Collapse of the native ruffe (*Gymnocephalus cernuus*) population in the Biesbosch lakes (the Netherlands) owing to round goby (*Neogobius melanostomus*) invasion.

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Key words: Biesbosch National Park, De Gijster, invasive fish species, Honderd en Dertig, Petrusplaat, Rhine-Meuse delta

**Abstract**

We investigated the change in benthic fish communities in three artificial lakes of the Biesbosch area in the Netherlands between two time periods: before and after the invasion of round goby (*Neogobius melanostomus*). Native ruffe (*Gymnocephalus cernuus*), the dominant species in benthic gillnet and littoral beach seining catches before the invasion, almost completely disappeared in all lakes only two years after the invasion. We found a significant increase in 0+ perch (*Perca fluviatilis*) and, in some lakes, pikeperch (*Sander lucioperca*) abundance in gillnet catches after invasion. In the post-invasion period, the 0+ fish community was dominated by perch, and the older fish community was dominated by round goby. The species richness of 0+ fish increased in the post-invasion period owing to the invasion of gobiids. However, it did not change for older fish between periods. Our results clearly show that, owing to a similar benthic lifestyle and high niche overlap, ruffe was the only species negatively influenced by the round goby invasion. The competitive superiority of round goby over ruffe is so

strong that the once-dominant species of the overall benthic fish community collapsed after only a few years of coexistence.

## 1. Introduction

Biological invasions are an important component of global change in aquatic ecosystems (Sala et al. 2000; Bauer et al. 2007) and are considered one of the major threats to worldwide biodiversity (Allendorf and Lundquist 2003). The appearance of exotic species may lead to a significant reduction in the occurrence of native species or even to their extinction (Jermacz et al. 2015). Round goby (*Neogobius melanostomus*), of the family Gobiidae, is a benthic, euryhaline species that is native to central Eurasia including the Black, Azov and Caspian Seas (Verreycken et al. 2011), but it was transported via ballast water to different parts of Europe and North America (Corkum et al. 2004). In newly colonized regions, round goby spread rapidly and reached densities over 100 individuals per $m^{-2}$ in some habitats (Cooper et al. 2009). Reasons for the proliferation of this species include its tolerance to a wide range of environmental factors; broad diet; aggressive behavior; ability to spawn repeatedly during the spring, summer and autumn; parental care by males to facilitate successful recruitment; large body size compared to species with similar benthic lifestyles (Charlebois et al. 1997); and pelagic larvae and juveniles (Jůza et al. 2016), which are pumped from the ballast water by boats and spread easily. The most important concerns related to round goby invasions are the detrimental effects on native fish species through predation of eggs and juveniles (Chotkowski and Marsden 1999), competition for food and competition for shelter from predators or spawning substrates (Janssen and Jude 2001). In addition, round goby is included on the list of 100 worst European invasive species (www.europe-aliens.org), which suggests its high risk potential.

The effects of round goby invasion on the native ichthyofauna have been studied, especially in North America after its first invasion in 1990 and subsequent rapid spread. Observations in the St. Clair River area of the Great Lakes region suggest that populations of mottled sculpin (*Cottus bairdi*) and logperch (*Percina caprodes*) have declined since the appearance of round gobies (Janssen and Jude 2001; Balshine et al. 1995). Lauer et al. (2004) also found a significant decrease in the mottled sculpin and the johnny darter (*Etheostoma nigrum*) in trawl catches in Lake Michigan after round goby invasion. Riley et al. (2008) describe the collapse of the deep water demersal fish community in Lake Huron owing to the invasion of exotic species, including the round goby. Studies by Janáč et al. (2016) and van Kessel et al. (2016) are, to the best of our knowledge, the only two European studies in which the authors investigated the influence of round goby invasion on native ichthyofauna in fresh water field surveys. Janáč et al. (2016) found that colonization of the Dyje River (Czech Republic) by round goby had no apparent effect on native 0+ fish abundance, species richness or habitat utilization. Significant diet overlap was found between the round goby and European flounder (*Platichthys flesus*) in the Baltic Sea. Therefore, Karlson et al. (2007) proposed that the round goby had a negative influence on the commercially important flounder. Invasion of gobies into the River Meuse in the Netherlands resulted in the rapid decline of native river bullhead (*Cottus perifretum*), most likely owing to predation and competition for shelter and/or food (van Kessel et al. 2011, 2016).

Similar to many other European and North American water bodies, the River Rhine and, subsequently, the River Meuse have been invaded by many Ponto-Caspian species (van Kessel et al. 2016). After the first record of round goby in the Netherlands in 2004, many other individuals were caught at different locations in the western part of the country (van Beek 2006). Because round goby may be capable of altering the community structure of benthic fish (Balshine et al. 2005), possible impacts of invasion may include competition for food and space with fishes such as the European bullhead (*Cottus gobio*) and European flounder. These species could become less abundant and possibly disappear locally when the round goby reproduces successfully (van Beek 2006). The effects of biological invasions are best studied when alien species reach high densities and sufficient pre- and post- colonization data are available (van Kessel et al. 2016); thus here, we compared abundances of fish species and age groups (0+ and older), as well as species richness in three lakes in the Netherlands during two periods (before and after round goby invasion). All three artificial lakes are the part of the Biesbosch National Park, which is one of the largest national parks in the Netherlands. We hypothesized that the species richness would be lower in the period after the invasion. Additionally, it was hypothesized that the abundance of species that have a significant niche overlap with round goby would be much lower as a result of competition with the new invader. Understanding the effects of invasion by new species is especially important for the appropriate management of this nature sanctuary.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in Biesbosch National Park in the Netherlands (Fig. 1), which consists of three interconnected cascading lakes: De Gijster (51.6773 N, 4.8041 E, area: 320 ha, max. depth: 27 m), Honderd en Dertig (51.7347 N, 4.7744 E, area: 219 ha, max. depth: 27 m) and Petrusplaat (51.7572 N, 4.7745 E, area: 105 ha, max. depth: 15 m). The lakes were constructed during the 1970s, and they provide high-volume storage and serve as the first step in the treatment of river water for drinking water production by several waterworks in the southern and western parts of the Netherlands, e.g., the municipality Rotterdam and its wide surrounding area (Oskam and van Breemen 1992). The lakes were built as basin-shaped embanked impoundments along the River Meuse, with artificial sides of asphalt-concrete and clay bottoms. The moderately polluted but highly eutrophic water from the River Meuse is first pumped into De Gijster, followed by Honderd en Dertig, and finally, Petrusplaat (Oskam and van Breemen 1992). The lakes do not stratify during summer because the water is artificially mixed with strong aeration. The bottoms of the first two lakes are smooth, with approximately 10-20 cm of mud based on location. The bottom of the last lake, Petrusplaat, consists of chalk, resulting from a liming process. A littoral zone with macrophytes is almost completely missing in the lakes owing to the asphalt-concrete banks that extend to a depth of 6 meters. There is no fish stocking, and fishing is prohibited, although some poaching has been observed (Wagenvoort unpublished observations). The average summer water transparency is approximately 2.5, 3.5 and 4 m in De Gijster, Honderd en Dertig and Petrusplaat, respectively and the trophic status (phosphorus concentration) decreases from De Gijster towards Petrusplaat.

