



They do not fear the unknown: *Ancylus fluviatilis* (Mollusca, Planorbidae) shows no predator avoidance behavior towards a novel invasive predator

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Abstract Biological invasion is a strong threat to native biodiversity, with limnic systems being especially vulnerable due to historical separation and resulting prey naivety. The prey naivety hypothesis states that native species may not be able to recognize novel predators due to a lack of common evolutionary background and, therefore, become easy targets. In a laboratory experiment, we added cues of native European bullhead (*Cottus gobio* Linnaeus, 1758) and invasive round goby [*Neogobius melanostomus* (Pallas, 1814)] to *Ancylus fluviatilis* Müller, 1774 originating from two different populations within the same river (one naive, one experienced towards round goby) and compared their predator avoidance behavior. Individuals from both populations recognized cues from the known predator *C. gobio* and reduced their locomotive activity. To round goby cues, however, naive individuals did not respond, thereby supporting the prey naivety hypothesis. Experienced individuals, in contrast, reduced their activity,

suggesting a learning effect due to the co-occurrence of invasive predator and prey. At fast moving invasion fronts of highly invasive species like *N. melanostomus*, prey naivety can, hence, enhance their negative impact on ecosystems. Behavioral adaptation of native species resulting in predator avoidance reactions could, therefore, play an important role in ecosystem resilience and temporal invasion dynamics.

Keywords Prey naivety hypothesis · Learning · Predator cues · Locomotive activity

Introduction

One of many hypotheses in aquatic invasion ecology is the prey naivety hypothesis, describing that native prey organisms may be naive towards introduced predators due to a lack of common history—and are, therefore, more vulnerable to these new predator species (Cox & Lima, 2006). Contrary to the neophobia hypothesis, which describes the fear of cues from unknown predators (Barnett, 1958), the prey naivety hypothesis states that naive prey organisms may not be able to recognize the potential predator and/or do not respond with an efficient avoidance behavior (Banks & Dickman, 2007). Therefore, predation of native prey species by newly introduced predators may increase with biological invasion effects potentially being enhanced (Sih et al., 2010). Some examples for this hypothesis include *Astyanax ruberrimus*

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Eigenmann, 1913 as naive prey fish for the invasive predator *Cichla monoculus* Agassiz, 1831 in Panama (Sharpe et al., 2021) or tadpoles of *Rana dalmatina* Bonaparte, 1840 that did not react to predator cues of the recent invader *Neogobius melanostomus* (Pallas, 1814) (Hettzey et al., 2016).

The round goby (*N. melanostomus*) is a small bottom-dwelling fish and one of the most invasive fish species worldwide (Kornis et al., 2012). Among others, *N. melanostomus* advantages are opportunistic and generalist feeding (Pennuto et al., 2010; Brandner et al., 2013; Nurkse et al., 2016), high reproduction rates (MacInnis & Corkum, 2000), affinity for artificial habitat structures (Brandner et al., 2015; Roche et al., 2021), and robustness against low oxygen concentrations (Dickey et al., 2021). Many studies relate round goby invasion with a decline in native fish (e.g., Balshine et al., 2005 and summarized by Corkum et al., 2004) as well as macroinvertebrates (e.g., Lederer et al., 2006; Deurs et al., 2021) due to competition or predation (summarized by Kornis et al., 2012). Consequently, the invasion by *N. melanostomus* may directly alter communities (Krakowiak & Pennuto, 2008) and ecosystem function by feeding on grazers and shredders with additional indirect effects on trophic cascades affecting periphyton or leaf litter decomposition (Pennuto et al., 2018). Originating from the Ponto-Caspian region, *N. melanostomus* spread in the 1990s to Europe and North America (summarized by Corkum et al., 2004). In Europe, round goby invaded the rivers Danube (Wiesner et al., 2000; Jurajda et al., 2005), Rhine (van Beek, 2006; Borcherdig et al., 2011), Weser (Brunken et al., 2012), Odra (Schomaker & Wolter, 2014) as well as the Baltic Sea (Sapota, 2004). In 2008, *N. melanostomus* was found in the lower River Elbe near Hamburg (Hempel & Thiel, 2013) and 2015 in the upper River Elbe, Czech Republic (Buřič et al., 2015), indicating an invasion from down- as well as upstream towards the Saxonian upper River Elbe (Tavares et al., 2020). Since 2018, round gobies have been found in lower stretches of several Saxonian River Elbe tributaries with increasing abundances as well as more invaded tributaries every year (unpublished data). In these rivers, the invading *N. melanostomus* occupy a similar ecological niche to the native European bullhead (*Cottus gobio* Linnaeus, 1758) (Roje et al., 2021) with similar substrate preferences (van Kessel et al., 2016) and food sources (Błońska et al., 2016). Although

