

ECOLOGY OF *PERCCOTTUS GLENII* DYBOWSKI, 1877 OF SMALL RIVERS AND LAKES IN THE EASTERN EDGE OF EUROPE

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DOI: 10.2478/trser-2026-0004

KEYWORDS: environmental factors, Amur Sleeper, occurrence, Tatarstan.

ABSTRACT

Our work offer information on the abundance, probability of occurrences, distribution, morphometric, and cohabitation abilities of *Perccottus glenii*. The study was conducted in the east edge of Europe in 562 small rivers and 122 lakes with high geographical and ecological heterogeneity. Probability of occurrence for *P. glenii* of lakes – 41% and 2.5% in small river, and it has been growing lately. The highest percentage (30.3) of coexisted for *P. glenii* was observed with *Carassius gibelio* – other invasive species. Elevation, depth and tree/bush cover were the factors influencing the distribution of *P. glenii* in lakes. In small rivers, the probability of occurrences of *P. glenii* increased in the eastern study areas in wide and deep areas with a low percentage of forest cover.

RÉSUMÉ: Écologie de *Perccottus glenii* Dybovski, 1877 des petites rivières et des lacs de la périphérie orientale de l'Europe.

Nos travaux fournissent des informations sur l'abondance, la probabilité de présence, la distribution, la morphométrie et les capacités de cohabitation du *Perccottus glenii*. L'étude a été menée à l'est de l'Europe, dans 562 petits cours d'eau et 122 lacs présentant une forte hétérogénéité géographique et écologique. La probabilité de présence du *P. glenii* est de 41% dans les lacs et de 2,5% dans les petits cours d'eau, et elle est en augmentation ces dernières années. Le pourcentage le plus élevé (30,3%) de coexistence du *P. glenii* a été observé avec le *Carassius gibelio* – une autre espèce invasive. L'altitude, la profondeur et le couvert arboré/arbustif sont les facteurs qui influencent la distribution du *P. glenii* dans les lacs. Dans les petits cours d'eau, la probabilité de présence du *P. glenii* a augmenté dans les zones d'étude orientales, notamment dans les zones larges et profondes à faible couverture forestière.

REZUMAT: Ecologia lui *Perccottus glenii* Dybovski, 1877 în râurile și lacurile mici de la periferia estică a Europei.

Lucrarea oferă informații despre abundența, probabilitatea de apariție, distribuția, caracteristicile morfometrice și de coabitare a speciei *Perccottus glenii*. Studiul a fost realizat în marginea estică a Europei, în 562 de râuri mici și 122 de lacuri, cu o heterogenitate geografică și ecologică mare. Probabilitatea de apariție a lui *P. glenii* în lacuri – 41% și 2,5% în râurile mici, a crescut recent. Cel mai mare procent (30,3%) de coexistență pentru *P. glenii* este cu *Carassius gibelio* – o altă specie invazivă. Altitudinea, adâncimea și acoperirea cu arbori/arbuști au fost factorii care au influențat distribuția lui *P. glenii* în lacuri. În râurile mici, probabilitatea de apariție a lui *P. glenii* a crescut în zonele estice de studiu, în zone largi și adânci, cu un procent scăzut de acoperire forestieră.

INTRODUCTION

Amur Sleeper – *Perccottus glenii* (Dybowski, 1877) a species of fish of the family Odontobutidae, in its natural habitat inhabiting East Asia, now, mainly due to human activity, has spread in a mosaic manner across different river basins of Eurasia (Reshetnikov et al., 2010). It is believed that *P. glenii* is one of the most rapidly spreading invasive fish in western part of Eurasia (Czeplédi et al., 2025, 2024; Ercoli et al., 2024). A similar trend of range expansion for this fish species is observed in Western Siberia (Reshetnikov et al., 2025). *P. glenii* is recognized in top-100 most dangerous invasive alien species in Northern Eurasia (Petrosyan et al., 2023). In the study area, *P. glenii* was not found during a comprehensive revision of the ichthyofauna in the late 19th and early 20th centuries (Berg, 1906; Ruzsky, 1887; Varpakhovsky, 1886); in the mid-20th century, *P. glenii* was also not present in Tatarstan (Popov and Lukin, 1949); the first captures of this species in the study area were dated 1981 in the Kuibyshev Reservoir (Kuznetsov, 2005) (according to unofficial data, the first discovery dates back to 1972 in the edge west part of the Republic of Tatarstan) and after that it began to spread rapidly and now lives throughout the study area. The latest study conducted in the lakes of Tatarstan showed that *P. glenii* is one of the most common fish species (Askeyev et al., 2023).

