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Research Article

Competitive interactions for food resources between invasive Ponto-Caspian gobies and their native competitors in the context of global warming

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Abstract

Climate warming can modify the process of biological invasions by affecting the outcomes of competition between alien species and their native counterparts in invaded environments. Inland freshwaters are particularly vulnerable to the intensification of such phenomena due to the accumulation of invaders, including thermophilic species that may benefit from warming. We intended to check whether an elevated summer temperature (25 vs. 17 °C) affects the abilities of the Ponto-Caspian gobies to compete for food. These fish are considered temperature-tolerant, highly invasive freshwater fish in Europe. In laboratory experiments, we tested single- and two-species pairs of juvenile specimens of two goby species and their native counterparts from the same ecological guild (the racer goby *Babka gymnotrachelus* versus European bullhead *Cottus gobio*, and monkey goby *Neogobius fluviatilis* versus native gudgeon *Gobio gobio*). The fish competed for food (live chironomidae larvae provided at rates below satiation) for 1 hour at night. We analysed behaviours associated with direct interactions (aggression acts) and foraging activity (time to enter the feeder and the time spent in the feeder). We found that although the gobies did not show higher aggression than the natives, they more actively accessed food compared to the latter, irrespective of temperature. Our results suggest that, in the wild, the invasive fish have a competitive advantage over the native ones due to better resource allocation (gaining food without incurring the costs of aggression) and will maintain this advantage as water warming continues.

Key words: Aggressive behaviour, biological invasions, climate change, food competition, freshwater species, nonnative species

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Introduction

Nowadays, biological invasions constitute a leading threat to global biodiversity (Chandra and Gerhardt 2008; Lambertini et al. 2011; Ricciardi et al. 2013; Reid et al. 2019) with adverse impact on native populations (Dudgeon et al. 2006). This is especially true for freshwater ecosystems exposed to strong human impact (Reid et al. 2019; Bernery et al. 2022), which have been colonised by non-native species to a greater extent than human-affected terrestrial habitats (Dudgeon et al. 2006; Ricciardi and MacIsaac 2010).

Invasions of alien species can be aided by changes in environmental conditions, such as climate warming (Walther et al. 2009; Bellard et al. 2013; Chown et al.

2015; Früh et al. 2017). Climate warming is a global phenomenon that causes multiple changes in the functioning and distribution of organisms, including animals (Isaak and Rieman 2013; Estay et al. 2014; Vázquez et al. 2017). Current scenarios predict an average temperature increase by 2–5 °C (depending on the assumed carbon dioxide emission) by the end of this century (Estay et al. 2014; IPCC 2014). It is worth noting that ectothermic animals are especially sensitive to temperature changes, as their physiology (Vinagre et al. 2014; Marras et al. 2015; Stoffels et al. 2017; Barker et al. 2018) and behaviour (Briffa et al. 2013; Magellan et al. 2019) depend on the ambient temperature. Many invasive species evolved under warmer conditions than their native counterparts, therefore their establishment in novel areas is correlated with ongoing global warming (Hellmann et al. 2008; Rahel and Olden 2008; Jones and Cheung 2015; Hesselschwerdt and Wantzen 2018).

The Ponto-Caspian region constitutes the major donor of alien taxa for European waters (Bij de Vaate et al. 2002; Galil et al. 2007), including several species of goby fish (Gobiidae) (Copp et al. 2005; Roche et al. 2013). The Ponto-Caspian invaders migrate to inland waters of Central and Western Europe through the European river network connected by artificial canals (Bij de Vaate et al. 2002; Pauli and Briski 2018; Soto et al. 2023). Since the 1990s, gobies have quickly increased their ranges throughout Europe (Bij de Vaate et al. 2002; Galil et al. 2007), exerting a strong impact on the environment. The gobies evolved in limans and deltas of Ponto-Caspian rivers where the water temperature reaches 29 °C in July, suggesting the higher upper-temperature tolerance limit of local organisms (Rewicz et al. 2014) compared to central, eastern, and northern European areas. Thus, the invasion of the Ponto-Caspian gobies in Central and Western Europe seems to be linked to the progressive increase in the mean annual temperature (Harka and Bíró 2007).

