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SPECIAL ISSUE: INVASIVE FISHES REVIEW

Tubenose goby – a discreet invader from the past goes higher

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Abstract. The tubenose goby has been reported to be the first non-native postglacial gobiid immigrant from the Lower Danube refuges. It is thus a pioneer species that was the forerunner of the extensive invasion of Ponto-Caspian gobies that ascended the River Danube and spread across Europe a century before other goby species. It appears that recently the tubenose goby invasion has accelerated. In this paper historical data on the distribution of the tubenose goby, together with data from extensive monitoring of fish communities in Slovakia are examined to evaluate both the temporal and spatial aspects of tubenose goby distribution dynamics. Until the 1990s, the species was recorded only in the River Danube and small water bodies in the Danubian Lowland (Slovakia). Since then the tubenose goby has spread upstream into tributaries of the River Danube. It was also recorded in several streams in eastern Slovakia after 2014, and the spatial data demonstrate that the tubenose goby has been colonising new water bodies, progressing to the north and ascending rivers, reaching higher altitudes than previously reported. These findings suggest that the tubenose goby deserves attention, even after two centuries following the onset of its invasion, and its further expansion across Europe should be carefully monitored.

Key words: Proterorhinus semilunaris, Danube, invasion, distribution dynamics, higher altitudes

Introduction

The River Danube is the most important aquatic migratory route in Europe, and the upstream expansion of biota from the Ponto-Caspian (P-C) region started in the 1800s. The western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) (hereafter tubenose goby) is thought to be a pioneer species, as its expansion took place before other P-C species, and thus was the first to colonise new territories (Roche et al.

2013). Some sources report this to have been a slow process resulting from active upstream migration (Kottelat & Freyhof 2007), but also from passive downstream dispersal (Janáč et al. 2013). Nevertheless, the expansion of the tubenose goby into novel environments may also progress rapidly (Grabowska et al. 2008). In fact, the tubenose goby should be viewed as the smallest and one of the most expansive species among the invasive P-C gobies in European waterbodies (Grabowska et al. 2019).

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One of the reasons behind this invasion success appears to be the overall biological plasticity of the tubenose goby. Indeed, several of its attributes predispose this species to success in new areas. Populations of tubenose goby were found to display plasticity in their life-history traits during different invasion stages (Grabowska et al. 2019, 2021), similar to what has been observed in invasive populations of other P-C gobies (Ľavrinčíková & Kováč 2007, Čápová et al. 2008, Kováč et al. 2009, Hôrková & Kováč 2014, 2015). Moreover, the tubenose goby also exhibits high feeding plasticity; it can opportunistically utilize available resources and is able to switch to other food items under specific conditions (e.g. high macrozoobenthos density; Ondračková et al. 2019, Tarkan et al. 2019).

This species also shows high plasticity in habitat use and thus is able to occupy a variety of habitats, including lakes, estuaries, rivers, streams, canals and backwaters, or even peatbogs (Botta et al. 1981, Kottelat & Freyhof 2007, Ondračková et al. 2019, Top et al. 2019). It is able to cope with various habitat parameters, such as rip-rap bank, mud, overhanging vegetation and littoral aquatic vegetation, slow flowing water or no current, rich in submerged vegetation, shallow littoral areas, alluvial habitats and warmer water (Lusk & Halačka 1995, Naseka et al. 2005, von Landwüst 2006, Koščo et al. 2014). The invasive tubenose goby population from the River Dyje basin inhabited sites displaying a wide range of environmental conditions and showed a great plasticity in macro and microhabitat use. Their habitats included lowland rivers, brooks, reservoirs, aquacultural carp ponds, borrow pits, oxbows, backwaters, with no preferences for substrate type or habitat variable (e.g. vegetation cover, presence of predators). Moreover, this population was able to cope with parasitic diseases with no effect on the fish condition (Ondračková et al. 2019).

Although the tubenose goby is a species with broad temperature tolerance, it seems to have lower temperature optima compared to the round goby (*Neogobius melanostomus* Pallas, 1814). Tubenose gobies showed a lower maximum feeding rate at 25 °C, but a slightly higher attack rate at 20 °C compared to round gobies (Gebauer et al. 2018). The tubenose goby is known to have a higher metabolic rate at low temperatures and to achieve a metabolic optimum at a lower temperature than the round goby (O'Neil 2013). This difference might be a comparative advantage for the tubenose goby in competition with other invasive gobies.

