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Several decades of two invasive fish species (*Perccottus glenii*, *Pseudorasbora parva*) of European concern in Lithuanian inland waters; from first appearance to current state

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Abstract. Following their first appearance, the invasive fishes *Pseudorasbora parva* and *Perccottus glenii* have been in Lithuania for several decades. However, until recently, information relating to their distribution and secondary spread was limited. For this reason, suitable habitats for these fish species were surveyed for their presence across the entire country. Additionally, all previously reported records on the presence of these species were summarized. Results revealed *P. glenii* to be widely distributed within the country with abundant populations in habitats suitable for the species. The recent distribution of *P. parva* is restricted to only a few water bodies. It was shown that both species are associated with human mediated transfer, while no natural dispersal of these invasive species was observed. The results of this study suggest that the invasion of Lithuanian inland waters by *P. parva* and *P. glenii* is still ongoing, and their occurrence in numerous water bodies, which are still devoid of these species, now seems probable. Demonstrated vectors of *P. parva* and *P. glenii* introductions in Lithuania highlight the importance of controlling and screening human activities related to aquaculture, recreational angling and the ornamental fish trade in order to restrict further *P. glenii* and *P. parva* expansion in this region.

Key words: aquatic invasion, alien species, fish introductions, central European invasion corridor

Introduction

There is good evidence that one of the main causes of biodiversity loss is the spread of introduced, invasive species. These species reduce local biodiversity through both indirect competitive and direct predatory impacts on resident native populations. Some invasive species have relatively narrow distributions, thus their negative impacts on local ecosystems are only regional while other species have a wide distribution. Furthermore, the

spread of invasive species is ongoing, and their impacts on local communities is often difficult to predict. As a consequence, the further spread of invasive species is now considered an international problem and all European countries are actively working to reduce their spread and impacts; since 2016 these species have been designated as “invasive species of European concern” (European Commission 2016). Currently, there are two invasive fish species of European concern present in Lithuania: *Perccottus glenii* (Dybowski, 1877) and

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Pseudorasbora parva (Temminck & Schlegel, 1846). The presence of both species was first recorded several decades ago.

The first official record of *P. parva* in Lithuanian inland waters dates back to 1963 (Krotas 1971, Virbickas & Maniukas 1971). The first few individuals were caught in a small enclosed water body, Lake Dunojus (Fig. 1A). *Pseudorasbora parva* was introduced unintentionally with imported stocks of juvenile *Ctenopharyngodon idella* (Valencienes, 1844) that were deliberately stocked in the lake (Virbickas 2010). For some time, the species was abundant at the site (Krotas 1971). Various age classes of *P. parva* were detected, showing a well-developed population with potential for spreading elsewhere in the country. However, later the species vanished without an apparent cause (Virbickas 2010). Interestingly, the same introduction, establishment and subsequent sudden disappearance was demonstrated in 2008–

2012. The contemporary status of *P. parva* in the inland waters of Lithuania is unknown.

The first record of *P. glenii* dates back to 1985 (Virbickas 2000). The first few individuals of *P. glenii* were caught in Lake Bevardis near Vilnius (Fig. 1A). The introduction of *P. glenii* originated from ornamental fish keeping. An abundant population of *P. glenii* with a large age variation was recorded in Lake Bevardis, thereby showing high potential for further spread within country. Contrary to *P. parva*, *P. glenii* started to expand from its first introduction, giving rise to several more numerous populations within and around Vilnius (Virbickas 2000). In 2014, it was shown that the species is widespread in some regions (Rakauskas et al. 2016a). However, there were no further data on the distribution of *P. glenii* in the inland waters of Lithuania.

Recent monitoring of invasive species has shown that *P. parva* is still present in Lithuania, and *P. glenii*