The success of the Ponto-Caspian gobies is often linked to their effective competition (Kakareko et al. 2013; Jermacz et al. 2015; Grabowska et al. 2016, 2019). Due to their competition with local ichthyofauna, they change the abundance and taxonomic composition of the local benthic fish communities (Gurevitch and Padilla 2004; Kornis et al. 2012; Jakovlić et al. 2015), sometimes contributing to the displacement of native species (Kakareko et al. 2013; Grabowska et al. 2016). The latest studies have shown that the outcomes of interspecific competition between Ponto-Caspian gobies and their native counterparts are variable and can depend on species, size, and reproductive status (Kakareko et al. 2013; Jermacz et al. 2015; Błońska et al. 2016; Grabowska et al. 2016). For example, the racer goby *Babka gymnotrachelus* (Kessler, 1857) revealed greater aggressiveness than the native European bullhead *Cottus gobio* Linnaeus, 1758 of comparable size, being a stronger competitor (Kakareko et al. 2013). On the other hand, the monkey goby *Neogobius fluviatilis* (Pallas, 1814) did not exhibit competitive advantage against European bullhead (Błońska et al. 2016).

Ongoing global warming can reconfigure interspecific interactions between invasive species and their native counterparts (Taniguchi et al. 1998; Oyugi et al. 2012; Carmona-Catot et al. 2013; Ramberg-Pihl et al. 2023), potentially increasing existing and generating new negative effects of invasions (Taniguchi et al. 1998; Carmona-Catot et al. 2013; Ramberg-Pihl et al. 2023). The ability of the Ponto-Caspian gobies to maintain their resting metabolism (SMR) within a range of 17–25 °C at a constant and relatively low level compared to their native

counterparts can be an important trait responsible for their invasive potential (Kłosiński et al. 2024). This way, the gobies can allocate saved energy to interspecific food competition and have an advantage over native species from the same ecological guild.

The tolerance to elevated temperature and competitive efficiency are separate issues which likely interact with each other, but their interacting effects are unknown. Therefore, we aimed to study these interactions experimentally. First, we assumed that interspecific competition between alien gobies and their native counterparts belonging to the same ecological guild is an effect of overlapping food niches (Peiman and Robinson 2010). Second, we assumed that the invasive status of the gobies has been already determined by earlier studies (Copp et al. 2005; Roche et al. 2013; Vilizzi et al. 2019, 2021), and we are looking for their traits contributing to their invasive potential, i.e. their capability to expand and thrive in new areas. In our study, we compared behaviours associated with interference (aggression) and consumptive (exploitative) competition (rapid access to the food source and time spent on feeding) at two different summer temperatures (17 and 25 °C). A temperature of 17 °C reflects the mean temperature recorded in the warm half-year in rivers in central Poland (Marszelewski and Pius 2014, 2016). In turn, 25 °C refers to the mean annual temperature in the warmest month in rivers in central Poland (Marszelewski and Pius 2014, 2016), but is expected to occur more and more often, and for longer periods with ongoing climate change. In contrast to the native species, the invasive gobies had a chance to evolve mechanisms that enabled them to tolerate relatively high temperatures. We hypothesized that the invasive gobies, compared to their native counterparts, are superior in a direct competition for food. Their advantage will be manifested by higher aggression towards their native competitors than towards conspecifics, visiting the food source faster, spending more time in the feeding area, and limiting the access of the natives to the feeding ground. Moreover, we hypothesized that this competitive advantage of gobies over the native species will become more pronounced at 25 than 17 °C.

Materials and methods

Animals

We tested two goby species of Ponto-Caspian origin, the racer goby and monkey goby, paired with their coexisting native competitors: the European bullhead and gudgeon *Gobio gobio* (Linnaeus, 1758), respectively. These two pairs of species were chosen as they co-occur in the same habitats of European freshwater environments sharing similar biology and ecology (Kakareko et al. 2016; Piria et al. 2016; Janáč et al. 2018; Płąchocki et al. 2020). Thus, interspecific competition between the alien gobies and their native counterparts can be an effect of their overlapping food niches (Peiman and Robinson 2010). The test species have similar food preferences: benthic invertebrates, especially chironomid larvae (Welton et al. 1991; Declerck et al. 2002; Grabowska and Grabowski 2005; Kakareko et al. 2005; Grabowska et al. 2009, 2024). We obtained juvenile fish from lowland rivers in October-November 2022. European bullhead and racer goby were caught in the River Brda (53°08'52.5"N, 17°58'10.5"E), a tributary of the lower River Vistula, by scuba divers using aquarium nets. At this locality, both species are quite