In the Middle Danube (from the Devín Gate in Slovakia to the Iron Gate, r.km 1880-1075) and its tributaries, the tubenose goby has been considered a native species by some authors (Oliva & Hrabě 1968, Hensel 1995). Others, on the contrary, claimed it to be a "Pontic immigrant" (Hankó 1931), or more precisely a postglacial immigrant from the Lower Danube refuges (Balon 1968, Ahnelt 1989, Ahnelt et al. 1998). Indeed, there has always been some doubt about the status of this P-C species in the Middle Danube. For example, The Act on Fisheries of the Slovak Republic (Fisheries Act No. 216/2018, Executing Decree No. 381/2018 Coll) still reports the tubenose goby in the list of native species of fishes and lampreys. But what if the tubenose goby is a discreet invader that may benefit from its great biological flexibility and ultimately prove problematic?

To disentangle this problem, well documented historical, as well as recent data from Slovakia as a case study are used. The main aim of the present paper is to review briefly historical data on the distribution of the tubenose goby (including grey literature), and to combine this review with recent data on the species' current distribution in Slovak streams and rivers. These new data (mainly from the EU Water Framework Directive monitoring) can help in evaluating the potential of the tubenose goby to spread further into other European water bodies situated in higher altitudes.

A brief history of spreading and distribution of the tubenose goby upstream the River Danube and further

The tubenose goby appears to be the most successful gobiid species colonising the entire River Danube (Ahnelt et al. 1998) and is perceived as non-native in most countries in the Danubian basin. The native range of this species is the lower part of the River Danube and the littoral zone of the Black Sea (Polačik et al. 2008, Jakovlić et al. 2015). Although it is considered native in Bulgaria (Vassilev & Pehlivanov 2005), in Croatia its status is more complicated, as the tubenose goby is considered native by some authors (Jakovlić et al. 2015). The first record of this species from Serbia comes from the 19th century where it is currently considered a well acclimatized non-native species (Lenhardt et al. 2010).

The tubenose goby was the first member of the Gobiidae family in the Central European region (Hárka & Bíró 2007). In the middle section of the River Danube it was first observed at the mouth

Table 1. Occurrence of the western tubenose goby (*Proterorhinus semilunaris*) with sites and year of record/monitoring in the River Danube.* first record of western tubenose goby in the country.

Country	Site	r.km	Year	Source
Romania		all		Bănărescu 1964
Ukraine-Romania	from Vylkove			Manilo 2008-2009
Romania-Bulgaria	Dunavets	423	2005	Polačik et al. 2008
	Pozharevo	464	2005	Polačik et al. 2008
	Sandrovo	477	2005	Polačik et al. 2008
	Ruse	502	2005	Polačik et al. 2008
	Belene – Hisarlaka	578	2005	Polačik et al. 2008
	Kozloduy	701	2005	Polačik et al. 2008
	Stanevo	724	2005	Polačik et al. 2008
	Dolno Linevo	735	2005	Polačik et al. 2008
	Lom	744	2005	Polačik et al. 2008
	Archar	770	2005	Polačik et al. 2008
	Simeonovo	776	2005	Polačik et al. 2008
	Vidin	791	2005, 2006	Polačik et al. 2008
	Koshava	811	2005	Polačik et al. 2008
	Gomotartsi	817	2005	Polačik et al. 2008
	Yasen	825	2005	Polačik et al. 2008
	Novo Selo	833	2005	Polačik et al. 2008
	Vrav	836	2005	Polačik et al. 2008
Serbia	Belgrade (above)	1,177		Medić 1896
Hungary	Baja	1,480	1951	Mihályi 1954
	Gerjen	1,515	1980	Botta et al. 1984
	Madocsa and Bölcske	1,545	1980	Botta et al. 1981
	Adony	1,601	1981	Botta et al. 1984
	Ercsi	1,613	1980	Botta et al. 1981
	Budapest	1,647	1879	Mihályi 1954
	Budapest	1,647	1957, 1959, 1993, 1994, 2004, 2007	Sevcsik & Erős 2008
	Felsőgöd	1,668	1951	Mihályi 1954
	Felsőgöd	1,668	1988, 2007	Sevcsik & Erős 2008
	Vác	1,680	1959, 1960, 2007	Sevcsik & Erős 2008
Slovakia-Hungary	Chľaba	1,710		Brtek 1953
	Kováčov	1,713		Brtek 1953
	Štúrovo	1,720	1953	Brtek 1953
	Obid	1,726	1950/1951	Brtek 1953
	Čenkov	1,736		Žitňan 1972
	Kravany nad Dunajom	1,738	1971/1972	Žitňan 1972
	Radvaň nad Dunajom	1,749	1971	K. Hensel, unpublished data
	Patince	1,754		Jurajda et al. 2005
	Iža	1,759		Jurajda et al. 2005
	Komárno	1,767		Jurajda et al. 2005
	Zlatná na Ostrove	1,779	2004	Jurajda et al. 2005
	Veľký Lel	1,781	1961	Kux & Weisz 1962

