 2011). In 2015, the monkey goby

penetrated the Neris River (Neman basin) in Lithuania where it established an abundant population in the sector close to the border with Belarus (Rakauskas et al. 2018). The origin of this population probably has Dnieper roots. Thus, the Central Corridor passes not only through the Vistula basin, but also through the small rivers in northern Belarus that connect the Dnieper basin with the Neman basin.

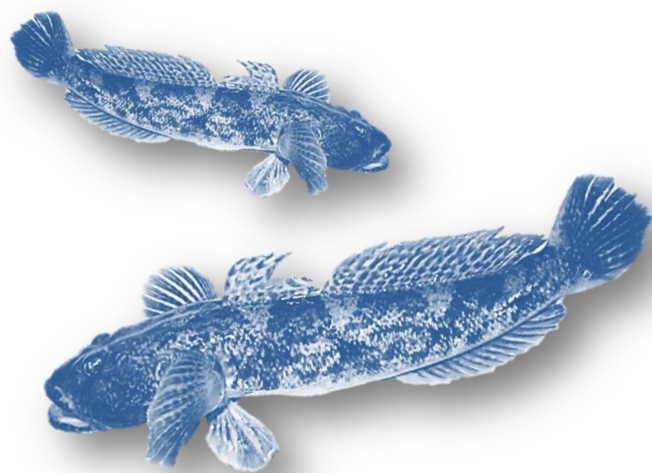
Except for the mentioned 7 goby species, which showed the large range expansion and considered invasive in many localities, some single facts of introduction of several other Ponto-Caspian gobiids were registered in the last decades. In the Sea of Aral, except for the round and the gorlap gobies, three other Ponto-Caspian gobiids, i.e. the white goby (*Neogobius pallasii*), the eastern tubenose goby (*Proterorhinus nasalis*), and the syrman goby (*Ponticola syrman* (Nordmann, 1840)), were introduced from the Caspian Sea in the 1950s (Mordukhai-Boltovskoy 1972; Plotnikov et al. 2012). The Don tadpole-goby (*Benthophilus durrelli* Boldyrev & Bogutskaya, 2004) (mentioned as *Benthophilus stellatus* (Sauvage, 1874) at the beginning), which has the natural range in the Lower Don River, has been registered in the Volga River since the 1970s, where it was introduced via the Volga-Don Canal (Boldyrev & Bogutskaya 2007). However, despite the wide range in the Volga, this species is always not numerous. The Black Sea tadpole-goby (*Benthophilus nudus* (Berg, 1898)) was registered in the Middle Dnieper basin in the mouth of the Olshanka River (a tributary) in 1981, but a bit later, in 1982, it was registered in the Desna River lower reach (Pinchuk et al. 1985). In 1997, the syrman goby (*P. syrman*) was found in the Danube River in Hungary (Guti 1999). A little bit later, the range expansion of the toad goby (*Mesogobius batrachocephalus* (Pallas, 1814)) was registered. Thus, in 1998 this fish occurred in the Middle Dnieper near Kyiv, and also in the Kaniv Reservoir (Movchan et al. 2003). Except for the Dnieper River, it was registered in the middle reach of the Dniester River in Moldova in the 2000s (Romanescu 2012). The rattan goby (*Ponticola ratan* (Nordmann, 1840)) was registered in the Kamyanske Reservoir in the Middle Dnieper basin in 2011 (Manilo & Didenko 2013).



Fig. 2. The toad goby (*Mesogobius batrachocephalus*), a Ponto-Caspian species which spread the range in the Dniester and Dnieper rivers. Photograph by Yuriy Kvach.

Thus, the current range of the Ponto-Caspian gobiids in the Old World is laid from the Sea of Aral in the east (round goby, gorlap goby) to the basins of the rivers Scheldt and Moselle in Belgium and France (round goby, bighead goby, western tubenose goby) in the west; from the Gulf of Bothnia of the Baltic Sea (round goby) in the north to the Tenedos Island in the Aegean Sea (also the round goby) in the south. Two species, the round goby and the western tubenose goby, were transferred to North America. The round goby is the most widespread invasive Ponto-Caspian gobiid species.

SYSTEMATIC STATUS OF THE PONTO-CASPIAN GOBIIDS



Order Gobiiformes Günther, 1880

Earlier, the fishes of this taxonomic group were related to the subfamily Gobioidae inside the perch-like fish order (Actinopterygii: Perciformes). In terms of the modern view of the systematic of this group, they are related to the separate order of goby-like fish (Actinopterygii: Gobiiformes) (Nelson et al. 2016). The order comprises nine families of fish (Eschmeyer 2021):

- Family Rhyacichthyidae Jordan 1905 (loach gobies)
- Family Odontobutidae Hoese & Gill 1993 (shovel-snouts, or Asian freshwater sleepers)
- Family Eleotridae Bonaparte 1835 (sleepers)
 - ✓ Subfamily Butinae Bleeker 1874 (gudgeons)
 - ✓ Subfamily Eleotrinae Bonaparte 1835 (bullies)
 - ✓ Subfamily Milyeringinae Whitley 1945 (freshwater cave gobies)
- Family Thalasseleotrididae Gill & Mooi 2012 (ocean sleepers)
- Family Gobiidae Cuvier 1816 (gobies)
 - ✓ Subfamily Sicydiinae Gill 1860 (rock-climbing gobies)
 - ✓ Subfamily Gobionellinae Bleeker 1874 (oxudercids)
 - ✓ Subfamily Oxudercinae Günther 1861 (mudskippers and allies)
 - ✓ Subfamily Amblyopinae Günther 1861 (mudburrowing gobies)
 - ✓ Subfamily Gobiinae Cuvier 1816 (true gobies)
- Family Kraemeriidae Whitley 1935 (1911) (sand darts)
- Family Microdesmidae Regan 1912 (wormfishes)
 - ✓ Subfamily Microdesminae Regan 1912
 - ✓ Subfamily Ptereleotrinae Bleeker 1875 (dart-gobies)

- Family Xenisthmidae Miller 1973 (collared wrigglers)
- Family Schindleriidae Giltay 1934 (infantfishes)

Family Gobiidae Cuvier 1816

The family consists of five subfamilies (Eschmeyer 2021). The Ponto-Caspian gobiids were considered to be isolated into the subfamily of Benthophilinae (Neilson & Stepien 2009a), which now joined the true gobies Gobiinae (Nelson et al. 2016; Eschmeyer 2021). The group of the Ponto-Caspian gobiids is characterized by the absence of the swimbladder. The fishes are endemics of the Ponto-Caspian brackish water zoogeographic zone and are part of its relict fauna. Part of them showed expansion into the freshwaters, forming the group of neolimnetic fishes (Kvach & Kutsokon 2017).

The group of the Ponto-Caspian gobiids consists of three tribes (Neilson & Stepien 2009a):

- Tribe Benthophilini
 - ✓ *Anatirostrum* Iljin, 1930 (duckbill pugolovka)
Anatirostrum profundorum (Berg, 1927) (duckbill pugolovka)
 - ✓ *Benthophiloides* Beling & Iljin, 1927
Benthophiloides brauneri Beling & Iljin, 1927
Benthophiloides turcomanus (Iljin, 1941)
 - ✓ *Benthophilus* Eichwald, 1831 (tadpole gobies)
Benthophilus abdurahmanovi Ragimov, 1978
 (Abdurahmanov's pugolovka)
Benthophilus baeri Kessler, 1877 (Baer pugolovka)
Benthophilus casachicus Ragimov, 1978
Benthophilus ctenolepidus Kessler, 1877

Benthophilus durrelli Boldyrev & Bogutskaya, 2004 (Don tadpole-goby)

Benthophilus granulosus Kessler, 1877 (Granular pugolovka)

Benthophilus grimmi Kessler, 1877

Benthophilus kessleri Berg, 1927

Benthophilus leobergius Berg, 1949 (Caspian stellate tadpole-goby)

Benthophilus leptcephalus Kessler, 1877

Benthophilus leptorhynchus Kessler, 1877 (Short-snout pugolovka)

Benthophilus macrocephalus (Pallas, 1787) (Caspian tadpole goby)

Benthophilus magistri Iljin, 1927 (Azov tadpole goby)

Benthophilus mahmudbejovi Ragimov, 1976 (Small-spine tadpole-goby)

Benthophilus nudus Berg, 1898 (Black Sea tadpole-goby)

Benthophilus pinchuki Ragimov, 1982

Benthophilus ragimovi Boldyrev & Bogutskaya, 2004

Benthophilus spinosus Kessler, 1877 (Spiny pugolovka)

Benthophilus stellatus (Sauvage, 1874) (Stellate tadpole-goby)

Benthophilus svetovidovi Pinchuk & Ragimov, 1979

✓ *Caspiosoma* Iljin, 1927

Caspiosoma caspium (Kessler, 1877)

