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Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead

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Received: 14 July 2015 / Accepted: 22 January 2016 / Published online: 14 March 2016

Handling editor: Vadim Panov

Abstract

Invasions by alien species may cause a decline in populations of vulnerable protected species through interference and resource competition. During the last decade, four invasive goby species of Ponto-Caspian origin have displayed rapid dispersal in The Netherlands. High densities of these species have been recorded in large rivers and hydrologically connected water bodies such as canals and floodplain lakes. In the River Meuse, alien tubenose goby (*Proterorhinus semilunaris*), round goby (*Neogobius melanostomus*) and bighead goby (*Ponticola kessleri*) occupy similar habitat to native, protected river bullhead (*Cottus perifretum*), i.e., coarse substrates with large pebbles, and groyne stones and riprap that protect river banks against erosion and preserve river channels. In the years following the arrival in 2011 of *N. melanostomus* in the River Meuse, a rapid decline in native *C. perifretum* average density from twenty to one individual per 100 m² was observed, most likely due to predation and competition for shelter and/or food. *C. perifretum* density also declined at sites colonized by *Ponticola kessleri* and/or *Proterorhinus semilunaris* only. However, when compared to sites where *N. melanostomus* was present, *C. perifretum* density remained relatively high. Similar effects on other native benthic fish species may occur in the near future due to the presence of alien gobies. Compliance with ecological status objectives relating to the European Habitats Directive and Water Framework Directive may not be achievable due to the loss of protected and endangered native fish species in areas invaded by alien gobies.

Key words: benthic fish, competition, European Habitats Directive, native species, non-native species, Ponto-Caspian gobiids, River Meuse, Water Framework Directive

Introduction

Biological invasions by alien species are considered a threat to native biodiversity due to the potential localized disappearance or even extirpation of species as a result of interference and resource competition (Van der Velde et al. 2006; Simberloff 2013). Protected species are often vulnerable to invasions by alien species. However, the impacts of invasions are context dependent and, in many cases, remain unknown. The effects of biological invasions are best studied when high densities of

alien species are reached and sufficient pre- and post-colonization data from invaded and control sites are available for statistically sound effect assessment.

Similarly to many other European and North-American water bodies, the River Rhine, and subsequently the River Meuse, has been invaded by many Ponto-Caspian species. Dispersal of these species is mostly facilitated by the interconnection of river basins by canals resulting in new invasion corridors (Bij de Vaate et al. 2002; Leuven et al. 2009) and by transport in the ballast water of sea

going vessels (Wonham et al. 2000; Corkum et al. 2004). Decades of water pollution and habitat degradation prior to the 1970s resulted in a severe depletion of macro-invertebrate and fish communities in the Dutch rivers Rhine and Meuse (Lelek 1987; Lelek and Köhler 1990; Van den Brink et al. 1990, 1991; Leuven et al. 2011). Water quality improvements resulting from waste water treatment initiated during the period 1970–1986 led to a (re)colonization of these rivers by macro-invertebrates and fish. However, the so-called Sandoz disaster in 1986 led to the extermination of almost all aquatic life in the River Rhine downstream of the Sandoz agrochemical storehouse in Schweizerhalle, near Basel in Switzerland (Plum and Schulte-Wülwer-Leidig 2014). As a result of this catastrophic event, a number of programmes aimed at the ecological rehabilitation of the Rivers Rhine and Meuse were launched (ICPR 1987; 1994; Hendriks et al. 1997; Nienhuis et al. 2002). In addition, because of water pollution control measures initiated in the 1990s, further improvements in water quality occurred, leading to signs of recovery in the native aquatic fauna (Admiraal et al. 1993). However, the aquatic fauna currently (re)colonizing Dutch rivers is dominated by alien species featuring high densities of Ponto-Caspian macroinvertebrates (Van den Brink et al. 1991, 1993; Tittizer et al. 1994; Ketelaars et al. 1999; Bij de Vaate et al. 2002; Van der Velde et al. 2002; Leuven et al. 2009) that preceded and are now facilitating invasions by Ponto-Caspian goby species. The colonization of Dutch rivers by Ponto-Caspian species accelerated following the opening of the Main-Danube canal in 1992, connecting the River Danube with the River Rhine (Leuven et al. 2009). These invasions can lead to an ‘invasional meltdown’ (cascade effect) as each invasion of a Ponto-Caspian species facilitates the colonization of other alien species from the same region (Simberloff 2013; Gallardo and Aldridge 2015).