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	Malé Kosihy	1,787	1950/1951	Brtek 1953
	Kližská Nemá	1,793	1968	K. Hensel, unpublished data
	Číčov	1,798		Jurajda et al. 2005
	Medveďov	1,805	1961	Balon 1968
	Kišpatkó side – arm (mouth)	1,809	1961	Balon 1962
	Sap (Palkovičovo)	1,811		Černý 1995
	Istragov side arms and Sporná Sihoť side arm	1,817	1991-1993	Černý 1995
Slovakia	Gabčíkovo	1,819	2004	Jurajda et al. 2005
biovakia	derivation channel of the Gabčíkovo waterplant	1,017	2015	Jakubčinová 2018
Hungary	Lipót	1,820	1989, 2007	Sevcsik & Erős 2008
Slovakia-Hungary	Bodíky	1,830	2015	Jakubčinová 2018
	Vojka	1,838	2013	Jurajda et al. 2005
Slovakia	Dobrohošť	1,843	2004	Jurajda et al. 2005
	Čilistov	1,844		Jurajda et al. 2005
	Šamorín	1,847		Jurajda et al. 2005
	Čuňovo	1,851	2004	Jurajda et al. 2005
	Hrušov Reservoir	1,853	1961, 2014	Kux & Weisz 1962, Jakubčinová 2018
	Rusovce	1,858		Brtek 1953
	Jarovce	1,860		Brtek 1953
	Bratislava – Petržalka	1,868		Brtek 1953
	Bratislava – Karlova Ves	1,872	1950/1951	Brtek 1953
	Bratislava*			Koelbel 1874
	Sihoť island	1,875	1999	Kautman 2001
	confluence of the rivers Danube and			
	Morava	1,880		Ahnelt 1989
Austria	Hainburg	1,884	1963	Ahnelt 1988
	Melk	2,035		Radda & Wallner 1973
	Wallsee	2,093		Balon et al. 1986
	to Linz	2,132		Jungwirth 1975
Germany	the whole stretch, even in tributaries			Wiesner 2003
	Passau	2,229	1985	Reinartz et al. 2000
	Vilshofen an der Donau	2,248	1985	Stemmer 2008
	Regensburg	2,382	1986	Reinartz et al. 2000

of a thermal stream flowing into the River Danube in old Buda (Óbuda), today part of Budapest and described as a new species under the name *Gobius rubro-maculatus* (Kriesch 1873). Its occurrence was also recorded later in Lake Balaton, including its tributaries (Herman 1887). Currently it is considered non-native in Hungary (Takács et al. 2017).

In the Austrian part of the River Danube, the first tubenose goby individuals were recorded in 1963

near Hainburg (Ahnelt 1988). According to Wiesner (2003), it occurs along the entire Austrian section of the River Danube as well as in its tributaries. Nevertheless, some authors claim the tubenose goby to be a native species (Rabitsch et al. 2013, Ramler & Keckeis 2019).

In contrast, in Germany; i.e. upstream of the River Danube, the tubenose goby is considered nonnative. It spread naturally to various water bodies via canals connecting individual river basins, as well as through ballast water (Wolter & Rörh 2010, Rabitsch et al. 2013). In Bavaria, the first record in the River Danube (1985) was followed by further expansion in subsequent years (Reinartz et al. 2000, Stemmer 2008). The distribution of the tubenose goby continued to increase, and the species colonised other European rivers via the Rhine-Main-Danube Canal. In 1999, it was first discovered in the River Main (Reinartz et al. 2000, Schadt 2000). Since then, this species has spread rapidly downstream. The tubenose goby also penetrated into the River Rhine in 1999 (Borcherding et al. 2011), and in 2002 it was recorded in the Netherlands (von Landwüst 2006). In 2005, its expansion upstream in the River Rhine was also observed (Manné et al. 2013). The tubenose goby was found in 2008 at the Belgian-Dutch border (Cammaerts et al. 2012), and in 2011 it was first recorded in Switzerland in Basel (Manné & Poulet 2008, see Table 1 for further details).

