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Research Article

Recovery of the ruffe (*Gymnocephalus cernua*) population after an invasion boom of round goby (*Neogobius melanostomus*) in De Gijster Lake (the Netherlands)

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Abstract

Studies dealing with invasive species usually focus on changes caused by invasion, however, natural recovery of the system after the initial population explosion (boom) has been much less studied. Ruffe dominated the benthic fish community in De Gijster Lake (Biesbosch National Park, the Netherlands) before a round goby invasion indicated by catches in both seines and gillnets. In 2012, the round goby was found for the first time and it was observed to undergo a boom in 2014, when ruffe almost completely disappeared. Nevertheless, gillnet sampling in 2016 indicated a decreasing trend in the number of round gobies and an increase in ruffe. These changes were confirmed during monitoring in 2019, when the density of round goby decreased seven times in comparison with 2014 indicated both in seine and gillnet catches. At the same time, the density of ruffe increased six times in gillnets and from zero to 396 ind/ha in seine catches. Densities of both species were clearly negatively correlated and the approximate theoretical threshold-values for coexistence of both species were estimated as 750 ind/ha in the littoral zone and 120–140 ind/1000 m^2 of standard CEN gillnets. Our results show the recovery of a native fish population after a natural decline of the invasive species density, which could be important when considering the management of invasive species.

Key words: Biesbosch, invasive fish species, Rhine-Meuse delta, gillnets; seining

Introduction

One of the most persistent ideas in invasion biology is the boom-bust concept (Strayer et al. 2017). According to this concept, invaders may go through an initial outbreak (boom) phase, in which their population becomes very large (population explosion), before declining to a much lower population size (bust). Declines in invasive species following the initial peak may be due to factors such as increased competition for resources, increased pathogen transmission and inbreeding depression (Cooling and Hoffmann 2015), predators (Carlsson et al. 2009) but also due to many other unknown reasons. Identifying the drivers and mechanisms behind such declines could have important implications for invasive species management worldwide. Ponto-Caspian gobies have successfully invaded many European and North American fresh waters in the last few decades, and their spreading continues (Jude et al. 1992; Corkum et al. 2004; Manné et al. 2013). In particular, the round goby *Neogobius melanostomus* (Pallas, 1814), a small Ponto-Caspian gobiid species, has become invasive in both Europe and North America (Corkum et al. 2004). The reasons for the rapid spread of this species are tolerance to a wide range of environmental factors, a broad diet, ability to spawn repeatedly during the whole growing season, and aggressive behaviour and parental care (Charlebois et al. 1997). The occurrence of early juveniles in the pelagic (Jůza et al. 2016) is also supposed to enable their rapid spread as the juvenile fish can be pumped into boats in ballast water and transported long distances (Hayden and Miner 2009).

The most important concerns related to round goby invasions are the detrimental effects on native fish species. For example, populations of mottled sculpin *Cottus bairdi* (Girard, 1850) and logperch *Percina caprodes* (Rafinesque, 1820) have declined since the appearance of round gobies in the St Clair River area of the Great Lakes region (Janssen and Jude 2001; Balshine et al. 2005). Lauer et al. (2004) also found a significant decrease in mottled sculpin and the johnny darter *Etheostoma nigrum* (Rafinesque, 1820) in trawl catches in Lake Michigan after a round goby invasion. Riley et al. (2008) described the collapse of the deep water demersal fish community in Lake Huron owing to the invasion of exotic species, including the round goby. In Europe, Janáč et al. (2016) found that the colonization of the Dyje River (Czech Republic) by round goby had no apparent effect on native 0+ fish density, species richness or habitat utilization. On the other hand, Janáč et al. (2019) found a significant negative correlation between round goby and older than 1+ chub *Squalius cephalus* (Linnaeus, 1758) density in the upper Elbe River (Czech Republic). The negative effect is often clearly visible, but how it happens is questionable. Native fish can be affected through predation on eggs and juveniles (Chotkovski and Marsden 1999). This behaviour was observed especially in laboratory conditions, whereas some recent studies have not proven round goby's significant predation on eggs and juveniles of other species in the field (e.g., Vašek et al. 2014). Karlson et al. (2007) proposed that round goby had a negative influence on the commercially important European flounder *Platichthys flesus* (Linnaeus, 1758) in the Baltic Sea because of significant diet overlap. Invasion of gobies into the River Meuse in the Netherlands resulted in the rapid decline of native river bullhead *Cottus perifretum* (Freyhof et al. 2005), probably owing to predation or competition for shelter and/or food (Van Kessel et al. 2011, 2016).