During the last decade, several Ponto-Caspian, bottom dwelling fish species have colonized the Rhine and Meuse river systems in the Netherlands, i.e. tubenose goby (*Proterorhinus semilunaris*, present since 2002), round goby (*Neogobius melanostomus*, present since 2004), bighead goby (*Ponticola kessleri*, present since 2007) and monkey goby (*Neogobius fluviatilis*, present since 2008) (Soes et al. 2005; Van Beek 2006; Van Kessel et al. 2009). All these species first appeared in the River Rhine and dispersed rapidly to its tributaries and associated canals. The River Meuse, which is connected to the River Rhine by several canals,

has been colonized since 2008 by *Proterorhinus semilunaris*. Three other goby species arrived in 2011 in the River Meuse (i.e., *N. melanostomus*, *Ponticola kessleri* and *N. fluviatilis*). At present, large parts of almost all Dutch rivers and canals are characterized by high densities of the aforementioned Ponto-Caspian gobiid species (Van Kessel et al. 2013; Cammaerts et al. 2012).

Several of these alien invasive gobies have earlier been linked to the decline and/or disappearance of mainly bottom dwelling native fish species in Europe and the North American Great Lakes, i.e. stone loach (*Barbatula barbatula*), European bullhead (*Cottus gobio*), slimy sculpin (*C. cognatus*), mottled sculpin (*C. bairdi*), spoonhead sculpin (*C. ricei*), Johnny darter (*Estheostoma nigrum*), common logperch (*Percina caprodes*), European flounder (*Platichthys flesus*) and Northern whitefin gudgeon (*Romanogobio belingi*) (Jude et al. 1995; Dubs and Corkum 1996; Janssen and Jude 2001; Jurajda et al. 2005; Balshine et al. 2005; Von Landwüst 2006; Karlson et al. 2007). However, discussion of causal factors has been based on merely anecdotal observations that may possibly be confounded by other environmental factors. Detailed quantitative studies are limited to analyses of the effect of *N. melanostomus* on *C. bairdi* in Lake Michigan, North America. In these studies populations of *C. bairdi* rapidly declined after the arrival of *N. melanostomus* (Janssen and Jude 2001; Lauer et al. 2004).

In Dutch rivers, true bottom-dwelling native fish species, especially those that prefer stony substrates, are relatively scarce. Only river bullhead (*C. perifretum* = *C. gobio* pro parte; see Freyhof et al. 2005) and *B. barbatula* occur in high densities in some river sections, whereas only an isolated population of brook bullhead (*C. rhenanus* = *C. gobio* pro parte; see Freyhof et al. 2005) is present in the upper stretches of the River Geul, a tributary of the River Meuse. Both *Cottus* species are protected under the European Habitats Directive (HD; Annex II; 92/43/EEC) and are important target species according to the European Water Framework Directive (WFD; 2000/60/EC). The species are primarily present in shallow habitat with hard stony substrates, such as pebbles and man-made deposits of basalt stones and cut rocks at groynes and river banks. Since these substrates are also preferred by three Ponto-Caspian goby species, i.e., *Proterorhinus semilunaris*, *N. melanostomus* and *Ponticola kessleri*, it may be supposed that colonization of the River Meuse by these invasive fish species will affect the presence and densities of *C. perifretum* and *C. rhenanus*,

Table 1. Overview of the survey sites, site coordinates (WGS 84) and the number of transects surveyed per site per year. Site numbers correspond with figure 1 (For more details see Supplementary materials: Table S1).

Site number	Site coordinates		2007	Number of surveyed transects per site per year				
	Latitude, °N	Longitude, °E		2009	2010	2011	2012	2014
1	51°83'65.73"	5°80'86.72"		3			4	
2	51°80'57.82"	5°64'89.68"		2			2	
3	51°77'63.50"	5°70'81.17"				5	3	3
4	51°75'37.71"	5°87'53.28"				3	2	
5	51°71'75.28"	5°92'94.86"				3	4	3
6	51°66'72.14"	5°96'48.77"		2			3	
7	51°66'75.60"	5°96'57.78"		2			2	
8	51°59'50.34"	6°02'78.32"				3	3	3
9	51°50'97.17"	6°16'60.43"				3	3	3
10	51°35'28.30"	6°13'86.91"		4			4	
11	51°33'53.60"	6°11'75.47"		3			2	
12	51°23'29.65"	6°00'17.50"				3	3	3
13	51°09'48.95"	5°83'50.41"	1				1	
14	51°06'82.57"	5°83'36.80"	4				4	
15	50°90'66.70"	5°71'78.55"			3		3	6