P. glenii has high ecological plasticity, adaptability to freezing of reservoirs (Jiang et al., 2023), low oxygen content and temperature differences in water (Kuznetsov, 2005), is a fish with a very wide range of food (Ercoli et al., 2024; Djikanović et al., 2023), including possible cases of cannibalism (Rau et al., 2017). All these, together with the ability to reproduce early (from two years old age) and protect its own nesting clutch of eggs (Kuznetsov, 2005; Kirczuk et al., 2024) the *P. glenii* is a very strong competitor and is capable of displacing or reducing the abundance of local fish species by predation (Czeplédi et al., 2025; Somogyi et al., 2023). On the other hand, in the Republic of Tatarstan, *P. glenii* is valued for its delicate meat and the almost complete absence of bones in its muscle fibers. Homemade canned *P. glenii* in oil, (à la Baltic Sprattus), is very popular. This, coupled with the fact that is often one of the few fish inhabitants of closed lakes, makes it a potential object of aquaculture on study area.

Climate change can additionally influence the composition of fish populations and exert additional pressure (Rumschlag et al., 2025; Bănăduc et al., 2021, 2022, 2024; Comte and Grenouillet, 2013; Moss et al., 2011). In the study area, climate change has a strong influence on various components of ecosystems at different part of the year (Askeyev et al., 2024a, 2022, 2020). As studies show (Askeyev et al., 2022), when certain temperatures are reached, individual components of ecosystems can react with an excessively nonlinear reaction. It is quite possible that the current rapid and strong increase in temperatures will lead to a strong increase in the growth of invasive fish species, including *P. glenii*. The interest in this species is also due to the fact that there is very little knowledge about its ecology and preferences for environmental conditions. All this makes this fish an interesting object for research especially in the context of possible future ecosystems perturbations and fisheries development.

The main objectives of this study were: 1) To calculate the probability of occurrences, abundance, and morphological features of body length of *P. glenii* in small rivers and lakes of the east edge of Europe; 2) to determine the fish species that coexist with *P. glenii* in water case of the east edge of Europe; 3) to identify the preferences of *P. glenii* in relation to environmental factors in lakes and small rivers; 4) to calculate the optimal points and widths of the ecological niche for *P. glenii* in the study area aquatic ecosystems.

MATERIAL AND METHODS

Study area and fish assemblage data

The study area is located in the extreme east of Europe (in the eastern part of the Ponto-Caspian biogeographic region) and covers the territory of the Republic of Tatarstan and the mountainous part of the Republic of Bashkortostan (detailed map is presented in Askeyev et al. (2023, 2025)). The study area represents an extremely wide range of diverse environmental conditions and reach fish species assemblages in rivers (Askeyev et al., 2021) and similar are in the lakes (Askeyev et al., 2023).

Rivers section

We focused on the fish assemblages of small rivers (length up to 500 km). We excluded rivers strongly impacted by large reservoirs. Fish sampling was conducted at 562 locations. Fieldwork was carried out from May to October in the years 2012-2025 during reduced summer flows. We used three different lengths of nets, depending on the width of the river. Three seining net were 5-15 m in length, 1.2-1.5 m high, 5x5 mm mesh in the wings, 3x3 mm in bags. Dip nets were of diameter 50-70 cm, with 4x4 mm mesh. Lengths of between 200 m (smaller rivers) and 400 m (larger rivers) of the river sites were sampled. For determining the length of the site, we followed the recommendations for catching fish by FAME CONSORTIUM (2004). The sampled fish individuals were placed in a plastic basin and identified, counted, and measured at the end of each catch session, after which $\geq 90\%$ of fish were returned to the water. The following eight environmental variables were obtained for each site: elevation (altitude) above sea level, mean width, mean depth, water velocity, tree/bush cover along banks, dominant bottom substrate (1 – mud, 2 – clay or peat, 3 – sand, 4 – gravel, 5 – small pebbles, 6 – large stones up to 150 mm, 7 – large stones 150-300 mm, 8 – boulders >300 mm), geographical latitude and longitude.