The River Rhine and subsequently the River Meuse have also been invaded by many Ponto-Caspian species including macroinvertebrates as

Dreissena polymorpha (Pallas, 1771) and *Limnomysis benedeni* (Czerniavsky, 1882) (Bij de Vaate et al. 2002; Leuven et al. 2009), and fish as tubenose goby (*Protherorhinus semilunaris*) (Heckel, 1837), bighead goby (*Ponticola kessleri*) (Günther, 1861) and monkey goby (*Neogobius fluviatilis*) (Pallas, 1814) (Van Kessel et al. 2016). In the Netherlands, round goby was first recorded in 2004 and in subsequent years many other individuals were caught in the western part of the country (Van Beek 2006). In the Biesbosch Lake system, round goby was first recorded in 2012 (Kruitwagen 2013) and in 2014 round goby was a dominant species of the benthic fish community in all lakes, including De Gijster Lake (Vašek et al. 2015). Ruffe *Gymnocephalus cernua* (Linnaeus, 1758) was very abundant before the round goby invasion, but disappeared almost completely in 2014, when the round goby density reached a peak probably due to significant niche overlap with round goby being a stronger competitor (Jůza et al. 2018).

To the best of our knowledge, evidence of a natural recovery of native fish populations after the invasion took effect is missing in the literature. A decrease in the alien fish population is often connected with direct human influence, such as removal of the alien fish using rotenone (Weyl et al. 2014) or by gillnetting or electrofishing (Haubrock et al. 2018). Prior et al. (2018), for example, performed a comprehensive review of 151 studies that removed invasive species and assessed ecological recovery over time. The current study extends the study of Jůza et al. (2018), which described the collapse of the ruffe population during the phase of high round goby density shortly after their invasion into De Gijster Lake. Our present study aims to follow further development of these two competing populations. Because a significant natural decline of round goby density was evident in 2016 and especially in 2019, the main aim of this study is to describe the reaction of the ruffe population, which was found to be strongly negatively correlated with round goby density (Jůza et al. 2018). We expect that with decreasing density of the invasive round goby, the population of ruffe would recover and start to slowly increase.

Materials and methods

Study area

The study was conducted in De Gijster Lake (51.7270N; 4.8104E, area: 320 ha, max depth: 27 m) situated in Biesbosch National Park, the Netherlands (Figure 1a). The lake was created during the 1970s and serves as the first step in the treatment of the Meuse River water for drinking water production by several waterworks in the southern and western parts of the Netherlands (Oskam and van Breemen 1992). The lake was built as a basin-shaped embanked impoundment along the River Meuse, with artificial sides of asphalt-concrete and a clay bottom. Approximately 10–20 cm of mud is located on the bottom deeper than 6 m. The lake does not stratify