In the Czech Republic, the tubenose goby is also listed among the non-native fish species (Musil et al. 2010). The first record dates back to 1994 from the Upper Mušov Reservoir, part of the Nové Mlýny reservoir system in the River Dyje basin (Lusk & Halačka 1995).

In Poland, the tubenose goby was first recorded in spring 2008 in the River Vistula basin, where it probably spread from Belarus through a canal connecting the Rivers Bug and Pripyat (Rizevsky et al. 2007, Grabowska et al. 2008, Nowak et al. 2008). Thus, it is also listed as invasive in Poland. In Ukraine, the species spread together with other gobiids from the natural area of brackish waters of the Black Sea through the reservoirs in the River Dnieper basin, where it found suitable conditions (Kvach & Kutsokon 2017).

Tubenose goby – a silent invader from two centuries ago?

The first record of the tubenose goby in Slovakia (middle Danube) comes from the late 19th century

from Koelbel (1874), who provided the most complete description of a population from the River Danube near Bratislava and from the River Morava near Devínska Nová Ves (the sample contained as many as 50 specimens, which is a large sample for that period). Other data on the first occurrence of the tubenose goby come from the marshes at the mouth of the River Morava at its junction with the River Danube (Steindachner 1899), followed later by data from the River Danube inundation near the village of Kamenica on the River Hron (Ferianc 1947), from the River Danube and from the Šúr Channel (Brtek 1951, 1953, 1964), as well as from other locations in Slovakia (Oliva 1956, 1962, Balon 1966, Oliva & Hrabě 1968, Spindler et al. 1992, Hensel 1995). Among the tributaries of the Slovak section of the River Danube the species has been found in the Rivers Ipel' (e.g. Jurajda et al. 2005, Kováč 2015b), Hron (Kux & Weisz 1962), Nitra (Kux & Weisz 1962), Váh (e.g. Kux & Weisz 1962, Jurajda et al. 2005, Kováč 2015b, Jakubčinová 2018) and Morava (e.g. Lisický 1995, Horváth et al. 2012), as well as in the River Little Danube (e.g. Nagy & Černý 1992, Kováč 2015b). However, in eastern Slovakia (the River Tisa drainage), the occurrence of the tubenose goby was not recorded earlier than 2014 (in the Rivers Bodrog and Ondava; Koščo et al. 2014). In 2015, it was further recorded in other parts of the River Bodrog, as well as in the Rivers Laborec and Roňava (Jakubčinová 2018, see Table 1 for further details).

Will the tubenose goby invade smaller rivers and higher altitudes in Europe?

Between 2011 and 2021, an extensive survey of fish communities was conducted in Slovakia. This sampling was associated with the monitoring of fish communities (implementation of the Water Framework Directive of EU in Slovakia), with monitoring aimed at implementation of the Council Directive on the conservation of natural habitats and of wild fauna and flora in Slovakia (also known as Natura 2000; European Community 1992). A total of 1,117 sites were sampled in all zoogeographical regions of Slovakia that covered all types of flowing waters in terms of fish communities. The fish samples were collected by electrofishing, and the sampling protocol followed the standards required under the Water Framework Directive, and thus was uniform for all sites (Kováč 2015a). In addition to this survey, monitoring of invasive species was performed in eastern Slovakia in 2014, 2015, 2017, 2018, 2019 and 2020.