Lakes section

Our scientific collection of ichthyological material was carried out during 2012-2025 period from a total of 122 waterbodies: 92 lakes and 30 ponds (hereafter lakes for brevity). The collection of the sampled fish fauna was carried out using various methods. In the littoral zone, at depths from 0.4 to 1.3 m, a seining net was used, eight m long and a maximum height of 1.5 m, with a mesh in the wings of five mm; in geomorphologically complex and cluttered (with many snags) sites, an ichthyological net with an area of 0.15 m² was used. Dragging was carried out manually, the passage was carried out along the bank, at a distance of 20-30 m, depending on the conditions of the possibility of fishing, with a convergence at one point at the time of pulling. Pelagial and benthal zones, in large lakes and ponds, at depths from 1.6 to 12 m, were fished with two 30 m universal fixed gill nets (consisting of six five m sections of various meshes (10, 16, 28, 36, 40, 45 mm × 35, 40, 45, 50, 55, 60 mm)), 1.8 m high. The setting and sampling of nets was carried out from a boat, the nets were installed from the evening until the next morning, standing for 10 to 12 hours. The following six continuous environmental variables were obtained for each site: elevation (altitude) above sea level, lake area, mean depth, tree/bush cover along banks, geographical latitude, and longitude. Identification of fish in all waterbodies was carried out according to Maitland and Linsell (2009) and Makeeva et al. (2011). The coexistence of *P. glenii* with each other fish species of the sampling areas was calculated separately for lakes and small rivers and expressed as a percentage. The details about morphometric analysis are included in the below sections results and discussion.

Data analysis

Relationship between fish species and environmental variables

For probability of occurrences of *P. glenii*, the nature and strength of relationships with the environmental parameters in small rivers and lakes (separately) were examined using binary logistic regression with the environmental variables as predictors. Only statistically significant variables were retained in these regressions. In order to assess the accuracy of the final models, we used the area under the ROC curve (AUC), which indicates the predictive performance expressed as an index ranging from 0.5 to 1. The accuracy of the model was interpreted after Swets (1988) as follows: 0.90-1.00 excellent; 0.80-0.90 good; 0.70-0.80 fair; 0.60-0.70 poor; and 0.50-0.60 fail.

Species optimums and niche breadth

Species optima in terms of abundance for environmental variables was calculated for *P. glenii* in rivers and fits Gaussian response models to species abundances along an environmental gradient. The fitted parameters are optimum (i.e. average) and niche breadth/tolerance (i.e. standard deviation). The algorithm is based on weighted averaging (ter Braak and van Dam, 1989). Calculation and visualization were done in PAST 4.12 and MINITAB 19.

RESULTS AND DISCUSSION

General information about *Perccottus glenii*

Compared with previous studies in small rivers (Askeyev et al., 2017), the number of *P. glenii* encounters doubled and amounted to 14, with a probability of occurrences of 2.5%. The total number of these species also increased and amounted to 104 individuals, with an average of $0.19 \pm 2.94SD$. In the lakes, *P. glenii* was found in 50 sites, with a probability of occurrences of 41%, which is also more than in the previous study (Askeyev et al., 2023). A total of 888 individuals were caught in the lakes with an average of $7.3 \pm 19.8SD$. The increase in the occurrence of *P. glenii* may indicate generally favorable conditions for it at the current time, and perhaps further warming of the climate will also have a favorable effect on the state of its populations.