- Tribe Neogobiini

✓ *Neogobius* Iljin, 1927

Neogobius caspius (Eichwald, 1831) (Caspian goby)
Neogobius fluviatilis (Pallas, 1814) (monkey goby)
Neogobius melanostomus (Pallas, 1814) (round goby)
Neogobius pallasii (L. S. Berg, 1916) (white goby)

- Tribe Ponticolini

- ✓ *Babka* Iljin, 1927

Babka gymnotrachelus (Kessler, 1857) (racer goby)

- ✓ *Mesogobius* Bleeker, 1874 (toad gobies)

Mesogobius batrachocephalus (Pallas, 1814) (toad, or knout goby)

Mesogobius nigronotatus (Kessler, 1877)

Mesogobius nonultimus (Iljin, 1936)

- ✓ *Ponticola* Iljin, 1927

Ponticola bathybius (Kessler, 1877)

Ponticola cephalargoides (Pinchuk, 1976) (Pinchuk's goby)

Ponticola constructor (Nordmann, 1840) (Caucasian goby)

Ponticola cyrius (Kessler, 1874) (Kura goby)

Ponticola eurycephalus (Kessler, 1874) (mushroom goby)

Ponticola gorlap (Iljin, 1949) (gorlap goby)

Ponticola iranica Vasil'eva, Mousavi-Sabet & Vasil'ev, 2015 (Iranian Goby)

Ponticola kessleri (Günther, 1861) (bighead goby)

Ponticola platyrostris (Pallas, 1814) (flatsnout goby)

Ponticola ratan (Nordmann, 1840) (ratan goby)

Ponticola rhodioni (Vasil'eva & Vasil'ev, 1994) (riverine goby)

Ponticola rizensis (Kovačić & Engin, 2008) (Iyidere goby)

Ponticola syrman (Nordmann, 1840) (syrman goby)

Ponticola turani (Kovačić & Engin, 2008) (Aksu, or Turan's goby)

✓ *Proterorhinus* Smitt, 1900 (tubenose gobies)

Proterorhinus marmoratus (Pallas, 1814) (marine tubenose goby)

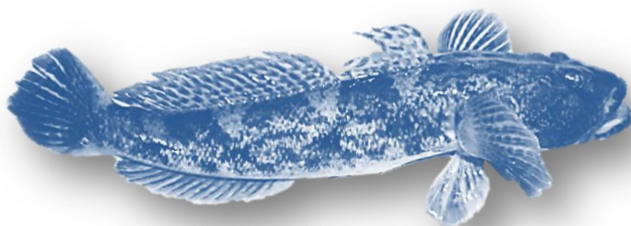
Proterorhinus nasalis (De Filippi, 1863) (eastern tubenose goby)

Proterorhinus semilunaris (Heckel, 1837) (western tubenose goby)

Proterorhinus semipellucidus (Kessler, 1863) (Caspian tubenose goby)

Proterorhinus tataricus Freyhof & Naseka, 2007 (Chornaya tubenose goby)

REVIEW OF THE PONTO-CASPIAN GOBIIDS SHOWING INVASIONS



MONKEY GOBY

***Neogobius fluviatilis* (Pallas, 1814)**

(Fig. 3)

Synonyms:

Gobius fluviatilis Pallas, 1814

Apollonia fluviatilis (Pallas, 1814)

Neogobius fluviatilis fluviatilis (Pallas, 1814)

Gobius sordidus Bennett, 1835 (questionable)

Gobius stevenii Nordmann, 1840

Gobius steveni Nordmann, 1840

Gobius fluviatilis nigra Kessler, 1859



Fig. 3. Monkey goby (*Neogobius fluviatilis*) from the Bug River, Vistula River basin, Poland. Photograph by Yuriy Kvach.

Native range

Mesohaline, oligohaline of the Black Sea (including the Sea of Azov) and the Sea of Marmara, also lower reaches of rivers, coastal and deltaic lakes (Fig. 4).

The Black Sea. Along all coasts on sandy bottoms, mainly in desalinated parts. In lagoons and estuaries of the North-Western Black Sea (Tylihul, Budaki, Tuzly Lagoons, Sasyk, Razelm-Sinoe, etc.), Lakes Varna and Burgas. Rivers: Kamchiya, Lower Danube with tributaries (Ogosta, Iskar, Vit, Osam, Yantra), Lower and Middle Dniester tributaries, Southern Bug, Lower Dnieper (including of the Kakhovka and Zaporizhzhia reservoirs), the rivers of Caucasus, i.e. Dagomys, Rioni, the small rivers in Abkhazia and Adjara, Lake Paliastomi (Smirnov 1986; Slastenenko 1955-1956; Vasilev et al. 2012).

The Sea of Azov. Everywhere, including of the estuaries and lagoons, such as Molochna Estuary and Sivash. Rivers: Lower Don and Kuban, the small rivers in northern Azov coast and Crimea (Smirnov 1986; Slastenenko 1955-1956).

The Sea of Marmara. It is distributed in the southern coastal lakes, such as Sapanca, Manyas, Uluabat, also the small rivers from the Biga Peninsula in the west to Bosphorus in the east (Sari et al. 2006; Karakuş et al. 2018).

Non-native range

The middle and upper reaches of the rivers of the Black Sea basin, the rivers of the Baltic and North Sea basins, Maritza River in Greece, and Volga River in Russia (Fig. 4).

The Black Sea. In the Dnieper, it is known in the middle reach in Ukraine, including the Lower Desna River, the upper Dniester and Southern Bug with tributaries (Pinchuk et al. 1985; Smirnov 1986; Manilo 2020). In Belarus, it is recorded in the Upper Dnieper and the Pripyat River (Semenchenko et al. 2009). In the Danube, it is recorded up to Bavaria, including also the Tisza river basin with the

Someș River in Romania (Pintér 1989; Harka 1993; Stráňai & Andreji 2001; Lenhardt et al. 2011; Cocan et al. 2014). Also, in Lake Balaton in Hungary (Bíró 1971).

The Sea of Azov. The Middle Don River with tributaries: Donets, Khoper, Medveditsa (Smirnov 1986).

The Aegean Sea. The expansion started in 2006 from the Tundzha River (Maritsa River tributary) in Bulgaria (Stefanov et al. 2008). Then, it spread to the Lower Maritsa in Greece (Zogaris & Apostolou 2011).

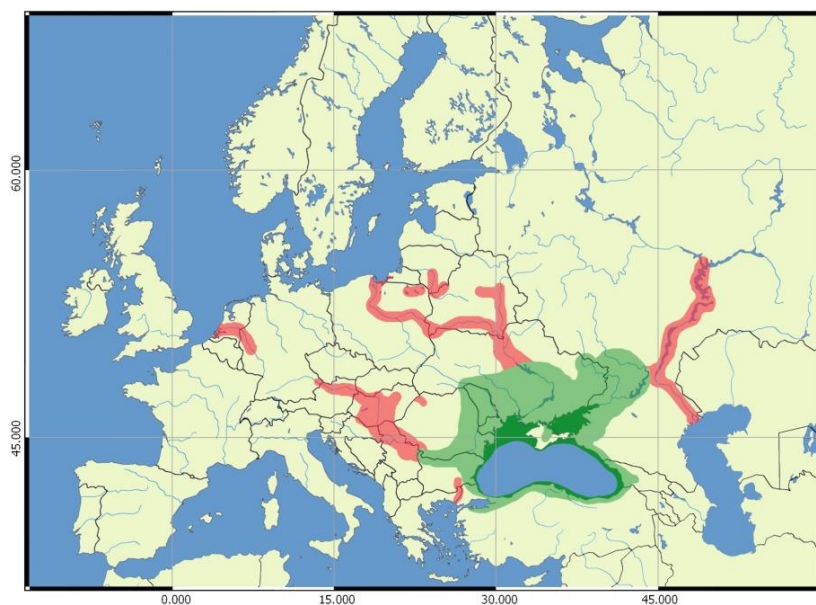


Fig. 4. The range map of the monkey goby (*Neogobius fluviatilis*) expansion. Green – native range, Red – non-native range (dark color – in the sea; light color – in the inland waters).

The Baltic Sea. This was first recorded in the Bug River basin in Poland in 1997 (Danilkiewicz 1998). Later, it became a common species in the Włocławek and Zegrze reservoirs (Kostrzewa &

Grabowski 2002). Now, its range in the Vistula basin borders on the Bug River drainage for the Mukhovetz River in Belarus, till the Vistula deltaic zone, together with the Vistula Lagoon and riverine forefront in the Gulf of Gdansk (Semenchenko et al. 2009; Lejk et al. 2013). Recently, this species has been reported in the waters of the Great Masurian Lakes system (Kapusta et al. 2020; Ulikowski et al. 2021).

The North Sea. Since 2009, it has been registered in the Waal River in the Netherlands and the Lower Rhine in Germany (van Kessel et al. 2009; Borcharding et al. 2011).

