



Chinese sleeper (*Perccottus glenii* Dybowski, 1877) (Pisces, Odontobutidae) in the reserves and National Parks of the middle and lower Volga (Russia): mini-review

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Abstract. A review of the distribution of the Chinese sleeper *Perccottus glenii* Dybowski, 1877 (Pisces, Odontobutidae) as an invasive species of fish in the territories of the reserves and national parks of the middle and lower Volga Region is presented. It occurs in 12 protected areas which is only 44.4% of the total number of protected areas. The invasion way of *P. glenii* in some protected areas is described, which is associated with stocking of fishery ponds. Data on habitats and the number of *P. glenii* in studied reserves and national parks are given, as well as the possible reasons for its absence in the ichthyofauna of other protected areas.

Key Words: Chinese sleeper, *Perccottus glenii*, invasion, distribution, Volga river basin.

Introduction. Biodiversity conservation is one of the most important tasks of the nature conservation as a whole. The federal-level Protected Areas as places of the greatest concentration of the biodiversity and dislocation of the most significant elements of its play a special role in the biodiversity conservation of natural complexes (Brooks et al 2006; Grebennikov 2016). In the Russian Federation for a century there is an important system of such Protected Areas – reserves and national parks. They are guarantors of protection stability and invariability of the natural complexes, reserves of rare plants and animals and, in fact, act as a kind of “islets” of the natural biodiversity of certain geographic zones (Vargot et al 2015; Kurhinen et al 2016; Barashkova et al 2017).

However, the problem of infusing of alien species did not bypass the above-mentioned Protected Areas with minimal anthropogenic load. The species number is emerging, the native ranges of which are located at a considerable distance from the new areas-recipients. Such invasive species include the Chinese sleeper *Perccottus glenii* Dybowski, 1877 (Odontobutidae, Pisces). It is a component of biocoenoses of the floodplain reservoirs of the Far East. However, it has become extremely widespread in the waters of the European Russia and abroad in the last century (Litvinov & O’Gorman 1996; Reshetnikov 2004, 2009; Ruchin 2004a; Vechkanov et al 2007; Novak et al 2008; Grabowska et al 2011; Lukina 2011; Nehring & Steinhof 2015; Kvach et al 2016; Kirilenko & Shemonaev 2017). In natural ecosystems, *P. glenii* has been involved in the trophic connections of the floodplain ecosystems, acting as a predator and fodder base (Reshetnikov et al 2013). Many aspects of the *P. glenii* biology were elucidated in the course of experimental work (Manteifel & Reshetnikov 2002; Konstantinov et al 2003; Ruchin 2004b; Ruchin et al 2004, 2005; Bagnyukova et al 2007; Golovanov et al 2016; Santalova et al

2018). An important feature is its resistance to various kinds of temperature anomalies. Thus, seasonal differences in the critical thermal maximum were revealed among two-year-old individuals. The maximum thermal stability was established at a slow heating rate. It turned out that in terms of its thermoadaptive characteristics, *P. glenii* is the closest to such heat-loving eurythermal species as *Carassius auratus* and *Cyprinus carpio* (Golovanov & Ruchin 2011). The aim of the study was to study the invasion, distribution, description of some aspects of the biology of the alien species *Perccottus glenii* in the reserves and national parks of some Russian regions.

Material and Method

Study site. The Volga is one of the largest rivers in Russia. Its catchment area is estimated at 1360 thousand km², which is 62% of the European Russia and 8% of the whole Russia, almost 13% of the whole Europe. The main part of the territory belongs to the basin of the Middle and Lower Volga. There are 16 reserves and 11 national parks in this area (Figure 1). All these Protected Areas are unique from the biodiversity viewpoint and they are objects of the federal protection. The natural conditions of those Protected Areas are described below, within which the most intensive studies of the invasive species of fish – *P. glenii* – were conducted.