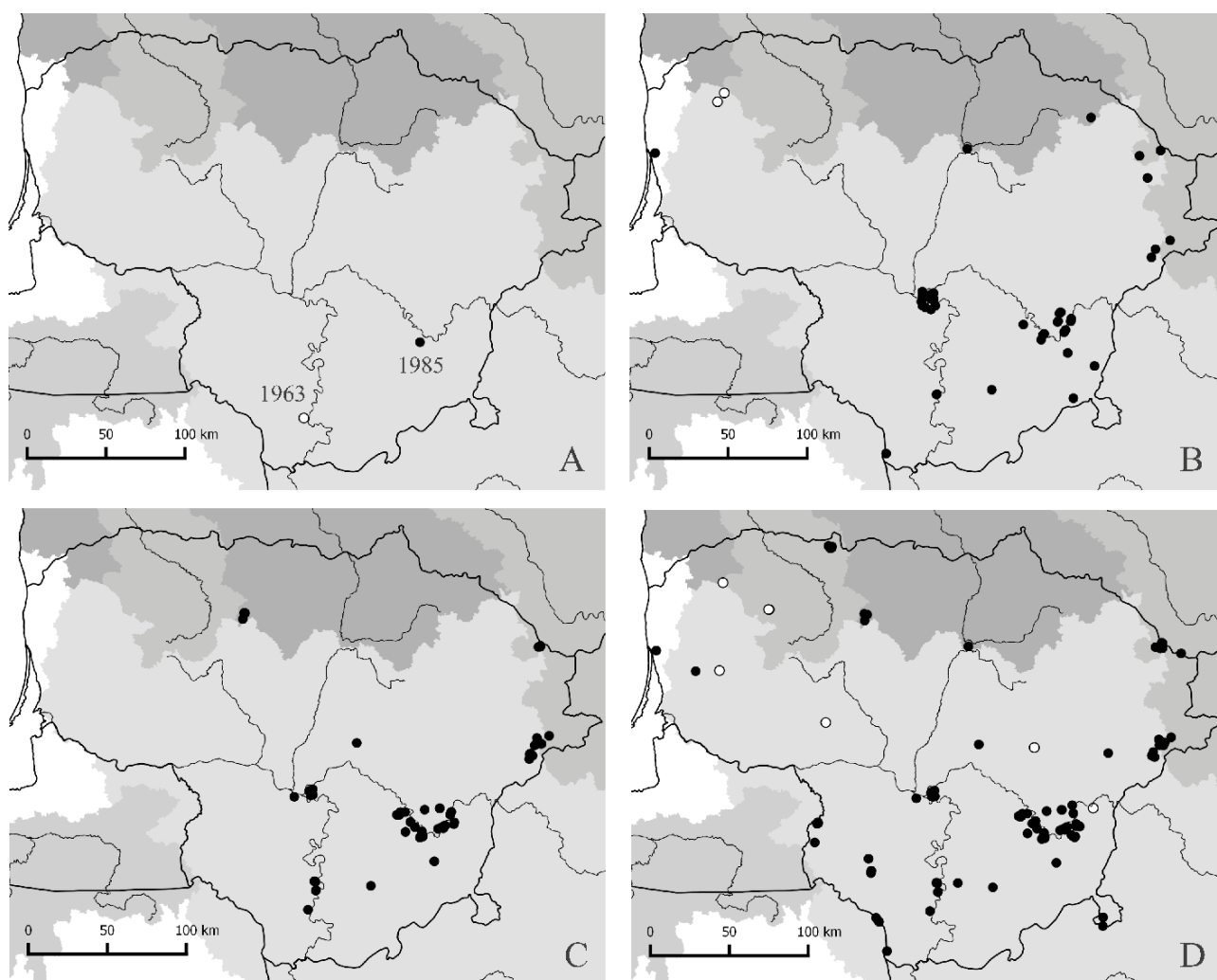


Fig. 1. Distribution of *Pseudorasbora parva* (open circles) and *Percottus glenii* (closed circles) in the inland waters of Lithuania: sites and year of first record (A), first inventory in 2008–2010 (B), second inventory in 2012–2014 (C), current (2019–2021) species distribution (D).

is still expanding its range in the country. Thus, an understanding of the vectors for the spread of *P. glenii* and *P. parva* may help to predict and prevent their further expansion and establishment in the region. Understanding the pattern of spread of these species within the country can help in the formulation of better strategies for control and the protection of endangered species.

Material and Methods

Study area

Lithuania is in the Baltic Sea drainage basin, situated along the south-east shore of the Baltic Sea and with a territory of approximately 64,800 km², which is divided by seven main river basins (Kažys 2013). There are 2,850 lakes with a surface area exceeding 0.005 km² in the country, and 3,150 smaller lakes with a total area of 913.6 km². In addition, there

are 1,132 reservoirs and more than 3,000 ponds in Lithuania (Kažys 2013). The River Nemunas has the largest catchment area in Lithuania, with 93% of Lithuanian territory is within or is connected by canals to the River Nemunas basin (Fig. 2). Of note is that the River Nemunas drainage basin is connected to the Rivers Pripyat and Vistula by the Oginski (opened in 1783) and Augustow (opened in 1839) canals (Fig. 2), forming a northern branch of the central European invasion corridor (Rakauskas et al. 2016a, 2018). Connections between watersheds of the Rivers Nemunas and Dnieper form the most probable pathway for new fish invasions of this region, primarily those of Ponto-Caspian origin (Rakauskas et al. 2016a, 2018).

Screening for non-indigenous fish species

Historical records of the presence of *P. glenii* and *P. parva* in Lithuania were assembled from both