co-occurrence of *N. melanostomus* and *C. gobio* can be observed (Roche et al., 2015; van Kessel et al., 2016; Janáč et al., 2018), several laboratory and field studies indicate negative effects of *N. melanostomus* on *C. gobio* populations (Dubs & Corkum, 1996; Janssen & Jude, 2001; Corkum et al., 2004; Jurajda et al., 2005; van Kessel et al., 2016). Considering the prey naivety hypothesis, one reason for this could be a competitive advantage of round goby over the native bullhead with prey organisms recognizing the known native predator but not the new invading one.

One of these potential prey organisms is the freshwater snail *Ancylus fluviatilis* Müller, 1774 (Western, 1969; Emde et al., 2012) that is widely abundant in Central European streams (Maitland, 1965; Cordellier & Pfenninger, 2008). Like other macroinvertebrates, such as gammarids (Wudkevich et al., 1997; Haddaway et al., 2014), *A. fluviatilis* is known to reduce its locomotive activity when perceiving predation risks (Malmqvist, 1992) rather than showing escape behavior in the form of crawl-outs as reported for limnophilic and phytophilic freshwater snails (e.g., Covich et al., 1994; Dalesman et al., 2007b; Turner, 2008; Mathers et al., 2021). For periphyton grazers like *A. fluviatilis* (Calow, 1973), the decreased activity may result in reduced food intake (Malmqvist, 1992) and, thus, cause a trade-off between feeding and minimizing predation risk. However, cost-intensive behavioral changes like hiding or reduced activity cannot be maintained for too long (Holomuzki & Hatchett, 1994). Therefore, a fine-tuned predator avoidance behavior, based on the ability to recognize predation risk resulting in an appropriate reaction, is significant for survival (Lima & Dill, 1990; Dodson et al., 1994; Sih et al., 2010). Various semiochemicals are transmitting information between organisms for intra- and interspecific interactions (Ferrari et al., 2010). Among these, alarm cues of injured conspecifics and predator cues are the most important cue types mediating predator-prey interactions—with the prey benefiting from the information (e.g., Dodson et al., 1994; Ferrari et al., 2010). The co-occurrence of both these cue types may enable associative learning and identification of new predators (Ferrari et al., 2005; Dalesman et al., 2006, 2007a). However, to our knowledge, few other studies have compared responses of native prey to native vs. introduced predators until now (e.g., Shave et al., 1994; Dunlop-Hayden & Rehage, 2011; Haddaway et al., 2014; Hettzey et al., 2016; Sharpe

et al., 2021), with none of them addressing *C. gobio* vs. *N. melanostomus*.

The aim of this study was to test the prey naivety hypothesis for *A. fluviatilis* with *C. gobio* as native and known vs. *N. melanostomus* as unknown predator and whether *A. fluviatilis* is able to learn to recognize *N. melanostomus* as predator. Therefore, we conducted a laboratory experiment, exposing *A. fluviatilis* to kairomones of both fish species. We used snails from two different sampling stretches of a River Elbe tributary: one, directly above the conjunction where *C. gobio* is native and *N. melanostomus* was first found two years ago, and second, about 5 km upstream, where *C. gobio* is native but *N. melanostomus* were not found.