In general, the trend of *P. glenii* distribution is clearly expressed in the regions to the west of our study area (Grabowska et al., 2020; Reshetnikov, 2010) and to the east (Reshetnikov, 2025). If until the 1960s the distribution of *P. glenii* in Europe was spotty, then starting from the 21st century the species has spread significantly, especially in the central part of the Europe (Reshetnikov et al., 2010). For example, in Hungary, *P. glenii* was discovered at the end of the 20th century (Harka, 1998) and subsequently began to spread widely throughout the country (Czeglédi et al., 2024; Takács et al., 2015; Takács and Vital, 2012; Harka et al., 2008; Erős et al., 2008); in Romania, the first catch occurred in 2001 (Nalbant et al., 2004) and gradually began to spread throughout different basins (Năstase et al., 2019; Covaciu-Marcov et al., 2011, 2017; Năstase, 2007; Popa et al., 2006). Currently, *P. glenii* continues to spread across Europe, so in 2022 it was discovered in Finland (Pihlström et al., 2022), it is also actively distributed in Lithuania (Rakauskas et al., 2021). In Croatia, the first finding was in the beginning of the second decade of the 21st century (Čaleta et al., 2011), now it has begun to spread to other river basins (Horvatić et al., 2022). In Latvia, *P. glenii* was first detected in 1974, in the second decade of the 21st century it was detected in more than 50 locations (Pupina, et al., 2015). Now it is distributed everywhere, mainly in closed water bodies (Birzaks, 2024). In the Cheboksary Reservoir, the relative abundance and probability of occurrences of this fish is increasing according to the catches of some fishing gear (Loginov et al., 2020). It appeared also in the center of the Russian Plain (Ivancheva and Ivanchev, 2025),

P. glenii is among the three most widespread non-native species. It should also be taken into account that due to the rather mosaic distribution of this species, it is sometimes worth using non-standard approaches to determining its exact distribution (Reshetnikov et al., 2025, 2017; Czeglédi et al., 2024, 2025; Šmejkal et al., 2024; Sokolov et al., 2023). The general trend is clear, *P. glenii* is spreading in all directions.

Morphometric relationships between total length (TL) and standard length (SL) for *P. glenii*. General information.

Total sample sizes: N – 34. Ranges for standard length and total length, the means, Stand. dev., Median: SL (min – max) – 90 – 196 mm; mean 114,8 mm, Stand. dev. 25,45915; Median 106,5 mm. TL – (min – max) - 107 – 245 mm; mean 137,8 mm, Stand. dev. 29,47627; Median 130 mm

Estimation length-length relationships

Relationships between measured fish lengths (length-length relationships – LLRs) are described by regression equations: Standard length and total length relationships were calculated by regression model $TL = bSL + a$, where “a” is the intercept and “b” is the slope. The descriptive statistics for the LLRs are presented in table 1, including sample sizes and 95% Confidence intervals (CIs) for both equation parameters “a” and “b” as well as the coefficient correlation (R^2). Length-length regressions were highly significant ($p < 0.001$). The regression equations were obtained from the database of collection measurements from recent (20th-21st century) *P. glenii* specimens in the Biomonitoring Laboratory, Institute of Problems in Ecology and Mineral Wealth, Tatarstan Academy of Sciences, Kazan, Russia.

Table 1: Relationships between measured fish lengths.

Species	n	Equation	a [95% CIs]	b [95% CIs]	R^2
<i>Perccottus glenii</i>	34	$TL = 1.1473 \times SL + 6,0945$	6,0945 [– 4.9065 18.875]	1,1473 [1.026 1.2451]	0.981

Coexistence of *P. glenii* with other fish species in lakes and small rivers

P. glenii coexisted with 23 (Tab. 2) out of 35 species (Askeyev et al., 2023) of fish for lakes of the Republic of Tatarstan. The highest percentage of cohabitation for *P. glenii* was noted with also invasive fish species for the region – *Carassius gibelio* (30.3%). A high percentage of cohabitation was also noted for *Leucaspis delineatus* (17.7%) and also for others for native fish species such as *Carassius carassius*, *Perca fluviatilis* and *Rutilus rutilus* (Tab. 2). The studied species was not observed to cohabit with such rare fish for the region as lake minnow (*Rhynchocypris percunurus*), bitterling (*Rhodeus sericeus*) and sterlet (*Huso rutenus*). In five lakes, *P. glenii* is the only fish species, in two of them cases of cannibalism were noted. In small rivers, *P. glenii* can coexist with 36 out 42 species (Askeyev et al., 2017) both shallow rivers at high elevations above sea level together with cold-loving fish species such as grayling (*Thymallus thymallus*), bullhead (*Cottus gobio*) and river minnow (*Phoxinus phoxinus*) (but has never been recorded in areas with Brown trout (*Salmo caspius morpha fario*), and in sites of potamal rivers with the participation of other 29 fish species (Askeyev et al., 2024b). These facts tell us that the *P. glenii* is a very flexible species that can live in reservoirs without competition and victims for predation, on the other hand, this fish is able to withstand competition in a site with a large number of other species, and also withstand the pressure of larger predators.