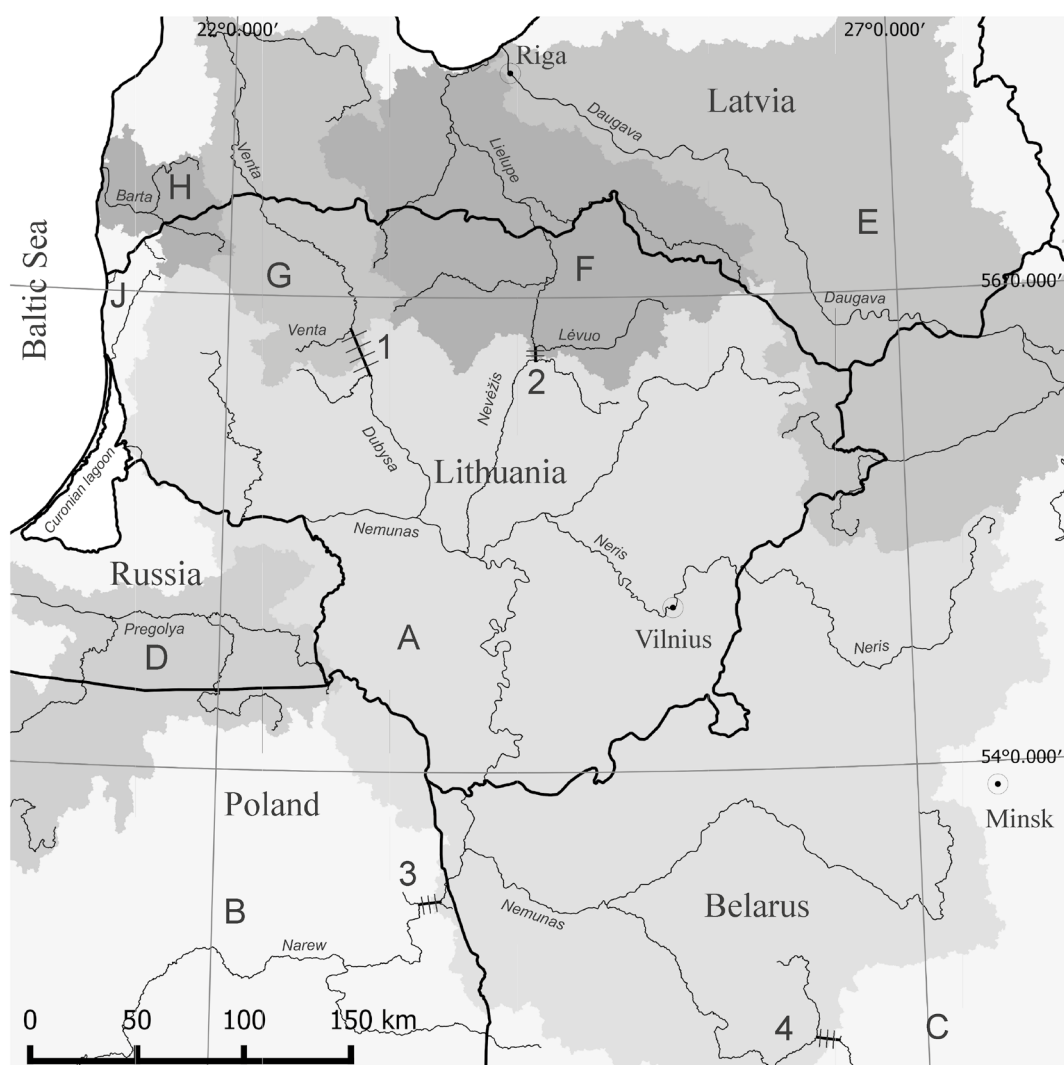


Fig. 2. Drainage basins of the main rivers in Lithuania. Different shading and capital letters indicate different river basins: Nemunas (A), Vistula (B), Pripyat (C), Pregolya (D), Daugava (E), Lielupe (F), Venta (G), Barta (H), Lithuanian coastal rivers (J). Canals connecting different basins are numbered: Windawski (1), Sanžilės (2), Augustow (3), Oginski (4).

published papers and “grey” literature (local scientific reports, verified reports in social media, etc.). After the initial records of the two species in inland Lithuanian waters, an inventory of records was compiled into three discrete periods: I – 2008-2010; II – 2012-2014; III – 2019-2021. In each of these periods, locations of invasive fish were identified from angler’s messages about the presence of invasive fish. When checking sites, several randomly selected water bodies potentially suitable for the studied fish species, located up to 2 km from the identified sites, were also screened for the presence of invasive species. Furthermore, already recognised populations of *P. glenii* and *P. parva* were re-investigated during each inventory. Information on the distribution of the studied invasive species during the first inventory period was collected from national scientific reports (Kaupinis et al. 2009, Virbickas 2010, 2011). During the second period, data were assembled from both the published literature (Rakauskas et al. 2016a) and scientific reports (Stakėnas et al. 2014). The data for the most recent period (2020-2021) was compiled from surveys conducted during a national invasive species-monitoring program. Occasional catches of single specimens of *P. glenii* recorded outside preferred habitats between 2000 and 2021 that were reported during national fish-monitoring or studies conducted for other purposes, were added to the overall inventory data. Notably, ichthyological studies are performed annually in a large number of lakes (~60) and river sites (~150) as a part of national monitoring programs in Lithuania.

Results also include data from 533 lentic water bodies with a surface area smaller than 0.5 km². Fish were captured using battery-powered electric fishing gear from May until October. Electric fishing was performed from a boat or by wading for 10 min intervals in water depths of 0.5-3.0 m for each catch per unit effort (CPUE). Fish taxonomy used in the present paper follows FishBase (<http://www.fishbase.se>, accessed 2021.06.15).

Results

First inventory (2008-2010)

Perccottus glenii

A total of 121 water bodies were investigated for the presence of *P. glenii* during the first inventory period. Anglers identified 53 waterbodies as harbouring specimens of *P. glenii*. Furthermore, 58 water bodies were investigated as potential habitats

around those identified by anglers, including one where *P. glenii* was recorded for the first time.

