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Interspecific differences in swimming performance, behavior and survival between native Italian gudgeon (*Gobio benacensis* Pollini, 1816) and non-native European gudgeon (*Gobio gobio* Linnaeus, 1758)

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Abstract
Introduction of non-native species is an important cause of biodiversity decline in rivers. Separated by mountains and salt water, the freshwater fish fauna in Italy has experienced a natural isolation from fish in continental Europe. As a consequence, several Italian fish species have diverged from their European sister species, likely with unique adaptations to the local environment. Relatedly, the region is also susceptible to the invasion of non-native fish, and today almost half the fish species present are of non-native origin. Several of these non-native species have Italian congeners susceptible to competition and hybridizations, and, in the long run, displacements and extinctions. One such example is the Italian gudgeon (*Gobio benacensis*) and its European congener European gudgeon (*Gobio gobio*). During the last few decades the European gudgeon was introduced in Italian waters and has since spread rapidly, causing progressive declines in the Italian species. As for several other similar species pairs, little is known about potential differences in ecology and behavior. Here we study differences between Italian and European gudgeons in a controlled laboratory environment, using a combined open field and provoked escape response test, as well as tracking their sympatric survival over time in the hatchery. The smaller Italian gudgeon displayed a lower maximum swimming speed compared to the larger European gudgeon. The Italian gudgeon also experienced substantially higher sympatric mortality, resulting in only European gudgeon surviving to the end of the experiment. Contrary to expectations, no difference was seen in boldness and the Italian gudgeon displayed a higher movement activity, moving a larger distance in an open field test, compared to its European sister species. The reported differences could play a role in the replacement process, and may also have impacts on the surrounding ecosystem, and the prey and predators that have coevolved with the Italian species.

Keywords: *Invasive species*, *maximum swimming speed*, *activity*, *freezing*, *boldness*, *mortality*

Introduction

Many freshwater fish populations are at risk from a range of anthropogenic stressors, including habitat degradation and invasive species, and introduction of non-native species is a primary cause of biodiversity decline in temperate rivers (Dudgeon et al. 2006; Stefani et al. 2020; Su et al. 2021). Active stocking of non-native fish, as well as accidental release from aquaculture, sportfishing or the ornamental fish hobby have resulted in introductions of non-native fish, with the rate of introduction increasing over the past century (Gherardi et al. 2008; Cucherousset & Olden 2011). Non-native species can have varying effects on the local ecology, such as alteration of food webs, pathogen dynamics and predation, and sometimes also cause a change in the behavior and distribution of native fish species (Cucherousset & Olden 2011). Competition and hybridization may constitute particularly important consequences for native species following the arrival

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of closely related non-native species (Cucherousset & Olden 2011; Carosi et al. 2017; Zaccara et al. 2020).

Although often relatively similar in morphology, ecology and behavior, there might be subtle differences between the native and non-native sister species, with potential effects not only on their interspecific competitive strength and fitness differences, but also on other species and processes in their environment (Wolf & Weissing 2012; Raffard et al. 2017). For example, successful non-native species have been scored higher for boldness, exploration or aggression compared to native species in species as different as wasps, crayfish and lizards (Usio et al. 2001; Monceau et al. 2015; Damas-Moreira et al. 2019). In fish, non-native *Gambusia* species have been observed to feed at higher rate and be more likely to disperse than closely related native species (Rehage & Sih 2004; Rehage et al. 2005) and invading round gobies are bolder than established conspecifics (Myles-Gonzalez et al. 2015; Thorlacius et al. 2015). Non-native fish have also been reported to be larger and have lower loads of parasites than local fish or compared to the species in its native range (Dove 2000; Colautti et al. 2004).