Mordovia State Nature Reserve is located in the Temnikov district of the Republic of Mordovia on the forested right bank of the Moksha River and covers the area of 321.62 km². From the north the border runs along the Satis River – the right tributary of the Moksha River, further to the east – along the Arga River, which flows into the Satis River. The western border runs along the Chernaya River, the Satis River and the Moksha River. The hydrographic network of the reserve is small and it is represented by these rivers, other small rivers, and streams (Pushta, Vyaz-Pushta, Vorsklay, Arga, etc.). In the floodplain of the Moksha River and Pushta River there is a network of flowing and low-flow lakes (Vargot 2016; Ruchin & Mikhailenko 2018).

National Park “Smolny” is located in the northeastern part of the Republic of Mordovia on the area of 365.0 km². The rivers of the National Park “Smolny” are typically flat and they are represented by small water flows and streams. They are characterized by a slight drop and relatively slow flow. Oxbow lakes of the National Park are concentrated mainly in the Alatyr River floodplain (Khapugin et al 2016; Ivanov et al 2019).

Nurgush State Nature Reserve, established in 1994, consists of two cluster sites currently, which are located in the southeastern part of the Kotelnich district (cluster “Nurgush”, the area of 56.34 km²) and the northwestern part of the Nagorny district (cluster “Tulashor”, the area of 17.81 km²) of the Kirov region. The first section can be completely flooded during heavy flow. It is limited to water bodies: from the north, east and south – Vyatka River, partly from the south – Lake Staritsa, from the west – the near-terrace Prost River. The hydrographic network of this site is represented by numerous (more than 80) floodplain lakes and five rivers. Lakes, floodplain rivers and channels form a unified water system that communicates with the present riverbed of the Vyatka River (Borodin 2014).

Volzhsko-Kamsky State Nature Biosphere Reserve was established in 1960 and it is located in the Republic of Tatarstan and consists of two clusters – Saralinsky, with the area of 39.22 km² (with the water area of the Kuibyshev reservoir 15.58 km²), located in Laishevsky district, and Raifsky cluster, with the area of 59.21 km², located in the Zelenodolsky district. The territory of the Protected Area lies on the left-bank ancient alluvial terraces of the Volga River and 82% of the area is covered by forests. The Saralinsky cluster is located in the interfluvium of the Volga River, the Kama River and the Mesha River and it is a peninsula pushed into the Volzhsko-Kamsky reach of the Kuibyshev reservoir. It includes an adjacent 500-meter strip of the water area of the reservoir. The Raifsky cluster is located 60 km upstream of the Volga Region; its hydrographic network is represented by small rivers – the Sumka River and its inflow Ser-Bulak River – and eight lakes, mostly of suffusion-karst origin (depths from 5 to 20 m). The Sumka River is represented by a fragment of its middle current of 9 km. During the summer period, within the limits of the Volzhsko-Kamsky Reserve the Sumka River and the Ser-Bulak River usually dry out. Most of lakes are confined to their valleys, the largest of which are flow-

ing. In 1996–2000, the beaver reintroduction was carried out. Beaver’s construction activity is associated with the appearance of “beaver ponds” on the watercourses in the Raifsky cluster.

Kerzhensky State Nature Biosphere Reserve is located in the Nizhny Novgorod region. The reserve area is 469.39 km². The Kerzhenets is the largest river of the Protected Area and it forms the western border of the reserve. Small rivers – Vishnya River, Chernaya River, Pugai River, Rustaychik stream are its left-sided tributaries. Lakes are represented mainly by oxbows and they are located in the Kerzhenets River floodplain, to a lesser extent the Vishnya River and the Chernaya River. Artificial reservoirs are represented by ponds, ditches, fire-fighting reservoirs along the roads. In the reserve there are about 40 marshes in natural state. The territory of the reserve is a part of water-marsh wetlands of international importance – the Kamsko-Bakaldinsky group of bogs (Lebedinskii et al 2019).