Perccottus glenii was found in 39 of 121 (32.2 %) investigated water bodies. Two sites were also discovered in rivers during national ichthyological monitoring (Virbickas 2008, 2009). Overall, the presence of this species was identified at 41 locations (Fig. 1B). The species was found at 38 (71.7 %) of 53 sites suggested by anglers. Preliminary analysis showed that the species was well established in some water bodies at the time of surveys and dominant in the fish community. At some sites *P. glenii* constituted up to 95% of the overall fish assemblage at a density exceeding 300 ind./100 m². A large age range of specimens were detected during the study (from 0+ to 11+), indicating well-developed populations and suggesting further potential for expansion in the country (Kaupinis et al. 2009, Virbickas 2011). Notably the species was still present and abundant in Lake Bevardis, the site of its first introduction in Lithuania. Only single individuals of *P. glenii* were found in river sites.

In all cases, abundant *P. glenii* populations were recorded from small, hypereutrophic or dystrophic water bodies with atypical fish assemblages. Such fish assemblages as a rule consisted of one to three fish species with no other piscivorous species except *P. glenii*. Fish species accompanying *P. glenii* were mostly represented by: *Leucaspius delineatus* (Heckel, 1843) and *Carassius gibelio* (Bloch, 1782), as well as single cases of *Tinca tinca*, (Linnaeus, 1758) and *Carassius carassius* (Linnaeus, 1758). Meanwhile in other habitats, such as relatively large lakes or river sites, only single specimens of *P. glenii* were captured, indicating accidental species presence in habitats unsuitable for viable *P. glenii* populations.

Pseudorasbora parva

A total of ten water bodies were investigated for the presence of *P. parva* during the first inventory period. Anglers identified fewer water bodies with *P. parva* during this period, although the first record of *P. parva* in Lithuania was much earlier than *P. glenii*. Two water bodies were investigated based on angler reports. One site was investigated as it was formerly known to support a population of *P. parva* and seven additional water bodies were investigated close to the locations identified by anglers.

Pseudorasbora parva was found at both the sites indicated by anglers but was not detected at the other

sites surveyed as potential habitats (Fig. 1B). Three (from 0+ to 2+) age groups of *P. parva* were caught at both sites, showing well-developed populations (Virbickas 2010). Notably the species was not found at its first recorded location. *P. parva* was not detected at any other sites, other than those identified by anglers, suggesting extinction at the previously inhabited water body and no further expansion around the locations at which it was recorded by anglers. This in total, *P. parva* was found in two of ten (20%) investigated water bodies. The appearance of all new *P. parva* populations were associated with unintentional introductions while stocking juvenile *C. idella* for controlling aquatic vegetation.

Second inventory (2012-2014)

Perccottus glenii

In total, 154 water bodies were investigated for the presence of *P. glenii* during the second invasive species inventory period. Forty-one sites were investigated as a result of previous records of *P. glenii* during the first inventory period. A further 47 water bodies were identified by anglers as harbouring *P. glenii* specimens and an additional 66 sites were investigated as further potential habitats.

Perccottus glenii was found at 67 (43.5%) of locations. One additional site was located in the River Mera during national riverine ichthyological monitoring, with a total of 68 locations showing the presence of this species (Fig. 1C). Of those 41 sites at which *P. glenii* was detected in the first phase, the species was present at 20 (48.8%) sites. This finding implies the disappearance of *P. glenii* from 21 (51.2%) water bodies at which the species was previously present. The species was also found at 36 (76.6%) sites (of 47) suggested by anglers. Overall, *P. glenii* was found at 48 new sites and was not detected at 21 where it had previously been found. It was still present in Lake Bevardis, the site at which it was first introduced. During this phase of data collection, eradication measures had been undertaken at sites where *P. glenii* was particularly abundant (Rakauskas et al. 2019).

In common with results from the first inventory, *P. glenii* was most abundant in small, hypereutrophic water bodies. Similarly, the fish species most frequently co-occurring with *P. glenii* were *L. delineatus* and *C. gibelio*.

Pseudorasbora parva

Only two sites previously known to harbour *P. parva* populations were investigated during the

second inventory period. Anglers failed to report new locations with *P. parva*, and none of the sites previously known to support *P. parva* gave evidence of its presence, indicating its possible disappearance from the inland waters of Lithuania (Fig. 1C).

Current distribution (2019-2021)

Perccottus glenii

A total of 533 water bodies were investigated for the presence of *P. glenii* during the third invasive species inventory period. Sixty-eight sites were investigated as locations at which *P. glenii* was present during the second inventory period and anglers identified a further 37 new locations. An additional 105 sites were investigated as potential habitats in proximity to those identified by anglers and around locations previously identified as harbouring *P. glenii*. A further 323 habitats were investigated in regions where there was no previous records for the presence of *P. glenii*.

One hundred and twenty-two (22.9%) sites were identified with *P. glenii* present. An additional three sites were also reported from national riverine ichthyological monitoring, giving 125 locations at which the species was known to be present (Fig. 1D). Of the 68 sites at which *P. glenii* was found in the second survey, the species was present at 65 (95.6%) of the sites; *P. glenii* disappeared from only three water bodies at which the species was present several years previously. The species was also found at 26 (70.3%) sites (of 37) suggested by anglers. Thirty-one new *P. glenii* populations were found in areas distant from sites previously known to support *P. glenii* in Lithuania. Overall, *P. glenii* was found at 60 new sites and was not detected at three where it had previously been found. Of note was a record of successful bio-manipulation on *P. glenii* (Rakauskas et al. 2019), with the species successfully removed from its original site of introduction in Lithuania. However, since its first introduction it has shown steady expansion, with the number of water bodies occupied constantly increasing.