Isolated by mountains and salt water, the freshwater fish fauna in Italy has experienced a natural isolation from the fish in continental Europe, resulting in allopatric speciation and relatively high endemism (Bianco 1995; Fortini 2016). Several Italian fish species have diverged from sister species in continental Europe (Fortini 2016), likely with unique adaptations to the local and regional environment (Carvalho 1993). The historical isolation, in combination with the recent surge in fish introductions, also makes the region susceptible to the invasion of non-native fish, and today almost half of the fish species present are of non-native origin (Bianco 1995; Gherardi et al. 2008; Lanzoni et al. 2018). Several of these non-native species have Italian sister species susceptible to competition and hybridizations, and, in the long run, displacements and extinctions (Bianco 1995; Bianco & Ketmaier 2005; Zaccara et al. 2020), with unknown consequences for the local ecosystem. This is the case, for example, for native Italian barbel (*Barbus plebejus*; Meraner et al. 2013; Zaccara et al. 2020), Tiberian barbel (*Barbo tyberinus*; Carosi et al. 2017), Italian spined loach (*Cobitis bilineata*; Delmastro et al. 2022), southern pike (*Esox cisalpinus*; Lucentini et al. 2011), marble trout (*Salmo marmoratus*; Polgar et al. 2022), and Italian gudgeon (*Gobio benacensis*; Bianco & Ketmaier 2005). Although there are studies on the sister species' respective morphology, distribution and genetics, little is known about potential differences in ecology and behavior (e.g. Bianco & Ketmaier 2005; Lucentini et al. 2011; Delmastro et al. 2022).

Gudgeons (*Gobio* sp.) are small-sized, riverine, gregarious fish that feed mainly on benthic invertebrates. Although relatively stationary, gudgeons may embark on substantial longitudinal movements (Kennedy & Fitzmaurice 1972; Reubens et al. 2013; Fortini 2016). In Northern Italy, the genus *Gobio* was historically represented by the native Italian gudgeon (*G. benacensis*; also referred to as *Romanogobio benacensis*). During the last several decades, however, the European gudgeon (*Gobio gobio*) was introduced in Italian waters and has rapidly spread throughout the country, contributing to the progressive decline in the Italian species (Bianco & Ketmaier 2005; Bianco 2014; Fortini 2016). Although the number of scales between the anus and anal fin distinguish the two species, *G. benacensis* is also typically smaller (maximum 10–12 cm vs 15–16 cm), has a shorter and rounder head, and reflects a more metallic glow compared to *G. gobio* (Fortini 2016). Little is known about behavioral differences between the Italian and European species, and how these might contribute to the simultaneous decrease of the former and expansion of the latter, or affect the local ecosystem differently.

Here we study behavioral differences between *G. benacensis* and *G. gobio* in a controlled environment. In arena tests, we compare boldness, activity and maximum swimming speed of the two species. In addition, we track their sympatric survival over time in a controlled environment – the hatchery. We hypothesized that the non-native *G. gobio* should be bolder and more active, and, as a consequence of its larger size, display a higher maximum swimming speed (Rehage & Sih 2004; Domenici 2010; Damas-Moreira et al. 2019).

Material and methods

Both species were collected in shallow, slow-flowing tributaries of the Orba River in the Province of Alessandria, Italy, using electrofishing on 19 September 2022. *G. gobio* ($n = 31$) were collected from the Canale Rocca Grimalda, (44°39′44.6″N, 8°38′56.8″E), while *G. benacensis* ($n = 31$) were caught in Lemme River (44°39′47.7″N, 8°49′51.5″E). Species were determined based on known presence in the respective stream and confirmed by morphological traits (Fortini 2016). The fish were brought to the Predosa Hatchery (Predosa, Alessandria, Italy) and left to recover in a spring-fed flow-through tank overnight, before being PIT-tagged for individual recognition. Only healthy-looking fish were included in the study.

Fish were anaesthetized in clove oil (Aromlabs, USA; approximately 0.05 mL clove oil/L water), before a 2–4 mm incision was made on the ventral side of the fish, slightly offset from the center, and anterior of the pelvic fins. A passive integrated transponder (PIT-tag; Oregon, USA; 12 mm × 2.1 mm; 0.10 g) was inserted through the incision and pushed forward in the abdominal cavity to align with the fish body (Bolland et al. 2009; Schiavon et al. 2023). Fish were measured for length and weight before being left to recover in an aerated fresh water tank.