Methods

Collection and maintenance of *Ancylus fluviatilis*

A. fluviatilis were collected from two different stretches of Zschonerbach brook in Dresden. Individuals from a downstream stretch near the mouth to the River Elbe (N 51° 04' 17.0, E 13° 40' 17.8) had been co-existing with *C. gobio* and *N. melanostomus* for two to four years (WFD monitoring data 2016: no gobies caught; 2019: first proof of gobies in Zschonerbach; LfULG, pers. communication). In contrast, individuals from the stretch 5 km upstream from the downstream stretch (N 51° 03' 32.2, E 13° 38' 34.7) were still naive towards *N. melanostomus*. During regular WFD monitoring in 2019 and 2022, no gobies were caught in that stretch and 16 barriers are registered between both sites, 12 of them marked as non-passable (LfULG iDA database v8.3.177, pers. communication).

From both sampling sites, stones with attached *A. fluviatilis* (mean shell length 5.6 ± 0.7 mm) were collected and transported to the laboratory in 10-L buckets filled with fresh river water. In case of stones being too big for transportation, snails were carefully detached and placed onto smaller stones. In the laboratory the stones including the snails were put into separate 30-L aquaria filled with aerated, artificial fresh water (Borgmann, 1996), according to the sampling site, and acclimated for three to seven days. For temperature control, the aquaria were placed into an artificial indoor stream channel with a mean

temperature of 14 °C (range 13–15 °C) in a tarp-covered glass house with natural light conditions but no direct sunlight. Since the stones were covered with natural periphyton biofilm, the snails had enough food available during the keeping.

Cultivation of biofilm

The effect of simulated predation risk on *A. fluviatilis* was tested measuring the crawling activity in the form of snail trails through biofilm comparable to Calow (1974). Therefore, standard glass microscope slides (7.6×2.5 cm) covered with biofilm were prepared. We used a natural biofilm community from the upstream stretch of Zschonerbach (see above). For each experiment 10 to 15 biofilm-covered stones were collected and brushed with stream water so that 1 L biofilm suspension was collected in glass bottles and transported in cooling boxes to the laboratory. The suspension was cleaned from debris or other coarse material by gentle vacuum filtration (85×78 mm, 370 µm, Nuova Ricambi srl, Italy) and added to aquaria which were already filled with 4 L artificial fresh water with additives for algal growth (Borgmann, 1996) and glass slides on the bottom. The aquaria were covered for 24 h in order to avoid growth of planktic algae and support settling of biofilm algae. After 24 h covers were removed and aquaria were aerated by air stones. The biofilm was kept in the same laboratory and under the same temperature and light conditions as *A. fluviatilis* for three days before being used for the experiments.

Kairomone production

Predator avoidance behavior of *A. fluviatilis* was investigated using kairomones (chemical cues) of *N. melanostomus* or *C. gobio* from different sampling sites. In September 2020, gobies were collected by angling from River Elbe (N 51° 03' 48.3, E 13° 46' 38.3), gently removed from the hook and transported to the laboratory in aerated boxes. Bullheads were caught from Biela (N 50° 55' 7.4, E 14° 04' 26.9) and Rauner Bach (N 50° 17' 41.3, E 12° 15' 59.5) in March 2021, as bycatch during macroinvertebrate sampling. They were freed from surber sampler or substrate cages, their length was measured and then transported to the laboratory in aerated boxes. After completing the experiments and

field sampling campaigns, bullheads were released into their respective streams. For this, a clear distinction of the individuals was possible due to different body length. Invasive round gobies were killed according to Saxonian Fisheries regulations after the experiments were completed.