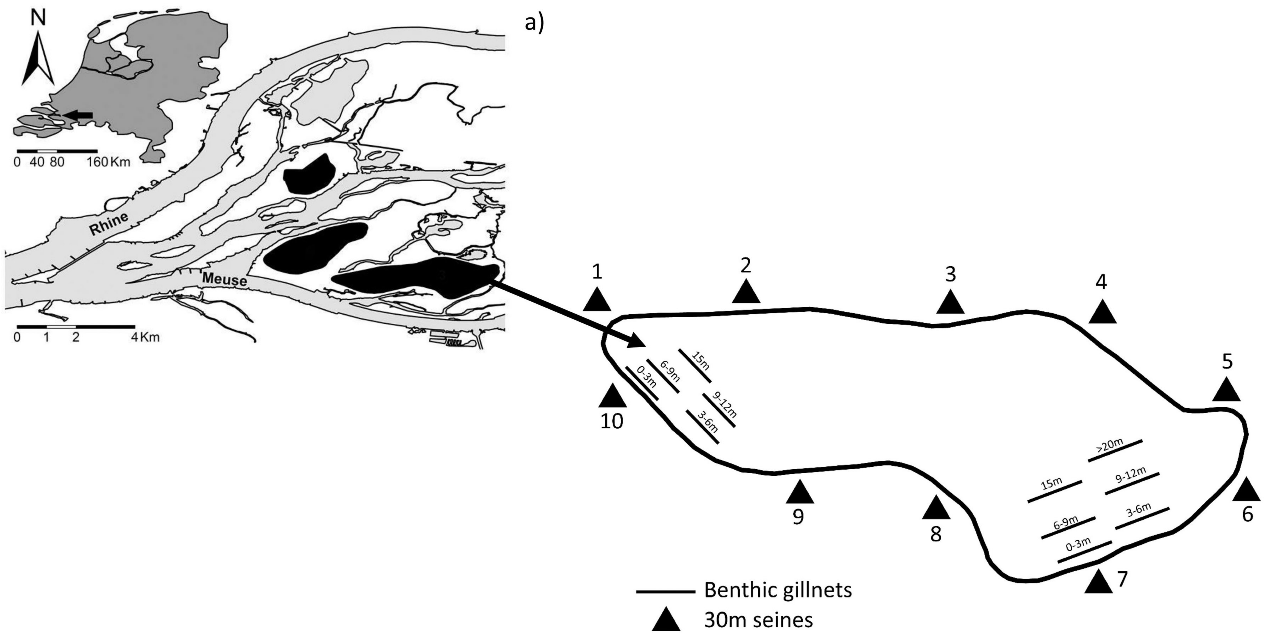

Figure 1. Map of the Biesbosch area and its location within the Netherlands and location of De Gijster Lake at the confluence of the Rhine and Meuse Rivers (a) and location of gillnet and seine samplings within the lake (b).

during the summer due to artificial mixing which provides strong aeration. There is no fish stocking and fishing is prohibited. The average summer transparency measured by Secchi disk is about 4 m. See Jůza et al. (2016) for the species composition of the fish stock in the lake.

Fish sampling

Fish were sampled in August 1998, 2000, 2002, 2008, 2014 and 2016, and in September 2019 using benthic gillnets and beach seining. The European sampling protocol (CEN 2015) was used for depth stratified sampling, total effort based on lake surface area and maximum depth sampled by gillnets. The depth layers sampled by benthic gillnets were 0–3, 3–6, 6–9, 9–12, 12–15, 15–20 and 20 m. The 15–20 m depth layer was not sampled in 2019 because of bottom modifications by heavy machinery. The multimesh gillnets consisted of 12 mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm knot to knot), as recommended by the European sampling protocol (CEN 2015). Each gillnet was 30 m long and 1.5 m high. Two locations were sampled in each year and three nets were deployed in every depth layer of each location (Figure 1b). All nets were set approximately 2 h before sunset and lifted after sunrise to cover the highest peaks of fish activity (Prchalová et al. 2010).

Because gillnets underestimate fish < 40 mm (Prchalová et al. 2009), a 30 m long and 3 m deep beach seine with a mesh size of 6 mm was used at night to capture the smallest 0+ round gobies and ruffe in the shallowest littoral area. The area quantitatively sampled with one seine haul was 270 m^2. Total effort was 10 seines per year performed around the perimeter of the lake (Figure 1b).

Table 1. Density of ruffe and round goby in seine and gillnet (average of all depth layers) catches in different years in De Gijster Lake. The horizontal line divides the pre and post invasion of round goby.

Year	Density in seines (inds./ha)		Density in gillnet (inds./1000 m^2)	
	Ruffe	Round goby	Ruffe	Round goby
1998	5673	0	570	0
2000	3589	0	298	0
2002	4126	0	196	0
2008	2974	0	538	0
2014	0	3359	38	258
2016	0	5170	103	164
2019	396	511	237	32

Fish from gillnets were processed immediately after removing the nets from the water, beach seine catches were processed immediately after each haul. All fish were identified to species and counted. For gillnets the round goby and ruffe density was expressed as number of fish per 1000 m^2 (ind/1000 m^2) of gillnet area per night and for beach seines, density was expressed as a number of fish per ha (ind/ha) of lake area.