As with the first and second inventory results, *P. glenii* was most abundant in small, hypereutrophic water bodies and co-occurring most often with *L. delineatus* and *C. gibelio*. In 13 water bodies (10.4% of all recently invaded sites) *P. glenii* formed mono-species fish assemblages.

Pseudorasbora parva

A total 19 water bodies were investigated for the presence of *P. parva* during the last inventory period.

Anglers identified eight new potential locations and a further 11 potential sites were also investigated.

Pseudorasbora parva was present only in seven (38.9%) of the surveyed locations (Fig. 1D), with seven of the eight sites indicated by anglers found to harbour populations of *P. parva*. Several (from 0+ to 2+) age classes of *P. parva* were caught in all sites, suggesting stable populations. None of the additionally investigated sites showed the presence of the species, indicating no further expansion around the locations reported by anglers.

For the first time *P. parva* was detected in rivers, indicating an elevated risk of expansion within the country. The appearance of new *P. parva* lentic populations were again associated with unintentional introduction while stocking juvenile *C. idella* for biomanipulation purposes. The lotic population was detected close to a fish farm that cultivated *C. idella*, suggesting *P. parva* had escaped from the farm and further implicating *C. idella* stocking as the source of *P. parva* introductions in Lithuania.

Discussion

Amur sleeper

Introduction history

The first official record of *P. glenii* in Lithuania comes from Lake Bevardis, a small enclosed lake, and dates back to 1985 (Fig. 1A). It was suggested that the introduction of *P. glenii* was a by-product of ornamental fish keeping (Virbickas 2011). An abundant population of *P. glenii* with large age variation was recorded at Lake Bevardis at that time, showing high potential for expansion within the country (T. Virbickas, unpublished data). Later, the species was translocated further and gave rise to several more numerous populations within and around Vilnius. A potential secondary pathway for *P. glenii* introduction was intentional, though illegal, introductions by local anglers. According to anglers, the presence of *P. glenii* in other ponds around Vilnius was recorded before 2000. A preliminary survey in 2010 showed that the species was already well established at that time in the water bodies surveyed and dominant in many fish communities. The species constituted 66-95% of total fish numbers in all water bodies investigated (more than 300 ind./100 m²) (Virbickas 2011). Since its first introduction, *P. glenii* showed consistent expansion in Lithuania, even in the face of measures to control its spread from 2013.

Habitats

The presence of *P. glenii* has recently been identified in a total of 125 water bodies. The large number of habitats surveyed provides an unambiguous view of the preferred habitats of *P. glenii* in Lithuania. It is clear the species is not able to establish and expand in environments with a good ecological status and balanced fish assemblage. Large *P. glenii* populations were typically associated with degraded, hyper-eutrophic ecosystems with atypical fish assemblages comprising 1-3 species. In 13 water bodies (10.4% of all recently invaded) *P. glenii* formed mono-species fish assemblages. A total of 92% of all recently known viable *P. glenii* populations are found in a small (< 10 ha), shallow lentic water bodies, with a thick sediment (sapropel) layer and a littoral zone densely overgrown with macrophytes. Most of these sites are subjected to irregular oxygen depletion events during prolonged ice cover. During the entire period of the investigation, there were only six sites at which *P. glenii* was found in lotic ecosystems, despite sampling in rivers during each survey period. Similar habitats preferences were shown in neighbouring countries in the region (Nowak et al. 2008, Grabowska et al. 2011, Lukina 2011, Reshetnikov 2013, Kutsokon 2017). The study also showed, that *P. glenii* is not capable of long-distance dispersal through small, cold-water, fast running rivers. For a decade *P. glenii* was recorded in the channelized upper reaches of the River Mera, where it disperses through the ditches from a small eutrophic lake. However, it has never been caught in a natural section of the river downstream, even though the natural site has been monitored annually for two decades as part of the Natura 2000 and salmonid species monitoring system (annual national reports).

Introduction vectors

The appearance of the first population of *P. glenii* in Lithuania is thought to be associated with ornamental fish keeping. Local anglers believe the source population is Russia and genetic studies of *P. glenii* populations in Europe also suggest Russian populations as the most probable source of introductions of Lithuanian *P. glenii* populations (Grabowska et al. 2020). Genetic analyses revealed that *P. glenii* in Europe consists of at least three distinct haplogroups that may represent independent introduction events from different parts of its native range. The haplogroup recorded in Lithuania was also found in neighbouring countries, such as Latvia (Daugava drainage),

Belarus (Dnieper drainage), and further away in Russia, in the lower River Volga drainage (Grabowska et al. 2020). First records of *P. glenii* in Latvia and Belarus were in the 1970s (Lukina 2011, Grabowska et al. 2020), while the first reports of *P. glenii* in Russia come from St. Petersburg in 1916 (Kuderskiy 1980); significantly earlier than in other countries. Thus, the hypothesis that the *P. glenii* haplogroup that is typical for Lithuania was introduced from the Volga drainage seems reasonable.

The secondary pathway for *P. glenii* dispersal in the inland waters of Lithuania is that of anglers. The observed pattern of fragmented dispersal of *P. glenii* suggests human mediated transfer (i.e. illegal, but intentional introductions), which has significantly facilitated the expansion of this species. Based on discussion with anglers, there are two main purposes for these introductions: a) to improve fish diversity for angling purpose in species-poor water bodies, b) to control unwanted populations of *C. gibelio* and/or amphibians. Strikingly, during this investigation anglers identified new viable *P. glenii* populations with 72.7% accuracy, indicating that anglers are familiar with the species.