Fish were kept in a common spring-fed flow-through tank (length × width × depth = 1.1 m × 1.2 m × 0.4 m) after tagging, and in a larger spring-fed flow-through tank after the arena tests (2 m × 2 m × 0.6 m). Temperature was kept stable at around 13°C under a natural day–night cycle (windows in the hatchery) and shelters were available in the tanks. Fish were regularly fed commercial aquaria fish pellets (Sera Koi Royal pellets) supplemented by wild-caught aquatic invertebrates, and the tank was checked frequently for mortalities until the experiment ended on 2 November 2022, 43 days after tagging.

On 25–26 September (6–7 days after tagging) the fish boldness, movement activity, and maximal swimming speed were quantified in an open field arena test. An individual fish was netted from the holding tank, placed in a small bucket and gently released into an arena (length × width × depth = 565 × 365 × 100 mm). The fish was left to move freely in the arena for 10 min. As gudgeons often freeze as a defense reaction to disturbance and potential predators, the time to start moving after the first freezing (longer than 10 s) was quantified as a measure of boldness (Thorlacius et al. 2015; Hirsch et al. 2017). After 5 min of habituation in the arena tank (Ashraf et al. 2024), the total distance moved for the subsequent 5 min was quantified as a measure of movement activity (Miklósi et al. 1992; Watz 2019; Haraldstad et al. 2021). After approximately 10 min (5 min of habituation +5 min of activity test) in the arena, a small spherical weight was released from about 1 m height to land in the proximity of the fish to provoke an escape response. The fish typically displayed an immediate escape response followed by some time swimming around. When the fish stopped, another escape response was provoked by dropping another weight close to the fish. This was repeated a third time, to provoke in total three escape responses, during which the fish's maximum swimming speed was quantified (Knaepkens et al. 2007; Tudorache et al. 2008; Nyqvist et al. 2022). After the third provoked escape response, the fish was netted, scanned for PIT-ID and left to recover in an aerated tank before being returned to the larger holding tank once all fish had been tested. Two trials were run in parallel. Water in the test tanks was changed regularly to maintain a stable temperature across trials. A separate tank, subject to identical conditions as the test tanks, was used to continuously measure temperature without influencing the test arena (Nyqvist et al. 2022).

The trials were recorded with an overhead video camera (Sony 4K, FDR-AX43, 25fps), and fish positions were manually tracked using a custom-made MATLAB (R2021b, The MathWorks Inc, Natick, Massachusetts, USA) script (derived from https://github.com/SilverFox275/manual-point-tracking). The fish was positioned (center of mass) manually on one frame per second for the total distance moved after the initial 5 min of habituation, and on five frames per second for the provoked escape response. The known dimensions of the arena were used to convert the distances moved in pixels to distances moved in meters. The fastest 400 ms (that is, longest distance moved over two tracked frames) during the provoked escape response period were used as an estimate of maximum swimming speed (Knaepkens et al. 2007; Tudorache et al. 2008; Nyqvist et al. 2022). Time to start moving after an initial freezing behavior was quantified manually using VLC (VideoLan, 2006. VLC media player, https://www.videolan.org/vlc/index.html). The actual tests as well as the manual tracking and postprocessing were performed with the researcher being blind to the treatment.

The difference between *G. benacensis* and *G. gobio* in latency to start moving after freezing was analyzed using Cox regression (Hosmer et al. 2008). Fish that remained frozen until the end of the trial were censored at this point and the output model was tested for the proportionality of hazard assumption (Fox 2002). Difference in total distance moved and maximum swimming speed (absolute and scaled to fish body size) between the two species was tested using Wilcoxon–Mann–Whitney tests as our data did not fulfill the criteria for parametric tests. Difference in distance moved was tested on the full set of fish, as well as on a dataset excluding fish freezing for the full experiment. Difference in mortality was analyzed using a chi^2 test as the data did not fulfill the proportionality of hazard assumption (Fox 2002) for a Cox regression.

Data management, plotting and statistical tests were performed in R (R Core Team 2021) involving the following packages: dplyr (Wickham & Francois

2015), ggplot2 (Wickham 2016) and plyr (Wickham & Wickham 2017), survival (Therneau & Lumley 2017), survminer (Kassambara et al. 2017) and patchwork (Pedersen 2019).