### 2.2. Fish sampling

Fish were sampled in August of 1998, 2000, 2002, 2008, 2014, 2015 and 2016 in all lakes, with the exception of 2015, when sampling in De Gijster was not performed owing to low water levels. Because round gobies were first found in all three lakes in 2012 using fyke nets (Kruitwagen 2013), the years between 1998 and 2008 are considered the pre-invasion period and the years from 2014 to 2016 are considered the post-invasion period.

The fish community was sampled with benthic gillnets and beach seining. The European sampling protocol (CEN 2005) was used for depth-stratified sampling, total effort based on lake surface area, and maximum depth sampled by gillnets. Depth layers sampled by benthic gillnets were 0-3, 3-6, 6-9, 9-12 and 15 m in the shallowest lake (Petrusplaat) and 0-3, 3-6, 6-9, 9-12, 12-18 and 20 m in Honderd en Dertig and De Gijster. 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 2005). Each multimesh gillnet was 30 m long and 1.5 m high. Two locations were sampled in each lake in each year, and three nets were deployed in every depth layer of each location. All nets were set approximately 2 hours before sunset and lifted after sunrise to cover the highest peaks of fish activity (Prchalová et al. 2010).

Because gillnets underestimate fish smaller than 40 mm (Prchalová et al. 2009), a 30 m long and 3 m deep beach seine net with a mesh size of 6 mm was used at night to capture the smallest 0+ fish in the shallowest littoral area. The area quantitatively sampled with one seine haul was 270 $m^2$. Age 0 and older fish were evaluated separately. Total effort was 7 seines per year in the smallest lake (Petrusplaat) and 10 seines per year in Honderd en Dertig and De Gijster; seines were performed around the perimeter of the lakes annually.

Captured fish were measured (standard length) and identified to the species level, and 0+ and older fish were distinguished based on scale annuli (roach, *Rutilus rutilus*) or otoliths (other fish species) from a subsample of 50 fish of a particular size group. For gillnets, fish abundance was expressed as number of fish per 1000 $m^2$ of gillnet netting per night and for beach seines, fish abundance was expressed as number of fish per hectare of water area. In our study, only the most abundant species were used for abundance comparisons between pre- and post-invasion periods. These abundant species included round goby, ruffe, perch, pikeperch and roach (Table 1).

### 2.3. Statistical analyses

Species richness (Hill number 0) was compared for periods before and after the invasion of round goby. Because of the relatively low number of samples, the relationship between number of species and number of individuals was plotted by rarefaction curves for observation and extrapolated up to the double value of its reference sample size. The significance of species richness differences between both periods was investigated by the overlap of 95% confidence intervals of the rarefaction curves. The analyses were carried out using the R package iNEXT (Hsieh et al. 2014) which is an update of the R code originally supplied as an Appendix in Chao et al. (2014).

Because our data were normally distributed ($p>0.05$; Kolmogorov-Smirnov test) a t-test was used for comparing fish abundance between pre- and post-invasion periods. Tests comparing fish abundance were performed separately for the most important species and age categories (0+ and older). All statistical analyses were performed in R 3.3.1 (R Core Team, 2016).

## 3. Results

### 3.1. Species composition of the catch

Twenty-five fish species were captured in all years and lakes (Table 1). After invasion, round goby was the most abundant gobiid. Other gobiid species that newly occurred together with round goby were tubenose goby (*Proterorhinus semilunaris*) and monkey goby (*Neogobius fluviatilis*). The densities of these species were very low in comparison to round goby (Table 1).

### 3.2. Abundance changes of dominant species between periods

Ruffe, which was abundant in catches using both methods during the pre-invasion period, practically disappeared immediately after invasion (Fig. 2). The decrease in ruffe abundance was significant in both sampling methods in all lakes for the 0+ and older categories catches (0+ ruffe: Petrusplaat: gillnet: t=2.5, df=82, p<0.05; seine t=4.9, df=45, p<0.001; Honderd en Dertig: gillnet: t=5.9, df=127, p<0.001; seine t=13.1, df=62, p<0.001; De Gister: gillnet: t=3.1, df=115, p<0.01; seine t=5.5, df=55, p<0.001; older ruffe: Petrusplaat: gillnet: t=3.1, df=82, p<0.01; seine t=2.3, df=45, p<0.05; Honderd en Dertig: gillnet: t=5.6, df=127, p<0.001; seine t=5.9, df=62, p<0.001; De Gister: gillnet: t=2.5, df=115, p<0.05; seine t=2.4, df=55, p<0.05; Fig. 3).

Another clear trend was the increase in 0+ perch abundance in the post-invasion period using both sampling methods; this trend was significant in Honderd en Dertig (gillnet: t=-8.3, df=127, p<0.001; seine t=-3.3, df=62, p<0.05) and De Gijster Dertig (gillnet: t=-8.8, df=115, p<0.001; seine t=-2.7, df=55, p<0.05) but not for seining in Petrusplaat (gillnet: t=-2.6, df=82, p<0.05; seine t=-0.8, df=45, p>0.05; Fig. 3). Additionally, the abundance of older perch increased significantly in the post-invasion period in all lakes in gillnets (older perch were rare in seine catches; Petrusplaat: gillnet: t=-2.7, df=82, p<0.01; Honderd en Dertig: gillnet: t=-7.4, df=127, p<0.001; De Gister: gillnet: t=-6.1, df=115, p<0.001; Fig. 3). Abundance of 0+ pikeperch increased in all lakes and both sampling techniques in the post-invasion period, except in seine catches in De Gijster, and this increase was usually significant, especially in gillnet catches (Petrusplaat: gillnet: t=-0.4, df=82, p>0.05; seine t=-2, df=45, p>0.05; Honderd en Dertig: gillnet: t=-4.1, df=127, p<0.01; seine t=-1.1, df=62, p>0.05; De Gister: gillnet: t=-3.4, df=115, p<0.01; seine t=2, df=55, p>0.05; Fig. 3). Older pikeperch were captured mainly in gillnets, and their abundance decreased significantly in all lakes in the post-invasion period (Petrusplaat: gillnet: t=2.7, df=82, p<0.01; Honderd en Dertig: gillnet: t=6.5, df=127, p<0.001; De Gister: gillnet: t=4.6, df=115, p<0.001; Fig. 3). Abundance of relatively abundant 0+ roach did not significantly change between periods (Petrusplaat: gillnet: t=-1.2, df=82, p>0.05; seine t=1.3, df=45, p>0.05; Honderd en Dertig: gillnet: t=0.1, df=126 p>0.05; seine t=0.2, df=62, p>0.05; De Gister: gillnet: t=0.9, df=,115 p>0.05; seine t=0.1, df=55, p>0.05; Fig. 3).