Three individuals of each species (bullheads: 7.0–10.3 cm, gobies: 7.0–11.0 cm) were kept in two separate aquaria (one per species) that were filled with 50 L aerated and filtered tap water, at a mean temperature of 14 °C (range 13–15 °C) and artificial light conditions (8:16 h). Stones as well as PVC half tubes and flowerpots provided shelter. Three times per week, one third of the water was exchanged and the fish were fed with standard chironomid larvae (not with *A. fluviatilis*), to avoid the production of alarm cues (Kats & Dill, 1998). For the same reason, the fish were starved for 24 h before each experiment. This setup was used to produce kairomones in a non-invasive way (e.g., Pettersson et al., 2000; Haddaway et al., 2014). Therefore, the filtration unit was removed for 24 h before each experiment to allow for the accumulation of kairomones and aeration was provided by an air stone only. 500 mL water from bullhead or goby aquarium was applied per fish treatment. As negative control, deionized tap water was used.

Experimental setup

The experiments were conducted in circular stream tanks (Schneider et al., 2014) (Fig. 1). Two thin lines of silicon marked a quarter of the tank bottom that was covered with gravel of 2 mm (experimental area). Opposite to the experimental area a submersible pump (Circulator 500, AQUAEL, Poland, 500 L h⁻¹, 4.4 W) produced a constant current of 0.07 ± 0.02 m s⁻¹ (mean \pm SE) in the tank center and aerated the water. Standing in the same laboratory and stream channels as the aquaria with *A. fluviatilis* and biofilms, the experimental tanks had the same temperature and light conditions. The experimental tanks were filled with 7.5 L of artificial fresh water (Borgmann, 1996) and 20 min before the start of the experiment 500 mL of either kairomone (goby or bullhead) or tap water was randomly added so that the simulated fish density was 0.004 individuals L⁻¹ (bullheads: 0.03 g L⁻¹, gobies: 0.04 g L⁻¹). Then, one snail (from either the upstream or the downstream

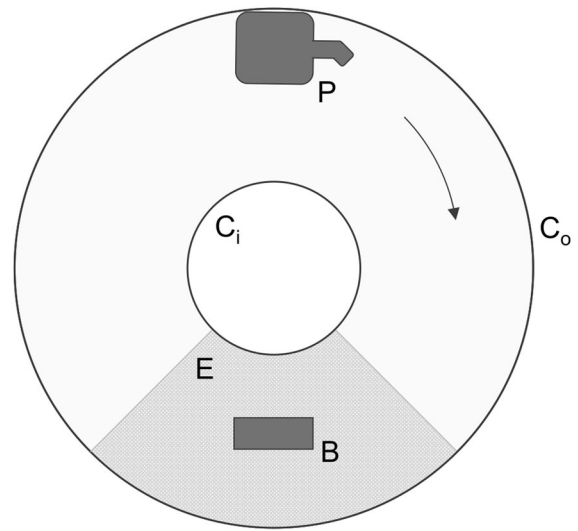


Fig. 1 Schematic top view on experimental tank: circular stream tank with outer cylinder (C₀) (diameter=29 ± 1 cm) and inner cylinder (C_i) (diameter=11 ± 1 cm). Experimental area (E) is one quarter of the tank covered with gravel of 2 mm. Opposite to the experimental area, a submersible pump (P) produces a constant current. In the middle of the experimental area, one glass slide (7.6 × 2.5 cm) covered with biofilm (B) is used as activity and feeding zone of *Ancylus fluviatilis*.

stretch) per tank was transferred carefully from its stone onto the right corner of a fresh biofilm-covered glass slide which was then placed in the middle of the experimental area. The flow velocity directly above the biofilm slide was 0.05 ± 0.01 m s⁻¹. The experiments lasted for 4 h. This duration is short enough to avoid the decay of kairomones (following Richter et al., 2018) and long enough to observe a response of the snails (as found in preliminary tests and supported by other studies, e.g., Rundle & Brönmark, 2001; Haddaway et al., 2014) without possibly masking the direct anti-predator response by any other stimuli such as hunger. At the end of each experiment, the snails were removed from the experimental tanks after noting their position. Afterwards, the biofilm slides were carefully removed and photographed from above (14.5 cm distance, mobile phone camera of Samsung Galaxy A3 mini, standard mode, 480 × 800 px). The area (cm²) where *A. fluviatilis* had crawled and cleared the biofilm was measured using ImageJ (1.53e, Wayne Rasband and Contributors, USA). In total, 144 snails were used. Due to limited space capacity, only four full treatment sets of the six combinations (bullhead/ goby/ tap water x