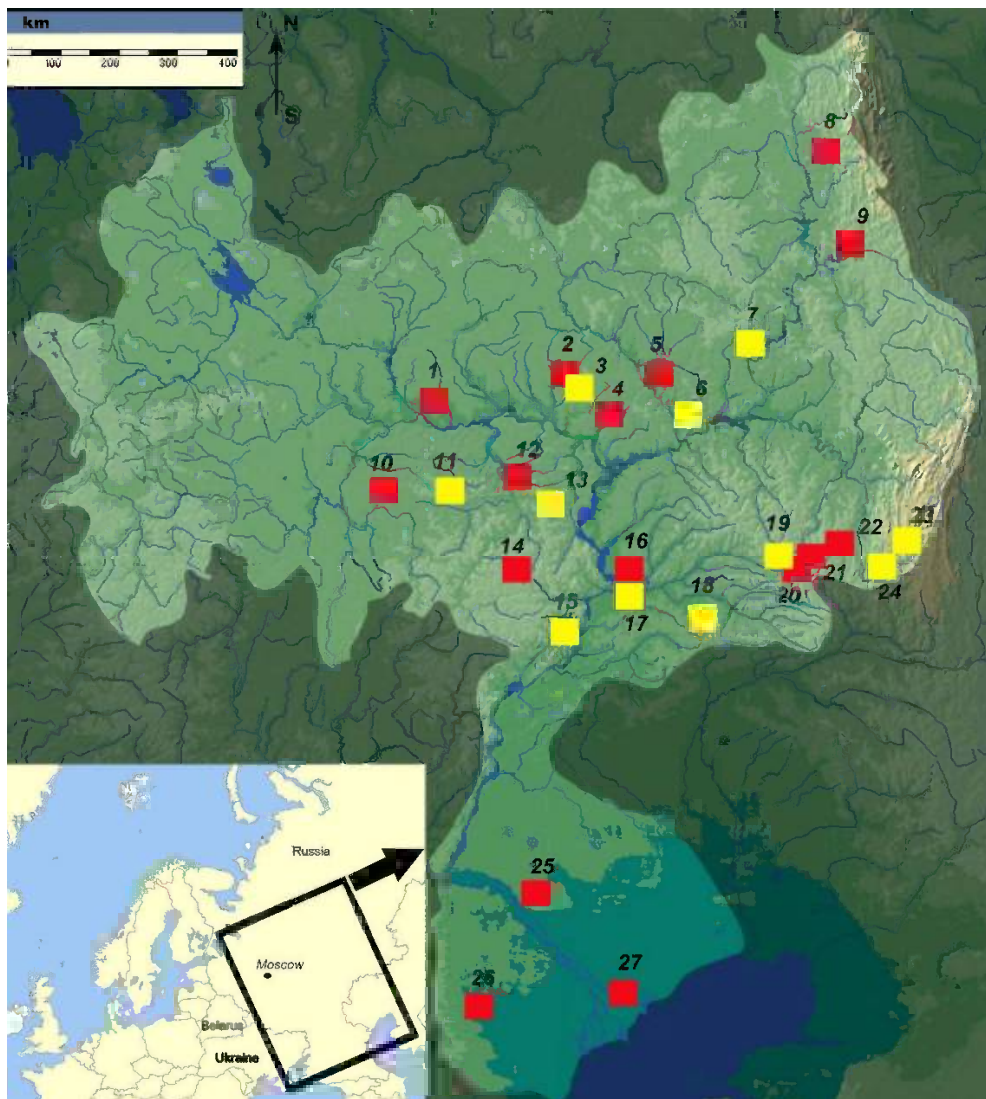


Figure 1. The location map of the reserves (red squares) and national parks (yellow squares) within the Middle and Lower Volga Region. 1 – Kerzhensky State Nature Biosphere Reserve; 2 – State Nature Reserve “Bolshaya Kokshaga”; 3 – National Park “Mariy Chodra”; 4 – Volzhsko-Kamsky State Nature Biosphere Reserve; 5 – Nurgush State Nature Reserve; 6 – National Park “Nizhnyaya Kama”; 7 – National Park “Nechkinsky”; 8 – State Nature Reserve “Vishersky”; 9 – State Nature Reserve “Basegi”; 10 – Mordovia State Nature Reserve; 11 – National Park “Smolny”; 12 – State Nature Reserve “Prisursky”; 13 – National Park “Chavash Varmane”; 14 – Privolzhskaya Lesostep State Nature Reserve; 15 – National Park “Hvalynskiy”; 16 – Zhigulevsky State Nature Reserve; 17 – National Park “Samaruskaya Luka”; 18 – National Park “Buzuluksky Bor”; 19 – National Park “Bashkiriya”; 20 – Shulgan-Tash State Nature Biosphere Reserve; 21 – Bashkirsky Nature Reserve; 22 – Yuzhno-Uralsky Nature Reserve; 23 – National Park “Taganay”; 24 – National Park “Zyuratkul”; 25 – Bogdinsko-Baskunchaksky Nature Reserve; 26 – Chornyye Zemli State Nature Reserve; 27 – Astrakhan Biosphere Nature Reserve.