### 3.3. Species richness changes between periods

The number of 0+ fish species in the post-invasion period was higher than in the pre-invasion period in all lakes and with both methods (Fig. 4). The average numbers of species (over all lakes) were 9 and 13 in the gillnet and 10 and 13 in the seine in the pre-invasion and post-invasion period respectively. The significant difference of species richness between both periods, based on the overlap of confidence intervals, was found in all lakes in gillnets and in Honderd en Dertig in the seine nets (Fig. 4).

The number of older fish species between the pre-invasion and post-invasion periods was not significantly different in any lake or sampling method, based on the overlap of confidence intervals (Fig. 5). The average number of species (over all the lakes) was 10 in gillnets in both periods and 11 and 10 in seine in the pre-invasion and post-invasion periods respectively.

### 3.4. The lengths of 0+ perch in different years

The lengths of 0+ perch, which became the dominant species of gillnet catches, fluctuated especially during the post-invasion period. In 2014, the largest 0+ perch were observed in all lakes but since then, the length of 0+ perch has decreased (Fig. 6).

## 4. Discussion

To the best of our knowledge, our study provides the first empirical (i.e. field-based) evidence of an almost total collapse of the native ruffe population caused by round goby invasion. The comparison of the fish community before and after the invasion of round goby in the Biesbosch lakes showed that both 0+ and older ruffe almost completely disappeared after invasion in all of the investigated lakes. Age-0 perch and pikeperch, on the other hand, reached the highest abundances in the post-invasion period, especially in gillnet catches. Roach was practically uninfluenced by the round goby invasion, and their annual changes in abundance were within the frame of expected between-year variations (Jůza et al. 2014). An increase in species richness was found in the post-invasion period for 0+ fish but stayed practically unchanged between periods for older fish. Other non-native gobiid species were rare in the catches. These results corroborate those by Manné et al. (2013), who also found tubenose goby in very small densities compared to round goby in the Rhine basin, and thus indicate that round goby is the key gobiid influencing the system.

Ruffe was the most negatively affected by the round goby invasion, and also has the highest niche overlap. Ruffe and round goby are both benthic species (Charlebois et al. 1997, Hölker and Thiel 1998) with high diet overlap. The diets of both species may include zooplankton, aquatic insects, fish eggs and larvae and small fishes (Ogle 1998; Charlebois et al. 1997). Both species are highly fecund. Ruffe do not provide parental care, and they spawn adhesive eggs in the open water over hard substrates or plants (Ogle 1998). In contrast, round gobies lay adhesive eggs in cavities and defend their nests aggressively (Corkum et al. 1998). As both ruffe and round gobies are prolific, aggressive, and share habitat and diet preferences, there is potential for ecological interactions between the two species that affect their population dynamics (Savino et al. 2007). The rapid spread of round gobies may have affected the colonization of ruffe, which have spread far less rapidly in newly colonized areas (Savino et al. 2007).

In goby – ruffe competition experiment, gobies grew faster than ruffe, suggesting the superiority of round goby over ruffe at low resource levels (Bauer et. al. 2007). Even a short-term reduction in growth rate can result in decreased population sizes over longer time frames (Bauer et al. 2007). Thus, in the presence of round goby, ruffe may be unable to establish sizable populations in areas where round gobies are already abundant (Bauer et al. 2007). Bauer et al. (2007) also mention that ruffe may be relegated to less preferred environments, resulting in low populations. Savino et al. (2007) found the round goby to be more aggressive than ruffe in laboratory conditions and they also noted that field studies on interactions between round gobies and ruffe were necessary.

The potential influence of round goby on other fish species is described in the literature, especially from research in the Great Lakes region (Janssen and Jude 2001; Balshine et al. 1995, Lauer et al. 2004), but round goby – ruffe interactions in field conditions are rare. Bauer et al. (2007) mentioned that the non-native ruffe population declined significantly in Thunder Bay (Lake Huron) in 2000, only one year after the establishment of round goby in the estuary, and two years later, round goby had replaced ruffe as the most abundant fish. In our study, the impact of the round goby invasion on the native ruffe population occurred extremely fast. In 2014, only two years after the first capture of round gobies in the Biesbosch lakes, the round goby became the dominant species in the benthic habitat. Ruffe, which was the dominant benthic species for many years before invasion, had almost disappeared by that time. Similar to non-native ruffe collapse in Lake Huron, we show the rapid decline of native ruffe following round goby invasion. However, in our study system native ruffe have been present in the man-made lakes since their construction in 1970`s, whereas non-native ruffe in the Great Lakes region occurred in 1987 (Pratt et al. 1992), only three years before the first occurrence of round goby in 1990 (Jude et al. 1992). The impact of the round goby invasion is not therefore influenced by the age of the ruffe population. Diet analyses of ruffe from the Biesbosch lakes in the pre-invasion period showed that gammarids and chironomids were dominant components of their diet; usually, more than 10 individuals were present in the digestive tract of each individual, and only 2% of investigated ruffe had empty stomachs (Evides unpublished data). Gastropods, chironomids and *Dreissena* dominated round goby diet in 2014 and 2016, whereas in this post-invasion period, most of the very few captured ruffe had empty stomachs (51% ruffe with empty stomach, Evides unpublished data). This indicates that ruffe feeding is probably less efficient when it has to compete with round goby and could be the main reason the ruffe are disappearing. A study by Janáč et al. (2016) did not find any influence of round goby invasion on native fauna owing to the lack of benthic fish with a high niche overlap in the lower Dyje River, where the study occurred. In the Biesbosch lakes, ruffe was the only abundant species that was strictly benthic. The next typically benthic species present in the Biesbosch lakes were European bullhead and spined loach (*Cobitis taenia*); however, the catch rates for these species were too low in the pre-invasion period to evaluate changes in their abundance in the post-invasion period. In our system, round goby and ruffe utilize the same benthic habitat and feed on benthic organisms, and round goby is clearly the more successful competitor.