Statistical analyses

The data were checked for normality, linearity and homogeneity of variance assumptions. Mean yearly round goby and ruffe densities (ln-transformed densities) in the years of their co-occurrence were compared separately for seining and gillnetting by the Welsh two paired sample *t*-test to see how dominance of particular species changed in time after the round goby invasion. *P*-values were calculated with significance set to 0.05. In the case of gillnets, mean density calculated from combined values at all depths was first used. In the years 2014–2019 the depth of gillnetting was also taken into account. Based on logarithmic equations, the same density at which both species can theoretically coexist were calculated for seining and gillnetting. The theoretical density values in which both species can coexist in the same densities in whole lake estimates, and also round goby density values, which mean complete suppression of ruffe, were calculated from these equations. Furthermore, a linear regression model was applied to test the relationships between ruffe and round goby densities in years 2014, 2015 and 2019 with log-transformed (ln(x+1)) catch data used for individual nets. Analysis and figures were performed in R version 4.0.0. (R Core Team 2020).

Results

In beach seine catches the density of ruffe in the period before round goby invasion (1998–2008) was 4,000 ind/ha approximately (Table 1). In the years of the massive round goby boom (2014 and 2016, 4,265 ind/ha in average) ruffe was not detected (Table 1). In 2019, the density of round goby decreased significantly to 511 ind/ha and an increase of ruffe density was observed in the same year to 396 ind/ha. There was no significant difference in density of ruffe and round goby in 2019 ($t = -1.23$, $p = 0.25$, $df = 9$) and the negatively