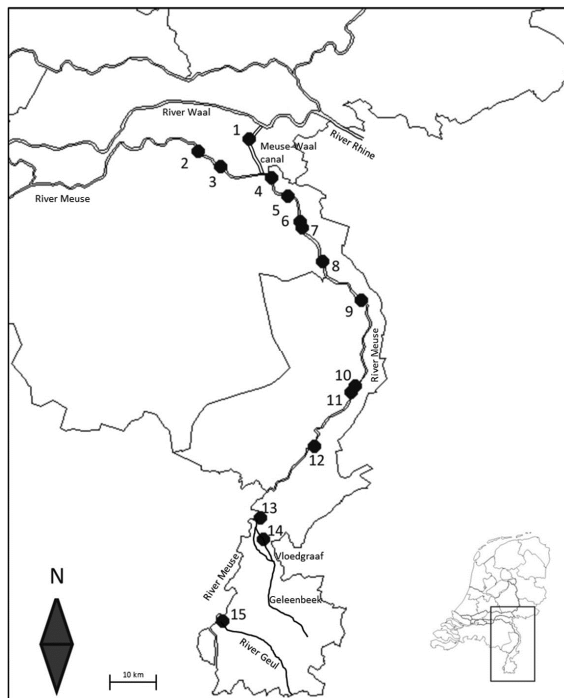


Figure 1. Geographical locations of the fish survey sites in the River Meuse and its tributaries in the Netherlands.

similarly to the North American Great Lakes where declines of *Cottus* species occurred after the arrival of *N. melanostomus*. These potential effects on native species may have implications for the achievement of ecological status objectives set by the HD and WFD.

Ecological survey data of fish assemblages in the littoral zones of the River Meuse and its tributaries were obtained from sites featuring

C. perifretum populations and included surveys carried out before and after colonization by alien gobies. The available data allowed the reconstruction of the process of colonization by Ponto-Caspian gobies and a statistical analysis of their impact on native *C. perifretum*. We hypothesized that invasive gobies outcompeted protected *C. perifretum*. As a result, a large increase in densities of Ponto-Caspian gobies is expected to coincide with a decline in *C. perifretum* densities.

Materials and methods

Study site

The present study was conducted at 15 sites in the River Meuse and its tributaries in The Netherlands during 2007–2014 (Figure 1; Table 1 and Table S1). Twelve sites were located along banks of the River Meuse and three sites in its tributaries, i.e., the River Geul, and the Geleenbeek and Vloedgraaf (both lowland streams). Substrates were dominated by hard stony structures, mainly large pebbles (up to 15 cm in diameter), riprap, polygonal cut rocks and basalt stones (e.g., in groynes). The discharge of the River Meuse varies between 100–500 m³ sec⁻¹ throughout the year on average (De Wit et al. 2007). During summer and other dry periods, discharge may be very low and water velocity in the River Meuse is near to 0 m sec⁻¹ as a result of dam and weir management in impounded sections in order to maintain the standard river water level for shipping. Passing vessels create dynamic currents in littoral zones (e.g., shipping induced water displacement and waves). Water discharge in the three tributaries is considerably lower than in the River Meuse (up to maximum

15 m³ sec⁻¹). Water velocity is always higher than 0.15 m sec⁻¹ in the River Geul and both lowlands streams because of the smaller channel dimensions relative to the River Meuse.

Fish surveys

Fish assemblages were monitored in multiple independent transects during daytime between July and September from 2007 to 2012 in the littoral zones of the River Meuse and its tributaries (Table 1). This formed part of the legally required ecological status assessments relating to the WFD and some environmental impact assessments. In 2012, all transects at the 15 sites were surveyed. Prior to 2012 all sites were surveyed once, but the sampling year varied, i.e., two sites were surveyed in 2007, six in 2009, one in 2010 and six in 2011. This data was used to investigate the effect of colonization of the sites by Ponto-Caspian gobies on *C. perifretum*. In addition, six of the 15 sites were also surveyed in 2014, allowing analysis of fluctuations in densities of the observed species over the years 2012–2014.

According to Flotemersch et al. (2011) multiple smaller transects per site were sampled. The number of replicate transects per site varied between two and five (Table 1). All transects consisted of a similar type of microhabitat (i.e., shallow littoral zones with riprap and groyne stones) and were sampled at similar water level (i.e., the standard water level maintained in impounded sections of the River Meuse). The length, width and depth of transects varied between 25–505 m, 2–4 m and 0.1–1.0 m, respectively. The entire transect area was sampled at each site. Fish surveys were conducted using a suitable electrofishing method for sampling small sized fish species in shallow littoral river habitats (handheld equipment: DEKA Lord 3000, Mühlenbein DEKA Gerätebau, Marsberg, Germany). After catching, fish were visually identified, counted and released. All fish surveys and identifications were performed by the same fisherman, reducing interpersonal variability.