ROUND GOBY

***Neogobius melanostomus* (Pallas, 1814)**

(Fig. 5)

Synonyms:

Gobius melanostomus Pallas, 1814

Apollonia melanostoma (Pallas, 1814)

Neogobius melanostoma (Pallas, 1814)

Gobius cephalarges Pallas, 1814

Neogobius cephalarges (Pallas, 1814)

Neogobius cephalarges cephalarges (Pallas, 1814)

Ponticola cephalarges (Pallas, 1814)

Gobius chilo Pallas, 1814

Gobius melanio Pallas, 1814

Gobius virescens Pallas, 1814

Gobius exanthematosus Pallas, 1814

Gobius sulcatus Eichwald, 1831

Gobius affinis Eichwald, 1831

Neogobius melanostomus affinis (Eichwald, 1831)

Gobius lugens Nordmann, 1840

Gobius grossholzii Steindachner, 1894



Fig. 5. Round goby (*Neogobius melanostomus*). A. An individual from the Unterwarnew, Baltic Sea, Germany (non-native range) in aquarium. Photograph by Yuriy Kvach. B. An individual in the natural invidonment near the Snake Island, Black Sea, Ukraine. Photograph by Sergey Snigirov.

Native range

Similar to the previous species, but more common in the coastal waters of the Black Sea (including the Sea of Azov) and the Sea of Marmara, also lower reaches of rivers, coastal and deltaic lakes, the Caspian Sea with the lower reaches of rivers (Fig. 6, A).

The Black Sea. Along all coasts, including all lagoons and estuaries. Rivers: Lower Danube with tributaries (Ogosta, Iskar, Vit, Osam, Yantra), Lower and Middle Dniester tributaries, Southern Bug, Lower Dnieper (including of the Kakhovka and Zaporizhzhia reservoirs), small rivers along all coasts, rivers of Caucasus, i.e. Mezib, Pshada, Vulcan, Kodori, and Çoruh (Smirnov 1986; Slastenenko 1955-1956).

The Sea of Azov. Everywhere, including the estuaries and lagoons. Rivers: Lower Don and Siverskyi Donets, Lower Kuban, small rivers in the northern Azov coast and the Crimea (Smirnov 1986; Slastenenko 1955-1956).

The Sea of Marmara. Recorded in the sea near-shores (Slastenenko 1955-1956; Bilecenoglu et al. 2014).

The Caspian Sea. In the Caspian Sea it is widespread along all coasts and in the lower reaches of all rivers of its drainage (Bogutskaya & Naseka 2004).

Non-native range

Middle and upper reaches of the rivers of the Black Sea basin, the Baltic Sea in rivers of its basin, rivers of the North Sea basins, the Aegean Sea, Middle and Upper Volga River in Russia, the Sea of Aral, Northamerican Great Lakes, Illinois and St. Laurence rivers (Fig. 6).

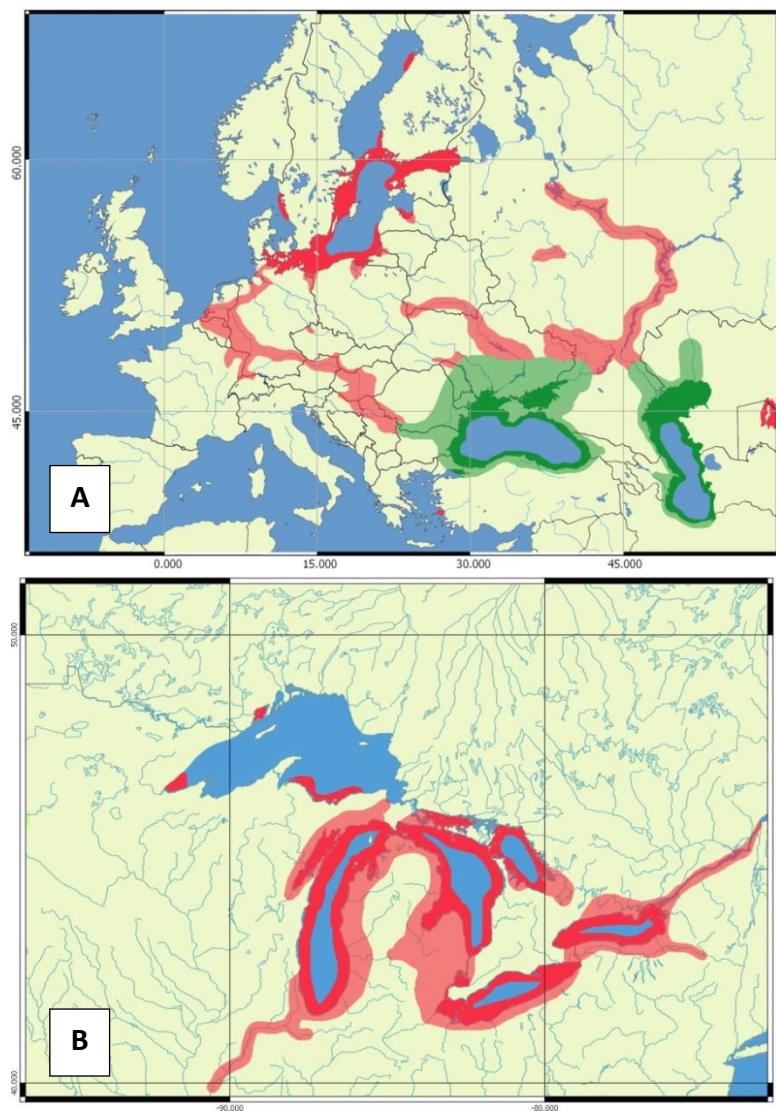


Fig. 6. The range map of the round goby (*Neogobius melanostomus*) expansion in the Old World (A) and North America (B). Green – native range, Red – non-native range (dark color – in sea and open lake waters; light color – in the other inland waters).

The Black Sea. The first spread of the species was registered in 1954 in the Upper Dniester, when the expansion was caused by the construction of the Dubossary Dam Reservoir in Moldova (Khudiyi 2002). The first finding in the Middle Dnieper was registered near Kaniv in 1960 (Babenko 1961). In Northern Ukraine, around the City of Kyiv, it occurred in 1983 (Pinchuk et al. 1985). Since 1993 it is known in the Upper Dnieper and the Pripyat River in Belarus (Gulyugin & Kunitsky 1999). Later, it spread the range along the Pripyat River including the Kanal Królewski (Semenchenko et al. 2009). In the Middle Danube River, the expansion started in 1997, when this species were found in Serbia (Simonović et al. 1998). Then, this species was found in the Middle Danube in Austria, Hungary, Slovakia (Wiesner et al. 2000; Guti et al. 2003; Stráňai & Bitter 2003; Stráňai & Andreji 2004), and in the Upper Danube in Germany (Paintner & Seifert 2006). It is known in the tributaries, i.e. river Morava, Dyje, Sava (Lusk et al. 2010; Piria et al. 2011).

The Aegean Sea. This species was registered in 2001 near the Tenedos (Bozcaada) Island, Turkey (Eryilmaz 2002). But no further expansion was observed.

The Baltic Sea. It was first registered in 1990 in the Puck Bay (a part of the Gulf of Gdańsk) near the Hel, Poland (Skóra & Stolarski 1993). Then, it invaded the western part of the Gulf of Gdańsk (Sapota 2004). Now, it is known along all coasts (Sapota 2004, 2012; Winkler 2006; Ojaveer 2006; Møller & Carl 2010; Florin & Karlsson 2011). Also, in the deltaic zones and lower reaches of rivers, including of Vistula, Oder and Neman (Borowski 1999; Bacevičius 2003; Sapota 2004; Czugala & Woźniczka 2010; Schomaker & Wolter 2014; Rakauskas et al. 2016). In 2006-2008, it was registered in the Mukhavetz River in Belarus (a tributary of the Bug River), located near the border with Poland (Semenchenko et al. 2009). Since 2010, it is registered in the Kiel Canal, Germany (Kvach & Winkler 2011).

The North Sea. The invasion started in 2004 when it occurred in the Lek River (branch of the Rhine) in the Netherlands (van Beek 2006). In the Middle and Upper Rhine, it is spread in Germany,

France and Switzerland (Borcherding et al. 2011; Kalchhauser et al. 2013; Manné et al. 2013). Since 2011, it occurred in the Moselle River in France (Manné et al. 2013). Since 2008, it is registered in the Elbe Estuary and the Lower Elbe, Germany (Hempel & Thiel 2013). The second place of invasion in this water drainage is the Upper Elbe in Czechia, where it was registered in 2015 (Buřič et al. 2015; Roche et al. 2015). Except for the Rhine and Elbe drainage, in the North Sea basin, it is registered in the Lower Meuse, Lower Scheldt (with the estuary) and Albert Canal, Belgium (Verreycken et al. 2011; Verreycken 2013), and the Lower Weser, Germany (Brunken et al. 2012). It inhabits the tidal zones of these rivers, including the brackish water parts of the Elbe and Sheldt Estuaries (Verreycken et al. 2011; Hempel & Thiel 2013).