upstream/ downstream snails) could be conducted in parallel, but the experiment was repeated six times in June 2021 (always 9 am to 1 pm) for a total $N=24$ per treatment set. An effect of daytime or light conditions on *A. fluviatilis* behavior is unlikely because it is known to be active at day as well as night (Meyer-Rochow & Bobkova, 2001).

Statistical analysis

The data analysis was performed using R 4.2.1 (R Core Team, 2022). Due to the non-normal distribution of the area cleared from biofilm, we employed a generalized linear mixed model (GLMM, glmmTMB package, Brooks et al. 2017) for Gamma distribution (log link) to describe the influence of both fixed and random effects on the response variable (biofilm free area). Under the assumption that a non-moving snail should at least clear the biofilm where it was placed, biofilm free areas smaller than 0.36 cm^2 were corrected to this threshold, ahead of performing the gamma GLM. This value is derived from the approximate snail “base area” of an average individual of 6 mm shell length. The two predictors representing fixed effects were the presence of kairomones (three factor levels: bullheads/gobies/no fish) and origin of the snail (two factor levels: upstream/downstream). Since replicate experiments could not be conducted synchronously, the day of conducting the experiment was added as random effect to the GLMM. The best fitting model was chosen by pair-wise model selection with a likelihood ratio test (X^2) depending on lowest AIC (Akaike Information Criterion). The model assumptions were checked and approved via residual diagnostics using the DHARMA package (Hartig, 2022). Specified differences between the treatments

were assessed by pair-wise post hoc comparisons and visualized via letter code based on estimated marginal means with Tukey HSD (emmeans package, Lenth 2021).

Snails that were not on the slide at the end of the experiment were not removed from the data set. To show that the snail position was independent of the kairomone treatment and/or origin, we employed an additional pair-wise model selection depending on lowest AIC: a mixed effects logistic regression to describe the influence of both fixed effects (kairomone treatment and individual origin) and random effect (day) on the binary response variable (position: snail on the slide or not).

Results

The best fitting model was a full model with interaction of both factors (Table 1). Both factors (kairomone treatment and river stretch) as well as their interaction had significant effects on the activity of *A. fluviatilis*. While snails in control treatments crawled more or less over the entire glass slide, individuals originating from both river stretches recognized kairomones of *C. gobio* and reduced their activity significantly compared to the control treatments (Fig. 2; Table 2). Significant differences between individuals from the upstream vs. the downstream stretch were only observed when treated with round goby kairomones, with significantly more snails from the downstream stretch (i.e., co-occurring with *N. melanostomus*) reducing their activity (Fig. 2, Table 2).

During the experiments, mortality was less than 1% (1 individual out of 144). At the end of the experiments, 68% of the snails had left their slide (snails

Table 1 Results of gamma GLMM (log link) for comparison using likelihood ratio test (X^2) and Akaike Information Criterion (AIC)

Response variable (locomotory activity) was measured as area cleared of biofilm. Best fitting model is indicated in bold

| Model | Npar | AIC | BIC | LogLik | Dev | X^2 | df | P |
|--|----------|------------|------------|-------------|------------|-----------|----------|------------------|
| Null model | 3 | 377 | 386 | -186 | 371 | | | |
| Activity ~ 1 + (1 run) | | | | | | | | |
| One-factor model with site | 4 | 369 | 381 | -181 | 361 | 10 | 1 | 0.002 |
| Activity ~ origin + (1 run) | | | | | | | | |
| One-factor model with kairomones | 5 | 312 | 327 | -151 | 302 | 59 | 1 | <0.001 |
| Activity ~ kairomones + (1 run) | | | | | | | | |
| Model without interaction | 6 | 305 | 323 | -147 | 293 | 9 | 1 | 0.002 |
| Activity ~ kairomones + origin + (1 run) | | | | | | | | |
| Full model | 8 | 280 | 304 | -132 | 265 | 29 | 2 | <0.001 |
| Activity ~ kairomones × origin + (1 run) | | | | | | | | |