Data analysis and statistics

The overall effect of the presence of *N. melanostomus* on *C. perifretum* was compared by fitting a linear mixed-effect model with a log-link function. The analysis aimed to determine whether the density of *C. perifretum* in the River Meuse changed between the periods before and after the invasion of *N. melanostomus*. Surveyed transects at a particular sample site functioned as replicates in

the model. The longitudinal arrangement of sites in the River Meuse (spatial effect) of different sites was included as a random factor, whereas the effect of the different sampling years before 2012 was set as a crossed random effect. Since *Ponticola kessleri* and *Proterorhinus semilunaris* occurred on sites with *N. melanostomus*, the pooled density of the first two species was set as an additional random effect. *C. perifretum* density was set as the dependent variable and log-transformed by $y = \log_{10}(x+1)$ in an attempt to achieve normality. Survey year and their interaction were set as fixed factors independent of whether a site was or was not invaded by *N. melanostomus*. Additional models were constructed to investigate whether the densities of *C. perifretum* between two sampled years significantly differed. In these models, sampling year was set as a fixed factor and the spatial effect of sites was included as a random factor. Likewise, models were constructed to investigate whether the densities of *Ponticola kessleri* and *Proterorhinus semilunaris* between two sampled years significantly differed between sites that were either colonized or not colonized by *N. melanostomus*.

Assumptions of normality were checked by residual analysis and by a Shapiro test of normality. Models were fitted with the lmer function in the lme4 package (Bates et al. 2011). To determine the effects of fixed factors, a likelihood ratio test was used to compare models with and without the variable of interest (Crawley 2007). All statistical analyses were performed in R version 2.15.0 (R Development Core Team).

Results

Effect of Ponto-Caspian goby colonization

Except site 13, *C. perifretum* was present at each site during the first year of sampling. During the 2012 survey, *Proterorhinus semilunaris* and *Ponticola kessleri* were present at nine and ten sites, respectively. Even though *N. melanostomus* was only present at six sites, the species reached the highest maximum densities of all alien gobies sampled and was therefore thought to have the largest potential impact on *C. perifretum*. *N. fluviatilis* was caught in very small numbers and was therefore not analyzed.

In 2012 twelve sites were colonized by invasive gobies, three remained uncolonized allowing a comparison between colonized and uncolonized locations (Table 2). Colonization of sites by *N. melanostomus* had a significant effect on

Table 2. Average densities of bighead goby (*Ponticola kessleri*), tubenose goby (*Proterorhinus semilunaris*), round goby (*Neogobius melanostomus*) and river bullhead (*Cottus perifretum*) during the years of survey (Site numbers correspond with Figure 1 and Table 1).