Another clear trend in the post-invasion period was the increase in 0+ perch abundance in gillnets and less so in seine catches. We did not find any positive connection between round goby invasions and abundance of 0+ perch in the scientific literature. In the case of the Biesbosch lakes 0+ perch, ruffe and pikeperch originate in the reservoir (Ketelaars unpublished observations) and are not usually pumped as larvae from the Meuse River, as many of other species are (Ketelaars et al. 1998). An extensive ichthyological survey of all lakes showed that the survival rate of 0+ perch into the next year of life is very low, and perch older than 0+ are rare (Kubečka et al. 2013).

A possible explanation of the low survival rate of 0+ perch could be their decreasing size in recent years (the late summer standard length of perch especially decreased in 2015 and 2016 in comparison with the pre-invasion period, Fig. 6). It is possible that size of 0+ perch can be influenced by the length of their co-existence with round gobies in reservoirs. Demersal 0+ yellow perch in Lake Michigan, for example, face a novel recruitment bottleneck caused by competition with round gobies, and 0+ yellow perch have obviously shifted their habitat and diet preferences (Houghton 2015). Because body size before the first winter of life significantly influences the probability of surviving into the second year of life (Sogard 1997), the survival rate can be low when there is much competition. It is very difficult to evaluate the influence of the round goby invasion on enhanced 0+ perch abundance but it seems that other factors, such as increased water transparency, could be responsible for this increase. The eggs of perch are unpalatable (Newsome and Tompkins 1985), and pikeperch males protect their nests (Lappalainen et al. 2003), so the clutches of these species are theoretically better protected against round goby predation in comparison with ruffe. This could also be a reason why ruffe is the only percid species negatively influenced by round gobies. Another clear trend was the decrease in abundance of older pikeperch in the post-invasion period in all of the lakes. This significant decline is most likely unrelated to the invasion of round goby because the decreasing trend started before the round goby invasion. Like perch, 0+ pikeperch have a survival rate of almost zero, and the pikeperch population of all lakes is represented by 0+ and few fish more than 10 years old, which are gradually disappearing from the population (middle-aged pikeperch are completely missing, Jůza et al. 2017). The reason for this decrease in older pikeperch is that these old pikeperch die out and are not replaced.

Invasive species are important drivers causing losses in global biodiversity (Sala et al. 2000). We therefore compared the number of fish species reached in all lakes by both sampling methods. For 0+ fish the number of species increased in the post-invasion period in all lakes, in both sampling methods. This increase was caused especially by the occurrence of three invasive gobiid species in the post-invasion period and by the disappearance of any species formerly present. A different situation occurred in the older fish community. Although three invasive gobiids occurred in the post-invasion period, the number of species stayed practically unchanged between both periods and with both sampling techniques. In the pre-invasion period adult benthic species such as bullhead, gudgeon (*Gobio gobio*) and flounder occurred in the fish community, however these species were missing in the post-invasion period. Abundance of these benthic species was very low (Table 1), so we do not have enough data to perform any deeper analyses. However, disappearance of these species in the post-invasion period can indicate a negative influence of the occurrence of round goby.

Our study provides clear evidence that concern about native fish fauna lost after a round goby invasion are justified and that a formerly abundant species with a similar lifestyle became marginalized shortly after invasion. The exact same trend was observed in all three investigated lakes. In Europe, the invasion of round goby into systems with a specific benthic fish community poses, first of all, danger to all species with significant niche overlap. Additionally, because round goby is able to outcompete common and ecologically unexacting species such as ruffe very quickly, it is probable that other ecologically susceptible benthic species, such as bullhead, spined loach, gudgeon and stone loach (*Barbatula barbatula*), may also decline in European waters owing to round goby spreading in the future.

## 5. Acknowledgements

We thank Zdeněk Prachař, Kateřina Soukalová, Afra Wagenvoort and Frank Jonker for their help with the data collection; Leslie Tse for English correction; Evides Water Company for financial support; and two anonymous referees for valuable comments that helped improve the manuscript. This work has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 677039" project CLIMEFISH and by program COST-CZ under contract number MSMT-LD15021. This publication reflects the views of only the authors, and the Commission cannot be held responsible for any use that may be made of the information contained therein.

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**Figure caption:**

Figure 1: A map of the Biesbosch lakes (1 - Petrusplaat, 2 - Honderd en Dertig, 3 - De Gijster) at the confluence of the Rhine and Meuse rivers and its location within the Netherlands.