Figure 1: The Astrakhanka Lake with one of the largest populations of *P. glenii* in Tatarstan.



Figure 2: *P. glenii* (bottom fish) and *C. carassius* are the most frequent coexist in the lakes of the Republic of Tatarstan.

Table 2: Percent of sites of lakes where two *P. glenii* and other fish species coexisted.

Fish species	%
Northern pike – <i>Esox lucius</i> (Linnaeus, 1758)	8.4
Common bream – <i>Abramis brama</i> (Linnaeus, 1758)	6.7
Blue bream – <i>Ballerus ballerus</i> (Linnaeus, 1758)	1.7
Silver bream – <i>Blicca bjoerkna</i> (Linnaeus, 1758)	3.4
Crucian carp – <i>Carassius carassius</i> (Linnaeus, 1758)	14.3
Gibel – <i>Carassius gibelio</i> (Bloch, 1782)	30.3
Gudgeon – <i>Gobio gobio</i> (Linnaeus, 1758)	2.5
Common bleak – <i>Alburnus alburnus</i> (Linnaeus, 1758)	5
Sunbleak – <i>Leucaspis delineatus</i> (Heckel, 1843)	17.7
Ide – <i>Leuciscus idus</i> (Linnaeus, 1758)	6.7
Common dace – <i>Leuciscus leuciscus</i> (Linnaeus, 1758)	0.8
Roach – <i>Rutilus rutilus</i> (Linnaeus, 1758)	10.9
Rudd – <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758)	7.6
Tench – <i>Tinca tinca</i> (Linnaeus, 1758)	7.6
Eurasian carp – <i>Cyprinus carpio</i> (Linnaeus, 1758)	6.7
Weatherfish – <i>Misgurnus fossilis</i> (Linnaeus, 1758)	1.7
Spined loach – <i>Cobitis taenia</i> (Linnaeus, 1758)	4.2
Stone loach – <i>Barbatula barbatula</i> (Linnaeus, 1758)	4.2
European perch – <i>Perca fluviatilis</i> (Linnaeus, 1758)	11.8
Ruffe – <i>Gymnocephalus cernuus</i> (Linnaeus, 1758)	2.5
Pikeperch – <i>Sander lucioperca</i> (Linnaeus, 1758)	2.5
Round goby – <i>Neogobius melanostomus</i> (Pallas, 1814)	2.5
Black-striped pipefish – <i>Syngnathus abaster</i> (A. Risso, 1826)	0.8

Distribution of *P. glenii* in environmental gradients in rivers and lakes of east edge of Europe. Relationship between fish species and environmental variables

The probability of occurrence for *P. glenii* had statistically significant relationships with four environmental variables in small river (Tab. 3) and three for lakes (Tab. 4). All final models had satisfactory predictive indicative power (AUC) (Tabs. 3 and 4). The probability of occurrence of *P. glenii* in small rivers was negative associated with trees and bushes cover (Tab. 3) and positive with the depth of the studied lotic ecosystems (Fig. 3), width and longitude (Tab. 3). The probability of occurrences for *P. glenii* species is higher in deep and wide and relatively open areas of rivers in the east of the study area. Thus, the probability of occurrences for *P. glenii* at depths of 0.4 m and below is close to or equal to 0 (Fig. 3). The probability of occurrence of *P. glenii* in lenitic ecosystems as well as small lotic ecosystems was negative associated with trees and bushes cover (Tab. 4; Fig. 4), in our opinion, the reduced probability of detecting *P. glenii* in areas with a high percentage of forest cover is due to the fact that greater shading prevents the abundant development of herbaceous plants in the water, which are necessary for the life of this species. Probability of occurrences of study species is also negative in association with elevation (Tab. 4). Thus, at elevation above 150 m, the probability of occurrences the species does not exceed 15% (Fig. 5). Unlike small rivers, in lakes in edge east of Europe the *P. glenii* has an increased probability of occurrences found in shallow areas; similar preferences for the species have been noted in Western Siberia (Reshetnikov et al., 2025).