The Caspian Sea. The range covers the Middle and Upper Volga basin in Russia. The first case of expansion was registered in 1968 in the Kuybyshev Reservoir (Tsyplakov 1974). Then, it was registered in the main river flow and reservoirs up to the Rybinsk Reservoir (Gavlena 1970; Teplyakov 2002; Nikulenko et al. 2005; Shemonaev & Kirilenko 2009; Stolbunov et al. 2013). Also, it is known in the Moskva River since 1988 (Sokolov et al. 1989), and in the Shatura Lakes since 2003 (Podushka 2004).

The Sea of Aral. The first case of artificial introduction of the round goby was registered in the water body. The fish was transported as hitchhikers by the gray mullets in the 1950s in Kazakhstan (Mordukhai-Boltovskoy 1972; Moskal'kova 1996).

The North American freshwaters. The first finding in North America was in 1990 in Lake St. Clair, USA (Jude et al. 1992). Now, it inhabits all the Great Lakes, i.e. Erie, Huron, Michigan, Superior, and Ontario, both in the USA and Canada (Charlebois et al. 1997; Vélez-Espino et al. 2010). The range covers the Great Lakes basin, such as Detroit, Calumet, Shiawassee, Niagara (Charlebois et al. 1997; Einhouse et al. 2002). Since 1997, it occurs in the Saint Lawrence River in Canada, from Lake Ontario down to the riverine mouth (Hickey & Fowlie 2005). Also, the range spreads to the Mississippi River basin, to be recorded in the Illinois River from north to lower reach (Kornis et al. 2012; Fuller et al. 2021a).

GORLAP GOBY

***Ponticola gorlap* (Iljin, 1949)**

(Fig. 7)

Synonyms:

Gobius kessleri non Günther, 1861

Neogobius kessleri (non Günther, 1861)

Neogobius kessleri gorlap Iljin, 1949

Neogobius gorlap Iljin, 1949

Neogobius iljini Vasil'eva & Vasil'ev, 1996



Fig. 7. Gorlap goby (*Ponticola gorlap*) from the Volga delta, Russia. Photograph by Yuriy Kvach.

Native range

The species is an endemic of the Caspian Sea where it is widespread along all coasts, also in the Volga River delta near the city of Astrakhan (Bogutskaya & Naseka 2004) (Fig. 8).

Non-native range

The range spreads via the Northern Corridor of Invasions: in the Volga River basin and in the Don River basin where it was introduced via the Volga-Don Canal (Fig. 8).

The Caspian Sea. The range covers the Volga basin in Russia. The first case of the expansion was registered in 1970 in the Volgograd Reservoir in Lower Volga, Russia (Gavlena 1977). Then, it spread to the Middle Volga, where it occurred in the Saratov (in 1982), Cheboksary (1990s) and Kuybyshev (2003) reservoirs (Kozlovskaya 1997; Aleev & Semenov 2003; Shemonaev & Kirilenko 2010). In the Moskva River, it is known since 1989 (Sokolov et al. 1989). The Northernmost finding of this species is in the reservoirs of the Upper Volga, i.e. Rybinsk and Ivankovo reservoirs (Slynko et al. 2001).

The Sea of Azov. The first spread of the species beyond the Caspian basin was registered in 1972, when this fish occurred in the Tsimlyansk Reservoir, Don River basin, Russia (Boldyrev 2002). Then, it invaded the Lower Don (in 2002) and Donets River (in 1957) (Troitsky 1961; Bogutskaya et al. 2004). Recently, it was found in the Don River mouth (Prishchepa & Karpova 2016).

The Sea of Aral. The first case of artificial introduction of the gorlap goby (together with the other gobiids) was registered in the water body. The fish was transported as hitchhikers by the gray mullets in the 1950s in Kazakhstan (Mordukhai-Boltovskoy 1972).

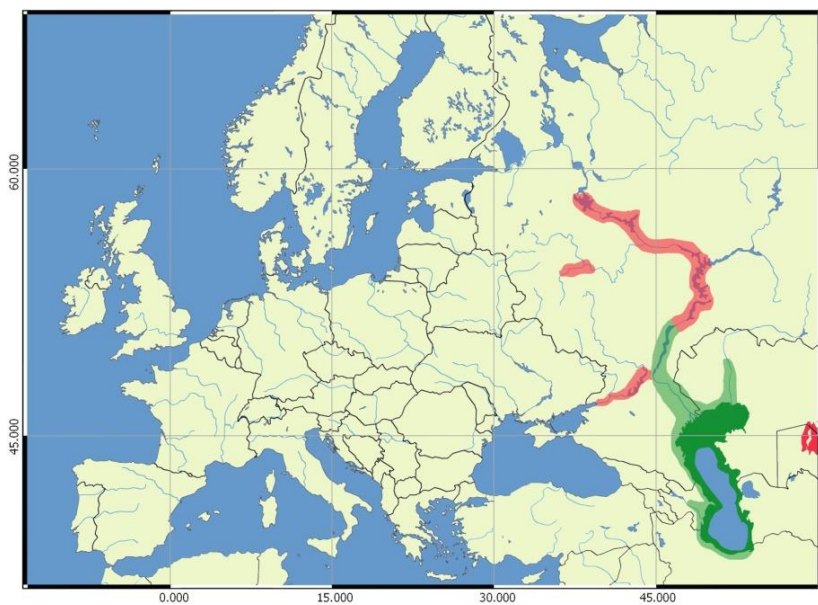


Fig. 8. The range map of the gorlap goby (*Ponticola gorlap*) expansion. Green – native range, Red – non-native range (dark color – in the see; light color – in the inland waters).

BIGHEAD GOBY

Ponticola kessleri (Günther, 1861)

(Fig. 9)

Synonyms:

Gobius kessleri Günther, 1861

Neogobius kessleri (Günther, 1861)

Gobius platycephalus Kessler, 1857 (homonym)



Fig. 9. Bighead goby (*Ponticola kessleri*) from the Dniester Estuary, North-Western Black Sea, Ukraine. Photograph by Yuriy Kvach.

Native range

Harboring the lower reaches of the rivers, mainly inflowing into the western part of the Black Sea, including of the coastal and deltaic lakes; also south-western Crimea and the rivers of the south-eastern Black Sea coast (Fig. 10).

The Black Sea. In the desalinated parts of the North-Western Black Sea, i.e. Dnieper-Bug Estuary, Dniester Estuary, Sasyk Lagoon, Razelm-Sinoe (Smirnov 1986). Recently confirmed for the rivers of the south-western Crimea (Boltachev et al. 2009). Along the Bulgarian coasts in the desalinated parts, such as lakes Mandra, Vaya, Varna, Beloslavsko (Smirnov 1986; Vasilev et al. 2012). In the Lower Danube up to Vidin with tributaries, the Dniester River up to the upper reach with tributaries, also, Southern Bug, Lower Dnieper, including of the Kakhovka and Zaporizhzhia reservoirs (Slastenenko 1955-1956; Smirnov 1986; Vasilev et al. 2012). In the south-eastern Black Sea region, it is registered in small rivers in Turkey (Balik & Turan 2004).

Non-native range

The middle and upper reaches of the Danube River, rivers of the North Sea basins, i.e. rivers Rhine (with tributaries) and Elbe (Fig. 10).

The Black Sea. The first case of expansion was recorded in the 1960s in the Middle Dnieper in the Kremenchuk Reservoir, Ukraine (Volkov 1969). Then, the species spread in the Middle Dnieper near Kaniv and Kyiv (Volkov 1971; Movchan et al. 2003) and in its tributaries, Olshanka and Desna (Pinchuk et al. 1985; Movchan et al. 2003). But, in the Dnieper basin, it is absent in the north of the Kyiv Reservoir (Pinchuk et al. 1985; Semenchenko et al. 2011). In the Middle Danube River, the expansion started in 1977, when this species was found in Serbia (Lenhardt et al. 2011). Then, this species was found in the Middle Danube in Austria, Hungary, Slovakia

(Zweimüller et al. 1996; Erős & Guti 1997; Kautman 2000), also in the Upper Danube in Germany (Seifert & Hartmann 2000).

The North Sea. Via the Maine-Rhine Canal, it penetrated the North-Sea basin, where it first occurred in 2006 in the lower reach and then spread along all the German part of the river (Borcherding et al. 2011). Now, it is distributed also in the Upper Rhine in Germany, France, and Switzerland (Kalchhauser et al. 2013; Manné et al. 2013). It is also known in the Moselle River (left tributary of the Rhine) in France and Waal River (a branch in the Rhine delta) in the Netherlands (van Kessel et al. 2009; Manné et al. 2013). Since 2015, it is registered in the Lower Elbe River to the south of the City of Hamburg (Thiel et al. 2017).