common and reach similar densities (ca. 60 specimens per 100 m^2 each) on the river bottom. There is some habitat overlap between small (juvenile) individuals of the two species, with an inverse relationship between their densities, suggesting that competition among them is likely (Kakareko et al. 2016). We collected the fish from four sites (each of about 25 m^2) from areas of a depth of ca. 1–2 m and moderate (0.3–0.6 m s^{-1}) water velocity over small stones and gravel, i.e. where their co-occurrence is most pronounced (Kakareko et al. 2016). Gudgeon and monkey goby were collected by electrofishing (EFGI 650, BSE Bretschneider Spezialelektronik, Germany) in the lower River Vistula (52°26'23.9"N, 19°56'32.5"E). Both species are, in general, common in the river, with the monkey goby considered more abundant than gudgeon in the near-shore fish assemblages (Kakareko et al. 2009; Błażejewski et al. 2022). We collected these species from several sites accessible from the shore by wading, with sandy or sandy-muddy bottoms, and low to moderate flow. Directly after capture, fish were transported to the laboratory (ca. 1–3 h transport time) in polythene bags with oxygenated water. In the laboratory, the fish were placed in 350-L stock tanks with 20–30 individuals of each species per tank, at a temperature measured in the wild (10 °C). After a few days, the temperature in the stock tanks was gradually raised to 17 °C. All specimens used for the tests were of 0+ age. They had no external signs of sexual maturity, thus we did not determine their sex. The stock tanks were filled with conditioned tap water and equipped with aquarium filters, aerators and stony and ceramic shelters, but no bottom substrate. The temperature was maintained by air conditioning at 17 °C. We fed the fish daily with unfrozen chironomid larvae *ad libitum* and uneaten prey were removed from the stock tanks. We exchanged ca. 30% of water volume in the stock tanks once a week. The fish were allowed to adapt to laboratory conditions for at least 1 month before the start of temperature acclimation.

Acclimation procedure to test temperatures

Fish were transferred from the stock tanks to 85-L acclimation tanks in groups of 10–12 individuals, at an initial temperature of 17 °C (as in the stock tanks). The acclimation tanks were filled with conditioned (24 h aged, aerated) tap water and furnished in the same way as the experimental tanks (see below, “Experimental setup”). The progressive adjustment of a temperature up to 25 °C was reached within 8 days using aquarium heaters with an accuracy of 0.25 °C (AQUAEL Ultra Heater 150 W; Suwałki, Poland). During acclimation, fish were fed *ad libitum* once a day with unfrozen chironomid larvae and uneaten prey were removed from the acclimation tanks. Food was delivered with a small amount of water to the acclimation tank on the Petri dish (a feeder placed on the bottom) through the PVC hose and the transparent glass tube. The fish to be tested at 17 °C were transferred from the stock tanks to the acclimation tanks for the same amount of time, but not subject to other temperature alterations. After 8 days in the acclimation tanks, when the temperature reached 25 °C, the fish were transferred to the experimental tanks.

Experimental setup

Experiments were carried out in 27-L tanks (30 × 30 × 30 cm) filled with aged (24 h), aerated tap water. To reduce the effects of handling and visual disturbance on the test fish, the experimental tanks were isolated on all sides by Styrofoam

screens. Each tank was furnished with an aerator, two shelters, aquarium heater (between the shelters), and feeder (Suppl. materials 1, 2). Each shelter was made of a PVC tile leaned against the tank wall at an angle of 49 degrees) in the corner of the tank. The two shelters ensured a refuge for both fish outside the feeding periods to mitigate competitive tensions them. The feeder was located opposite the shelters and heater. The feeder consisted of a Petri dish (attached to the experimental tank bottom with silicone glue), a transparent glass tube (attached to the tank wall with silicone glue, suspended 0.5 cm above the Petri dish bottom) and a PVC hose (coming out of the glass tube on the top and extending beyond the tank) (Suppl. material 1). Food (live chironomid larvae) was flushed with a small volume of water into the Petri dish through the hose and glass tube. The construction allowed us to apply food while minimizing the disturbing effect of the experimenter's presence on the fish. We recorded the experiment using an IP video camera (SNB–6004P, Samsung, Changwon, South Korea) suspended 0.8 m above the water level. Because the test species are nocturnal (see below, "Experimental procedure"), we used infrared lamps (MFL-I/ LED5-12 850 nm, eneo, Rödermark, Germany) for recording in darkness.