Site number	Year of survey	Average densities (# 100 m ⁻² ± SE)			
		<i>Ponticola kessleri</i>	<i>Proterorhinus semilunaris</i>	<i>Neogobius melanostomus</i>	<i>Cottus perifretum</i>
1	2009	0.0	0.0	0.0	8.0 ± 3.5
	2012	1.5 ± 1.0	0.0	16.0 ± 2.3	0.5 ± 0.5
2	2009	0.0	0.0	0.0	9.0 ± 1.0
	2012	13.0 ± 5.0	1.0 ± 1.0	1.0 ± 1.0	0.0
3	2011	8.0 ± 4.5	0.0	0.0	4.4 ± 2.9
	2012	23.3 ± 2.9	3.3 ± 3.3	71.3 ± 37.8	0.0
	2014	3.6 ± 1.0	0.0	37.9 ± 4.3	0.0
4	2011	22.0 ± 2.0	3.0 ± 3.0	0.0	22.0 ± 12.0
	2012	8.7 ± 5.9	1.3 ± 0.7	56.0 ± 9.2	3.3 ± 1.8
5	2011	18.0 ± 2.3	0.67 ± 0.67	0.0	44 ± 4.2
	2012	3.0 ± 1.7	0.0	145.0 ± 7.9	0.5 ± 0.5
	2014	0.6 ± 0.6	0.0	38.5 ± 17.7	0.0
6	2009	0.0	0.0	0.0	7.0 ± 5.0
	2012	8.0 ± 1.2	0.0	113.3 ± 4.8	0.0
7	2009	0.0	0.0	0.0	19.3 ± 2.7
	2012	3.0 ± 3.0	6.0 ± 4.0	0.0	14 ± 0.0
8	2011	4.7 ± 1.8	2.7 ± 1.8	0.0	38.7 ± 1.3
	2012	33.3 ± 7.5	62.3 ± 19.8	0.0	10.7 ± 4.8
	2014	4.1 ± 2.6	1.2 ± 0.6	55.7 ± 12.2	0.0
9	2011	0.0	0.0	0.0	35.3 ± 7.0
	2012	84.7 ± 4.4	18.0 ± 4.6	0.0	53.3 ± 2.9
	2014	3.6 ± 2.1	3.6 ± 1.0	118.0 ± 23.4	0.0
10	2009	0.0	0.0	0.0	8.0 ± 2.0
	2012	71.5 ± 3.4	5.5 ± 1.7	0.0	3.5 ± 2.2
11	2009	0.0	0.7 ± 0.7	0.0	31.3 ± 16.2
	2012	55.0 ± 5.0	0.0	13.0 ± 11.0	0.0
	2014	0.0	2.7 ± 1.3	0.0	32.0 ± 5.3
12	2011	0.0	2.7 ± 1.3	0.0	11.3 ± 3.3
	2012	0.0	4.7 ± 1.8	0.0	0.0
	2014	0.6 ± 0.6	7.7 ± 1.2	33.8 ± 2.1	0.0
13	2007	0.0	0.0	0.0	0.0
	2012	0.0	0.0	0.0	2.5 ± 0.0
14	2007	0.0	0.0	0.0	0.2 ± 0.2
	2012	0.0	0.0	0.0	3.1 ± 1.2
15	2010	0.0	0.0	0.0	10.7 ± 4.9
	2012	0.0	0.0	0.0	24.1 ± 7.2
	2014	0.0	0.0	0.0	14.1 ± 3.2

C. perifretum density (AIC=139; $\chi^2=23.45$; df=7; $P<0.0001$, AIC_{full model}=119; df_{full model}=9). Survey year (AIC=119; $\chi^2=18.80$; df=7; $P<0.0001$), as well as the interaction between invasion and survey year (AIC=133; $\chi^2=16.18$; df=8; $P<0.0001$) had a significant effect on *C. perifretum* density. The average densities of native *C. perifretum* at sites 1, 2, 6 and 11 (2009 vs. 2012) and the sites 3, 4 and 5 (2011 vs. 2012) in the River Meuse before colonization by *N. melanostomus* were 20.8 ± 6.1 (SE) and 19.8 ± 6.2 (SE) individuals per 100 m², respectively (Figure 2a; grey bars). After colonization of these sites by *N. melanostomus*, a significant decline in average density of *C. perifretum* was recorded (Figure 2a; 2009 vs. 2012: AIC=52; $\chi^2=22.75$; df=3; $P<0.0001$, AIC_{full model}=31; df_{full model}=4, 2011 vs. 2012: AIC=46; $\chi^2=11.98$; df=3; $P=0.0001$, AIC_{full model}=36; df_{full model}=4). Within the first year of colonization, the density of *N. melanostomus* at all sites was on average 66.4 ± 12.6 (SE) individuals per 100 m² with

a maximum of 145.0 ± 15.9 individuals per 100 m² occurring at site 5 (Table 2).

Sites that were not colonized by *N. melanostomus* in 2012 showed a different pattern (Figure 2b). Sites 13 and 14 (2007 vs. 2012), situated in the River Meuse tributaries Geleenbeek and Vloedgraaf showed a significant increase in *C. perifretum* density (AIC=10; $\chi^2=13.47$; df=3; $P=0.0002$, AIC_{full model}=-1; df_{full model}=4). The density of *C. perifretum* did not significantly change at sites 7 and 10 (2009 vs. 2012: AIC=16; $\chi^2=2.96$; df=3; $P=0.086$, AIC_{full model}=16; df_{full model}=4) and 15 (2010 vs. 2012: AIC=9; $\chi^2=2.47$; df=3; $P=0.11162$, AIC_{full model}=9; df_{full model}=4). However, average *C. perifretum* density decreased significantly ($P<0.05$) despite the absence of *N. melanostomus* in 2012 at sites 8, 9 and 12 (2011 vs. 2012: AIC=14; $\chi^2=5.27$; df=3; $P=0.0217$, AIC_{full model}=11; df_{full model}=4), but remained high in comparison with other sites where *C. perifretum* was still present in 2012 (Figure 2b).

