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Review

Spatio-temporal dynamics of the expansion of rotan *Perccottus glenii* from West-Ukrainian centre of distribution and consequences for European freshwater ecosystems*

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* This publication is devoted to the memory of Nikanor Yu. Sokolov, a young Ukrainian ichthyologist, who passed away early; one of the first investigators of *Perccottus glenii* in West-Ukrainian subrange of this fish.

Abstract

The invasive fish rotan or Amur sleeper, *Perccottus glenii* (Perciformes, Odontobutidae), arrived in Western Ukraine during the stocking of commercial cyprinid fish in the 1960s. Three periods were identified in its expansion. Period I: during the first two decades post-arrival, the fish was restricted to the upper section of a local river basin. Period II: rotan penetrated the adjacent river basins and over the following two decades, it rapidly self-distributed over huge distances, using rivers as long-distance, one-way natural corridors (*natural conveyors*). This expansion resulted in the invasion of many European river systems including the Danube, Dniester, western part of the Dnieper basin, Southern Bug (all belonging to Black Sea basin), and the Vistula (Baltic Sea basin). During colonization, rotan was found in Lviv, Zakarpatie, Volynskaya, Povno, Ivano-Frankovsk, Chernovtsy and Khmelnitskiy provinces of Western Ukraine, as well as in territories of south-western Belarus, Poland, Slovakia, Hungary, Serbia, Bulgaria, Romania, Croatia, and Moldova. This invader demonstrated comparatively rapid expansion from riverheads to downstream river mouths, but slower or negligible expansion upstream in tributaries. This example of the West-Ukrainian centre of distribution demonstrates the significance of upper parts of river basins for rapid distribution of this species, as well as the important function of rivers in crossing country borders. Period III relates to the period from approx. 2005 to the present day. During this period, perceived to be the longest in terms of colonization, its invaded range extends to tributaries and isolated water bodies filling gaps in areas between already colonized main rivers. Rotan did not reach high densities in the main river channels or deep, well-oxygenated lakes because of the presence of native fish predators. However, this alien species did form numerous dense populations in shallow lentic water bodies. The expansion of rotan may lead to adverse economic impacts upon European aquaculture farms, as well as predictable, ecological consequences for populations of some native European aquatic animals including invertebrates, fish and amphibians. Rotan has the potential to also influence adjacent terrestrial ecosystems. A review of rotan and native species interactions is presented.

Key words: Amur sleeper; Chinese sleeper; rotan; biological invasions; invasive fish species; Odontobutidae

Introduction

The invasive fish rotan, also known as Amur or Chinese sleeper, *Perccottus glenii* Dybowski, 1877 (Perciformes, Odontobutidae) (Figure 1) is native to the Far East of Eurasia. This species naturally inhabits oxbow lakes, ponds and other similar water bodies in river basins of the west coast of the Pacific Ocean from North Korea (in the south), to the Uda River basin, Russia (north) (Reshetnikov 2010). The main part of its native range is restricted to the Amur River basin. Rotan is also known to live in drainage of rivers flowing into the northern gulfs of the Yellow Sea: rivers Gou, Liao, Never, and Yalu (China, North Korea) (Reshetnikov 2010; Liu Xiaogang, pers. comm.). The most eastern native populations are from the north-western Sakhalin Island, Russia, opposite the mouth of the Amur (Taranets 1937).

The history of the introduction of rotan has been described in several papers (Elovenko 1981; Vasilyeva and Makeyeva 1988; Reshetnikov 2001 and Reshetnikov 2004). Since 1916, the fish has been introduced into more than 13 distinct localities throughout Eurasia (Reshetnikov and Ficetola 2011). Some initial introductions were documented;

Figure 1. Invasive fish rotan *Perccottus glenii* (Odontobutidae). Photo by author.

other introductions were distinguished using spatio-temporal analysis of information regarding this invader. These introductions led to the emergence of several new sources of secondary distribution (Saint Petersburg; Moscow; Nizhniy Novgorod, Ilev; Baikal; Lithuania; Minsk; Western Ukraine, Lviv; Arkhangelsk, Plestsy; Tomsk; Upper-Amur; Balaton amongst others). Many of these new subranges expanded rapidly and extensively and have since merged. Thus, the shape of the current invaded range is partially determined by the location of initial introduction points. Before 2011 non-native populations of rotan were recorded in Russia, Mongolia, Kazakhstan, Belarus, Ukraine, Lithuania, Latvia, Estonia, Poland, Slovakia, Hungary, Serbia, Croatia, Bulgaria, Romania, and Moldova (Reshetnikov and Ficetola 2011). Two climatically suitable corridors provide potential connection of colonized areas to Western Europe; a northern corridor which includes Poland, Germany and western countries, and a southern corridor extending from the Danube river basin through Croatia, Slovenia and Italy to France (Reshetnikov and Ficetola 2011). The northern corridor includes artificial canals connecting many rivers (Leuven et al. 2009). Most of the territory in Europe is climatically suitable for the species. Rotan's intense invasiveness, the lack of geographical barriers and the absence of reliable methods to prevent its spread are reasons for further expansion in Europe (Reshetnikov and Ficetola 2011).

The aim of the current paper is to analyse the long-term spatio-temporal dynamics of the West-Ukrainian (also known as Lviv) subrange of *P. glenii,* and review information concerning its potential impact on European freshwater ecosystems.

Methods

Updated information from the database "Non-native range of rotan, *Perccottus glenii*" (Reshetnikov A.N., 2003; # 0220309453®, STC "Informregister") was used for assessing both the past and current geographical distribution of the fish. Data were gathered by analyzing literature and also by a questionnaire survey of specialists in regions of interest. The validity of all data was examined; where cases were questionable, collected material or photos were requested. All records received before October 2012 were considered and analysed by using GIS software ArcViewGIS 3.2. To date, rotan records from 372 water bodies were recognised as part of the West-Ukrainian expanded subrange. Information concerning ecology and behaviour of rotan was obtained from personal research, as well as literature.