The study was performed in accordance with the Ufficio Tecnico Faunistico e Ittiofauna of the Provincia di Alessandria (no. 65493 of 11 november 2021), under the provisions of art. 2 of the national Decree no. 26/2014 (implementation of Dir. 2010/63/EU).

Results

G. benacensis were significantly smaller than *G. gobio* (Wilcoxon, $p < .001$). *G. benacensis* ($n = 31$) were on average 7.4 cm long (median, range = 7–10 cm) with a weight of 4.7 g (median, range 3.4–12.3 g), while *G. gobio* ($n = 31$) had a median length and weight of 9.3 cm (range 8.6–10.5 cm) and 9.3 g (7.1–13.7 g), respectively. Tag-to-fish-length ratios were 0.7–3% for weight and 11–16%, in line with current recommendations for natural fish behavior (Brown et al. 1999; Jepsen et al. 2005; Vollset et al. 2020).

All but two fish, both *G. benacensis*, froze at some point during the arena test. Time to freezing was on average 8 s (median, Inter Quartile range (IQR) = 3–24 s) for *G. benacensis* and 5 s (median, IQR = 2–20 s) for *G. gobio*. Overall, 8 *G. benacensis* and 16 *G. gobio* did not move again after freezing. Median latency to start moving after freezing was 85 s (IQR = 44–136 s) for *G. benacensis* and 43 s (IQR = 31–170 s) for *G. gobio*. There was no significant difference in latency to move between the species (Cox regression, $p = .1$, Figure 1).

In the open field test, the average total distance moved was significantly longer for *G. benacensis* compared to *G. gobio* for the full dataset (Mann-Whitney, $p = .03$; Figure 2) as well as when excluding fish that were freezing (no distance moved) for the full open field test (Mann-Whitney, $p < .01$; Figure 2). *G. benacensis* moved a median of 11.9 m (IQR = 0–18.5 m) while the median total distance moved for *G. gobio* was 0 m (IQR = 0–4.1 m).

During the escape response tests, *G. gobio* reached on average higher maximum swimming speeds compared to *G. benacensis* (Mann–Whitney, $p < .001$; Figure 3(a)) while there was no significant difference in maximum swimming speed scaled to body length (Mann–Whitney, $p = .87$; Figure 3(b)). *G. benacensis* reached maximum swimming speeds of 0.9 m/s (median, IQR = 0.8–1.1 m/s) corresponding to 12.5 Body Length / second (BL/s) (median, IQR = 11.0–14.7 BL/s) while the average maximum swimming speeds quantified for *G. gobio* were 1.2 m/s (median, IQR = 1.1–1.4 m/s) corresponding to 13.3 BL/s (median, IQR = 11.6–14.4 BL/s).

Three weeks after tagging the first mortalities were observed and within 9 days all *G. benacensis* and 32% of *G. gobio* died. The mortality was