Secondary dispersal pathways were also demonstrated to be operating in neighbouring countries. Fish release by aquarists and anglers is considered one of the primary reasons for the expansion of *P. glenii* in Belarus, Ukraine and Poland (Nowak et al. 2008, Lukina 2011, Kutsokon 2017). Anthropogenic introductions have also facilitated further expansion via natural mechanisms, particularly through drainage ditches, streams and rivers that may serve as invasion highways at the river drainage scale (Lukina 2011, Kutsokon 2017, Grabowska et al. 2020). Our study on the distribution of *P. glenii* in Lithuanian waters only revealed human-mediated translocations as a secondary dispersal pathway. Only in a few cases were single *P. glenii* individuals captured in rivers, despite the implementation of intensive ichthyological studies in Lithuanian rivers. Furthermore, all reported lotic cases were in proximity to known abundant lentic *P. glenii* populations, suggesting recent isolated individual migration. Similar results were obtained from studies of the distribution of *P. glenii* in Belarus and Ukraine, which revealed only a few cases when single individuals of the species were found in natural, well-preserved fluvial river stretches

(Lukina 2011, Kutsokon 2017). Furthermore, our studies on the River Mera, revealed the presence of *P. glenii* in upper river stretches, connected to the lake population, though the species was never found in the river downstream of the lake. This finding indicates that the species probably cannot persist in the presence of local piscivorous fish assemblages in rivers.

There is no evidence that *P. glenii* can be translocated accidentally by birds, boats or by other means, as their eggs are sticky, and once removed from the spawning site they never hatch (Reshetnikov 2003). Consequently, human-mediated translocation seems to be the primary vector by which *P. glenii* dispersal will occur in the inland waters of Lithuania in the future.

Impact

It is recognised that following their introduction, *P. glenii* seriously deplete the abundance of juvenile *C. gibelio*, thereby disrupting the sustainability of the species, as well as depleting the abundance of *L. delineatus* (unpublished data). One study was conducted on the possible impact of *P. glenii* on local European pond turtles, *Emys orbicularis* (Linnaeus, 1758). The study revealed that large specimens of *P. glenii* are not capable of preying on juvenile pond turtles, and thus cannot directly threaten pond turtle populations through predator-prey interactions, though their habitats and current distribution are overlapping in the inland waters of Lithuania. In contrast, it was shown that mature adult *E. orbicularis* can prey on juvenile *P. glenii*. Therefore, abundant turtle populations could potentially control the invasive *P. glenii* where their distributions overlap (Rakauskas et al. 2016b). No studies of the impact of *P. glenii* on local aquatic ecosystems have yet been completed.

However, the potential impact on local ecosystem can be extrapolated from locations with similar climatic conditions. In general, it was concluded that *P. glenii* is capable of depleting the diversity of water macroinvertebrates, amphibians, reptiles, and fishes (Koščo et al. 2008, Grabowska et al. 2009, 2019, Pupinš & Pupina 2012, 2018, Reshetnikov 2013), making it a serious threat to European freshwater ecosystems.

Eradication

Perccottus glenii was included on the list of Lithuanian invasive species since 2004 (Republic of Lithuania 2004). The species has also been

placed on the list of invasive species of European concern since 2016 (European Commission 2016). As a consequence experimental eradication and control measures for the most abundant *P. glenii* populations in Lithuania have been applied. Although control measures were applied at a small scale, the results were optimistic. It was shown that stocking local piscivorous fishes *Esox lucius* Linnaeus, 1758 and *Perca fluviatilis* Linnaeus, 1758 could be a valuable measure for the eradication of *P. glenii* from invaded water bodies (Rakauskas et al. 2019). Furthermore, this eradication measure was popular with pond owners, and this control measure was independently applied by some pond owners. As a result, *P. glenii* was eradicated from 24 water bodies during the study period.

Future threats

Our study results clearly indicate that *P. glenii* is widely distributed in Lithuania (Fig. 1D), showing consistent expansion of viable populations in the country. The observed pattern of fragmented dispersal implies human-mediated translocation (i.e. illegal, but intentional introductions), which has significantly facilitated the expansion of this species. The occupation of Lithuanian waters by *P. glenii* is still current, and its invasion into numerous water bodies, from which it is currently absent, seems probable. Although the species was eradicated from several ponds, over the long-term, this invader will likely occupy most small, stagnant and eutrophic water bodies that are overgrown with vegetation, such as oxbow lakes, floodplain pools, bogs and ponds, both natural and artificial, in Lithuania. Unfortunately, a similar prediction for further expansion of *P. glenii* has also been made for neighbouring countries (Lukina 2011, Kutsokon 2017). A public opinion poll showed that citizens lack information on *P. glenii* and its potential damage to freshwater ecosystems. Therefore, ecological education for the public is of primary importance to protect Lithuanian waters from further intentional illegal introductions of *P. glenii*.