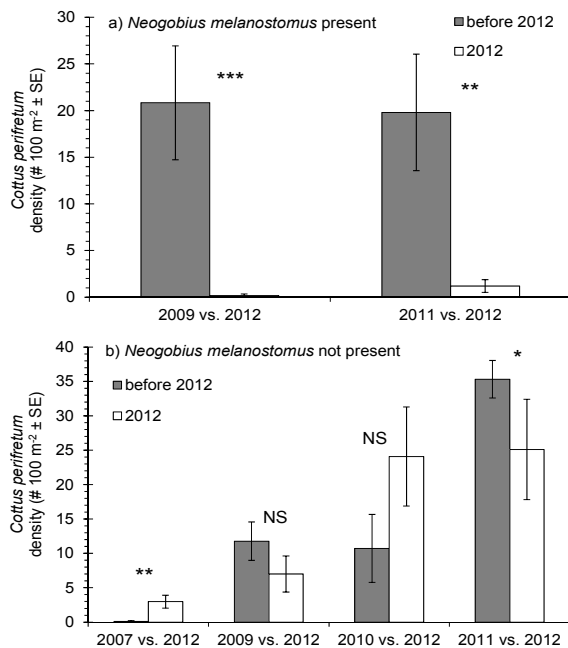


Figure 2. River bullhead (*Cottus perifretum*) densities in the River Meuse. a) Before (grey bars) and after (white bars) colonization of round goby (*Neogobius melanostomus*) in 2012, and b) At control sites that were not colonized by round goby in 2012. *C. perifretum* densities in 2012 are compared with densities in earlier survey years, i.e., 2007, 2009, 2010, or 2011. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant ($P \geq 0.05$).

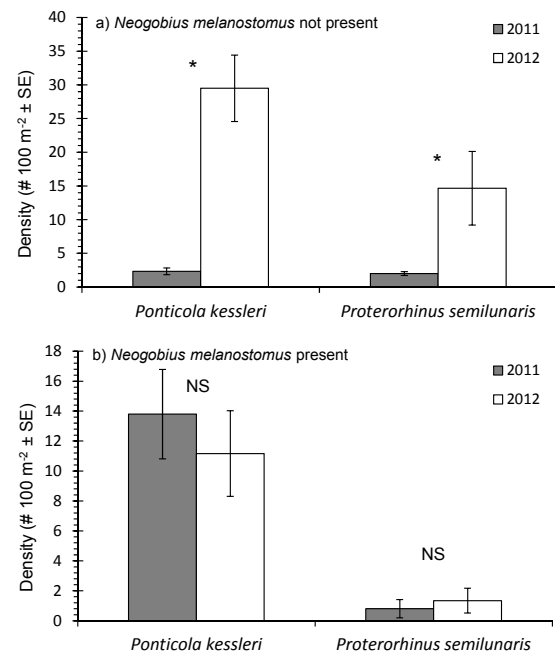


Figure 3a-b. Densities of bighead goby (*Ponticola kessleri*) and tubenose goby (*Proterorhinus semilunaris*) in 2011 and 2012 at sites in the River Meuse that were colonized (a; sites 3, 4 and 5, see table 1) and not colonized (b; sites 8, 9 and 12) by round goby (*Neogobius melanostomus*) in 2012. * $P < 0.05$; NS = not significant ($P \geq 0.05$).

Although sites 8, 9 and 12 were not colonized in 2012 by *N. melanostomus*, they were colonized by *Proterorhinus semilunaris* and *Ponticola kessleri* (Table 2, Figure 3a-b; site 12 was only invaded by *Proterorhinus semilunaris*). At these three sites, densities of *Proterorhinus semilunaris* (AIC=28; $\chi^2=4.59$ df=5; $P=0.0322$, AIC_{full model}=25; df_{full model}=6) and *Ponticola kessleri* (AIC=6; $\chi^2=3.85$ df=5; $P=0.0498$, AIC_{full model}=4; df_{full model}=6) increased significantly between 2011 and 2012 (Figure 3b). In contrast to these three sites, sites 3, 4 and 5 (2011 vs. 2012) were colonized by *N. melanostomus* in 2012. At these sites the densities of *Proterorhinus semilunaris* (AIC=22; $\chi^2=0.20$ df=5; $P=0.6526$, AIC_{full model}=20; df_{full model}=6) and *Ponticola kessleri* (AIC=152; $\chi^2=0.22$; df=5; $P=0.6392$, AIC_{full model}=150; df_{full model}=6) did not change significantly either in the year 2011 or after colonization by *N. melanostomus* in 2012 (Figure 3a).