National Park "Nizhnyaya Kama", organized in 1991, includes two clusters of the Kama floodplain remained of the flooding (cluster "Yelabuga meadows" with the area of 30.0 km² and cluster "Tanaisk meadows" with the area of 50.0 km²). It is located in the Republic of Tatarstan (Lukyanova 2011).

Catchings in the reservoirs of the Protected Areas were carried in 1999-2003, 2005, 2007-2010, 2012-2018. To study the distribution and the current state of populations, a variety of fishing gears (nets, seines, dragnets, box nets) were used, as well as visual observations. To analyze the state of the *P. glenii* populations, as well as the time of appearance of this species in studied reserves and national parks, we used information stored in scientific organizations. In addition, all available published data have been studied. The taxonomy and nomenclature is given according to Eschmeyer et al (2018).

Results and Discussion. According to our data, the *P. glenii* is known in the ichthyofaunas of six reserves and six national parks, which is only 44.4% of the total number of the Protected Areas (Table 1). Thus, it can be stated that this invasive fish does not have a significant distribution in the reserves and National Parks.

Table 1

Distribution of *P. glenii* in the Protected Areas of the middle and lower Volga Region
(a dash indicates the absence of the species in fauna)

<i>Protected areas</i>	<i>Presence/ absence</i>	<i>Years of first record</i>	<i>Authors of observations</i>
<i>Reserves</i>			
Astrakhan Biosphere Nature Reserve	–	–	N. A. Tsymlyansky
State Nature Reserve "Basegi"	–	–	Kovalev & Naumkin (2012)
Bashkirsky Nature Reserve	–	–	F. F. Zaripova
Bogdinsko-Baskunchaksky Nature Reserve	–	–	K. A. Grebennikov
State Nature Reserve "Bolshaya Kokshaga"	–	–	A. V. Isaev
State Nature Reserve "Vishersky"	–	–	P. N. Bakharev
Volzhsko-Kamsky State Nature Biosphere Reserve	+	1985	O. V. Bakin
Zhigulevsky State Nature Reserve	+	late 1990s	Kirilenko & Shemonaev (2011)
Kerzhensky State Nature Biosphere Reserve	+	early 1990s	O. L. Korablev
Mordovia State Nature Reserve	+	1979	Potapov et al (1998)
Nurgush State Nature Reserve	+	2016	L. G. Tselischeva
Privolzhskaya Lesostep State Nature Reserve	–	–	V. V. Osipov
State Nature Reserve "Prisursky"	–	–	V. V. Osipov
Chornye Zemli State Nature Reserve	–	–	B. I. Ubushaev
Shulgan-Tash State Nature Biosphere Reserve	–	–	M.V. Bakalov
Yuzhno-Uralsky Nature Reserve	+	2004	R. G. Bayteriakov
Total	6/10		
<i>National Parks</i>			
National Park "Bashkiriya";	+	2000	M. N. Kosarev
National Park "Buzuluksky Bor"	+	2012	A. I. Fayzulin
National Park "Taganay"	–	–	A. I. Fayzulin
National Park "Zyuratkul"	+	not installed	F. F. Zaripova
National Park "Mariy Chodra"	–	–	O. V. Palagushkina
National Park "Nechkinsky"	–	–	B. G. Kotegov
National Park "Nizhnyaya Kama"	+	not installed	S. P. Monakhov
National Park "Samarskaya Luka"	+	1998	Kirilenko & Shemonaev (2011)
National Park "Smolny"	+	1983	G. F. Grishutkin
National Park "Hvalynskiy"	–	–	E. Yu. Mosolova
National Park "Chavash Varmane"	–	–	Yakovlev (2012)
Total	6/5		
Total for the protected areas	12/15		