Results and discussion

An example of the process of *colonization of a river basin* by rotan may be briefly described as follows: (i) introduction in an oxbow lake; (ii) latent period of development of initial population (increase of population density); (iii) movement downstream during a flooding event and consequent rapid colonization of flood-plain water bodies, located downstream of the initial population; (iv) latent period of development of several populations in flood-plain water bodies and increase of the population density; (v) high population density in these water bodies and comparatively rapid systematic colonization of the river flood-plain habitats downstream; (vi) comparatively slow colonization of tributaries and isolated lakes and ponds in a given river basin; this stage of colonization is mainly as a result of uncontrolled translocations by local people. The process may be accelerated by unpredictable secondary translocations of the fish by humans within and between river basins. Stages (i)-(iii) and even (iv) may be named as "hidden" because detection of scarce, previously unknown species is difficult. Obviously investigators commonly find rotan at stage (v) or later, i.e., after its self-distribution and marked increasing of population density. So, there is generally an unavoidable time span (several years) between the actual introduction of the fish species into a water body and it being located and recorded. Regarding the above-presented arguments, small-scale approaches including reports of exact km/year velocity of distribution of rotan in rivers (Witkowski 2002; Andrzejewski et al. 2011) are not correct. On the other hand, analysis of species distributional data using large spatial and temporal scales may be regarded as a valuable tool for the investigation of biological laws regulating the invasion because large-scale analysis decreases significance of inexactitudes and lack of data (e.g., Reshetnikov and Ficetola 2011).

To describe the process of geographical distribution of rotan in the studied area, I used the following terms: a. initial introduction, or the point of the first introduction in a new region; b. centre (source) of the secondary distribution, i.e., the region invaded by rotan around the point of the first introduction serving as a source for further expansion; c. invaded subrange, i.e., part of the invaded range assumed to have originated from a single or a limited number of initial introductions, geographically separated from other invaded subranges, which may be temporally separated and later merged.

The first records and the early stage of development of the newly invaded subrange of rotan in Western Ukraine

At the end of the 1960s rotan was brought unintentionally, from the more eastern parts of its native or invaded range to Lviv province, Western Ukraine, during stocking of commercial fish. This fish was recorded in a fish farm near Sambor town in 1967 (N.Y. Sokolov, pers. comm.) and in a fish farm near Lisnevichi settlement in 1972–73 (O.V. Fedonyuk, pers. comm.). The above-mentioned fish farms are located in the upper part of the river basin of the Dniester flowing into the Black Sea (Figure 2). Obviously these fish farms became a source for secondary dispersion of rotan to other water bodies of Western Ukraine. In 1980 rotan had already inhabited ponds in Lviv town (Reshetnikov 2010), located at the watershed of Dniester and Vistula river basins. Before 1982 it was numerous in the water bodies of the Vereshchitsa River (tributary of the Dniester) in the Yavor district of Lviv province (Yu. Grinjuk, pers. comm.). The Vereshchitsa River supports fish ponds and numerous canals, promoting the dispersal of this species between neighboring water bodies. The source area of the Vereshchitsa River, colonized by rotan, is located less than 1 km from the sources of tributaries of the Western Bug River (tributary of the Vistula). In 1994 rotan was recorded in the rivers Luga and Svinoryika (tributaries of the Western Bug), in the Volynskaya province of the Ukraine (Bigun 2012). As early as 1988, four individuals of rotan were caught in the Vishnya River flowing into the San (another tributary of the Vistula) near the Ukrainian-Polish border (Movchan 1989). This confirms that colonization of the Vistula happened simultaneously through two large tributaries, i.e. the Western Bug and the San. Indeed, by 1992-1993 rotan was recorded in the lower sections of these waterways (Terlecki and Pałka 1999; Obukhovich 2009) (Figure 3).

In 1995–1996, the expansion of rotan in the West-Ukrainian centre of distribution resulted in records in the Zakarpatie province (separated from the contiguous Lviv province by the Carpathian Mountains). Before 1997 this species became abundant in many water bodies of Zakarpatie. It was detected in ponds in the village Chervone, as well as in lakes Chopskoe, Platnoe, Morotva, Tsyganskoe, Karna, and Siren, in the vicinity of Chop town (Sivohop 1998; Kozub and Sivohop 2000). Zakarpatie is the source of streams and rivers of the Danube river basin. It became a source of further colonization of the Danube River basin by rotan (Figure 3). Expansion of this invader from Zakarpatie to the middle Tisza happened simultaneously via three rivers, namely Uzh, Latorica, and the upper section of the Tisza.

Records of the cestode *Nippotaenia mogurndae* Yamaguti and Miyata, 1940 (the host-specific parasite of *P. glenii* and some other odontobutids) in populations of rotan in the Vistula and Danube river basins (Kosutova et al. 2004; Mierzejewska et al. 2010) concur with the idea that the suspected fish-farms are the vector of rotan introduction in the Western Ukraine (see explanations in Reshetnikov et al. 2011).

Further spatio-temporal dynamics of the West-Ukrainian subrange of rotan

The West-Ukrainian source of expansion of rotan is located at the watershed of several large European river drainage systems, namely the Danube, Dniester, Southern Bug, Dnieper (Black Sea basin) and Vistula (Baltic Sea basin) (Figure 2). These river basins are all climatically suitable for this species (Reshetnikov and Ficetola 2011).