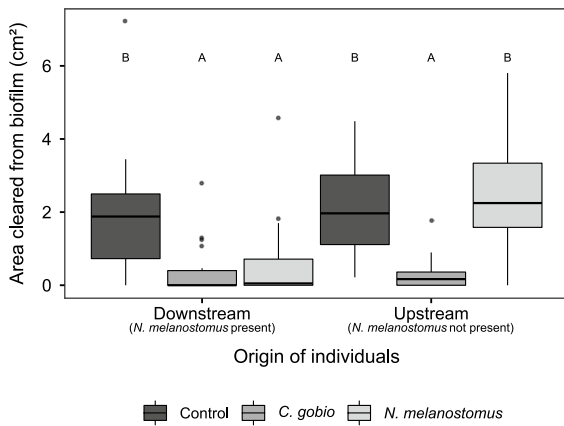


Fig. 2 Effect of kairomone treatments (dark gray: *Cottus gobio*, light gray: *Neogobius melanostomus*, medium gray; tapwater/control) on area (cm²) cleared from biofilm by *Ancyclus fluviatilis* originating from either a downstream (where both fish species are established) or an upstream river stretch (where only *C. gobio* is established) in 4 h. Significant differences ($\alpha=0.05$) between treatments * origin are indicated by letters A/B (based on EMM test with Tukey HSD correction) with bars having the same letter being not significantly different. Data of laboratory experiment, $n=24$ per treatment

Table 2 Results of pairwise post hoc comparisons (Tukey HSD, $df=135$) on gamma GLMM (log link) with area cleared of biofilm depending on kairomone treatment and origin of individuals as fixed effects and day as random effect

Significance ($\alpha=0.05$) is indicated in bold

| Comparisons | Estimate | SD | Error | Z | P |
|---|----------|-------|---------|------------------|---|
| Control (upstream–downstream) | 0.110 | 0.184 | 0.599 | 0.984 | |
| <i>C. gobio</i> (upstream–downstream) | − 0.174 | 0.182 | − 0.954 | 0.931 | |
| <i>N. melanostomus</i> (upstream–downstream) | 1.209 | 0.182 | 6.646 | <0.001 | |
| Upstream (<i>C. gobio</i> – <i>N. melanostomus</i>) | − 1.639 | 0.181 | − 9.052 | <0.001 | |
| Upstream (<i>C. gobio</i> –control) | − 1.510 | 0.182 | − 8.295 | <0.001 | |
| Upstream (<i>N. melanostomus</i> –control) | 0.129 | 0.182 | 0.706 | 0.981 | |
| Downstream (<i>C. gobio</i> – <i>N. melanostomus</i>) | − 0.256 | 0.183 | − 1.403 | 0.723 | |
| Downstream (<i>C. gobio</i> –control) | − 1.226 | 0.184 | − 6.657 | <0.001 | |
| Downstream (<i>N. melanostomus</i> –control) | − 0.970 | 0.184 | − 5.283 | <0.001 | |

Table 3 Results of binomial GLMM comparison using likelihood ratio test (X^2) and Akaike Information Criterion (AIC)