In most cases, the first records of *P. glenii* were noted at the late 1990s and the early 2000s. Exceptions are the Protected Areas of the Republic of Mordovia. In the Mordovia State Nature Reserve, *P. glenii* was first recorded in 1979 in Lake Krivaya Lipa (Potapov et al 1998). In the Moksha River basin *P. glenii* appeared during the acclimatization activities of 1970-1971. Then this species, with *C. carpio* was introduced into the ponds of the Ilevsky fish farm in the Gorky (Nizhny Novgorod region) (Kudersky 1980). These reservoirs are on the Sarma River, only in 20 km from the Mordovia State Nature Reserve (Figure 2). Thus, it overcame this distance for eight-nine years and it has been already found in the Moksha River floodplain.

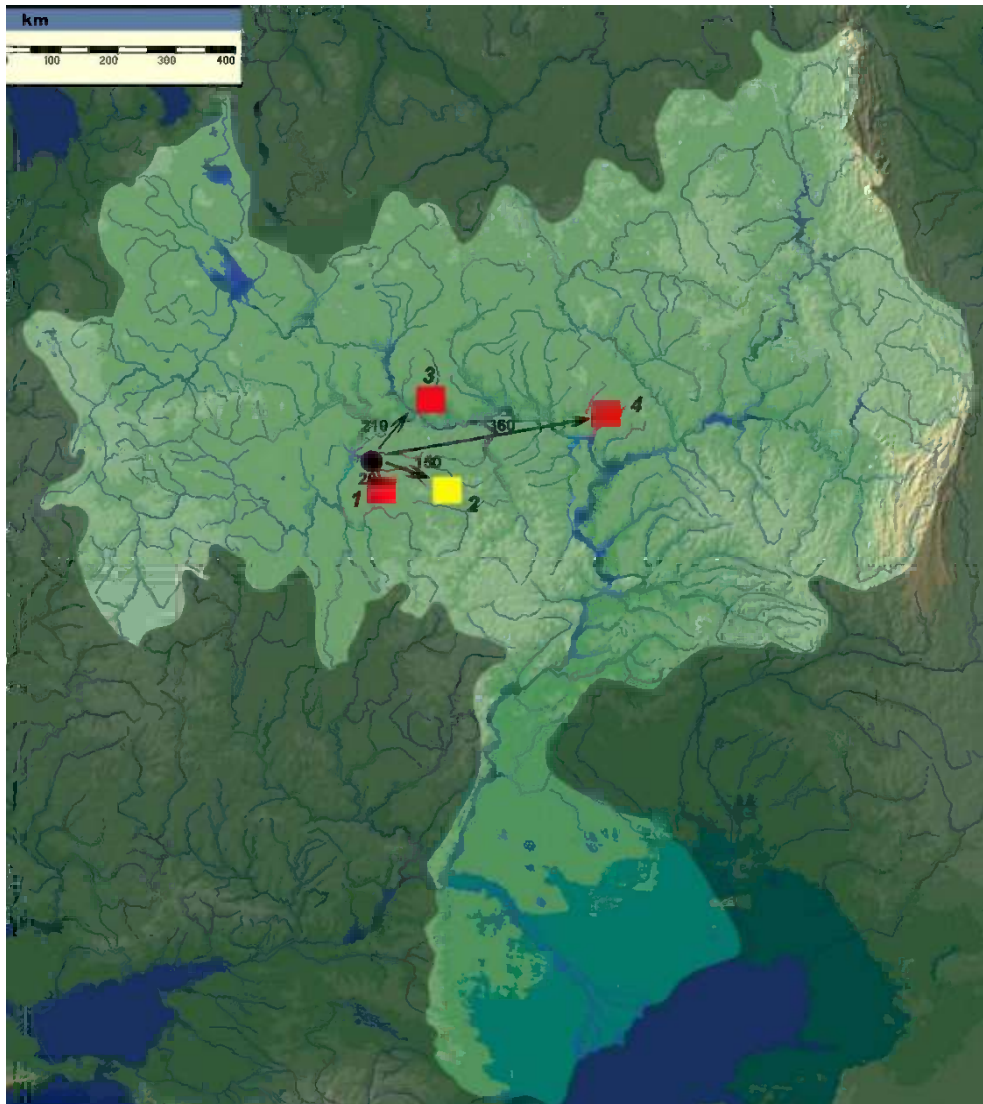


Figure 2. Distribution of *P. glenii* in some Protected Areas in the 1970s and 1980s. The black circle is the Ilevsk fish farm (invasion source). 1 – Mordovia State Nature Reserve; 2 – National Park “Smolny”; 3 – Kerzhensky State Nature Biosphere Reserve; 4 – Volzhsko-Kamsky State Nature Biosphere Reserve. The arrows indicate the probable distribution vectors of *P. glenii*, above them there are the distances (in km) from the invasion source.

In the next years *P. glenii* began to spread along lakes and ponds of the Mordovia State Nature Reserve. However, its records and the abundance are irregular in water bodies. Thus, in the flowing lakes, it has a low abundance currently and prefers to live in the coastal thickets and roots of trees near the shores. At the same time, in the suffocated lakes, *P. glenii*, *Misgurnus fossilis* (Linnaeus, 1758) and *Carassius gibelio* (Bloch, 1782) form the entire ichthyofauna of the biocoenosis (Artaev & Ruchin 2016). Sometimes it occurs in small rivers of the Mordovia State Nature Reserve (Artaev 2016). In the Moksha River basin, the highest occurrence rate of *P. glenii* is observed in the oxbows as well as

the karst and suffusion lakes (75.0-87.6%); moderate rate, in ponds (28.6%); lower rate (10.3%), in rivers to the distance of 25 km from the source; and very low rate (1.9%), in rivers to the distance of 25-100 km from the source.