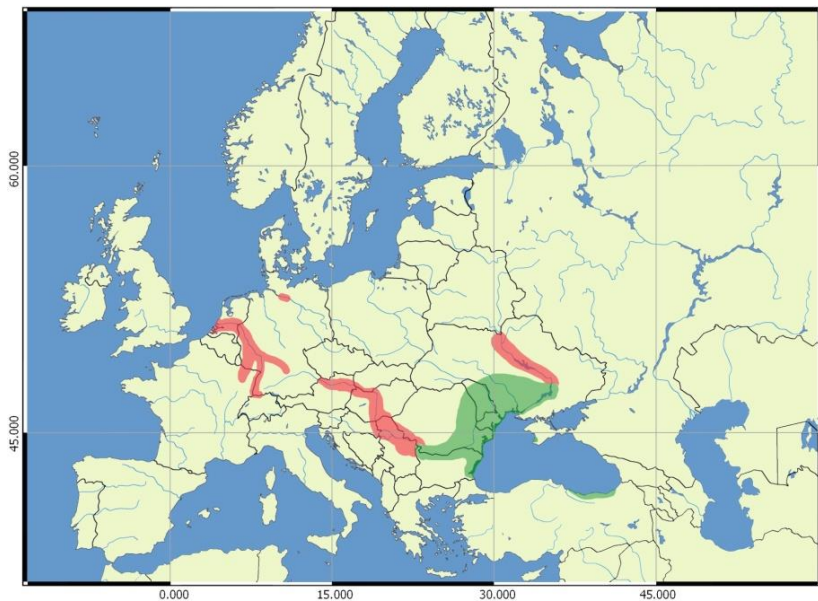


Fig. 10. The range map of the bighead goby (*Ponticola kessleri*) expansion. Green – native range, Red – non-native range (dark color – in the sea; light color – in the inland waters).

RACER GOBY

***Babka gymnotrachelus* (Kessler, 1857)**

(Fig. 11)

Synonyms:

Gobius gymnotrachelus Kessler, 1857

Mesogobius gymnotrachelus (Kessler, 1857)

Neogobius gymnotrachelus (Kessler, 1857)

Gobius macropus De Filippi, 1863

Gobius burmeisteri Kessler, 1877

Gobius macrophthalmus Kessler, 1877

Neogobius macrophthalmus (Kessler, 1877)

Neogobius gymnotrachelus macrophthalmus (Kessler, 1877)

Mesogobius gymnotrachelus otschakovinus Zubovich, 1925

Native range

The mesohaline and oligohaline waters, lower reaches of rivers, coastal and deltaic lakes of the Black Sea basin and Lake Sapanca in the Sea of Marmara basin, also in the Caspian Sea (Fig. 12).

The Black Sea. In the desalinated parts of the Black Sea along all coasts and in the freshwaters of its basin (Smirnov 1986; Slastenenko 1955-1956; Vasilev et al. 2012; Çiçek et al. 2015; Manilo 2020). In the North-Western Black Sea, it inhabits the Dnieper-Bug Estuary, Dniester Estuary, near the Tendra sandbar and Berezan Island, also in the brackish estuaries and lagoons. In the western

Black Sea coast, it is in the Kamchiya River and Lake Shablensko in Bulgaria. It is common in the lower parts of the Southern Bug and Dnieper. In the Danube River, it is native in tributaries and lakes of the Danube delta, including Brateş, Kahul, Yalpug, Katlabuh, Kitay, Razelm, etc., and in the main reach up to Vidin. In the Dniester River, it is native up to the upper reach, including the tributaries, i.e. Zbruch, Zhvanchik, Smotrych, Răut, Bîc. Inhabits the coasts of Turkey, the rivers of the Caucasus, including Inguri, Rioni, and the small rivers, coastal lagoons and lakes of Kolkhida.



Fig. 11. Racer goby (*Babka gymnotrachelus*) from the Bug River, Vistula River basin, Poland. Photograph by Yuriy Kvach.

The Sea of Azov. It is found in the Taganrog Bay and the lower reaches of rivers Don, Aksay, Seversky Donets (Smirnov 1986; Slastenenko 1955-1956).

The Sea of Marmara. It is known in the brackish coastal lake Sapanca (Özuluğ et al. 2007).

The Caspian Sea. It is known near all coasts, but absent in the rivers of its basin; the taxonomic status is discussable, probably another species (Bogutskaya & Naseka 2004).

Non-native range

The middle and upper reaches of the rivers of the Black Sea basin, rivers of the Baltic Sea basin, Evros River in Greece; the presence in the Sea of Aral is not confirmed (Fig. 12).

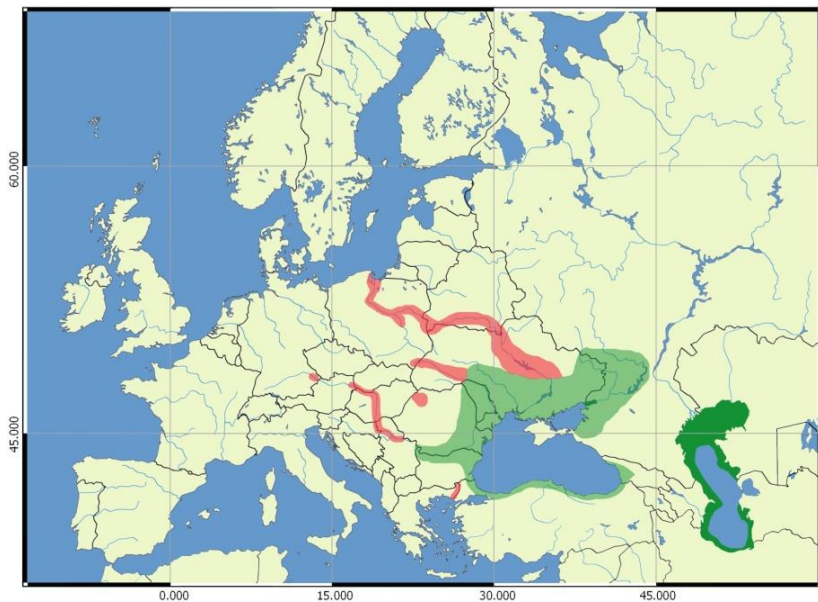


Fig. 12. The range map of the racer goby (*Babka gymnotrachelus*) expansion. Green – native range, Red – non-native range (dark color – in the sea; light color – in the inland waters).

The Black Sea. In the Middle Dnieper, it is known since 1978, when it was recorded near the city of Kyiv, Ukraine (Pinchuk et al. 1985). Now, it is spread along the middle reach in Ukraine, including

the Lower Desna River (Pinchuk et al. 1985; Smirnov 1986; Manilo 2020). In Belarus, it is recorded since 1993 in the Upper Dnieper and the Pripjat River (Gulyugin & Kunitskiy 1999; Semenchenko et al. 2009, 2011). Via the Crimean Canal it spread into the Crimean inland waters (Karpova 2009). In the Dniester River basin, it is recorded in 2009 in the Polish sector, in the Strwiąż River (Kukuła & Bylak 2013). In the Middle Danube, the expansion started in 1991, when it occurred in Serbia (Hegediš et al. 1991). Later, it is invaded the Hungarian, Slovakian and Austrian sectors of the river (Kautman 2000; Ahnelt et al. 2001; Guti 2004). In 2015-2016, it was found in small rivers of Transilvania in the Someş River basin, Tisza River drainage, Romania (Cocan et al. 2016). In the Upper Danube, it is recorded in Germany (Haertl et al. 2012).

The Aegean Sea. It is recorded in several localities along the Lower Maritsa River in Greece in 2018 (Zogaris et al. 2019).

The Baltic Sea. It was first recorded in the Bug river basin in Poland in 1995 (Danilkiewicz 1996). Later, it became a common species in the Włocławek and Zegrze reservoirs (Kostrzewa & Grabowski 2001). Now, its range in the Vistula basin harbors the Bug River drainage from the Mukhovetz River in Belarus, down to the Vistula deltaic zone (Grabowska et al. 2010; Semenchenko et al. 2011).

WESTERN TUBENOSE GOBY

***Proterorhinus semilunaris* (Heckel, 1837)**

(Fig. 13)

Synonyms:

Gobius marmoratus non Pallas, 1814

Proterorhinus marmoratus (non Pallas, 1814)

Gobius rubromaculatus Kriesch, 1873

Gobius semilunaris Heckel, 1837



Fig. 13. Western tubenose goby (*Proterorhinus semilunaris*) from the Danube delta, Ukraine. Photograph by Yuriy Kvach.