In 1995–1997, rotan became abundant in ecosystems of lentic water bodies (>60% of fish specimens; 1st out of 17 positions in the appropriate fish species list) in the Dniester River basin, and was rare in running water (0.7% of all fish specimens; 20th position in the fish species list) (Korte et al. 1999). By 2001 rotan was self-distributed

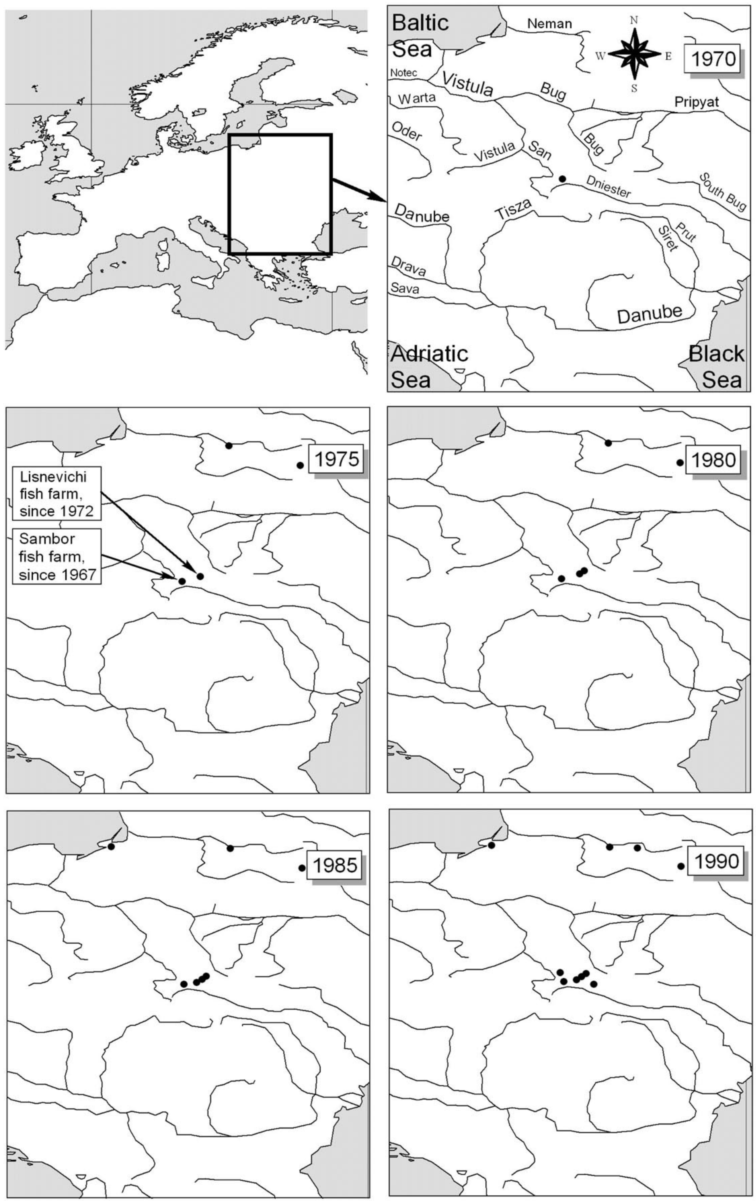

Figure 2. Spatio-temporal dynamics of records of the fish *Perccottus glenii* (Odontobutidae) for the West-Ukrainian centre of distribution of this species using information from database 1970–1990 (A.N. Reshetnikov, 2003; # 0220309453®, STC Informregister). Records in the Neman river basin and more northern ones do not belong to this centre.

down the Dniester and was found in Ivano-Frankovsk and Ternopol provinces of Western Ukraine (N.Y. Sokolv, pers. comm.). The fish also appeared lower downstream in the Chernovitskaya province (Moshu and Gusun 2002).

By 2001 rotan was already widely distributed in canals, ponds, rivers and other water bodies of the Western Bug basin (N.Y. Sokolov, pers. comm.). This dispersion contributed to the colonization of the lower Vistula. During this period, rotan crossed Poland from south to north, via the Vistula (Brylińska 2000) and crossed Hungary from north to south along the Tisza and appeared in Serbia in a pond near the Tisza (Gergely and Tucakov 2003; Harka et al. 2003; Simonović et al. 2006). In 2001 this species was also recorded in the Suceava River in north-eastern Romania (Nalbant et al. 2004). The upper Suceava runs close to the West-Ukrainian source of distribution and hence could be colonized from the Ukraine. This river flows into the Siret River (a tributary of the Danube). Expansion of rotan from the Western Ukraine resulted in a wide distribution downstream in the Dniester, Vistula and some tributaries of the Danube (Figure 3).