The highest abundance is observed in the landlocked oxbows, where its average share in catches is 30.9% (Artaev & Ruchin 2017). According to our observations it was quite numerous in the upper pond and lower pond in Pushta village (manor of the Mor-dovia State Nature Reserve) in 2004-2008. And fishes of all sizes and ages were captured. However, later its abundance decreased sharply and at present it is represented in these reservoirs only by large individuals. We assume that its abundance was significantly influenced by the appearance and subsequent sharp increase in the number of *Rhynchocypris percunurus* (Pallas, 1814). This assumption should be tested in future.

The Chinese sleeper was first found in the National Park "Smolny" in 1983. Apparently, it has also spread from the ponds of the Ilevsk fish farm. Currently it can be found in the floodplain water bodies and ponds of all forest areas of the National Park, and also it is found in the Alatyr River. In closed standing water bodies, it is a mass species, in contrast to the lakes with a good oxygen regime. The species prefers river parts with slow flow or stagnant water bodies. It inhabits water bodies with strongly developed aquatic vegetation (Grishutkin et al 2013).

In the Kerzhensky State Nature Biosphere Reserve *P. glenii* appeared almost at the same time in all oxbows near the rivers in the early 1990s. Since the Kerzhensky State Nature Biosphere Reserve is located at a distance of about 210 km from the Ilevsky fish farm, it can not be ruled out that the fish species appeared from this fish farm in the Protected Area as a result of its further spreading along the basins of the Oka River and the Volga River.

Currently the species occurs in the Kerzhenets River, the Rustaychik stream, in the oxbows of the Kerzhenets River, in the ponds of Rustay village. It primarily prefers oxbows remote from the Kherenets River, which, as a rule, are smaller and largely swamped. In these oxbows, *P. glenii* dominates among the fish species. Oxbows have a good connection with the river, a high degree of flowage and the possibility for entering the large fish from the river. In such conditions, *P. glenii* is either completely absent or its population is extremely small and in a depressed state. *P. glenii* is completely absent in the tributaries of the Kerzhenets River in the depths of the Kerzhensky Reserve (Bolshaya Chernaya River, Malaya Chernaya River), where its survival is impeded by *Esox lucius* Linnaeus, 1758.