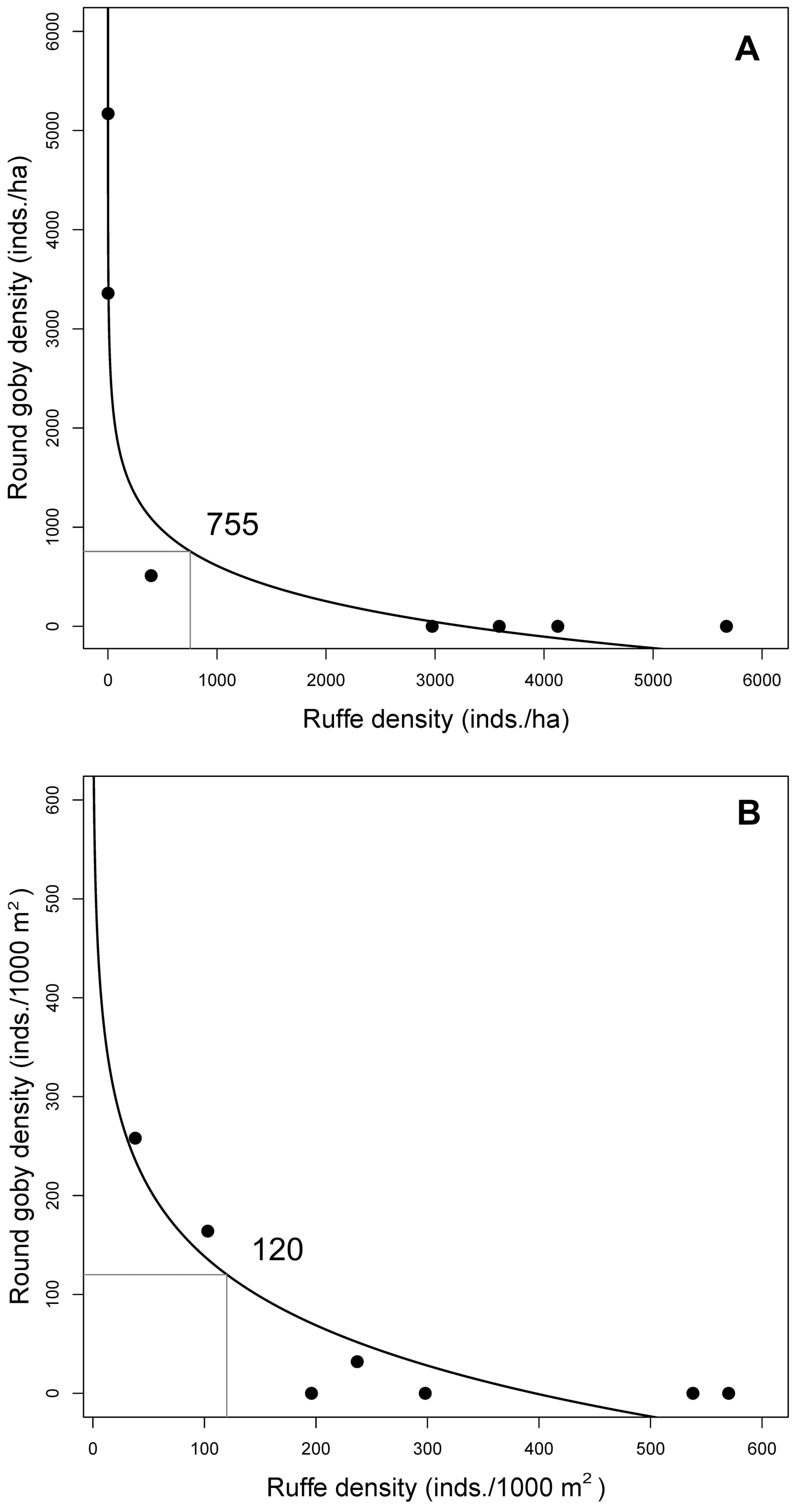

Figure 2. Logarithmic regression curves between round goby and ruffe density in beach seining (a) and gillnet (b) catches in De Gijster Lake in 1998, 2000, 2002, 2008, 2014, 2016 and 2019 (means of data for all depths combined for gillnets). The numbers on the curves provide theoretical values at which round goby and ruffe can coexist at the same density.

correlated relationship between ruffe density (x) and round goby density (y; Figure 2a) was described by the equation y = 4177.0 – 516.2*ln(x). The coefficient of determination was 0.92. The theoretical value, in which both species can coexist at the same density, was 755 ind/ha (Figure 2a).

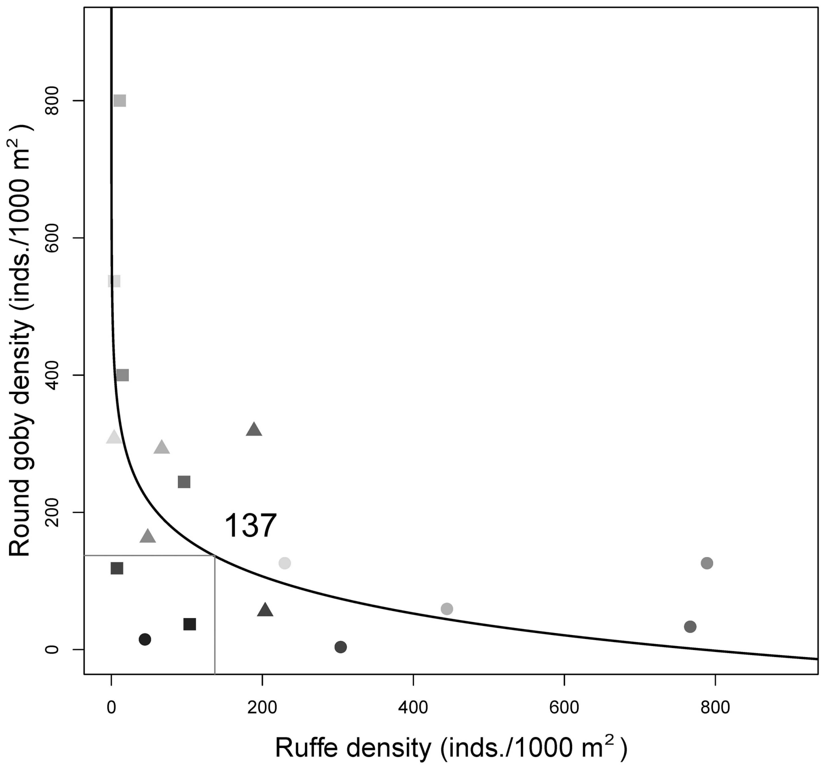

Figure 3. Logarithmic gillnet regression curves between round goby and ruffe density from different depths (the darker color the deeper strata) for years 2014 (square), 2016 (triangle) and 2019 (circle). The number on the curve provides the theoretical value of round goby and ruffe at which both species can coexist at the same density.