Stone moroko

Introduction history

The first official record of *P. parva* in Lithuanian inland waters dates back to 1963 (Krotas 1971, Virbickas & Maniukas 1971). The first few individuals were caught in Lake Dunojus, a small enclosed water body (Fig. 2A). After investigation of this introduction, it was concluded that *P. parva* was introduced unintentionally with imported stock of

juvenile *C. idella* during lake stocking (Virbickas 2000). For some time, the species was abundant at the site of introduction (Krotas 1971), and various age classes of *P. parva* were discovered, showing a well-developed population with species invasion potential. However, the species subsequently disappeared from the site without clear reason (Virbickas 2000), though it appears that *P. parva* suffers from predation pressure and interspecific competition from other fish species. During fish surveys in Lake Dunojus in 1995, a diverse fish assemblage, including native piscivorous *E. lucius* and *P. fluviatilis*, was observed (T. Virbickas, unpublished data). Luckily, the species was not translocated further within the country from its first introduction at that time. Until 2008 there was no record of the species in the country. However, *P. parva* was again inadvertently introduced into private ponds in 2008. Again, its introduction was associated with unintentional release with imported stocks of *C. idella* (Virbickas & Sidabras 2007, Virbickas 2010). However, similarly to the first *P. parva* introduction, the species again disappeared from the water bodies into which it was introduced. During the 2012-2014 survey, the absence of *P. parva* in its former introduction sites was confirmed, indicating the extinction of the species in the country (Fig. 1C). Finally, the species has once again been recorded in Lithuanian waters in 2021. This time the species was recorded in up to seven water bodies, including in a river site, suggesting high potential for its further spread within the country.

Habitats

Relatively little information is available on the habitat use of *P. parva* in Lithuania as the species has a relatively small distribution and most studies provides basic macro habitat information only (Virbickas 2000, Rakauskas et al. 2016a). For the first time *P. parva* was found in a natural, relatively small (20 ha), eutrophic lake. The fish community of the lake was primarily composed of warm-water fish, characteristic of ecosystems at late succession stages, dominated by *Rutilus rutilus* (Linnaeus, 1758), *Abramis brama* (Linnaeus, 1758) and *T. tinca*. In addition to these dominant species, fishes of other ecological groups also inhabited the lake, such as *Gymnocephalus cernua* (Linnaeus, 1758). Piscivorous fish comprised *E. lucius* and *P. fluviatilis* (T. Virbickas, unpublished data). However, the species did not persist in this habitat, which thus was considered unsuitable for *P. parva*. The species was later recorded from slightly different habitats.

During the second species introduction wave, *P. parva* was found in private, small (< 1 ha) artificial ponds, often overgrown by water plants, with no possibility for further spread. Similar habitat preferences were also reported from neighbouring countries where *P. parva* was generally associated with submerged vegetation (Kapusta et al. 2008, Karabanov et al. 2010). However, in Lithuania its occurrence in specific habitats may be coincident with its main introduction vector, *C. idella*, which is usually stocked to remove aquatic vegetation. Again these habitats appear unsuitable for the long-term persistence of *P. parva*, as the species again did not last long in recorded water bodies. It appears that *P. parva* perform poorly under interspecies competition and heavy predation pressure, and private ponds are usually under intensive fishery usage. However, more data are needed to demonstrate this hypothesis. Finally, in 2021 the species was found in the River Upė. This small river possesses muddy substrates, a eutrophic status, warm-water, slow current, and with a degraded fish assemblage.

Outside Lithuanian waters, *P. parva* in its introduced range demonstrates great plasticity in habitat utilization, occupying a diverse range of lentic and lotic waters, including rivers, reservoirs, drainage, ditches and canals, ponds and shallow lakes (Gozlan et al. 2010a, Karabanov et al. 2010). Although *P. parva* may form populations under lotic conditions (Sunardi & Manatunge 2005, 2007, Sunardi et al. 2007), the species occurs at higher densities in lentic conditions (Arnold 1990, Pollux & Korosi 2006). However, *P. parva* is known to tolerate a variety of environmental conditions.

Introduction vectors

The primary introduction pathway of *P. parva* into Lithuanian inland waters was unintentional species release associated with *C. idella* stocking (Virbickas 2010). Until now there was no secondary pathway for *P. parva* dispersal within Lithuanian inland waters. However, in 2021 the species was recorded in a river connected to the entire the River Nemunas basin. Sadly, after its recent discovery in this river, natural dispersal may represent a secondary pathway for future expansion of *P. parva* in Lithuanian inland waters. It is known that small rivers with low flow, and main river channels may serve as dispersal corridors for *P. parva* in Europe (Muchacheva 1950, Gozlan et al. 2010b, Karabanov et al. 2010). Overall, further expansion of *P. parva* by natural dispersal is to be

expected in Lithuania, which may be substantially facilitated by human-mediated introductions. This review should serve as an early warning for other countries, particularly for those importing *C. idella* for aquaculture or biomanipulation purposes. In general, the expansion of *P. parva* in neighbouring countries has also been associated with aquaculture (Karabanov et al. 2010).

Impact

Until now no impact of *P. parva* on local ecosystems have been investigated in Lithuania. However, the potential impact on local ecosystem can be extrapolated from other regions with similar conditions. Inter-specific competition for food between *P. parva* and native fish species has been observed in water bodies in Belgium (Declerck et al. 2002), Czech Republic (Adámek & Sukop 2000), Germany (Stein & Herl 1986), Greece (Rosecchi et al. 1993) and Poland (Witkowski 2002). In a mesocosm experiment, larval *P. parva* feeding reduced abundance of planktonic cladocerans and rotifer species (Hanazato & Yasuno 1989, Nagata et al. 2005). High grazing pressure exerted by dense *P. parva* populations can also result in changes in the prevalent environmental conditions through top-down effects characterized by increased development of phytoplankton and accelerated eutrophication (Arnold 1990, Adámek & Sukop 2000).