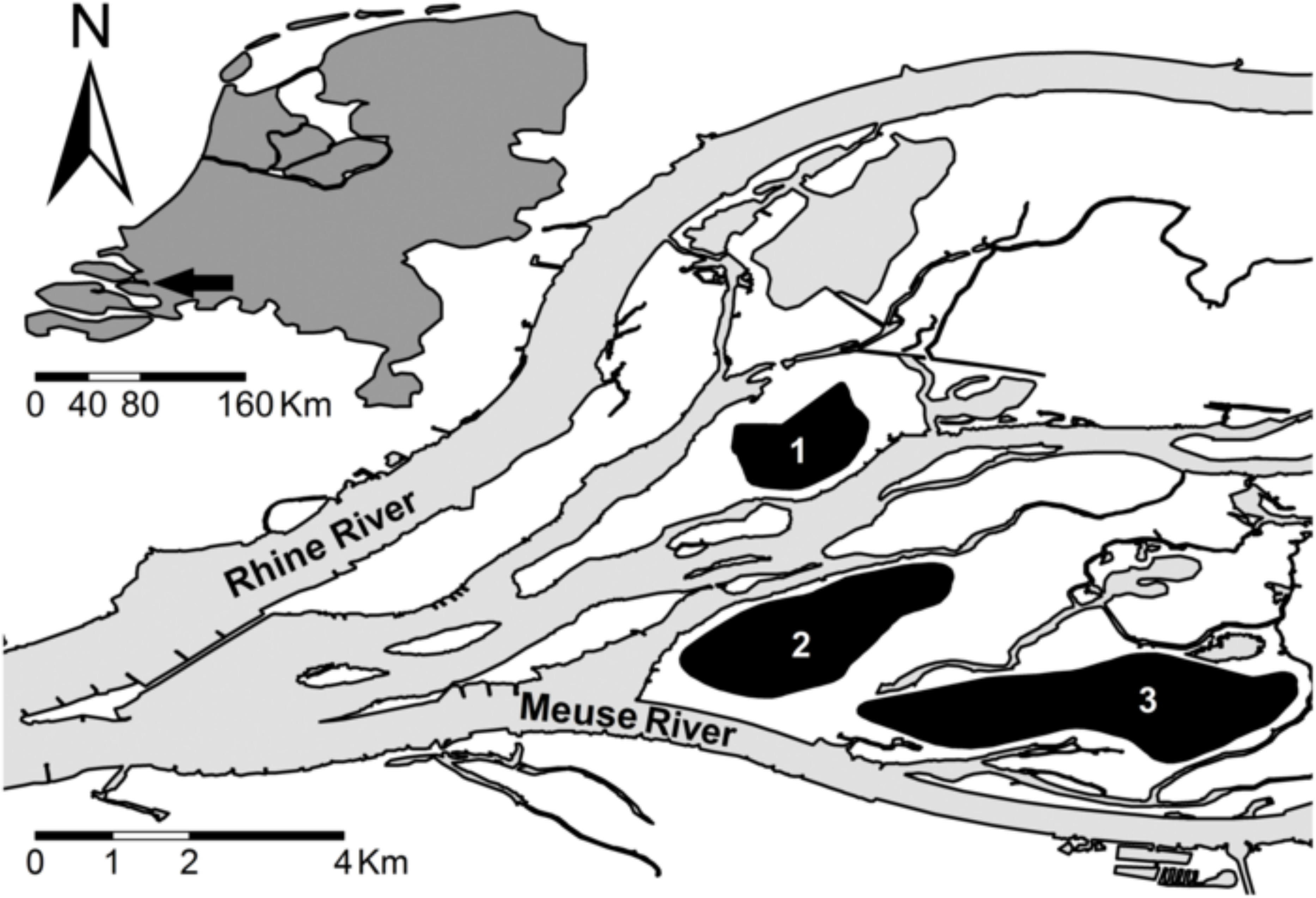
Figure 2: Abundance of ruffe (squares) and round goby (circles; 0+ and older fish are combined) in different years in Petrusplaat, Honderd en Dertig and De Gijster, estimated by gillnetting and seining. Mean values and standard deviations are shown. NA means not sampled. Black vertical lines separate pre-invasion and post-invasion periods.

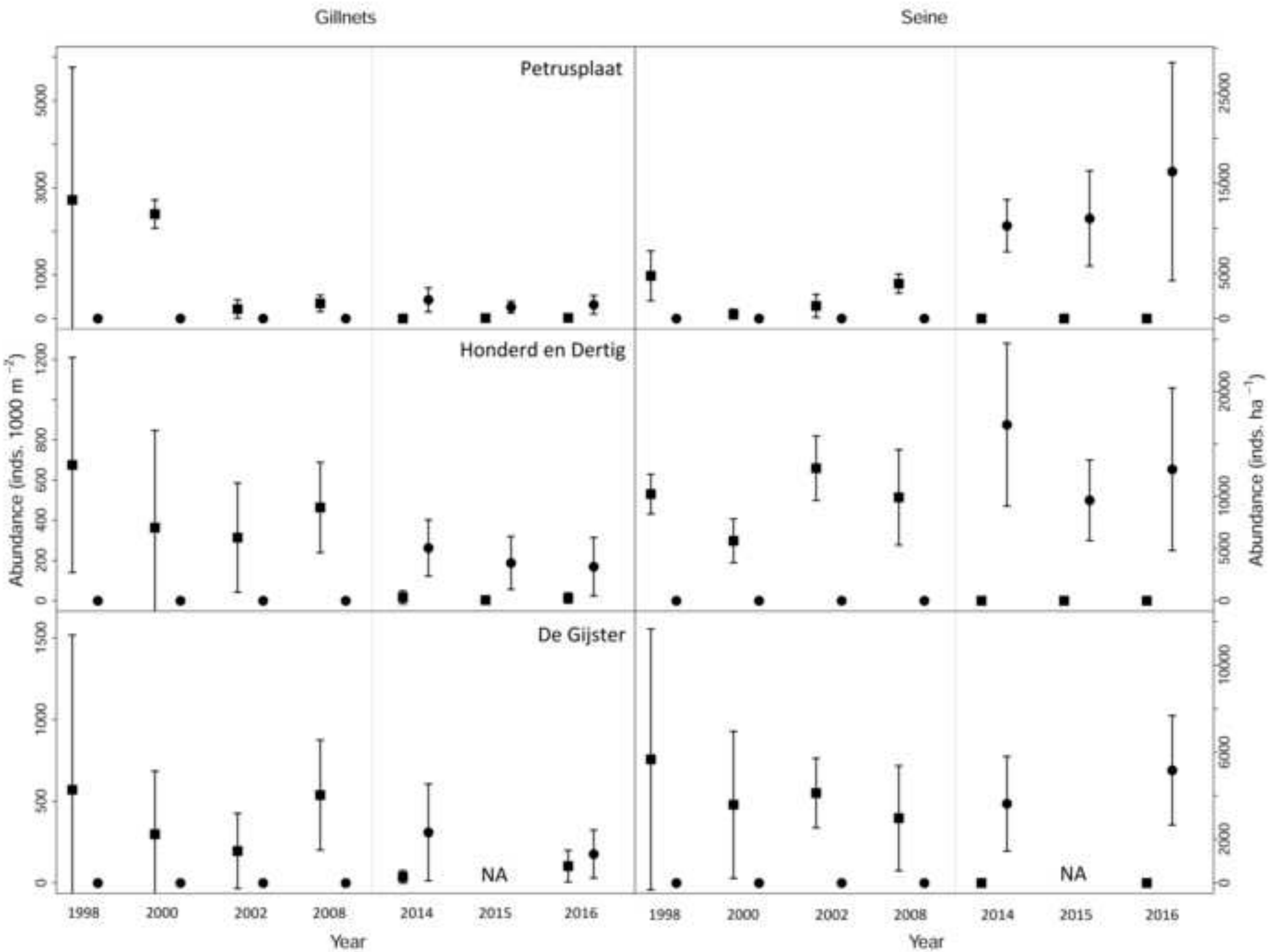
Figure 3: Abundance of 0+ and older fish of dominant species in pre-invasion and post-invasion periods in Petrusplaat, Honderd en Dertig and De Gijster, estimated by gillnetting and seining. Mean values and standard deviations are shown. Significance of abundance comparison between pre- and post-invasions periods is shown by star(s).