In gillnet catches, the density of ruffe in the period before the round goby invasion (1998–2008) was 400 ind/1000 m^2 approximately from all depths combined (Table 1). In 2014, when the round goby density in gillnet catches reached a peak (258 ind/1000 m^2), ruffe density decreased to 38 ind/1000 m^2. The difference in round goby and ruffe density was significant at this time ($t = -2.63$, $p = 0.02$, $df = 11$). In 2016, the decreasing trend of round goby density became evident in gillnet catches. In comparison with 2014, the round goby density decreased to 164 ind/1000 m^2 and ruffe density increased to 103 ind/1000 m^2 in 2016. The difference in round goby and ruffe density was not significant in 2016 ($t = -1.06$, $p = 0.31$, $df = 11$). The increasing trend in ruffe density and the opposite one in round goby density were found also in 2019 when round goby density decreased to 32 ind/1000 m^2, whereas the density of ruffe increased to 237 ind/1000 m^2. Density of ruffe was significantly higher than that of round goby in 2019 ($t = 5.03$, $p = 0.0005$, $df = 10$). The negatively correlated relationship between ruffe density (x) and round goby density (y) in gillnet catches (Figure 2b) was described by the logarithmic equation $y = 601.8 - 100.6*\ln(x)$. The coefficient of determination was 0.85. The theoretical density of both species, at which they could coexist at the same density was 120 ind/1000 m^2 (Figure 2b). The relationship between ruffe density (x) and round goby density (y), calculated from catches at separate depths, also showed the negatively correlated relationship: $y = 378.94 - 58.32*\ln(x)$ (Figure 3). The

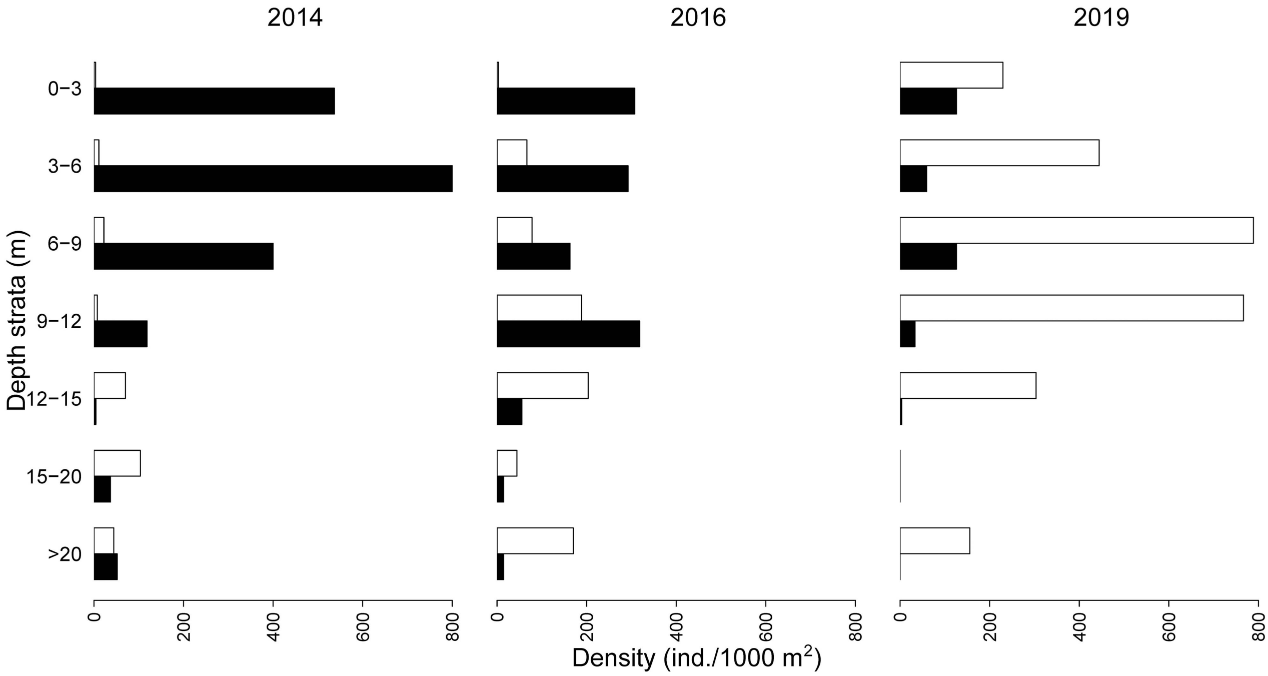

Figure 4. Depth distribution of round goby (black) and ruffe (white) in benthic gillnets in De Gijster Lake in 2014, 2016 and 2019.

coefficient of determination was 0.38 and the theoretical density of both species, in which they could theoretically coexist at the same densities, was 137 ind/1000 m^2 of the gillnets area in whole lake estimates, which is similar to the density calculated from the equation for averaged values of all years and depths (Figure 3).