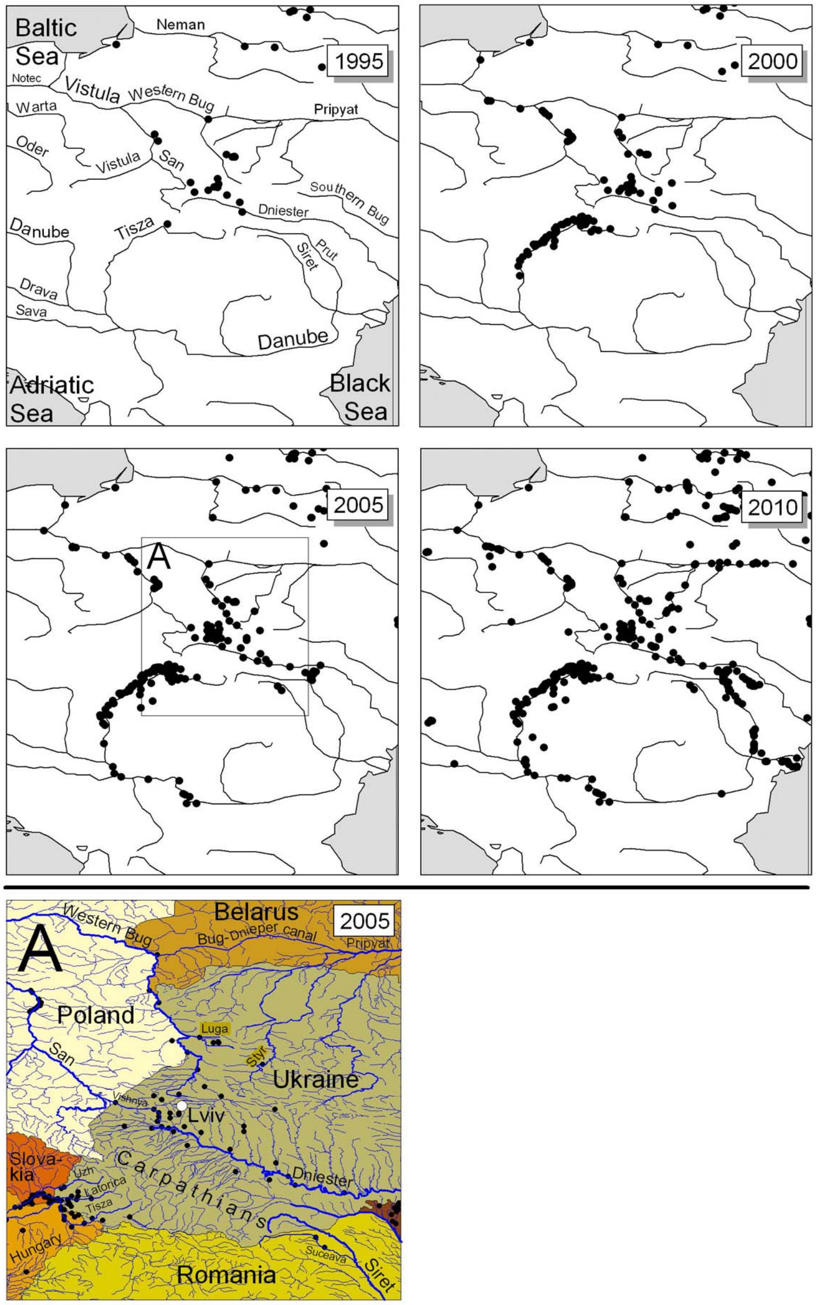

Figure 3. Spatio-temporal dynamics of records of fish *Perccottus glenii* (Odontobutidae) for the West-Ukrainian expanded subrange (1995–2010).

Rotan appeared at the watershed of the Dniester and Dnieper river basins before the beginning of the 21st century. For example, a record from station Zaliztsy, in the Zborovskiy district of Ternopol province, Western Ukraine, is known since 1997 (N.Y. Sokolov, pers. comm.). Later, populations were found in the adjacent part of the Dnieper river basin. The earliest hitherto known record of this species in the western part of Dnieper River basin is from 2003, from the Khrennitskoe (Khrenniki) reservoir in the Demidovka district of the Rovno province of Western Ukraine. In 2008, rotan had already been reported from many points of the Styr River basin (Sondak et al. 2009; Bigun 2012). Styr River is the right tributary of the Pripyat (the right tributary of the Dnieper).

The fish is also known from left tributaries of the Pripyat. For example, populations were established in the Soligorsk reservoir and neighbouring ponds (Soligorsk district of Minsk province, Belarus) before 2005 (M.V. Pluta, pers. comm.). However, those populations have a different origin (Minsk subrange) and do not belong to the Lviv subrange.

By 2005, rotan had crossed Serbia via the Tisza and Danube and was recorded in Romania and Bulgaria (Jurajda et al. 2006; Popa et al. 2006). Rotan movement was also via a parallel system of canals and rivers originating from the town Tiszalok (at Tizsa), which merges once more with the Tisza, at the mouth of Körös River (Harka and Szepesi 2007; Poór et al. 2009; Halasi-Kovács et al. 2011). During this period, rotan was also found in many water bodies in the upper part of the Prut (Moshu et al. 2007). Prut is a left tributary of the Danube.

Before 2010, rotan had travelled downstream in the Danube and occupied the delta (Nastase 2008; Nastase and Navodaru 2010). It was also found east of the Tisza, in water bodies of western Romania (Copilas-Ciocianu and Parvulescu 2011; Covaciu-Marcov et al. 2011). Several records of this species confirmed its westward expansion from the previously colonized Vistula – San and Bodrog – Tisza – Danube hydrological line. For example, rotan was found in the drainage system of the Nida River (tributary of the Vistula) as well as outside the Vistula basin, in the Glowna River (a tributary of the Warta) belonging to the Oder River basin (Andrzejewski et al. 2011; Klaczak et al. 2011). Appearance of rotan in Glowna River may be a result of uncontrolled translocation by humans. Populations in the Glowna could serve as a source for colonization of the Oder River, since the basin of the Oder is climatically suitable for this species (Reshetnikov and Ficetola 2011). During the same period (2005-2010), rotan was recorded in the upper part of the Vistula in Poland (Nowak et al. 2008). It was found also in a canal connected to the Sava River (right tributary of the Danube) in Croatia (Ćaleta et al. 2010) and in canals located closely to Balaton Lake, Hungary (Eros et al. 2008; Harka et al. 2008; Antal et al. 2009). Balaton Lake has a separate drainage system, but is artificially connected with the Danube by canals as well as with the Mura River, which flows into the Drava River (tributary of the Danube). During this period, rotan was already common along all the Prut River (Moshu et al 2007; Moshu and Kiriyak 2011). The Prut connects Ivano-Frankovsk and Chernovtsy provinces of Western Ukraine with the Lower Danube. Thus, spatio-temporal dynamics of records confirm that colonization of the lowest section of the Danube (including Danube delta) was from one source (West-Ukrainian source of distribution of rotan) via three routes: Route 1: small tributaries of Tisza – Tisza – Danube; Route 2: small tributaries of Siret – Siret – Danube and the third route of rotan was from main river channel of Prut downstream to the Danube. The dynamics of colonization of the West-Ukrainian subrange of *P. glenii*, between 1995 and 2010 is shown in Figure 3.