In the Saralinsky cluster of the Volzhsko-Kamsky State Nature Biosphere Reserve, individuals of *P. glenii* were first recorded in 1985. Later in the mid-1980s the species has widely spread along the channels of the lower part of this area (Kuznetsov 2005). Currently *P. glenii* adheres to the peaks of the bays with silted soils and macrophyte thickets. Its abundance is low. In total, the ichthyofauna of the bays includes 28 species. *P. glenii* is often the only fish species in the small overgrown water bodies separated from the bays; its size does not exceed 11 cm. In 1995, V. I. Garanin found a juvenile fish of *P. glenii* in the buffer zone of the Raifsky cluster of the Volzhsko-Kamsky Reserve in Lake Pridorozhnoe (Kuznetsov & Bortiakov 2002). In spring, sometimes this lake has a connection with the Sumka River. Directly in the Raifsky site, *P. glenii* was recorded in Lake Ilantovo in 1998. This lake with the area of 4.7 hectares is located near the Sumka River and has an average depth of 0.7 m. Lake Ilantovo is strongly overgrown by aquatic vegetation. Before suffocation in 2011 the lake was inhabited by *E. lucius* and *Leucaspis delineatus* Heckel, 1843; at the present time, besides of *P. glenii*, *C. gibelio* and *Carassius carassius* (Linnaeus, 1758) are remained in the lake. In other water bodies of the Raifsky cluster, *P. glenii* has not been detected yet, although in a some of shallow water bodies of the buffer zone has the high abundance.

In the numerous floodplain water bodies of the National Park "Nizhnyaya Kama" *P. glenii* is a common species now. It is not possible to determine the time of the appearance of *P. glenii* in the ichthyofauna of the Protected Area. Apparently, it appeared much earlier than the foundation of the National Park (1991), i.e. before the time of the beginning of the ichthyological studies on its area. Nearby of the Protected Area the Volzhsko-Kamsky State Nature Biosphere Reserve is located, in which *P. glenii* appeared in 1985.

Probably, at the same time *P. glenii* appeared in this National Park. The vector of *P. glenii* distribution in the Protected Areas (Figure 2) is similar to that previously described (Reshetnikov et al 2011).

In the Nurgush State Nature Reserve *P. glenii* was first discovered in May 2016 in the following lakes: Nurgush, Maloe Krivoe, Mogilnoe. In the reserve, *P. glenii* (1–2 years old) were collected by nets and stationary traps. One *P. glenii* specimen was probably caught by an otter and partially eaten. We found its remnants on the lake shore nearby with the otter tracks. At the same time, *P. glenii* were collected using a water net in the buffer zone in the Krutets stream. For the first time information about the appearance of *P. glenii* in the buffer zone (right bank of the Vyatka River) came from fishermen in the summer of 2011. It was caught in Lake Kaleichi (on the north border of the reserve) and Lake Gnilukha (on the south border of the reserve). In the lakes of the left-bank side of the Vyatka River (opposite the reserve), they were known even earlier – approximately since 2000. The current abundance of the species in the Nurgush Reserve is unknown, as well as trend of its further distribution. *Perca fluviatilis* (Linnaeus, 1758), *E. lucius*, *Leuciscus idus* (Linnaeus, 1758), *Rutilus rutilus* (Linnaeus, 1758) dominate in the lakes of the Protected Area.

Conditions for the distribution of *P. glenii* in the mountain-forest zone of the Southern Ural are unfavorable, because that lakes and oxbows, in which the species could be inhabited, are practically absent here. For the first time the species appeared in the Belaya River (a fragment of the southern border of the Bashkirsky Nature Reserve) in 2000, probably in connection with the construction of the Yumaguzinsky reservoir. The first record was noted in the Belaya oxbow artificially created near Irgizly village (National Park “Bashkiriya”, the zone of wedging 10 km above the boundary of the upper dam of the reservoir). In next years, it was registered in the Belaya River near the oxbow, but it is not marked in the tributaries. In catches the species is rare, the size of the specimens caught by fishers is 10–20 cm. The species coexists with *P. fluviatilis*, *R. rutilus*, *Alburnus alburnus* (Linnaeus, 1758), *E. lucius*, *Sander lucioperca* (Linnaeus, 1758).