Figure 4: Sample-based rarefaction (solid line) and extrapolation (dashed line, up to the double value of its reference sample size) with 95% confidence intervals (shaded area) of species richness for 0+ fish in gillnets and seine samples before (line with triangles representing reference sample) and after (line with circles representing reference sample) the invasion of round goby.

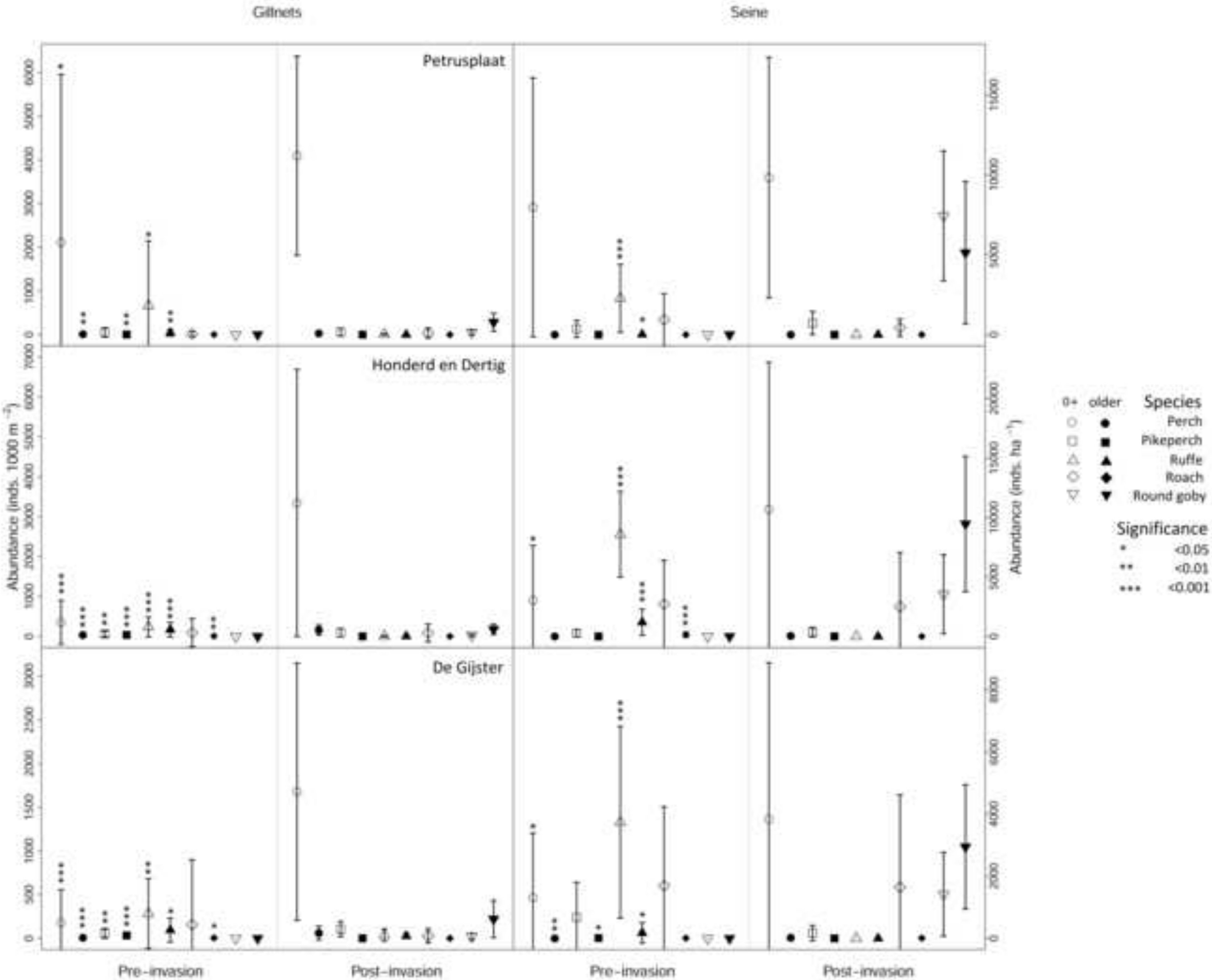
Figure 5: Sample-based rarefaction (solid line) and extrapolation (dashed line, up to the double value of its reference sample size) with 95% confidence intervals (shaded area) of species richness for older fish in gillnets and seine samples before (line with triangles representing reference sample) and after (line with circles representing reference sample) the invasion of round goby.

Figure 6: Standard lengths of 0+ perch captured by both sampling techniques in different years and lakes. Mean values and standard deviations are shown.