Position of snail at the end of the experiment was categorized in on slide or not on slide. Best fitting model is indicated in bold

| Model | Npar | AIC | BIC | LogLik | Dev | X^2 | df | P |
|--|----------|------------|------------|-------------|------------|-------|----|-------|
| Null model | 2 | 184 | 190 | − 90 | 180 | | | |
| Position ~ 1 + (1lrun) | | | | | | | | |
| One-factor model with site | 3 | 185 | 194 | − 90 | 179 | 0.43 | 1 | 0.510 |
| Position ~ origin + (1lrun) | | | | | | | | |
| One-factor model with kairomones | 4 | 186 | 198 | − 89 | 178 | 0.77 | 1 | 0.381 |
| Position ~ kairomones + (1lrun) | | | | | | | | |
| Model without interaction | 5 | 188 | 203 | − 89 | 178 | 0.44 | 1 | 0.507 |
| Position ~ kairomones + origin + (1lrun) | | | | | | | | |
| Full model | 7 | 191 | 212 | − 89 | 177 | 0.73 | 2 | 0.693 |
| Position ~ kairomones × origin + (1lrun) | | | | | | | | |

from upstream: $n_{\text{control}}=9$, $n_{\text{bullhead}}=10$, $n_{\text{goby}}=6$; snails from downstream: $n_{\text{control}}=6$, $n_{\text{bullhead}}=8$, $n_{\text{goby}}=7$). Because this behavior was not correlated to the kairomone treatment and/or origin of the snails (Table 3), we think it is very unlikely that it biased the response (area cleared of biofilm).

Discussion

In limnic ecosystems, gaining and adequately interpreting information by chemical signals is of great importance (Dodson et al., 1994). With this study, we tested whether naive *A. fluviatilis* display different avoidance behaviors towards a known compared to an unknown predator, using exclusively the predator kairomones without alarm cues. In accordance with the prey naivety hypothesis and other studies comparing prey responses to native vs. introduced predators (Shave et al., 1994; McLean et al., 2007; Smith et al., 2008; Hettzey et al., 2016; Sharpe et al., 2021), naive *A. fluviatilis* from the upper river stretch displayed a

behavioral response when treated with bullhead kairomones – but not when treated with kairomones of the unknown invader round goby.

In contrast to the population from the upper river stretch, *A. fluviatilis* originating from the lower river stretch responded to bullhead and round goby kairomones in the same intensity. Although there are studies that could not verify the prey naivety hypothesis (Kovalenko et al., 2010; Dunlop-Hayden & Rehage, 2011; Haddaway et al., 2014), a generalized predator recognition, as it is mainly suggested for related predator species (Ferrari et al., 2007; Dunlop-Hayden & Rehage, 2011), can be excluded, because the upstream population showed naive behavior. Therefore, the most likely explanation for *A. fluviatilis* recognizing the novel predator in the lower river stretch may be learning (Turner et al., 2006; Ferrari et al., 2007). Because *N. melanostomus* had been known to be present in that exact river stretch for at least two (max. four) years before the study was conducted, the behavioral adjustment of *A. fluviatilis* is probably based on associated learning of predation risks by novel predator cues co-occurring with alarm cues (Chivers & Smith, 1998; Kristensen & Closs, 2004; Ferrari et al., 2010). Although we did not test the response of *A. fluviatilis* to alarm cues, this kind of learning seems plausible for *A. fluviatilis* and has been shown for the freshwater snail *Lymnaea stagnalis* Linnaeus, 1758 by Dalesman et al. (2006) who treated laboratory-reared snails with a mix of alarm and predator cues. Eight days after a 48 h conditioning period, snails still showed an increased predator recognition when treated with predator cues compared to snails that were pre-exposed to control water only. While round gobies ingest small prey organisms like *A. fluviatilis* usually in one bite (pers. observation), conspecific prey cues could be released through digestion (Hettyey et al., 2015) or by hurting the foot during a forced detachment. Additionally, Dalesman et al. (2007a) observed that *L. stagnalis* was able to recognize and learn from heterospecific alarm cues, which is conceivable for *A. fluviatilis* as well.