Native range

The fresh waters in lower reaches of rivers, the coastal and deltaic lakes of the Black Sea, the northern Aegean Sea, and the Sea of Marmara drainages (Fig. 14, A). It is closely related to the marine tubenose goby *Proterorhinus marmoratus*, which inhabits the Black

Sea coastal waters, brackish lagoons and estuaries (Neilson & Stepien 2009b). It is absent in the Chorna River in Crimean, Ukraine, where it was replaced by the Tartar goby, *Proterorhinus tataricus* (Freyhof & Naseka 2007).

The Black Sea. In the Dnieper River, the natural range is from the estuary to Trubizh River; also the lower and middle reaches of the Dniester and Southern Bug rivers. In the Danube River, it is natural from the delta (together with the Danube Lakes) to Vienna, together with the Prut River to Iași, and Lake Neusiedler in Austria (Slattenenko 1955-1956; Smirnov 1986). In the western sea coast, it lives in the rivers Kamchiya, Ropotamo, Veleka, and Rezovska in Bulgaria (Smirnov 1986; Vassilev et al. 2007). In the eastern coast, it is in the Rioni River basin, together with Lake Paleastomi, also Lake Inkiti in Georgia (Slattenenko 1955-1956; Smirnov 1986).

The Sea of Azov. In the basin of the Sea of Azov, it lives in the small rivers of the north coast, Don, Seversky Donets (to Sviatohirsk), in the estuary of the Kuban River (Slattenenko 1955-1956; Smirnov 1986).

The Sea of Marmara. The coastal lakes of the southern coast: Manyas, Uluabat, İznik and Sapanca (Özuluğ et al. 2007; Karakuş et al. 2018; Top et al. 2018).

The Aegean Sea. The Maritsa River in Bulgaria (together with Toundzha River) and Greece, also the lower Struma River in Greece (Economou et al. 2007; Vassilev et al. 2012).

Non-native range

Upper reaches of the rivers of the Black Sea basin, rivers of the Baltic and the North Sea basins, also in the North American Great Lakes and St. Laurence rivers (Fig. 14).

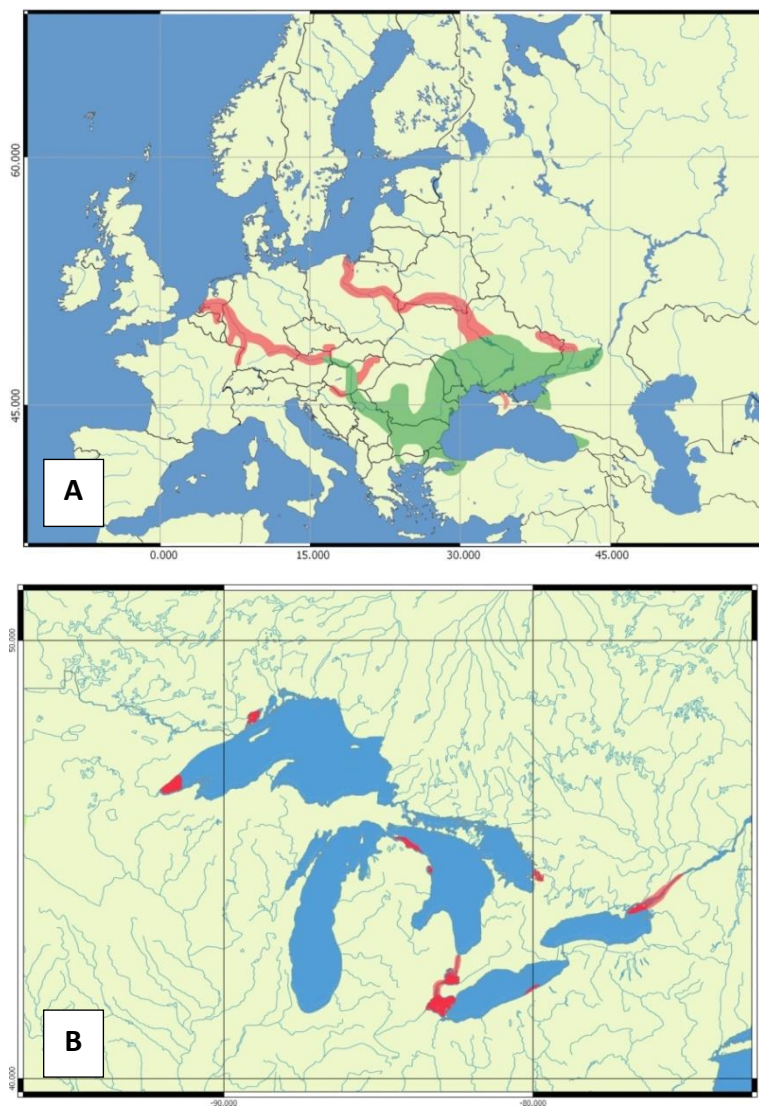


Fig. 14. The range map of the western tubenose goby (*Proterorhinus semilunaris*) expansion in the Old World (A) and North America (B). Green – native range, Red – non-native range (dark color – in the lakes open waters; light color – in the other inland waters).

The Black Sea. The expansion started in the 1930s from the tributaries of the Middle Dnieper basin, Ukraine (Beling 1937). Then, it spread in Ukraine into the Olshanka River (in 1981), Middle Dnieper in Kyiv (in 1982), Desna River (in 2000) (Pinchuk et al. 1985; Movchan et al. 2003). Via the Crimean Canal, it spread to the Crimean small rivers. In the Belarus part of the Dnieper basin, it is found in the Upper Dnieper and the Pripyat River (Rizevsky et al. 2007; Semenchenko et al. 2009). In 1976, it was registered in the Danube River upper of Vienna, Austria, and reaches the Upper Danube in Germany (Ahnelt 1988; Reinartz et al. 2000). Also, it is recorded in the Danube tributaries, i.e. the Tisza River in Hungary and Slovakia (Sterbetz 1963; Koščo et al. 2014), Drava River in Hungary (Sallai 1995), Morava River in Austria, Czechia and Slovakia (Spindler et al. 1992; Prášek & Jurajda 2005), Dyje River in Czechia (Lusk & Halačka 1995).

The Baltic Sea. It was first registered in 2008 in the Włocławek Reservoir, Vistula River, Poland (Grabowska et al. 2008). Now, it is distributed in Poland from the Vistula delta in the north to the Bug River in the southeast (Grabowska et al. 2008, 2010).

The North Sea. The invasion started in 1997, when it penetrated from the Danube River into the Main River, Germany, via the Main-Rhine Canal (Reinartz et al. 2000; Schadt 2000). Now, it is common in the Rhine River from the France-German border in the south to the riverine delta in the Netherlands (Dönni & Freyhof 2002; Freyhof 2003; von Landwüst 2006; Manné & Poulet 2008). Also, it is recorded in the Moselle River (Rhine tributary) in Germany and France (von Landwüst 2006; Manné et al. 2013). Except for the Rhine basin, it is recorded in the Meuse River in the Netherlands and Belgium, also in the Zuid Willems Canal, Belgium (Cammaerts et al. 2012).

The North American freshwaters. The first finding in North America was in 1990 in Lake St. Clair, USA (Jude et al. 1992). Then, it spread into the St. Clair River and western Lake Erie, in the USA and Canada (Leslie et al. 2002; Kocovsky et al. 2011). In 2001, it was recorded in the Saint Louis Bay of Lake Superior, USA (Vanderploeg

et al. 2002). In the last decade, it inhabits the Georgian Bay of Lake Huron, eastern parts of lakes Erie and Ontario (Grant et al. 2012; Goretzke et al. 2019). Since 2016, it is recorded in the Upper reach of the St. Laurence River in Canada (Goretzke et al. 2019).

CASPIAN TUBENOSE GOBY

***Proterorhinus semipellucidus* (Kessler, 1877)**

(Fig. 15)

Synonyms:

Gobius marmoratus non Pallas, 1814

Proterorhinus marmoratus (non Pallas, 1814)

Gobius semipellucidus Kessler, 1877



Fig. 15. Caspian tubenose goby (*Proterorhinus semipellucidus*) from the Lower Volga, Russia. Photograph by Yuriy Kvach.

Native range

The species is an endemic of the Volga River lower reach and deltaic zone, also some water bodies of the north-western Caspian coasts (Neilson & Stepien 2009a,b) (Fig. 16). It is closely related to the eastern tubenose goby *Proterorhinus nasalis*, which inhabits the Caspian Sea and the mouths of some rivers of its basin (Freyhof & Naseka 2007).

Non-native range

It spread via the Northern Corridor of Invasions: in the Volga River basin, in the Don River basin where it was introduced via the Volga-Don Canal, also in the Neva delta and Gulf of Finland of the Baltic Sea (Fig. 16).

The Caspian Sea. The expansion started in 1982 when this fish occurred in the Saratov Reservoir (Kozlovskaya 1997). Along the Volga River main stream, it is distributed in the reservoirs of Cheboksary, Kuybyshev, Rybinsk (Reshetnikov 2002; Klevakin et al. 2003; Naseka et al. 2005). Also, the isolated population is known in the Moskva River since the 1980s (Sokolov et al. 1989).