Current distribution of rotan within West-Ukrainian expanded subrange and predictions of further expansion

Publications on the presence of rotan in the middle and lower sections of the Dniester are absent. However in 2009, this fish was found in the Kuchurgan reservoir (lower Dniester) (O. Strugulya, pers. comm.) (Figure 4). This fish may already have colonized all the Dniester River, but reliable records are absent from the border between Moldova and the Pridnestrovian Moldavian Republic. Similarly, there are no records from the lower sections of the main tributaries of the Vistula: Western Bug and San (Figure 4). However, analysis of spatio-temporal dynamics of rotan, confirms that flood-plain water bodies of the Western Bug are already colonized by this species. However the lower section of the San has a comparatively less-developed flood plain and hence fewer suitable habitats for the invader. It has not yet been recorded in the lower sections of the Dnieper (Bulakhov et al. 2008). Rotan first appeared in water bodies of the Khmelnitskiy province of the Ukraine, in the upper part of Southern Bug basin (Figure 4). Further colonization of the Southern Bug basin is expected in the next years. The invaded range of rotan is also gradually moving to the upper part of Danube River basin. This fish has in fact just recently been recorded in the middle section of the Danube basin, approximately 115 km south of Budapest, Hungary (Takács and Vitál 2012), as well as in the upper part of the same basin in Bavaria, Germany (Reshetnikov and Schliewen, in press).

To date, the expansion of rotan from the Western Ukraine has resulted in the colonization by this invasive species of several large European rivers namely, the Dniester, Danube, Dnieper (Black Sea basin), and the Vistula (Baltic Sea basin). Throughout the colonization period, rotan has been recorded from Lviv, Zakarpatie, Volynskaya, Povno,

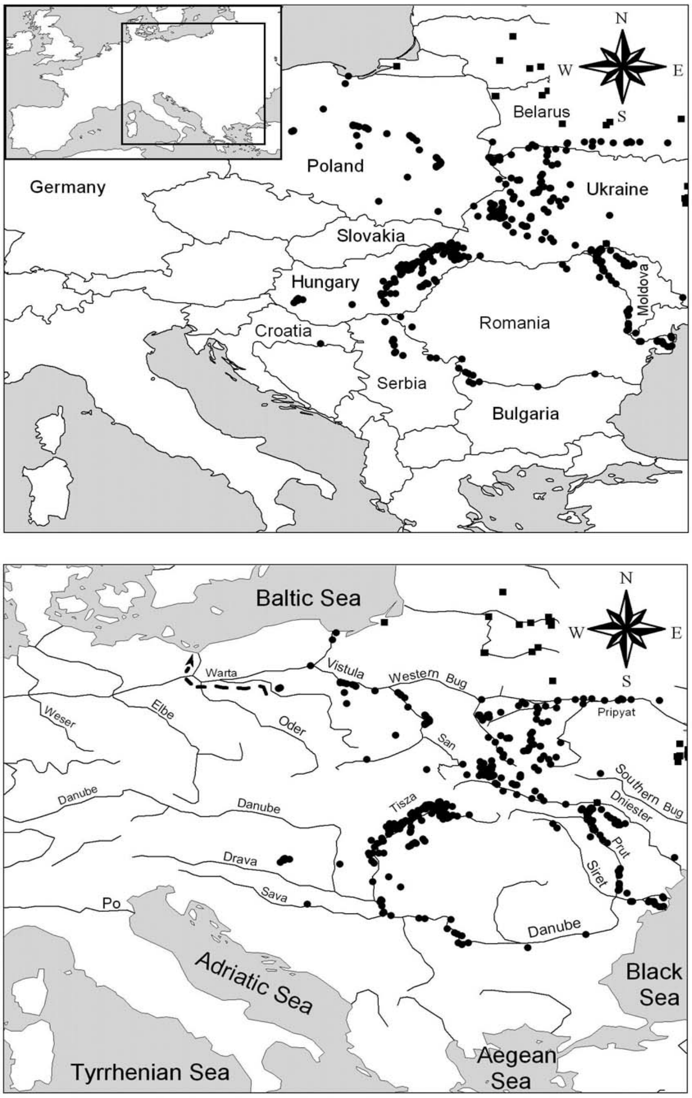

Figure 4. The current distribution of the fish *Perccottus glenii* (Odontobutidae) in the region of the West-Ukrainian subrange using records (black circles) known pre 2012 from database (A.N. Reshetnikov, 2003; # 0220309453®, STC Informregister). The records of rotan outside the West-Ukrainian subrange are shown by black squares. Names of the countries where rotan could potentially appear from the West-Ukrainian source of distribution are presented on the map (above). The hydrological network is also shown (below). The main invasion corridor of the next stage of expansion is shown using dotted line with an arrow.

Ivano-Frankovsk, Chernovtsy, and the Khmelnitskiy provinces of Western Ukraine as well as in territories of Poland, south-western Belarus, Slovakia, Hungary, Serbia, Bulgaria, Romania, Croatia, Moldova and Germany. The current known distribution, in the research area is shown in Figure 4.

Possible consequences for European ecosystems

Investigations, both internal and external to the West-Ukrainian, expanded subrange of rotan, reveal that rivers are common natural corridors/vectors for self-dispersal of this species (Harka et al. 2003; Hegediš et al. 2007; Reshetnikov and Petlina 2007; Reshetnikov and Chibilev 2009). Distribution of this invader within a river system can be described through the metapopulation concept (Hanski and Gilpin 1997), with source populations located in flood-plain water bodies and producing emigrants, especially during floods, whereas large rivers serve as important long-distance, one-way transmission corridors (Reshetnikov and Ficetola 2011). Spatio-temporal dynamics of the West-Ukrainian subrange entirely confirm this point of view. Rivers Dniester, Western Bug, Vistula, and Tisza, Siret, Prut and Danube served as such transmission corridors and a propagule source and determined the invasive success of this fish in flood-plain habitats (Figure 4). In the West-Ukrainian subrange, rotan is most numerous in flood-plain water bodies, canals, ponds, and shallow lakes (Harka and Sallai 1999; Korte et al. 1999; Terlecki and Pałka 1999). Ecosystems of such comparatively shallow water bodies are more vulnerable to rotan impact, compared to large rivers and deep lakes.