Population fluctuations

In 2014, additional surveys at six sites (i.e., site 3, 5, 8, 9, 12 and 15) were conducted to determine inter-annual population fluctuations of Ponto-Caspian

gobies and *C. perifretum* (Table 2). At sites 3 and 5, *C. perifretum* densities declined after colonization by *N. melanostomus* in 2012. *C. perifretum* was not recorded in 2014, whereas densities of *N. melanostomus* remained high. At sites 8 and 9, *N. melanostomus* was firstly observed in 2014. This colonization coincided with disappearance of *C. perifretum* and decline in densities of *Proterorhinus semilunaris* and *Ponticola kessleri*. At site 12 *Proterorhinus semilunaris* was present during all sampling years, *Ponticola kessleri* and *N. melanostomus* were only recorded in 2014 and *C. perifretum* disappeared. At site 15 Ponto-Caspian gobies were not recorded and *C. perifretum* densities remained constant.

Discussion

The colonization of shallow littoral zones of the River Meuse by the alien invasive goby *N. melanostomus* coincided with a rapid decline and virtual disappearance of native *C. perifretum* densities. In contrast, the density of *C. perifretum* increased or remained stable at two sites in the River Meuse and three sites in adjacent tributaries

that were not colonized by *N. melanostomus*. These patterns support the hypothesis that the colonization of the River Meuse by *N. melanostomus* has a strong negative impact on *C. perifretum*.

Average *C. perifretum* density also decreased at three sites in the River Meuse that were not colonized by *N. melanostomus* in 2012. However, these sites were colonized by two other alien gobies in 2012 (*Ponticola kessleri* and *Proterorhinus semilunaris*) that may have had an impact on the density of the native species. Similar to *N. melanostomus*, the densities of these alien species significantly increased at these sites between 2011 and 2012. The decline of *C. perifretum* between 2011 and 2012 is most likely related to the increase in densities of these two invasive goby species. Additionally, the increase of *Ponticola kessleri* and *Proterorhinus semilunaris* was not observed in 2012 at sites that were colonized by *N. melanostomus*, although these species were also present.

Additional survey data showed a further upstream colonization of the River Meuse by *N. melanostomus*. At sites colonized by *N. melanostomus* in 2012 *C. perifretum* remained absent and at sites colonized in 2014 *C. perifretum* disappeared. At the site without records of Ponto-Caspian gobies *C. perifretum* densities remained at the same level. These data support the hypothesis that *N. melanostomus* has a negative impact on *C. perifretum* and that the decline of *C. perifretum* in 2012 was not a result of inter-annual population fluctuations of this species. The occurrence of *N. melanostomus* also coincided with the decline in densities of other goby species, indicating that *N. melanostomus* is the superior competitor.

The mechanisms causing the decline of *C. perifretum* densities are not yet fully understood and empirical evidence is scarce. Impacts of Ponto-Caspian gobies are likely to result from predation and competition for shelter and food (French and Jude 2001; Kornis et al. 2012 and literature therein). The aggressive behaviour of gobies may give these species an advantage over their native competitors (Kakareko et al. 2013). Experimental evidence suggests that ecological effects of invasive gobies may be reduced at high densities (Kornis et al. 2014). However, densities at our study sites were four to seven times lower than that used for these experiments.

Various fish species have been observed to be excluded from shelter by alien gobies as a result of territorial behaviour (Dubs and Corkum 1996; Van Kessel et al. 2011; Jermacz et al. 2015). For example, *N. melanostomus* appeared to outcompete

Percina caprodes during territorial conflicts (Balshine et al. 2005). This territorial behaviour was not associated with spawning activities, although Janssen and Jude (2001) found that *N. melanostomus* interfered with the spawning activities of *C. bairdi*, resulting in a loss of *C. bairdi* eggs.

Outcomes of studies on diet composition and the effects of feeding activities of gobies are inconsistent, probably due to the high flexibility of gobies in adapting to and dominating local food resources (Bergstrom and Mensinger 2009; Polačik et al. 2009; Brandner et al. 2013; Števove and Kováč 2013). Most studies describe a preference of gobies for macroinvertebrates, particularly molluscs, whereas diet composition strongly depends on what is available (French and Jude 2001; Skora and Rzeznik 2001; Adámek et al. 2007; Raby et al. 2010; Kipp and Ricciardi 2012). However, some studies reveal that alien gobies predation on other fish, fish fry and eggs sometimes limits the recruitment success of native species (Chotkowski and Marsden 1999; French and Jude 2001; Janssen and Jude 2001; Adámek et al. 2007; Borchering et al. 2013a,b).