The Sea of Azov. The first confirmed case of this species in the Sea of Azov basin was in the Buzuluk River and Volgo-Don Canal in Russia in the 2000s (Neilson & Stepien 2009b). But, the same species is known from the Middle Don basin in Russia. The previous findings of *Proterorhinus* sp. in the Middle Don (Smirnov 1986) need confirmation.

The Baltic Sea. In 2006, the tubenose goby is recorded in the Neva River delta in Saint Petersburg, Russia (Antsulevich 2007). Also, it was confirmed for the eastern Gulf of Finland of the Baltic Sea where it spread into the Berezovye Islands (near Gulf of Vyborg) and Kopor Bay (Uspenskiy 2020).

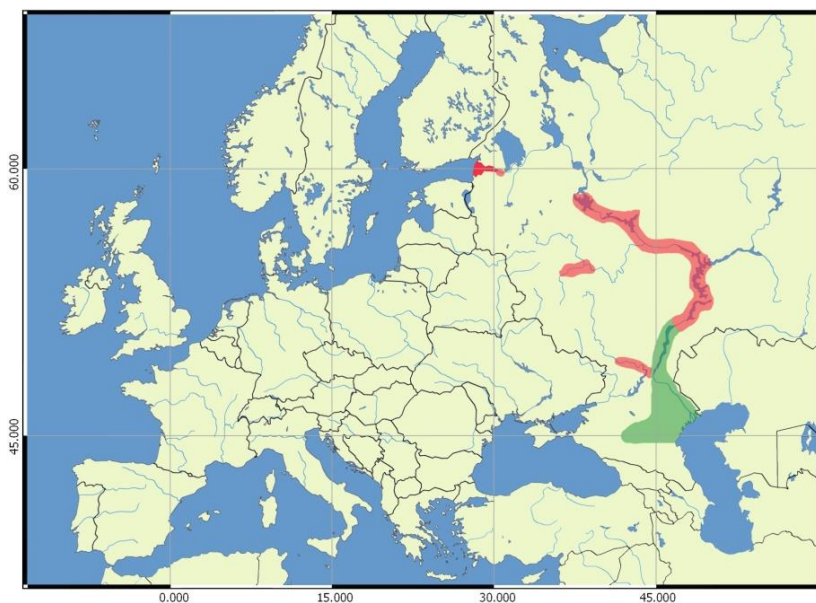


Fig. 16. The range map of the Caspian tubenose goby (*Proterorhinus semipellucidus*) expansion. Green – native range, Red – non-native range (dark color – in the lakes open waters; light color – in the other inland waters).

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Supplement Table

HISTORY OF THE PONTO-CASPIAN GOBIIDS EXPANSION IN THE WORLD

Fish species	Drainage	First occurrence in the basin	Further findings in the basin
1	2	3	4
Monkey goby, <i>Neogobius fluviatilis</i>	Dnieper River	1914, Middle Dnieper, Kyiv, Ukraine (Beling 1914)	1935, Desna River, Ukraine (Beling et al. 1935)
			1936, Upper Dnieper, Belarus (Vorontsov 1937)
			1950s, Pripjat River, Belarus (Peniaz 1956)
			1950s, Sozh River, Belarus (Zhukov 1961)
			1960s, Upper Dnieper, Belarus (Zhukov 1965)
	Volga River	1963, Lower Volga, Russia (Baranova 1967)	
	Danube River	1970, Lake Balaton, Hungary (Bíró 1971)	1977, Middle Danube, Serbia (Lenhardt et al. 2011)
			1984, Middle Danube, Hungary (Pintér 1989)
			1993, Tisza River, Hungary (Harka 1993)
			2001, Middle Danube, Slovakia (Strážnai & Andreji 2001)
			2013, Someş River, Romania (Cocan et al. 2014)

1	2	3	4
<i>N. fluviatilis</i>	Vistula River	1997, Bug River, Poland (Danilkiewicz 1998)	2002, Włocławek Reservoir, Poland (Kostrzewa & Grabowski 2002)
			2004, Lower Vistula, Poland (Kostrzewa et al. 2004)
			2006-2008, Mukhovetz River, Belarus (Semenchenko et al. 2009)
	Baltic Sea	2007, Vistula Lagoon, Poland (Lejk et al. 2013)	2011, Gulf of Gdańsk, Poland (Lejk et al. 2013)
	Rhine River	2009, Waal River, Netherlands (van Kessel et al. 2009)	2009, Lower Rhine, Germany (Borcherding et al. 2011)
	Neman River	2015, Neris River, Lithuania (Rakauskas et al. 2018)	
	Maritsa River	2006, Tundzha River, Bulgaria (Stefanov et al. 2008)	2011, Lower Maritsa, Greece (Zogaris & Apostolou 2011)
	Masurian Lakes	2018, Lake Tałty, Poland (Ulikowski et al. 2021)	2018–2020, 9 lakes of the same system, River Pisa, Canal Mioduński (Kapusta et al. 2020; Ulikowski et al. 2021)
Round goby, <i>Neogobius melanostomus</i>	Sea of Aral	1950s, Kazakhstan (Moskal'kova 1996)	
	Dniester River	1954, Upper Dniester (Khudyi 2002)	

1	2	3	4
<i>N. melanostomus</i>	Dnieper River	1960, Middle Dnieper, Kaniv, Ukraine (Babenko 1961)	1983, Middle Dnieper, Kyiv, Ukraine (Pinchuk et al. 1985)
			1990, <i>Upper Dnieper</i> ; 1993, <i>Pripyat River, Belarus</i> (Gulyugin & Kunitsky 1999)
	Volga River	1968, Kuybyshev Reservoir, Russia (Tsyplakov 1974)	1970, Saratov Reservoir, Russia (Gavlena 1970)
			1988, Moskva River, Russia (Sokolov et al. 1989)
			2003, Shatura Lakes (Podushka 2004); Kuybyshev Reservoir, Russia (Shemonaev & Kirilenko 2009)
			2000s, Udmurtia (Teplyakov 2002); Samara (Nikulenکو et al. 2005)
			2010, Rybinsk Reservoir, Russia (Stolbunov et al. 2013)
	Baltic Sea	1990, Puck Bay, Hel, Poland (Skóra & Stolarski 1993)	1997, western part of the Gulf of Gdańsk, Poland (Sapota 2004)
			1998, Rügen Island, Germany (Winkler 2006)
			1999, Vistula Lagoon, Poland (Borowski 1999)
			2002, Curonian Lagoon, Lithuania (Bacevičius 2003); Gulf of Finland and Gulf of Riga, Estonia (Ojaveer 2006)

1	2	3	4
<i>N. melanostomus</i>	Baltic Sea		2003–2004, Polish coastal waters (Sapota 2004), German coastal waters (Winkler 2006), Lithuanian, Latvian, Finnish coastal water (Sapota 2012)
			2008, Sweden (Florin & Karlsson 2011); Denmark (Møller & Carl 2010)
			2009, Szczecin Lagoon, Poland (Czugała & Woźniczka 2010)
			2010, Kiel Canal, Germany (Kvach & Winkler 2011)
	Great Lakes	1990, Lake St. Clair, USA (Jude et al. 1992)	1993, Detroit River, Calumet River (Lake Michigan basin), Lake Erie, USA (Charlebois et al. 1997)
			1994, Lake Huron, Lake Michigan, USA (Charlebois et al. 1997)
			1995, Saint Louis Bay, Lake Superior, USA (Charlebois et al. 1997)
			1996, Shiawassee River, Michigan, USA (Charlebois et al. 1997)
			1997, Saint Lawrence River, Quebec, Canada (Hickey & Fowlie 2005)
			1999, Niagara River, USA (Einhouse et al. 2002)
			2001, Lake Ontario, USA (Vélez-Espino et al. 2010)

1	2	3	4
<i>N. melanostomus</i>	Danube River	1997, Middle Danube, Serbia (Simonović et al. 1998)	1999, Middle Danube, Austria (Wiesner et al. 2000)
			2001, Middle Danube, Hungary (Guti et al. 2003)
			2003, Middle Danube, Slovakia (Stráňai & Bitter 2003; Stráňai & Andreji 2004)
			2004, Upper Danube, Germany (Paintner & Seifert 2006)
			2008, Morava River, Dyje River, Czechia (Lusk et al. 2010)
			2011, Sava River, Croatia (Piria et al. 2011)
	Aegean Sea	2001, Tenedos (Bozcaada) Island, Turkey (Eryilmaz 2002)	
	Vistula River	2001, Lower Vistula, Poland (Sapota 2004)	2006–2008, Mukhavetz River, Belarus (Semenchenko et al. 2009)
	Rhine River	2004, Lek River, Netherlands (van Beek 2006)	2008, Upper Rhine, Germany (Borcherding et al. 2011)
			2009, Middle Rhine, Germany (Borcherding et al. 2011)
			2011, Upper Rhine, France (Manné et al. 2013)
			2011, Moselle River, France (Manné et al. 2013)