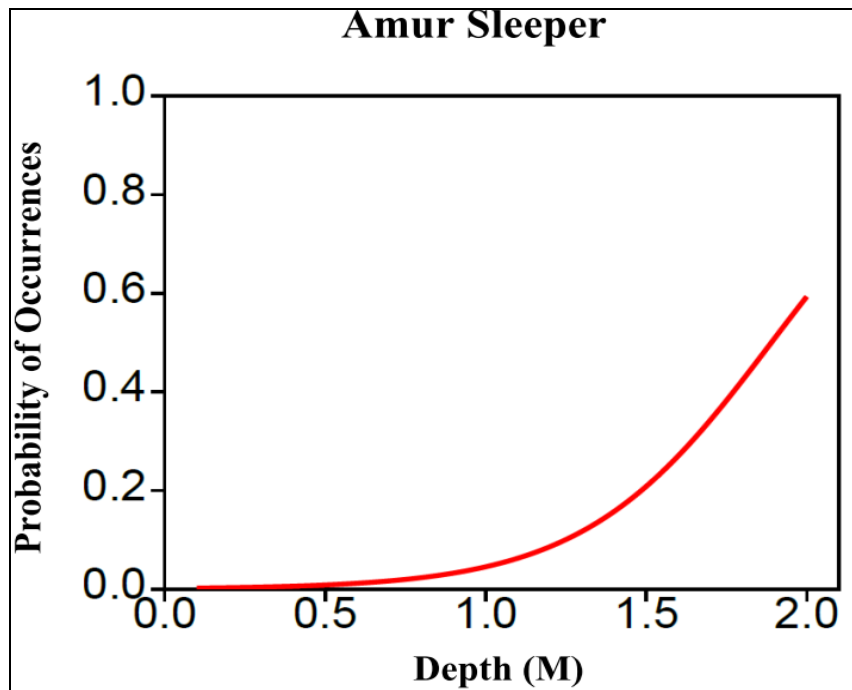


Figure 3: Relationship between the probability of occurrence of *P. glenii* and depth in rivers.

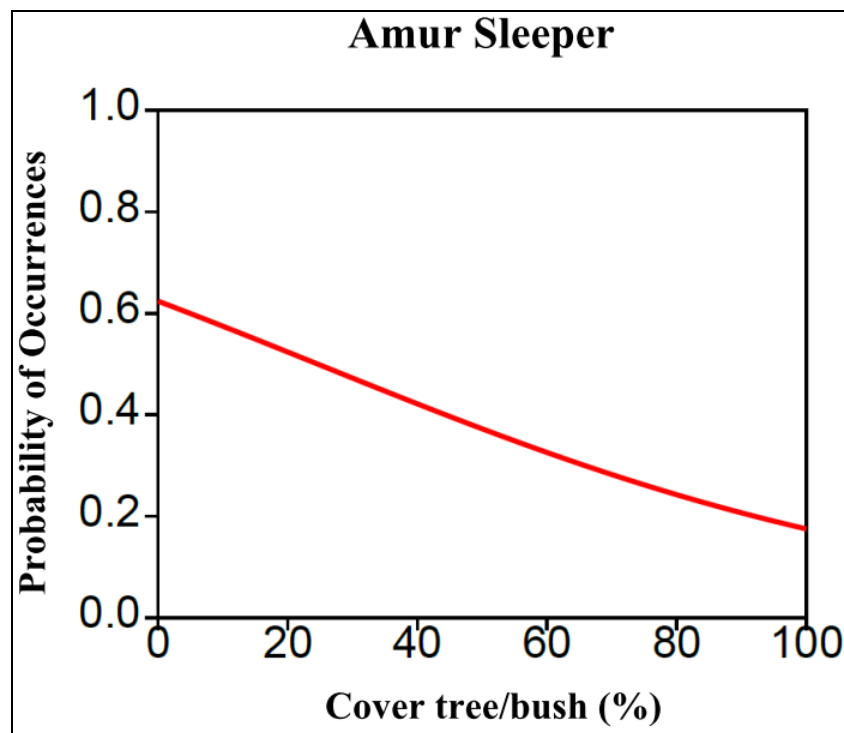


Figure 4: Relationship between the probability of occurrence of *P. glenii* and tree/bush cover in lakes.