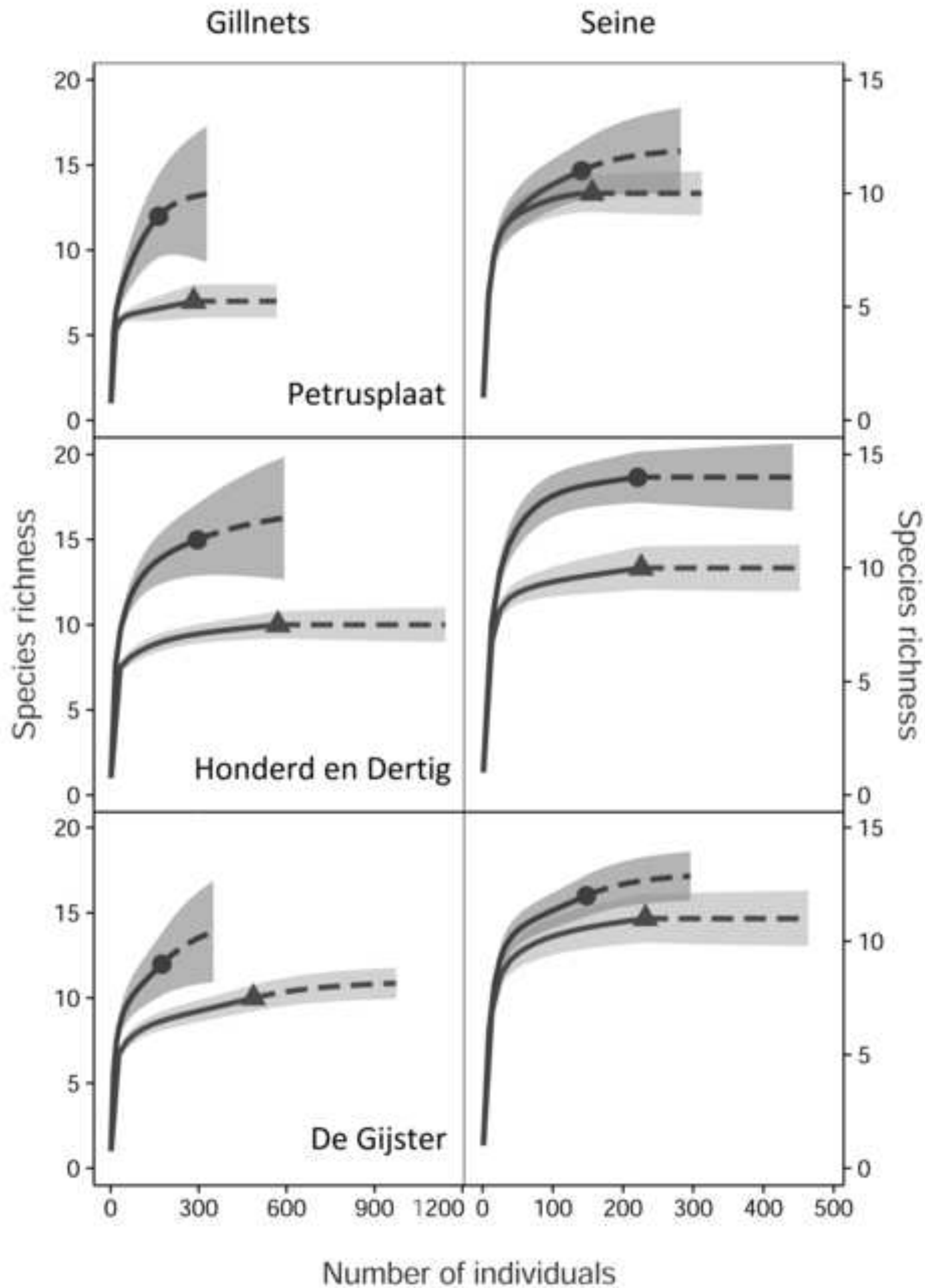

N
0 40 80 160 Km
Rhine River
Meuse River
1
2
3
0 1 2 4 Km

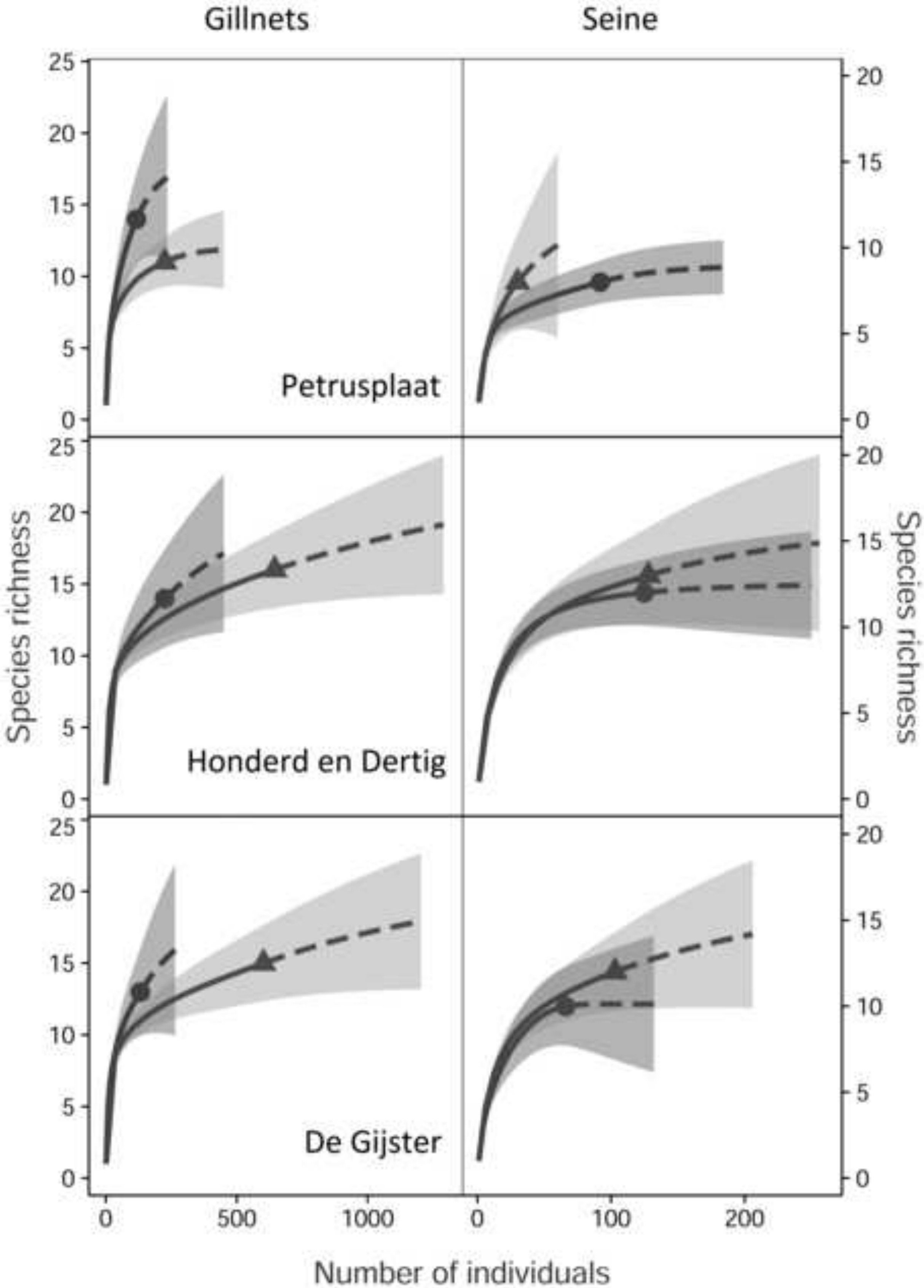


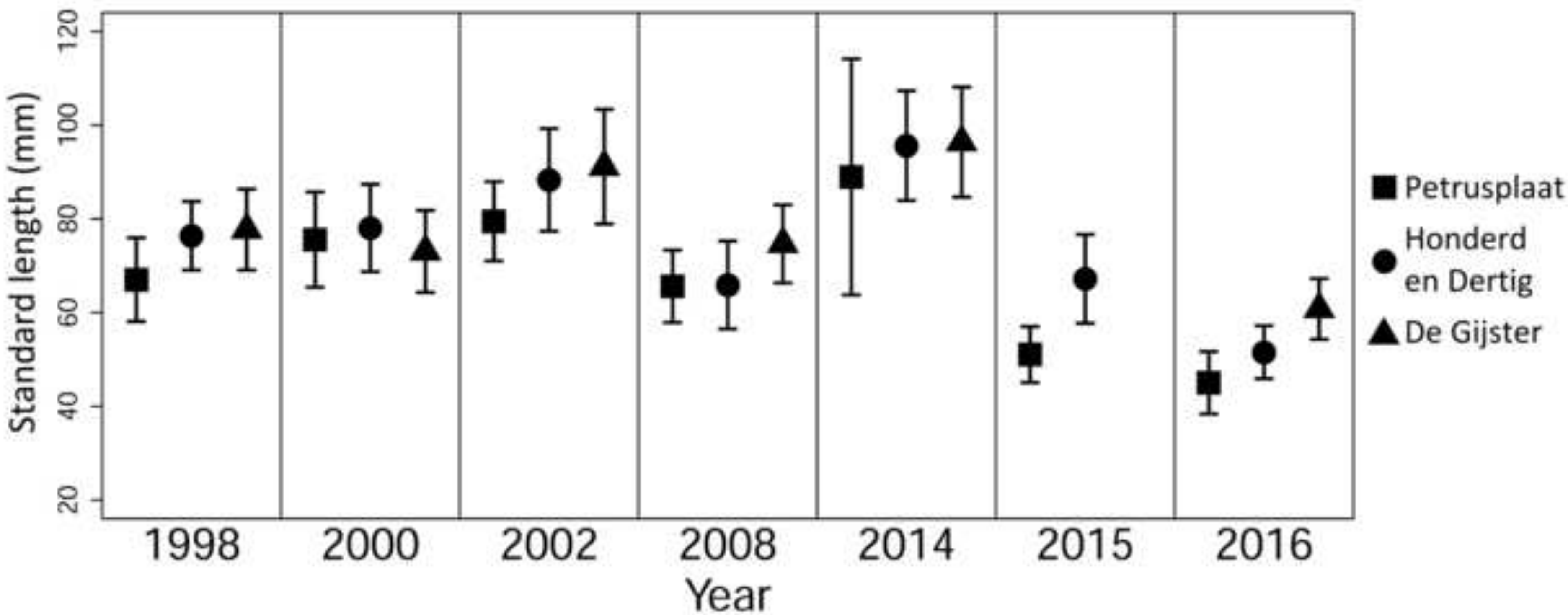
Gillnets
Seine
Petrusplaat
Honderd en Dertig
De Gijster
NA
NA
Abundance (inds. 1000 m $^{-2}$)
Abundance (inds. ha $^{-1}$)
1998
2000
2002
2008
2014
2015
2016
Year
Year



Gillnets
Seine
Petrusplaat
Honderd en Dertig
De Gijster
Abundance (inds. 1000 m⁻²)
Abundance (inds. ha⁻¹)
Pre-invasion
Post-invasion
Pre-invasion
Post-invasion
0+ older Species
Perch
Pikeperch
Ruffe
Roach
Round goby
Significance
* <0.05
** <0.01
*** <0.001


Gillnets
Seine
Petrusplaat
Honderd en Dertig
De Gijster
Species richness
Species richness
Number of individuals
0
5
10
15
20
0
300
600
900
1200
0
100
200
300
400
500


Gillnets
Seine
Petrusplaat
Honderd en Dertig
De Gijster
Species richness
Species richness
Number of individuals
0
5
10
15
20
25
0
500
1000
0
100
200


Standard length (mm)
120
100
80
60
40
20
1998
2000
2002
2008
2014
2015
2016
Year
Petrusplaat
Honderd en Dertig
De Gijster

| English name | Scientific name | Mean abundance in gillnets (inds. 1000 $m^{-2}$) | Mean abundance in seines (inds. $ha^{-1}$) |
| --- | --- | --- | --- |
| Perch | *Perca fluviatilis* | 1303 | 5784 |
| Pikeperch (Zander) | *Sander lucioperca* | 76 | 738 |