Eradication

Currently *P. parva* is not included in the list of Lithuanian invasive species (Republic of Lithuania 2016). Thus, no measures to date have been applied for *P. parva* eradication in Lithuanian waters. However, the species has been on the list of invasive species of European concern since 2016 (European Commission 2016). Therefore, if the species continues to spread and establishes stable and abundant populations in Lithuanian inland waters, local authorities will be obliged to impose control measures. It is known that natural predators such as *E. lucius* and *P. fluviatilis* (fishes native for Lithuanian waters) could be used for *P. parva* control in lentic water bodies (Davies & Britton 2015, Lemmens et al. 2015), and similar measures could be applied in Lithuania for *P. parva* eradication.

Alternatively, early prevention of introduction is the best measure for invasive species control. To date, all *P. parva* introductions in Lithuania have been associated with stocking of juvenile

C. idella. Therefore, prevention measures, such as prohibiting trade in live 0+ *C. idella* would considerably decrease the chance of *P. parva* introductions in Lithuania. Since 0+ specimens of both species are difficult to distinguish, stocking only with 1+ *C. idella*, which are substantially bigger than adult *P. parva*, would help prevent accidental introduction of *P. parva*. Other prevention options might include monitoring fish farms for intentional or unintentional breeding of invasive species.

Future threats

The first few introductions of *P. parva* ended favourably, with the species introduced into relatively small, discrete water bodies, with no means of further spread. So far, only primary introduction pathways were observed for *P. parva* in Lithuanian waters, with no secondary pathway cases observed. All introductions were associated with *C. idella* stocking. In all cases the species has subsequently disappeared from sites in which it was recorded. However, the recent record of the species in the River Upė, connected to the entire River Nemunas basin, may permit this species to expand further. Despite its strong preference for lotic conditions, small rivers or canalised parts of main rivers may serve as dispersal corridors for *P. parva* (Muchacheva 1950, Gozlan et al. 2010a, Karabanov et al. 2010). Life-history traits of *P. parva* include early maturity, relatively high fecundity, multiple reproductive events during the course of one reproductive season, and the expression of male nest guarding all serve to maximize rapid population growth and, hence, the rapid establishment of sustainable populations. Its appearance in small rivers connected to the River Nemunas basin is particularly troubling. The River Nemunas is connected to the central invasion corridor, giving access to Latvian inland waters. To date, *P. parva* was not recorded from the inland waters of Latvia (Aleksjevs & Birzaks 2011, Birzaks et al. 2011, J. Birzaks pers. comm.). However, the Rivers Venta and Lielupe flowing from Lithuania to Latvia may serve as donors of this species to the Latvian ichthyofauna as they are connected with the River Nemunas drainage area by canals. Two such invasion pathways may be operating: 1) the River Nemunas → the River Nevėžis → the Sanžilė canal → the River Lėvuo → the River Mūša → the River Lielupe and 2) the River Nemunas → the River Dubysa → the Windawski canal → the River Venta (Fig. 2). Overall, there is a high risk that *P. parva* will occupy degraded water bodies within the entire the River Nemunas basin,

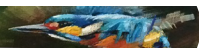
potentially establishing as a common fish species in such habitats in the future. Further expansion of *P. parva* by natural dispersal is to be expected, which may be substantially facilitated by human-mediated introductions. However, the important question about the potential of *P. parva* to expand their range further remains unclear.

Concluding remarks

Currently, *P. glenii* and *P. parva* are present in Lithuania. Both species have been repeatedly recorded within this region for several decades. However, their current distribution, primary and secondary introduction vectors and pathways are different. *Perccottus glenii* is widely distributed within the country with abundant populations in habitats suitable for the species. In contrast, the recent distribution of *P. parva* has been restricted to only a few water bodies. The observed fragmented pattern of dispersal of *P. glenii* indicates that human mediated transfer (i.e. illegal, but intentional introductions) is facilitating the expansion of this species. The unintentional release of *P. parva* associated with *C. idella* stocking is the only currently recognised pattern of *P. parva* introduction. However, with the recent discovery of *P. parva* in a major riverine ecosystem, it is expected that natural dispersal of the species could occur in the country. Overall, the occupation of Lithuanian inland waters by both species is ongoing, and their invasion into multiple water bodies that are currently devoid of these species, seems probable in the future. It is clear that both species are associated with human-mediated transfer. A public opinion poll showed that anglers lack information on invasive fish species and their potential damage to freshwater ecosystems and ecological education of the public is of primary importance to protect Lithuanian waters from further introductions of *P. glenii* and *P. parva*. This review should also serve as an early warning for other countries that face invasion by *P. glenii* and *P. parva*. Vectors of *P. parva* and *P. glenii* introductions in Lithuania highlight the importance of controlling and screening human activities related to aquaculture, recreational angling and the ornamental fish trade in order to avoid further *P. glenii* and *P. parva* expansion in Europe.

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