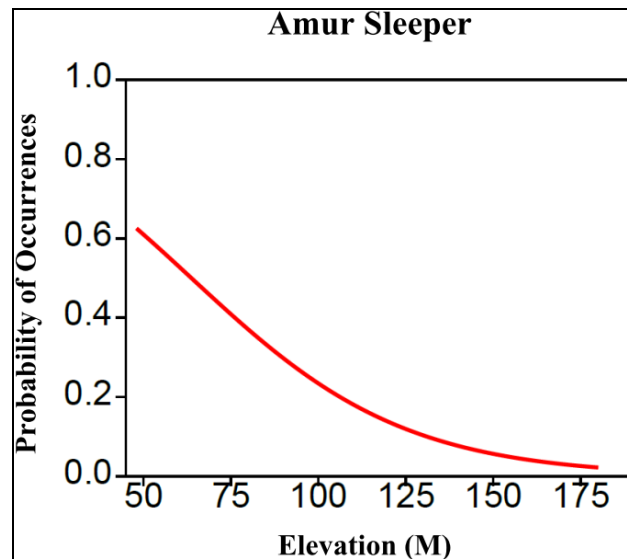


Figure 5: Relationship between the probability of occurrence of *P. glenii* and elevation in lakes.

Table 3: Coefficients and model summary for models summarising the relationship between presence/absence of *P. glenii* and environmental variables in small rivers.

Species	Constant	Cover	Width	Depth	Longitude	AUC
<i>P. glenii</i>	−9.58	−0.48	0.29	1.41	0.68	0.881

Table 4: Coefficients and model summary for models summarising the relationship between presence/absence of *P. glenii* and environmental variables in lakes.

Species	Constant	Elevation	Cover	Depth	AUC
<i>P. glenii</i>	−6.14	−0.40	−0.61	−0.52	0.891

Species optimums and niche breadth

Table 5 shows the optimal points and breadths for *P. glenii* in the gradient of the five environmental variables in small rivers, values for lakes are presented in Askeyev et al. (2023). The optimum point for *P. glenii* about elevation is very high, only three fish species in the study area have a higher point (Askeyev et al., 2017). According to the width and depth of the river, the optimum point for *P. glenii* has average values among other fish species, and according to cover tree/bush it is very low (Askeyev et al., 2015). In general, *P. glenii* shows very high tolerance for a number of factors. So, in terms of the width of the ecological niche by elevation above sea level in small rivers, it is second only to the bullhead (Askeyev et al., 2017), living both in the lowest sites of rivers and at elevations above 500 m. High tolerance is also observed for the velocity, this species is able to live in rivers with middle velocity speed, as well as in very fast mountainous sites. At the same time, in terms of width, depth and forest cover, the width of the *P. glenii* niche is in the middle position among fish species in the study region (Askeyev et al., 2015).

Table 5: *P. glenii* optimum values and tolerance (niche breadth) against five environmental variables (based on abundance data) in small rivers.

Fish species	Elevation (m)	Width (m)	Cover tree/bush (%)	Depth (m)	Velocity (m/s)
			Optimum values		
<i>P. glenii</i>	293.5	14.3	36.9	0.85	0.19
			Tolerance (niche breadth)		
<i>P. glenii</i>	191.3	13.0	22.4	0.28	0.17

CONCLUSIONS

Our study is the first in eastern Europe to illustrate the ecological preferences of *P. glenii* relative to environmental factors. We observe widespread ecological plasticity and a relatively rapid spread of *P. glenii* over a short period of time in East edge part of Europe. We urge our colleagues, especially those from the western part of Eurasia, to look at the lakes of the Republic of Tatarstan, where invasive species such as the *P. glenii* and *C. carassius* have spread widely and are gradually displacing native fish species, and to take measures to limit them before it is too late.

ACKNOWLEDGEMENTS

We thank Lily and Madina Askeyeva for their generous help in organizing logistics for the field surveys. We especially express our gratitude to Harold Flowers for revising the text of the early drafts of the manuscript.

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