The ability to recognize novel predator species relatively fast by learning is of great importance for prey organisms. While evolutionary adaptations to new predators require many generations (Anton et al., 2020), behavioral adjustments are much faster. Therefore, they may facilitate the survival of a native prey population, especially if the generation time of

the prey species (one to two generations per year in *A. fluviatilis*, Geldiay, 1956; Maitland, 1965) is rather long compared to the invasion speed of the predator (five to six batches per year in *N. melanostomus*, summarized by Charlebois et al., 1997). This could become even more important in case known predators that trigger innate responses disappear as a direct consequence of the invasion or other associated stressors. In the River Elbe tributaries, this is a possible scenario because studies from other ecosystems already observed negative effects of *N. melanostomus* on *Cottus* spp. as well as other benthivorous fish species (e.g., Janssen & Jude, 2001; van Kessel et al., 2016; Gaye-Siessegger et al., 2022).

On the other hand, learning to associate a behavior that is effective against a known predator with a new predator may be even disadvantageous if the new predator differs in some important way from the known one. At least for *A. fluviatilis* in the main River Elbe, this possibility seems to be corroborated by *N. melanostomus* showing an increasing preference for gastropods [*A. fluviatilis* and *Potamopyrgus antipodarum* (J. E. Gray, 1843)] with rising invasion age, as observed by Tavares et al., (2022) for rip-rap habitats. Because prey preferences in the field are a result of (often learned) active predator selectivity (Sih & Moore, 1990; Reiriz et al., 1998) and prey vulnerability, it is unclear which mechanism dominates in this specific case. However, round goby is known to feed efficiently on mollusks due to its well-suited pharyngeal teeth (Ghedotti et al., 1995; Andraso et al., 2011), in particular on sessile bivalves such as *Dreissena* spp. (Ray & Corkum, 1997; French & Jude, 2001; Lederer et al., 2006). Thus, reduced activity which normally helps avoid visual predators (Kats & Dill, 1998) as *C. gobio* (Ladich, 1989; Welton et al., 1991) and *N. melanostomus* (Diggins et al., 2002), might become an “evolutionary trap” for *A. fluviatilis* in the context of certain predator invasions. Escape behavior such as crawl-out (e.g., Covich et al., 1994; Hoverman et al., 2005; Turner, 2008; Mathers et al., 2021), which would be more appropriate, seems to occur in *A. fluviatilis* under abiotic conditions like low oxygen concentrations (Berg, 1952) rather than as a direct predator response and we only once observed it at temporarily elevated temperatures during the keeping. However, even if behavioral adjustments by *A. fluviatilis* would not match certain predators, this is probably an exception rather than a common case.

The great variety of anti-predator behavior existing in aquatic macroinvertebrates (e.g., Stewart et al., 1999; Schäffer et al., 2013; Haddaway et al., 2014; Szokoli et al., 2015) suggests that for most species of the benthic community, learning to recognize new predators will “on average” reduce predation risk. Prey adapting its behavior to novel predators may limit invasion success (Sih et al., 2010). This might be one of the reasons for the often observed “saturation” or “accommodation” phase with lower or stable goby abundances following the initial expansion phase (Roseman & Riley, 2009; Vélez-Espino et al., 2010; Young et al., 2010). Another likely reason can be native top predators (e.g., perch or trout) benefitting from the prey naivety of the introduced species (Pintor & Byers, 2015; Mumby et al., 2018; Vřetičková et al., 2018). Therefore, the outcome of this highly dynamic process is yet unclear and the further development has to be monitored in upper River Elbe and its tributaries.

In summary, the results of this study show prey naivety of *A. fluviatilis* towards the invasive round goby, which could further support invasion of *N. melanostomus* (Ricciardi & Atkinson, 2004). Nevertheless, the long-term effects of predator novelty are unknown. While genetic adaptations require many generations, *A. fluviatilis* adjusted its behavior after two years of co-occurrence with the invader. The effectiveness of this adjustment has to be seen, but the ability of native prey to recognize novel predator species by learning is of great importance and may affect the resilience of native biodiversity.

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Declarations

Competing interests The authors declare no conflict of interest.

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