Theoretically rotan can be a vector for the distribution of zoosporic fungi, since at least 34 such organisms can grow on this species (Czeczuga et al. 2001). This research was conducted *in vitro*, using only samples of fish tissue, however many of the studied fungi are known as parasites of fish eggs and adult fish (e.g., Srivastava and Srivastava 1977; Lartseva and Dudka 1990; Czeczuga and Kieziewicz 1999).

Within the colonized range, rotan transforms parasite systems and demonstrates parasitological interactions with indigenous fish and some other animal species (Sokolov et al. 2012; Reshetnikov et al. 2013). Rotan can harbour at least 67 parasite taxa within its native range and may be a host for appr. 100 parasitic taxa in its invaded range (Sokolov and Frolov 2012; Sokolov et al. 2013). Some of these parasites species have already been registered on/in rotan in the region of West-Ukrainian expanded subrange (Košuthová et al. 2004; Oros and Hanzelová 2009; Davydov et al. 2012; Mierzejewska et al. 2012). Rotan may play a significant role in the circulation of some European native parasites of fishes (Sokolov et al. 2012). Theoretically, this may influence other fish species inhabiting the same ecosystems. Moreover, host-specific parasites *Nippotaenia mogurndae* and *Gyrodactylus perccotti* Ergens et Yukhimenko, 1973 were introduced into the region via rotan (Košuthová et al. 2004; Ondračková et al. 2012). The cestode *N. mogurndae* has a complex life cycle and infects native copepod species. Up to 10% of copepod *Mesocyclops leuckarti* (Claus, 1857) individuals (one of the first intermediate hosts of *N. mogurndae*) may be infected by this cestode (Sokolov et al. 2011). However, the impact of this introduced parasite on populations of native crustaceans has not yet been assessed comprehensively.

In the Far East, rotan is an intermediate host for the trematode *Clonorchis sinensis* Looss, 1907 (family Opisthorchidae), causing a debilitating human (and some other mammal) parasitic disease, known as clonorchiasis (Wang 1983; Liu et al. 2011). Western parts of Eurasia including territories of the Ukraine, Belarus, and other European countries have natural loci of similar human disease called opisthorchiasis (Be'er 2005) which can drastically affect the liver, pancreas and gall bladder. Agents of this disease are opistorchid trematodes: *Opisthorchis felineus* (Rivolta, 1884), *Metorchis bilis* (Braun, 1890), and *Pseudamphistomum truncatum* (Rudolphi, 1819) are carried by some fish species (second intermediate hosts). The term "western opisthorchiidosis" is introduced to separate this disease from the above-mentioned Chinese clonorchiasis. Reshetnikov and Chibilev (2009) hypothesized that rotan can influence the natural loci of western opisthorchiidosis, since rotan is numerous in shallow flood-plain water bodies where members of this parasite system (mollusks and small fish) are concentrated. Trematodes, agents of western opisthorchiidosis were not found in rotans from flood plain of the Irtysh River, Siberia (region of well-known natural locus of this disease) (Sokolov et al. 2011). So, there is no evidence that this fish species may be a host for these parasites. On the other hand, rotan actively consumes gastropod mollusks and young-of-the-year cyprinid fish (first and second intermediate hosts). Rotan may therefore actually have a positive (for humans) impact on the natural loci of western opisthorchiidosis in these waterbodies, through elimination of the intermediate hosts (Reshetnikov and Chibilev 2009).

Rotan consumes a wide spectrum of animal prey items from ciliates to vertebrates (Sinelnikov 1976; Reshetnikov 2003; Dgebuadze and Skomorokhov 2005; Grabowska et al. 2009; Lukina 2012). Selectivity in its feeding habits have been reported (Manteifel and Reshetnikov 2001; Koščo et al. 2008; Reshetnikov 2008). In water bodies supporting rotan, significantly lower diversity of some species of large macroinvertebrates such as leeches, water spiders, dragonfly and beetle larvae, and adult beetles was observed (Reshetnikov 2003). Theoretically, this invader can compete for food with other fish species especially for larvae of Chironomidae (Litvinov and O'Gorman 1996). Rotan's diet also includes fish eggs and small fishes. Fish eggs at later developmental stages are more vulnerable for predation by rotan since the embryo's movements attract the attention of a predator (Reshetnikov 2008). Fish eggs may constitute one third of rotan stomach content during the spawning period of native fish (Bigun 2012). In shallow water bodies with high population densities of *P. glenii*, relative abundance of some native fish species may be decreased or the species may be even eliminated e.g., *Carassius carassius* (Linnaeus, 1758), *Phoxinus phoxinus* (Pallas, 1814), *Leucaspius delineatus* (Heckel, 1843) (Shlyapkin and Tikhonov 2001; Reshetnikov 2003; Reshetnikov and Chibilev

2009). In the region of the expanded West-Ukrainian subrange, rotan is mentioned as a possible reason for the decline of the endangered fish: the European mudminnow *Umbra krameri* Walbaum, 1792 in Slovakia, as well as lake minnow *Ph. percnurus* (Pallas, 1814) and bitterling *Rhodeus sericeus* (Pallas, 1776) in Poland (Koščo and Košuth 2002; Wolnicki and Kolejko 2008; Kuczynski and Pieckiel 2012).