Specimens in museum collections show that *C. perifretum* was already present in the Netherlands before 1900 (Dorenbosch et al. 2008). Until the nineties of the former century populations of several fish species, including *C. perifretum*, declined in Dutch rivers owing to severe water pollution and habitat deterioration (e.g., Van den Brink et al. 1996). Due to ambitious rehabilitation plans, the water and habitat quality of the river Meuse significantly improved and populations of *C. perifretum* recovered several years before goby invasions (e.g., Admiraal et al. 1993; Dorenbosch et al. 2008; Leuven et al. 2011; Nienhuis et al. 2002). However, Nolte et al. (2005) suggest that the current population in the River Meuse originates from recent colonization by an invasive lineage of *C. perifretum*. In spite of its origin, *C. perifretum* is considered as a native species in the Netherlands and is a protected species that requires special areas of conservation according to the European Union HD (Annex II; 92/43/EEC). Within the national ecological status objectives relating to the European Union WFD, *C. perifretum* is a designated rheophilic target species for river habitat. Moreover, parts of the River Meuse are designated as special areas of conservation. The main objective for the protection of *C. perifretum* in this area is the conservation of the range and quality of its native habitat and population. Therefore, the impact of goby invasion on *C. perifretum* has implications for the achievement

of the ecological status objectives of HD and WFD. It is likely that none of these conservation objectives will be achieved as a result of the negative effects of alien goby invasions on *C. perifretum*. A decline in the number of rheophilic species as a result of alien goby invasion will potentially limit the achievability of biological quality objectives and negatively affect the overall ecological status of water bodies within the framework of the WFD.

Further spread of alien gobies to tributaries of the River Meuse may also negatively impact other native (benthic) fish species designated within the HD and the WFD, i.e., brook bullhead (*C. rhenanus*), spined loach (*Cobitis taenia*), European weather loach (*Misgurnus fossilis*), sea lamprey (*Petromyzon marinus*), European river lamprey (*Lampetra fluviatilis*) and European brook lamprey (*L. planeri*). Some tributaries of the River Meuse, designated as a special conservation area under the HD, are inhabited by diverse fish communities, including rare and protected species such as *C. rhenanus*. This species is present in a stretch of the River Geul (The Netherlands) isolated by a weir. *C. rhenanus* occupies a similar habitat to *N. melanostomus*, *Ponticola kessleri* and *Proterorhinus semilunaris* and is therefore likely to be negatively affected if the weir were to be removed and the system colonized by alien gobies.

River systems in Europe and North America accommodating the non-native range of Ponto-Caspian gobies feature similar habitats for benthic littoral zone species as the River Meuse. Therefore, negative impacts, similar to those witnessed in the River Meuse, are likely to occur within these river systems. Species rich aquatic ecosystems were thought to demonstrate biotic resistance against invasions by gobies (Ricciardi 2001). However, *N. melanostomus* has been able to spread into the tributaries of the Great Lakes resulting in a suspected substantial negative impact on several endangered fish species (Poos et al. 2009). These findings point to the need for future research on potential impacts of the voracious feeding activity of goby species and the mitigating effects of habitat restoration efforts. An extensive vulnerability assessment of specific systems and species to goby invasions, especially regarding systems and populations that are still isolated due to natural or anthropogenic barriers is recommended. Until mechanisms that result in increased invasion success of Ponto-Caspian species are well understood, isolated populations of endangered and/or protected species may only be preserved by maintaining anthropogenic barriers and restoring natural barriers

to goby invasion (cf. Rahel 2013). Therefore, it may be concluded that the current practice in ecological rehabilitation of restoring the connectivity between isolated water bodies and the river channel may be counter-productive to vulnerable native species due to rapid spread and impact of invasive alien species.

Acknowledgements

This study was financially supported by the Netherlands Food and Consumer Product Safety Authority (Bureau for Risk Assessment & Research Programming) and the district water board 'Waterschap Roer en Overmaas'. We thank the Netherlands Ministry of Infrastructure and Environment ('Rijkswaterstaat') for the use of their survey data, our colleagues of Natuurbalans – Limes Divergens BV and the RAVON Foundation for their help during the fieldwork and Jon Matthews MSc for linguistic improvement of the manuscript. We also thank two anonymous reviewers for their constructive comments on the manuscript.

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The following supplementary material is available for this article:

Table S1. Primary geo-referenced fish species records in the River Meuse in 2007–2014.