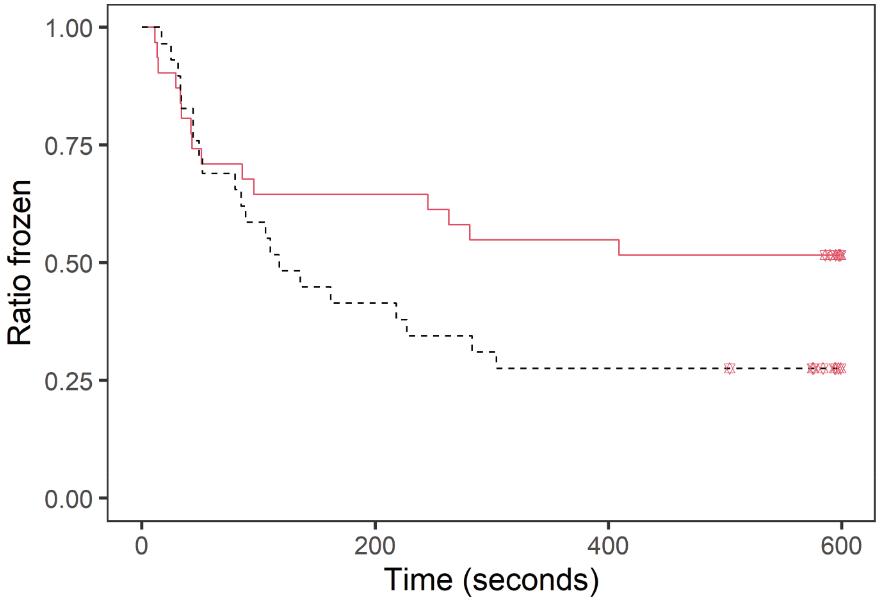

Figure 1. Kaplan-Maier plot of the latency to move for *G. benacensis* (dashed line) and G. gobio (solid line) with ratio of frozen fish on the y-axis (n = 60) and time in seconds on the x-axis. Stars represent censored observations at the end of the experiment.

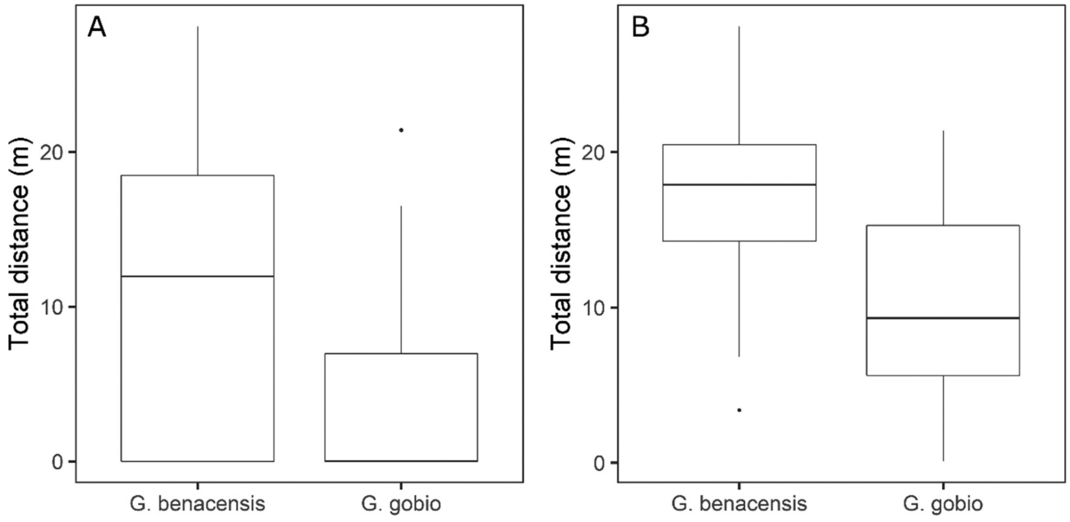

Figure 2. (a) Total distance moved for *G. benacensis* (*n* = 31) and *G. gobio* (*n* = 31) in the open field test. (b) Total distance moved for *G. benacensis* (*n* = 18) and *G. gobio* (*n* = 13) in the open field test, excluding fish that were freezing for the full experiment (distance = 0). The horizontal line represents the median value, the box the interquartile range (IQR), the vertical line the third quartile plus 1.5 × IQR, and outliers are shown as points.