The relationship between ruffe and round goby was significantly negative in 2014 (y = 123.825 − 18.057*ln(x+1), $F_{1,31}$ = 16.003, p < 0.001), but not in 2016 (y = 136.615 − 7.337*ln(x+1), $F_{1,34}$ = 0.283, p = 0.598), and in 2019 (y = 371.093 + 39.822*ln(x+1), $F_{1,31}$ = 3.048, p = 0.091). In 2016, when round goby density was generally high, ruffe utilized deeper habitats, where round goby density was lower. In 2019, when the general round goby density decreased significantly, ruffe shifted to the shallower habitats, where its coexistence with round goby was possible (round goby density close to 130 ind/1000 m^2 between 0–9 m calculated as a theoretical density equilibrium for both species, see above, Figure 4). The year 2016 was a transitional year for round goby density, where we saw that ruffe still prefer deeper habitats (12–20 m) but its density in shallower habitats (3–12 m) started to increase in comparison with 2014 (Figure 4).

Discussion

Invasive alien species are among the greatest threats to native species, often causing a decline in population numbers of the native species. For example, of 680 critically endangered animal species, invasive species were the sole cause cited for their extinction in 34 cases (Clavero and García-Berthou 2005). The management or eradication of invasive species could therefore theoretically support the recovery of the suppressed native species (Simberloff 2013). Castaneda et al. (2020), for instance, described that the successful removal of an invader led to recovery and stability of the native fish community. The successful removal of alien fishes resulted in an almost instantaneous increase in biodiversity in the South African Rondegat River (Weyl et al. 2014). Ecological recovery is more likely in animal populations and communities than in plant ones (Prior et al. 2018). In some cases, reducing invader density below some threshold may be almost as effective as total eradication (Green et al. 2014). Our data showed that significant natural decrease of invasive round gobies returns lost space for ruffe, a weaker competitor with similar environmental requirements.

Ruffe and round goby are both benthic species (Hölker and Thiel 1998) with highly overlapping diets. The diets of both species may include zooplankton, aquatic insects, fish eggs and larvae, and small fishes (Charlebois et al. 1997; Ogle 1998). In goby-ruffe competition experiments, gobies grew faster than ruffe, suggesting the superiority of round goby over ruffe at low resource levels (Bauer et al. 2007). Savino et al. (2007) found the round goby to be more aggressive than ruffe in laboratory conditions. Bauer et al. (2007) noticed that the non-native ruffe population declined significantly in Lake Huron in 2000, only 1 year after the establishment of round goby in the Thunder Bay River estuary. Two years later, round goby had replaced ruffe to become the most abundant fish in the system. The data presented in the study of Jůza et al. (2018) and partly also in this study showed that the impact of the round goby invasion on the native ruffe population was extremely fast. In 2014, only 2 years after the first capture of round goby in De Gijster Lake, ruffe was completely absent in beach seine catches and was very rare in gillnet catches. In 2016, the same picture of a very high density of round goby and the absence of ruffe was noted in seine catches. However, in gillnet catches the density of round goby decreased by almost two times in comparison with 2014. This decrease was reflected immediately in ruffe density, which increased almost three times in comparison with 2014. The decreasing round goby density, which was indicated in gillnet catches of 2016, was evident in 2019 when round goby gillnet density decreased five times in comparison to 2016 and ruffe density increased more than two times. Due to the round goby decrease, ruffe density in gillnet catches in 2019 was comparable with some years from the period before the round goby invasion (Table 1).