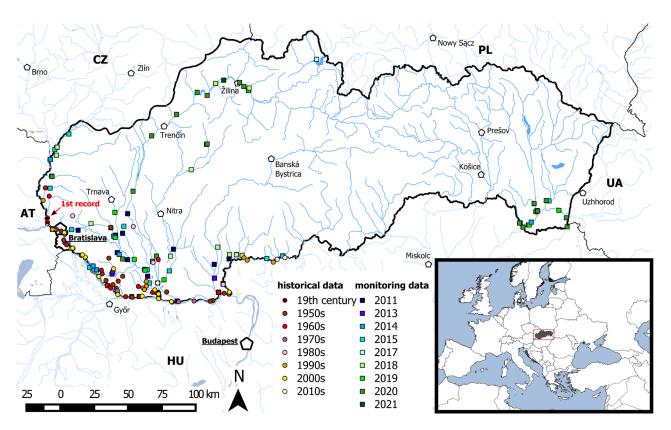


Fig. 1. Temporal (historical data) and spatial (monitoring data) patterns of the distribution of the western tubenose goby (*Proterorhinus semilunaris*) in Slovakia.

Until the 1990s, the tubenose goby was recorded in Slovakia only in the River Danube and small water bodies in the Danubian Lowland. However, since then it has expanded up the River Danube tributaries, the Rivers Morava, Váh, Hron and Ipeľ (e.g. Oliva & Hrabě 1968, Hensel 1995, Jurajda et al. 2005, Kováč 2015b, Jakubčinová 2018).

After 2014, the tubenose goby was also recorded in several streams in eastern Slovakia (i.e. the river Tisa drainage) and its occurrence is currently limited to the southern part of this region at lower altitudes only (Fig. 1).

In western Slovakia the occurrence of the tubenose goby is no longer limited to lower altitudes and latitudes. Over the last decade, its occurrence has been recorded in the upper sections of the Rivers Váh and Orava, as well as in the River Nitrica (both after 2017; Fig. 1), located at altitudes ranging from 140 to 597 m a.s.l. The record from the Orava Reservoir (the River Orava is a tributary of the River Váh) near the village of Bobrov in northern Slovakia (597 m a.s.l.; Fig. 1) in 2017 raises the question how the tubenose goby reached this part of the river. The River Váh is a non-navigable river, and due to many transverse barriers, active upstream migration is virtually impossible. The most likely explanation is a release of live fish used as baitfish by anglers, or unintentional introduction with fish stocks (Prášek & Jurajda 2005, Ondračková et al. 2019).

Such repeated introductions have probably occurred for decades, therefore, there is a question why a new range expansion of tubenose gobies to the north and upstream have started relatively recently, especially considering that the species was recorded in the River Danube as early as in the 19th century. The most likely explanation is elevated water temperatures resulting from the synergic effect of climate change and reservoirs built decades ago. This would be a process analogous to that in the River Danube, where repeated introductions of all P-C gobies in the hulls of ships is believed to have occurred for an extended period, though these species were able to establish populations only after water temperatures in the River Danube increased to the levels they could tolerate (e.g. Wiesner 2005, Hárka & Bíró 2007). Be it as it may, this example from northern Slovakia can serve as a warning that the tubenose goby may colonise further European smaller river systems at higher altitudes and colder climates than previously expected.

Based on all available historical data on the distribution and occurrence of the tubenose goby (see Table S1 for details, including grey literature representing valuable sources that have not yet been published in a comprehensive form), we can assume that it is the most widespread P-C fish species, with presumably the greatest capacity to establish riverine populations (Table S1, Grabowska et al. 2008) and one of the most widely distributed invasive fish species in European freshwaters (Grabowska et al. 2021). Moreover, it appears to be the fastest spreading P-C invasive species with an estimated rate of expansion of 608 km per year (Semenchenko et al. 2011). Another salient fact is that, together with the round goby, these are the only two species of P-C gobies that have successfully invaded the Great Lakes region of North America (Jude et al. 1992).

Nonetheless, competition with its larger relatives could be a limiting factor for further spread of the tubenose goby into new areas. The tubenose goby is a small species with a largely annual life cycle and is a poor competitor when confronted with other gobiid species, such as the larger round goby (Valová et al. 2015). When these two species cooccur, the round goby can suppress tubenose goby population size through its aggressive behaviour and greater competitive abilities. The round goby has even been observed to replace the tubenose goby in some locations (Baer et al. 2017, Cartwright et al. 2019). On the other hand, in the absence of goby competition, tubenose goby populations can reach high abundances and become numerically dominant in fish assemblages, and thus could pose negative impacts on native ecosystems (Valová et al. 2015).

The co-occurrence of tubenose and round gobies is limited to western and southern areas of Slovakia and to lower altitudes. In eastern and northern regions only the tubenose goby occurs (Fig. 2). Moreover, as the abundance of round goby populations in the Slovak stretch of the River Danube gradually decreases in the course of its invasion, it seems that tubenose goby abundance has begun to increase slightly (Bammer et al. 2021, D. Grul'a, unpublished data).