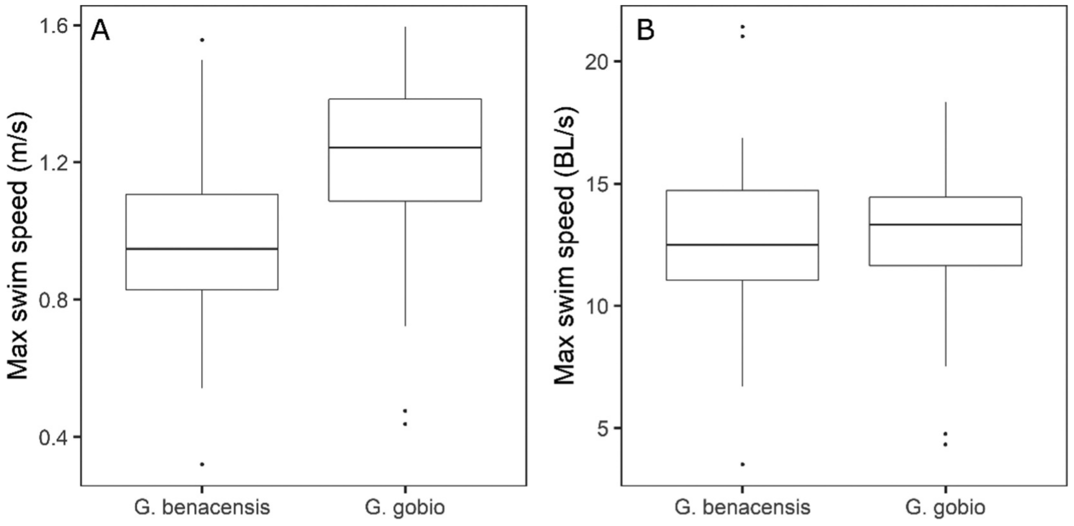

Figure 3. Maximum swimming speed over 400 ms in absolute terms (a) and scaled to the body length of the fish (b) for *G. benacensis* (*n* = 31) and *G. gobio* (*n* = 31). The horizontal line represents the median value, the box the interquartile range (IQR), the vertical line the third quartile plus 1.5 × IQR, and outliers are shown as points.

significantly higher among *G. benacensis* compared to *G. gobio* (df = 1, N = 62, $chi^2 = 28.8$, $p < .001$).

Discussion

The smaller native *G. benacensis* displayed a lower absolute maximum swimming speed compared to the larger non-native *G. gobio*. *G. benacensis* also experienced substantially higher sympatric mortality in the hatchery, resulting in only *G. benacensis* surviving to the end of the experiment. Contrary to expectations, no difference was seen in boldness and *G. benacensis* displayed a higher movement activity, moving a larger distance in the open field test, compared to its European sister species.

As expected from the size differences (Domenici & Blake 1997), *G. gobio* had a higher maximum swimming speed compared to *G. benacensis*. Maximum swimming speed – and related escape responses – is crucial for predator–prey interactions

(Domenici & Blake 1997) and this difference may have implications for the two species' relative success within, and impact on, the surrounding ecosystem. For example, lower escape velocities might result in higher predation mortality, and swimming speeds achieved might affect feeding success in relation to mobile prey (Christensen 1996; Watkins 1996; Strobbe et al. 2010). Burst or maximum swimming speed is also important for passing natural or anthropogenic hydrodynamic velocity barriers (Starrs et al. 2011; Katopodis & Gervais 2012), potentially positioning *G. benacensis* at a comparative disadvantage to its European congener.

The maximum swimming speeds scaled to the body length were approximately 13 BL/s for both species and in line with what has previously been reported for *G. gobio* with a similar volitional methodology (10–15 BL/s; Tudorache et al. 2008). These maximum swimming speeds are achieved using mainly white muscles and anaerobic processes (Videler 1993; Domenici & Blake 1997; Domenici 2010), and can only be maintained over very short time periods. For longer swimming periods the attained swimming speeds are lower, and the fish is also deploying slower red muscles and aerobic processes (Videler 1993). For example, critical swimming speeds at around 5 BL/s and critical burst speeds slightly higher than that have been reported over minutes and seconds, respectively (Tudorache et al. 2008; Egger et al. 2021). How the swimming performance of *G. gobio* and *G. benacensis* compares at lower velocities and over longer time remains to be investigated, but the larger size of the latter suggest a higher swimming capability also at these velocities (Kolok 1999; Katopodis & Gervais 2012).

In contrast to our results, non-native species often display higher movement rates compared to native species (Rehage & Sih 2004; Monceau et al. 2015; Damas-Moreira et al. 2019). Although simple arena trials (open field tests) may appear to be very artificial tests with little real-life application, their scores often correlate with behavior in the wild. In fish, for example, individual open field test scores have correlated with individual movement (Fraser et al. 2001; Watz 2019) and activity (Závorka et al. 2016) in nature, and with passage behavior in relation to in-stream barriers (Haraldstad et al. 2021; Nyqvist et al. 2024). Future field studies may verify whether the lower movement rates of *G. benacensis* compared to *G. benacensis* follow the fish into their natural environments.