| Ruffe* | *Gymnocephalus cernuus* | 785 | 5600 |
| Roach | *Rutilus rutilus* | 71 | 1688 |
| Ide | *Leuciscus idus* | 0.2 | 153 |
| Asp | *Leuciscus aspius* | 0.2 | 7 |
| Bleak | *Alburnus alburnus* | 0.1 | 8 |
| Bream | *Abramis brama* | 5 | 1183 |
| Round goby** | *Neogobius melanostomus* | 277 | 9980 |
| Tubenose goby** | *Proterorhinus semilunaris* | 0.5 | 382 |
| Monkey goby** | *Neogobius fluviatilis* | 0.7 | 11 |
| Three-spined stickleback | *Gasterosteus aculeatus* | 0.9 | 236 |
| Spined loach | *Cobitis* sp. | 0.1 | 9 |
| Houting | *Coregonus sp.* | 0.8 | 1 |
| Smelt | *Osmerus eperlanus* | 5 | 217 |
| Flounder | *Platichthys flesus* | 0.1 | 0 |
| Carp | *Cyprinus carpio* | 0.1 | 0 |
| Eel | *Anguilla anguilla* | 19 | 10 |
| Bullhead | *Cottus gobio* | 0.1 | 5 |
| Thicklip grey mullet | *Chelon* sp. | 0 | 0.2 |
| Rudd | *Scardinius erythrophthalmus* | 0.1 | 0.4 |
| White bream | *Abramis bjoerkna* | 0.6 | 0.8 |
| Crucian Carp | *Carassius carassius* | 0 | 0.2 |
| Nase | *Chondrostoma nasus* | 0 | 0.2 |
| Gudgeon | *Gobio gobio* | 0.01 | 0 |

Table 1: List of species captured in the Biesbosch lakes during all years of sampling together with average (over all lakes and years) abundances from gillnet and seine catches. * abundance average of the pre-invasion period only. ** abundance average of the post-invasion period only.