The habitat parameters that characterise the current distribution limits of the round goby in Slovakia were found to be river wetted width,

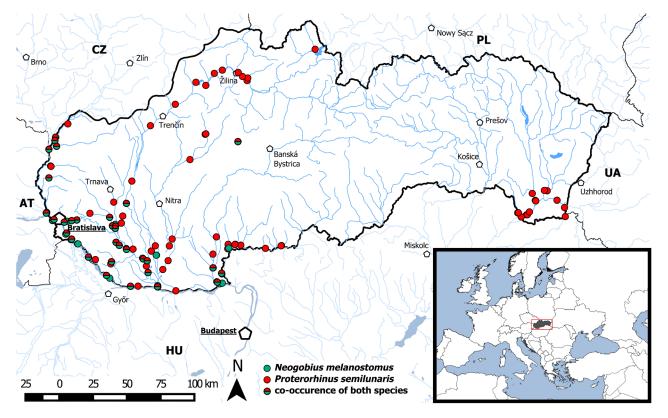


Fig. 2. Current distribution of the round goby (*Neogobius melanostomus*) and western tubenose goby (*Proterorhinus semilunaris*) in Slovakia.

slope, temperature and conductivity (Jakubčinová et al. 2018). The round goby was found to prefer a wider wetted width and shallower slope, as well as higher oxygen saturation. Such characteristics correspond to the River Danube and lower sections of its tributaries. These conditions may explain why the distribution of the round goby across Europe is currently limited to large water bodies, and the species is not known to penetrate too far upstream in smaller tributaries. According to an analysis of key factors of the current distribution of the round goby it is assumed that its future invasion of small and mid-size tributaries of large rivers is unlikely (Jakubčinová et al. 2018). This situation raises the possibility that the tubenose goby may successfully invade and dominate fish communities in smaller streams and higher altitudes, when competing with native species only (Valová et al. 2015). What the possible negative impacts of tubenose goby invasions on native fish communities, or whole ecosystems, still remains questionable.

The potential negative impacts of the tubenose goby on native fish fauna could be either direct (e.g. predation on fish eggs or larvae, or from competition) or indirect (e.g. alterations of food webs). In fact, scant information on the tubenose goby and its possible impacts on aquatic communities is currently available (Gebauer et al. 2018). However, some studies show that the tubenose goby may play an important role in trematode life cycles (Ondračková et al. 2019) and thus may promote the occurrence and further spread of these parasites. Moreover, the tubenose goby can have a possible negative impact on specific native fish species. For example, in the case of the European bullhead (Cottus gobio Linnaeus, 1758), which is a species of European concern, the numbers of bullhead decreased sharply following the appearance of non-native gobiids (Baer et al. 2017). Even in smaller streams located at higher altitudes in Slovakia, the tubenose goby could have a negative impact on European bullhead, as well as on other native species, and its impact may not be limited only to fish.

To mitigate potential negative impacts, effective monitoring of range expansion of the tubenose goby across Europe is recommended. Traditional methods of sampling, such as electrofishing should be supported by new methods, especially those aimed at species detection using environmental DNA (eDNA). Indeed, detection of invasive species based on eDNA extracted from water could provide more detailed information on the actual distribution and spread of the tubenose goby into smaller streams, backwaters and tributaries.

Conclusions

The tubenose goby is a pioneer species that appeared at the beginning of the invasion of Ponto-Caspian gobies up the River Danube and across Europe, two centuries before the other goby species that have subsequently invaded the region. In many European countries the tubenose goby is considered non-native or invasive, and its current status in Slovakia (representing an upper section of the Middle Danube) should also be re-stated as invasive. Spatial data from Slovakia demonstrate that the tubenose goby has been colonising new water bodies, progressing to the north and ascending rivers and establishing viable populations at higher altitudes than previously recorded. These developments suggest that the tubenose goby deserves attention, even after two centuries following its initial invasion, and its further expansion across Europe should be carefully monitored.

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Supplementary online material

Table S1. Occurrence of the western tubenose goby (*Proterorhinus semilunaris*) with sites and year of record/monitoring in Europe (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-4-2021-Slovak-Svolikova-et-al.-Table-S1.pdf).