Mature individuals of many rheophilic fish species inhabit larger main river channels, but commonly use oxbows for reproduction and early development. Population densities of rotan are high in temporally isolated flood-plain lakes where they actively consume eggs and small fish of other species. Reshetnikov and Chibilev (2009) underlined that data on the distribution of *P. glenii* in such water bodies should be taken in account when analyzing the general dynamics of fish communities of large rivers. On the other hand, deep, well-oxygenated reservoirs and lakes tend not support dense populations of rotan (Korte at al. 1999; Reshetnikov 2003; Nastase and Navodaru 2010). Large fish predators readily consume rotan (Litvinov and O'Gorman 1996; Bigun 2012) and may control its population density. Rotan can inhabit shallow riparian zones with dense submerged vegetation in large water bodies with diverse fish fauna (Litvinov and O'Gorman 1996; Reshetnikov 2003). In such biotopes this species can consume fish eggs and young fish. However, the effect of rotan on the reproduction and population dynamics of other fish species in large lotic and lentic water bodies has not been assessed quantitatively yet.

Rotan does not consume amphibian eggs (Reshetnikov 2008), but feeds selectively on amphibian larvae (Manteifel and Reshetnikov 2001). Noxious tadpoles of the common toad *Bufo bufo* (Linnaeus, 1758) are comparatively well-protected against predation by this fish (Manteifel and Reshetnikov 2002). Nevertheless, this invader readily consumes tadpoles of newts (*Lissotriton*, *Triturus*) and frogs (*Pelophylax*, *Rana*) as well as adult *Lissotriton* sp. In small water bodies this results in the entire elimination of all newt and frog larvae before metamorphosis (Reshetnikov and Manteifel 1997; Reshetnikov 2003). This transforms the metapopulation structure of amphibian species, since these amphibians are unable to use optimum permanent breeding ponds colonized by rotan (Reshetnikov and Manteifel 1997). On the whole, species diversity of amphibians in small water bodies inhabited by rotan is considerably lower, compared to rotan-free water bodies (Reshetnikov 2003). In the region of the expanded West-Ukrainian subrange, urodelians were recorded in the stomachs of rotans in Hungary, adult newts *Lissotriton* in the Lviv province and the larvae of *Triturus cristatus* (Laurenti, 1768) in three lakes of the Volynskaya province of Western Ukraine (Szito and Harka 2000; Fedonyuk 2005; Bigun 2012; V.K. Bigun, N.Y. Sokolov, pers. comm.). Litvinchuk and Borkin (2002) observed the disappearance of the newt *Triturus dobrogicus* (Kiritzescu, 1903) from several water bodies in the Zakarpatie province, Ukraine, following the introduction of *P. glenii*. The impact upon native species of newts is one of the most dramatic consequences of the expansion of rotan in Europe (Reshetnikov 2003).

Rotan may be, but rarely is, consumed by the adult frogs of *Pelophylax esculentus* species complex (Reshetnikov et al. 2013). Some pond terrapins (e.g., *Emys orbicularis* (Linnaeus, 1758)) do not hunt for live rotans (A.N. Reshetnikov, unpublished experimental data). However European semi-aquatic snakes (*Natrix natrix* (Linnaeus, 1758) and *N. tessellata* (Laurenti, 1768)) readily include rotan in their diets. In these cases, the snakes may contract the parasitic cestode *Ophiotaenia europaea* Odening, 1963 from rotan and become infected with 100% prevalence. Rotan therefore has the potential to influence animals in adjacent terrestrial ecosystems (Reshetnikov et al. 2013).

Rotan may be a source of food for many native fish, waterfowl and mammals within its invaded range: fishes European perch *Perca fluviatilis* (Linnaeus, 1758) and pike *Esox lucius* (Linnaeus, 1758) as well as birds grey heron *Ardea cinerea* (Linnaeus, 1758), common gull *Larus canus* (Linnaeus, 1758), black-headed gull *L. ridibundus* Linnaeus, 1766, herring gull *L. argentatus* Pontopiddan, 1763, mallard *Anas platyrhynchos* (Linnaeus, 1758), spot-billed duck *A. poecilorhyncha* Forster 1781, tufted duck *Aythya fuligula* (Linnaeus, 1758), greater greenshank *Tringa nebularia* (Gunnerus, 1767), common kingfisher *Alcedo atthis* (Linnaeus, 1758), and even mammals like the American mink *Mustela vison* Schreber, 1777, another invader (Tupitsin 1995; Litvinov and O'Gorman 1996; Kotyukov and Numerov 2004; Reshetnikov and Reshetnikova 2002). In large well-developed delta systems, rotan may be a significant component of a bird's diet. Distribution of this fish species may be a reason of an abrupt increase in the number of individuals and colonies of gulls and herons in the Selenga River delta, Russia (Tupitsin 1995). For example, the abundance of three gull species increased twice in four years; the number of