In De Gijster Lake, ruffe usually utilized deeper benthic habitats (below 12 m) in the years with high round goby density (2014 and 2016) and it was relatively rare in the shallowest littoral between 0 and 3 m (Figure 4), whereas round goby dominated the shallower zone down to 9 m (Vašek et al. 2015; Jůza et al. 2017, Figure 4). This is a complete change in comparison with 2008, when round goby was missing and ruffe was homogeneously distributed within the water column (Kubečka et al. 2009). Competition with round goby probably forced ruffe to move into deeper habitats, which was the reason for absence of ruffe in seine catches in 2014 and 2016. In the shallowest littoral, which was sampled by both techniques, density of ruffe was very low and the density of round goby was the highest in 2014. Ruffe density increased especially in deeper layers in 2016 (Figure 4), which were not accessible by beach seining. This is why the increasing capture of ruffe was observed only in gillnets and not in seines. Gillnets set at different depths therefore gave a better picture of the overall density of ruffe in the whole lake. In 2019, when density of round goby decreased significantly, ruffe started to utilize the shallowest littoral again, which was the case both in seine catches (Table 1) and also gillnets (Figure 4). Nevertheless, ruffe did not reach the before-invasion densities in seine catches, as observed in gillnet catch (see above) in 2019, probably because part of the space in shallow littoral was still utilized by round goby (Figure 4).

The data from De Gijster Lake showed that 750 ind/ha in seine catches and 137 ind/1000 m^2 in gillnet catches at combined depths are the theoretical values for coexistence of both species at the same density. A density increase of round goby above this level would mean a decrease in ruffe density, and an increase of round goby density to 2,000 ind/ha would mean the complete absence of ruffe in the seine catch. In the case of gillnet catches, a very similar theoretical value for coexistence of both species was found for the combined (Figure 2b) and non-combined depth densities (Figure 3). We are aware that these calculated densities, related specifically to the De Gijster Lake, are only theoretical and because we have data only from the beginning of the ruffe recovery period, we are not able to predict if the densities of both species will oscillate around estimated values over a long-term period.

It is also difficult to identify why the decline of round goby density occurred in De Gijster Lake only. Two other lakes in the Biesbosch area (Petrusplaat and Honderd en Dertig) continued to have a very high round goby density in 2019, whereas ruffe density was still very low (Jůza et al. 2020a, b). We can only hypothesize that there could be a connection to the trophic status of the lakes, because De Gijster Lake is more eutrophic than Petrusplaat and Honderd en Dertig Lakes. The position of De Gijster Lake (first lake in the cascade) can also play a role. Round gobies were introduced into the system from the Meuse River and De Gijster Lake was the first lake to be colonized. We unfortunately do not have data for the period 2011–2013, when the lakes were invaded. Nevertheless, if De Gijster Lake was the first to be invaded, the declining phase of the round goby cycle should theoretically occur in this lake earlier than in other two lakes. As the more oligotrophic lakes were invaded later, future years will show if the round goby decline in the post invasion phase (Strayer et al. 2017).

The results from De Gijster Lake indicate that there exists an interrelationship between densities of round goby and ruffe, two species with very similar benthic and niche requirements. During the initial invasion phase, when the round goby density increased rapidly, ruffe were suppressed to a very low level. Four years after the invasion, a decline of round goby density was observed, which was accompanied by an increase in ruffe density. This decline of round goby density was confirmed in 2019 and was followed by an immediate rapid increase of ruffe density, which reached almost before invasion values in gillnet catches (average over all depths, Table 1). Our observations indicate that at high round goby densities, ruffe is almost completely outcompeted from the system. Both the invasion of round goby and the partial recovery of ruffe were very fast. Ruffe was strongly suppressed by high round goby density but after its reduction, ruffe seems to be able to immediately fill the vacant space. Both round goby and ruffe are small fish species with relatively short life spans (usually not more than 6 years, Hölker and Thiel 1998; Sokolowska and Fey 2011) which probably enables an extremely fast turnover with very fast reaction of one species to changes in density of the other. We are aware that more years of data collection on declining round goby density are necessary, although this limited dataset shows the close interaction between the species.

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Author’s contribution

TJ – research conceptualization, sampling design, methodology, investigation, data collection, data analysis and interpretation, ethics approval, writing – original draft. PB – research conceptualization, sampling design, methodology, investigation, data collection, data analysis and interpretation, writing – reviewing and editing HAMK – financial support, research conceptualization, sampling design, methodology, writing – reviewing and editing DB, MČ, VD, JF, MH, LK, JK, MM, MP, MŘ, ZS, MŠ, MT, MV, LV, IV, AJW, JP – research conceptualization, sampling design, methodology, investigation, data collection, writing – reviewing and editing.

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Ethics and Permits

With submission of this article the authors have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects, and the authors are willing to share the original data and materials if so requested. The permission for this research was provided by Evides Water Company.

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