Freezing is used as an anti-predator behavior by many animals (Vilhunen & Hirvonen 2003; Eilam 2005), including gudgeons. We used latency to start moving as a measure of boldness (Thorlacius et al. 2015; Hirsch et al. 2017). Many, but not all, individuals of both species displayed some degree of freezing behavior after being introduced into the test arena. About half of *G. gobio*, and only about a third of *G. benacensis*, did not resume voluntary movement during the experiment. The latency to start moving, however, was highly variable among individuals, and no statistically significant difference between species was detected. Importantly, the high proportion of *G. gobio* not moving at all depress the total distance moved metric, indicating that anti-predator behavior may have a strong confounding effect on the result of the open field test and the unanticipated interspecific difference in total distance moved.

Unexpectedly, 3 weeks after the initiation of the experiments fish in the hatchery tank started to die, and within 9 days all *G. benacensis* and one third of *G. gobio* were lost. Although not initially part of the study design this represent a difference in survival in a heavily altered but controlled and predator-free environment. The ability to cope with stressful or degraded environments is often associated with successful species invasion, either from original characteristics or through introduction bottlenecks acting as a selective filters within the species (Moyle & Marchetti 2006; Chapple et al. 2012). Having evolved in a separate ecosystem, non-native species might also be less susceptible to local pathogens (Dove 2000) or be tolerant carriers of pathogens that have a detrimental effect on the local fauna (Reynolds 1988; Tompkins et al. 2003; Gozlan et al. 2005). For example, the invasive topmouth gudgeon has, as a healthy carrier of an intracellular eukaryotic parasite, caused mass mortalities in native sun bleak under controlled conditions (Gozlan et al. 2005). In our case, the mortality observation comes from one tank that housed all our fish, and the cause and mechanism of the mass mortality observed are unknown. Although the high mortality in *G. benacensis* in sympatry with its European congener – be it from pathogens, environmental stress or their interaction – highlights potential mechanisms for the ongoing replacement process (Bianco & Ketmaier 2005), and calls for future controlled and replicated experiments.

The potential loss of *G. benacensis*, and its replacement by its European sister species, constitutes an irreversible loss of biodiversity, in line with the homogenization of the freshwater fauna that is ongoing, at various scales, around the globe (Rahel 2007). The reported differences in swimming capability, behavior and sympatric survival, together with the previously acknowledged size difference, between *G. benacensis* and *G. gobio* may play a role in the replacement of the former with the latter (Bianco & Ketmaier 2005; Fortini 2016). The larger size alone likely increases fecundity (Nagendran et al. 1981) and reduces susceptibility to predation from gape-restricted predators for the European compared to the Italian gudgeon (Christensen 1996). Higher swimming capabilities, in addition, may increase feeding success and opportunity, as well as further facilitate predator avoidance (Christensen 1996) affecting the two species' relative fitness. In addition, inter-population differences have been reported to cause cascading ecosystem effects in guppies and alewifes (Post et al. 2008; Bassar et al. 2010). Similarly, the rise of *G. gobio* in Italy, in combination with interspecific differences, may also have impacts on the surrounding ecosystem, and the prey and predators that have coevolved with the Italian species.

The ongoing replacement of *G. benacensis* with its non-native European sister species is not a problem unique to gudgeons. Just in Italy, a multitude of Central European species are, more or less silently, replacing their native sister species (Lucentini et al. 2011; Carosi et al. 2017; Zaccara et al. 2020; Delmastro et al. 2022; Polgar et al. 2022) with behavioral and ecological differences remaining unknown. In this paper, the comparison of swimming performance, behavior and survival in the laboratory contribute to fill this knowledge gap. Future work, however, must go beyond simple arena trials and also study the species' behavior and ecology in the wild, including their respective responses to different environmental conditions (Lobon-Cervia et al. 1991) and stressors.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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