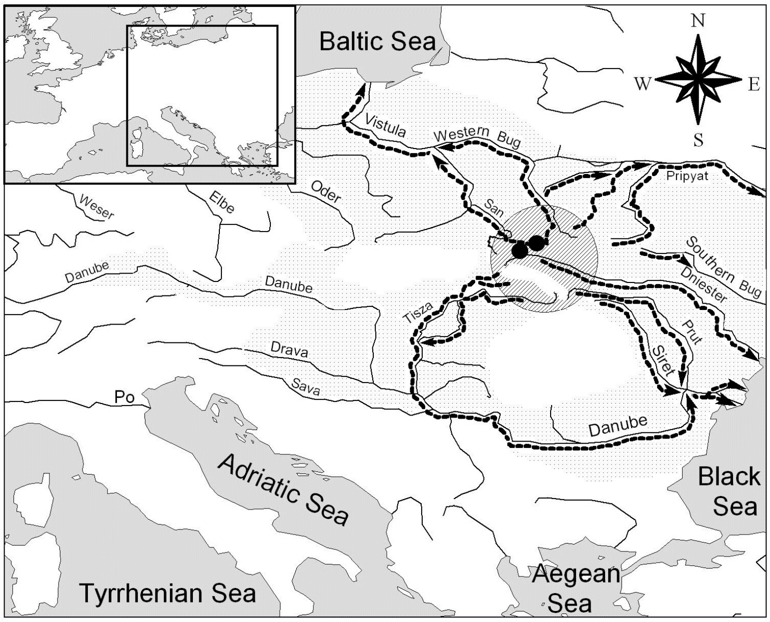

Figure 5. The functional scheme of development of the West-Ukrainian subrange of the fish *Perccottus glenii* (Odontobutidae). Initial populations = black circles. The West-Ukrainian centre (source) of secondary distribution of *P. glenii* = large circle with oblique lines. Long-distance one-way corridors promoted rapid self-dispersion during the Period II of expansion process = dotted lines with arrows. Area of the West-Ukrainian subrange (will be filled during the Period III) = light-grey colour. See text for explanation of the periods.

colonies of the common gull increased from 34 to 92. Grey herons increased from 1700–1900 to 4500–5000 individuals and colonies from 1 to 8, over 6 years. Rotan became the main food for nestlings of herons (Tupitsin 1995). Similar alterations in bird communities within the West-Ukrainian subrange can be assumed. The numbers of colonized lakes and population densities of rotan are growing in the Danube delta (Nastase 2008; Nastase and Navodaru 2010). Rotan is not abundant in large lakes of the delta (Nastase 2012), but in other locations the density of this species reached 92 individuals per 100 m^2 (Y. Kvach, pers. comm.). Alteration of bird foraging habits and population growth or enlarging of winter aggregations of some piscivorous bird species is expected. The inclusion of rotan in the diet of birds and mammals underlines its high potential to influence terrestrial ecosystems.

Conclusions

Thus, rotan self-distributed from local fish farms to the Dniester drainage system and colonized many water bodies during the 1970s and 1980s. This first period (period I, approximately two decades) of rotan expansion is characterized as slow and was locally restricted to the upper part of the Dniester basin. The second period (post 1988 approx.) is characterized by the movement of rotan to adjacent river basins and rapid self-distribution over long distances via rivers (Figure 5). Regarding the one-way direction of the movement of this fish species by strong river flows, these aquatic corridors act as *natural conveyors*. These same rivers may work as two-way corridors for other fish species. The West-Ukrainian source of expansion of rotan became consist of two contiguous regions: Lviv and Zakarpatie separated by the Carpathian Mountains. Since approximately 2005, the third period of rotan expansion has occurred. In this third longest period, rotan began and continues colonization of tributaries and isolated water bodies spreading within already invaded river basins filling gaps between large rivers (Figure 5).

Uncontrolled human-mediated fish dispersal is possible within and among river basins. However the presented spatio-temporal analysis of records confirms that the expansion of rotan from the West-Ukrainian source of distribution could be the main reason for the gradual invasion of several European huge drainage river systems listed above. Rotan demonstrated a comparatively rapid expansion from riverheads downstream to river mouths, yet a notable absence or much slower expansion upstream of tributaries. The example of the development of the West-Ukrainian subrange demonstrates the importance of the upper parts of river basins for the rapid distribution of rotan downstream, as well as the overall important role of water systems for the crossing of this species over country borders.

Analysis of spatio-temporal dynamics of dispersion of the fish under study from Western Ukraine shows that the so-called central European invasive corridor (Bij de Vaate et al. 2002) did not work for *P. glenii*. This conclusion coincides with the opinion of Semenchenko et al. (2011). Indeed, records of this species are still absent in the Dnieper–(Western) Bug canal (one of the links of this corridor), which connects the Dnieper and Vistula basins. Probably, contrary water flows and/or sluices may be temporary or permanent obstacles for rotan self-distribution. One of the actual natural corridors for rotan self-distribution in the region of the above-mentioned canal was the right tributaries of the Pripyat – Pripyat – Dnieper; the second route was via tributaries of the Western Bug – Western Bug – Vistula (Figure 5). Rotan was not recorded yet in another canal in the central European invasive corridor (the Bydgoszcz canal connecting the Vistula and Oder basins). Rotan is present in the Vistula, and was recorded close to the confluence of the Vistula and Brda River (part of Bydgoszcz canal system) before 2004 (Andrzejewski and Mastynski 2004). However rotan was not recorded from Brda to date, possibly because of the above-mentioned limited ability for the distribution potential upstream. Current analysis of data confirms that this fish did not use the central European invasive corridor for its expansion from east to west during more than 45 years of the development of the West-Ukrainian subrange. In addition, there is no evidence of its east-west movement through the Augustów canal, connecting the Neman and Vistula rivers.

The enlarging of the West-Ukrainian expanded subrange of *P. glenii* is ongoing. For the first time rotan was recorded recently in the middle and upper parts of the Danube river basin, in Hungary as well as in the Oder river basin, Poland (Figure 4). These introductions may have happened due to the secondary human translocations of this undesirable species within the territory of the West-Ukrainian expanding subrange. Such translocations may have been conducted unintentionally together with the movement of commercial fish species from one aquaculture farm to another, despite published recommenddations concerning the necessity of rigorous fish stock control (Reshetnikov and Ficetola 2011). The same mechanism of secondary dispersion was also documented for other parts of the invaded range of the species under study (Elovenko 1981; Reshetnikov 2004).

The described expansion of rotan will result in negative consequences for European waters. This invader is an undesirable deleterious species for European fish farms causing negative consequences for their economical effectiveness. Rotan may also be actively included in local parasite systems and may be a vector for introduction of host-specific parasites in new regions. This fish is capable of decreasing the abundance or even eliminating native hydrobionts. Rotan dramatically decreases species diversity of native freshwater ecosystems of various small shallow water bodies and also has the potential to influence adjacent terrestrial ecosystems.

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