1	2	3	4
<i>N. melanostomus</i>	Rhine River		2012, Upper Rhine, Switzerland (Kalchauer et al. 2013)
			2012, Mittelland Canal, Germany (Matteikat et al. 2016)
	Mississippi River	2004, Illinois River (Irons et al. 2006)	
	Saint Lawrence River	2005, Saint Lawrence River mouth, Ontario, Canada (Hickey & Fowlie 2005)	
	Elbe River	2008, Elbe Estuary and Lower Elbe, Germany (Hempel & Thiel 2013)	2015, Upper Elbe, Czechia (Buřič et al. 2015; Roche et al. 2015)
	Scheldt River	2010, Scheldt Estuary and Lower Scheldt, Belgium (Verreycken et al. 2011)	2010, Albert Canal, Belgium (Verreycken et al. 2011)
	Neman River	2010, Neman River delta, Lithuania (Rakauskas et al. 2016)	
	Weser River	2012, Lower Weser, Bremen, Germany (Brunken et al. 2012)	

1	2	3	4
	Meuse River	2013, Lower Meuse, Belgium (Verreycken 2013)	
<i>N. melanostomus</i>	Oder River	2013, Schwedt, Germany (Schomaker & Wolter 2014)	
Gorlap goby, <i>Ponticola gorlap</i>	Sea of Aral	1950s, Kazakhstan (Mordukhai-Boltovskoy 1972)	
	Volga River	1970, Volgograd Reservoir, Russia (Gavlena 1977)	1982, Saratov Reservoir, Russia (Kozlovskaya 1997)
			1989, Moskva River, Russia (Sokolov et al. 1989)
			1990s, Cheboksary Reservoir, Russia (Shemonaev & Kirilenko 2010)
			1993, Rybinsk and Ivankovo reservoirs, Russia (Slynko et al. 2001)
			2003, Kuybyshev Reservoir, Russia (Aleev & Semenov 2003)
	Don River	1972, Tsimlyansk Reservoir, Russia (Boldyrev 2002)	1957, Donets River, Russia (Troitsky 1961)
			2002, Lower Don, Russia (Bogutskaya et al. 2004)
			2015, Don River mouth, Russia (Prishchepa & Karpova 2016)

1	2	3	4
Bighead goby, <i>Ponticola kessleri</i>	Dnieper River Дніпро	1960s, Kremenchuk Reservoir, Ukraine (Volkov 1969)	1960s, Kaniv Reservoir, Ukraine (Volkov 1971)
			1965, Middle Dnieper, Kyiv, Ukraine (Movchan et al. 2003)
			1981, Olshanka River, Ukraine (Pinchuk et al. 1985)
			2000s, Desna River, Ukraine (Movchan et al. 2003)
	Danube River	1977, Middle Danube, Serbia (Lenhardt et al. 2011)	1994, Upper Danube, Austria (Zweimüller et al. 1996)
			1996, Middle Danube, Hungary (Erős & Guti 1997), Slovakia (Kautman 2000)
			1999, Upper Danube, Germany (Seifert & Hartmann 2000)
	Rhine River	2006, Lower Rhine, Germany (Borcherding et al. 2011)	2007, Waal River, Netherlands (van Kessel et al. 2009)
			2010, Upper Rhine, France (Manné et al. 2013)
			2011, Moselle River, France (Manné et al. 2013)
			2010s, German sector of the Rhine River (Borcherding et al. 2011)
			2011, Upper Rhine, Switzerland (Kalchhauser et al. 2013)
	Elbe River	2015, Lower Elbe (Thiel et al. 2017)	

1	2	3	4
Racer goby, <i>Babka gymnotrachelus</i>	Dnieper River	1978, Middle Dnieper, Kyiv, Ukraine (Pinchuk et al. 1985)	1981, Middle Dnieper, Cherkassy, Ukraine (Pinchuk et al. 1985)
			1993, Upper Dnieper, Pripjat River, Belarus (Gulyugin & Kunitskiy 1999)
	Dniester River	2009, Strwiąż River, Poland (Kukuła & Bylak 2013)	
	Danube River	1991, Middle Danube, Serbia (Hegediš et al. 1991)	1999, Middle Danube, Slovakia (Kautman 2000), Austria (Ahnelt et al. 2001)
			2004, Middle Danube, Hungary (Guti 2004)
			2015, Someş River, Tisza River basin, Romania (Cocan et al. 2016)
			2011, Upper Danube, Germany (Haertl et al. 2012)
	Vistula River	1995, Bug River, Poland (Danilkiewicz 1996)	2000, Włocławek Reservoir, Poland (Kostrzewa & Grabowski 2001)
			2007, Lower Vistula, Poland (Grabowska et al. 2010)
	Maritsa River	2018, Lower Maritsa, Greece (Zogaris et al. 2019)	
Western tubenose goby, <i>Proterorhinus semilunaris</i>	Dnieper River	1930s, tributaries of the Middle Dnieper, Ukraine (Beling 1937)	1981, Olshanka River, Ukraine (Pinchuk et al. 1985)
			1982, Middle Dnieper, Kyiv, Ukraine (Pinchuk et al. 1985)

1	2	3	4
<i>P. semilunaris</i>	Dnieper River		2000, Desna River, Ukraine (Movchan et al. 2003)
			2007, Pripjat River, Belarus (Rizevsky et al. 2007)
			2006-2008, Upper Dnieper, Belarus (Semenchenko et al. 2009)
	Danube River	1957, Lower Tisza, Hungary (Berinkev 1966)	1960s, Middle Tisza, Hungary (Sterbetz 1963)
			1976, Middle Danube (upper of Vienna), Austria (Ahnelt 1988)
			1991, Morava River, Austria (Spindler et al. 1992)
			1994, Dyje River, Czechia (Lusk & Halačka 1995)
			1996, Morava River, Slovakia; 1998, Morava River, Czechia (Prášek & Jurajda 2005)
			1990s, Drava River, Hungary (Sallai 1995); Upper Danube, Germany (Reinartz et al. 2000)
			2014, Upper Tisza and tributaries, Slovakia (Koščo et al. 2014)
	Great Lakes	1990, Lake St. Clair, USA (Jude et al. 1992)	1994, Lake St. Clair and western Lake Erie, Canada (Leslie et al. 2002)
			1997, western Lake Erie, USA (Kocovsky et al. 2011)

1	2	3	4
<i>P. semilunaris</i>	Great Lakes		2001, Saint Louis Bay, Lake Superior, USA (Vanderploeg et al. 2002)
			2011, Georgian Bay, Lake Huron (Goretzke et al. 2019)
			2012, eastern Lake Erie (Grant et al. 2012)
			2011, eastern Lake Ontario (Goretzke et al. 2019)
	Rhine River	1997, Main River, Germany (Reinartz et al. 2000; Schadt 2000)	2002, Lower Rhine, Netherlands (Dönni & Freyhof 2002)
			2000, Middle Rhine, Germany (von Landwüst 2006)
			2000-2002, German sector of the Rhine River (Freyhof 2003)
			2005, Moselle River, Germany (von Landwüst 2006)
			2007, Upper Rhine, France (Manné & Poulet 2008)
			2011, Moselle River, France (Manné et al. 2013)
	Vistula River	2008, Włocławek Reservoir, Poland (Grabowska et al. 2008)	2008, Bug River, Poland (Grabowska et al. 2008, 2010)
			2011, Lower Vistula, Poland (Kvach et al. 2014)
	Meuse River	2008-2009, Netherlands, Belgium (Cammaerts et al. 2012)	2010, Zuid Willems Canal, Belgium (Cammaerts et al. 2012)

1	2	3	4
	St. Lawrence River	2016, Wolf Island, Headwaters St. Lawrence (Goretzke et al. 2019)	2016, Upper St. Lawrence River (Goretzke et al. 2019)
Caspian tubenose goby, <i>Proterorhinus semipellucidus</i>	Volga River	1982, Saratov Reservoir, Russia (Kozlovskaya 1997)	1980s, Moskva River, Russia (Sokolov et al. 1989)
			2000, Kuybyshev Reservoir, Russia (Naseka et al. 2005)
			2001, Cheboksary Reservoir, Russia (Klevakin et al. 2003)
			2002, Rybinsk Reservoir, Russia (Reshetnikov 2002)
	Don River	2000s, Buzuluk River, Bolgo-Don Canal, Russia (Neilson & Stepien 2009b)	
	Neva River	2006, Saint Petersburg, Russia (Antsulevich 2007)	
	Baltic Sea	2007, Gulf of Finland, Russia (Antsulevich 2007)	2013, Berezovye Islands (Uspenskiy 2020)
			2015, Kopor Bay (Uspenskiy 2020)



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