In some Protected Areas, *P. glenii* is also absent for quite objective reasons. For example, in the Bogdinsko-Baskunchaksky State Nature Reserve there are no fresh water bodies. In the National Park “Hvalynskiy” and National Park “Chavash Varmane” there are no water bodies for possible invasion of *P. glenii*. In these National Parks there are small rivers, but there are no weakly flowing lakes and ponds, which are convenient for living of *P. glenii*.

In the State Nature Reserve “Basegi” also there is a developed network of the small rivers, but there are no floodplain lakes (Kovalev & Naumkin 2012).

As a rule, the appearance of a new species is preceded by a range of changes that modify the initial (natural, intact) biocenosis into the state of susceptibility (Biological invasions ... 2004). The success of the invasion depends on the peculiarities of the recipient systems, violations, deviations from normal or natural state of each particular system. At the same time the Protected Areas are shielded from the anthropogenic influence for a long time. Thus, they are guarantors of the high biodiversity and stability, and therefore the biocenoses in these areas should be less disturbed than in adjacent territories. Accordingly, they are stable and can not “receive” the invasive species due to their low susceptibility to the bioinvasions. This is observed in some Protected Areas. For example, in the State Nature Reserve “Prisursky”, *P. glenii* inhabits only the lakes and ponds located nearby the border, where the species appeared in the late 1990s, and has not been found directly on the area of the reserve yet.

Another feature of this species is its wide ecological plasticity. Within secondary range, it occupies a variety of water bodies, both anthropogenic (quarries, ponds, ditches, etc.) and natural floodplain water bodies. Due to the absence of specialized predators, sometimes *P. glenii* can become an absolute dominant in a water body (Novak et al 2008; Lukina 2011; Reshetnikov et al 2011; Reshetnikov 2013; Artaev 2016; Kvach et al 2016).

We assume that *P. glenii* will appear in the State Nature Reserve “Vishersky” in the further years. At present, it has already spread in the basin of the lower and middle Kama River basin and reached the mouth of the Vishera River (Sokolov et al 2014). It

should be noted that there is already information (Fish in the reserves of Russia 2010), that it inhabits this Protected Area, but it is not confirmed by the researchers of this reserve. *P. glenii* has not been found in the National Park "Mariy Chodra" yet. However, in the nearest water bodies outside the Protected Area it is the most common species and, if possible (for example, fish suffocation phenomena in the lakes), it will take its ecological niche and become one of the elements of the ichthyofauna. At the same time, mass dying of fish, leading to the disappearance of predators, can serve as one of the factors affecting the rapid dispersal of *P. glenii*. In addition, *P. glenii* sharply decreases the growth rate when pH is shifted to acid (below 7.6) and alkaline (pH above 8.0) (Ruchin et al 2004). It should be noted that exactly in the conditions of the forest-steppe zone of the middle Volga Region most water bodies have optimal pH conditions. In the undisturbed small water bodies of the forest zone, it shifts to a more acidic side, and in the conditions of the steppe zone – to a more alkaline side (Gashkina et al 2012).

Thus, *P. glenii* has not invaded in many Protected Areas of the Volga river basin yet. Apparently, this is due to the low disturbance level and the highest stability of the biocoenoses and, as a consequence, to the reduction of possible invasion ways of the alien species into the natural community. This can be indirectly confirmed by the fact that practically in all cases, *P. glenii* has penetrated into the Protected Areas through buffer zones, which are quite intensively visited by people and where, unlike Protected Areas, fishing is not prohibited. At the same time, the main invasion way is precisely the fishermen, contributing to the distribution of *P. glenii* in the water bodies.

Conclusions. Based on the analysis of the distribution and invasion of the *P. glenii*, it is possible to indicate the possible reasons for its absence in some Protected Areas in the middle and lower Volga basins:

- 1) the sustainability of the undisturbed biocoenoses in the Protected Areas does not contribute the invasion;
- 2) the Protected Areas are distant from the invasion "corridors" (from large rivers, vast floodplains, etc.);
- 3) the stagnant water bodies, favorable for invasion, are absent (some Protected Areas are located on watersheds or in the upper reaches of the rivers where there are not water bodies suitable for the invasion);
- 4) the predatory fish regulate the abundance of *P. glenii* and prevent active dispersal;
- 5) winters are very severe with low temperatures (typical for northern Protected Areas).

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