Experimental procedure

We took the fish for the research randomly, firstly from the field and then from the stock tanks. The total length of the fish was measured from digital photographs taken during tests using ImageJ 1.53k (freeware by W.S. Rasband, U.S. National Institutes of Health, Bethesda, Maryland, USA: https://imagej.net/ij/). Mean (± SD) total lengths (TL) were: 4.68 ± 0.58 cm, 4.87 ± 0.67 cm, 4.70 ± 0.69 cm and 5.31 ± 0.52 cm for the racer goby, bullhead, monkey goby and gudgeon, respectively. Within each species pair, the fish were tested in dyads of similar TL (average difference in TL of 0.10–0.26 cm). Mean TLs of fish in pairs were not significantly different between the species (Student's t tests for dependent samples; see Suppl. material 3 for details). The fish were tested either at 17 or 25 °C in (1) single species treatments: two conspecifics, invasive or native; and (2) mixed species treatments: one individual of the invasive species and one individual of the native species. Altogether, we used 71 individuals of the racer goby, 65 individuals of the European bullhead, 78 individuals of the monkey goby and 78 individuals of the gudgeon. In total, we conducted 146 replicates (n for a specific treatment = 7–14, see Suppl. material 3 for specific numbers of replicates in particular treatments).

The last feeding took place 40 h before the beginning of the experiment. Two fish (depending on the treatment) were selected from the acclimation tanks and placed in the experimental tank 16 h (at 15:00) before the start of the trial to get familiar with the experimental arena (the adaptation period) (Suppl. material 2). The air stone was turned off before the beginning of the experimental test to prevent water surface movement, which could disturb the video analysis. The tests were always conducted on the following day at 07:00. In the stock, acclimation, and experimental tanks, the photoperiod was set at 12:12 h light:dark cycle with lights on at 10:00 and off at 22:00. Experiments were carried out during the nighttime because the test species are nocturnal and thus their activity (including foraging) is highest at night (Prenda et al. 2000; Erös et al. 2005; Grabowska and Grabowski 2005; Kobler et al. 2012;

Kakareko et al. 2013; Grabowska et al. 2016; Nowak et al. 2019, our preliminary observations). The video camera was turned on at 07:00 and immediately the food (live chironomidae larvae) was delivered manually to the feeder (Suppl. material 2). Fish behaviour was recorded for the next 1 h (07:00–08:00) (Suppl. material 2). This timing was established based on preliminary research, and literature data (Bachman 1984; Taniguchi et al. 1998). Food dose was established as 20–25 mg of live chironomid larvae (2.12–2.65% of the fish weight), which was below the satiation level for one individual (estimated based on preliminary observations). This allowed us to maintain competitive tension between the individuals for limited food resources at the start of the test. Specimens were used only once during the experiments, and subsequently transferred to separate post-experimental tanks with the same water temperature as in the test (Suppl. material 2). After the tests, the elevated temperature in post-experimental tanks was gradually decreased to 17 °C.

Processing video data

Analysis of all the video recordings of fish behaviour was carried out manually, always by the same person, to avoid bias due to differences in the interpretation of fish behaviour. We noted one variable related to aggression and two variables related to foraging: (1) the number of aggressive actions directed towards the opponent, when one fish moved quickly towards the other, which ended in a physical contact between the individuals, such as hitting or pushing (so, the opponents had to touch each other at some moment of the interaction to count the event as aggression). This allowed us to establish clear, strict and objective criteria of aggressiveness, which did not raise any doubts about their correct assessment by the observer; (2) the time to enter the feeder for the first time by each individual; (3) the percentage of time spent by the fish directly in the feeder, which was used as a proxy for food consumption, as it was challenging to observe it directly in darkness. We assume this as a good proxy for foraging, especially in the initial period of the exposure, directly after the food application, when the food was present in the feeder for sure. The animal needed to be present inside the feeder at this moment to have access to the food. In the one-species treatments, because of the visual similarity of the individuals, it was not possible to track them without mistaking particular individuals on video frames. Instead, the two individuals of the same species were tracked together and the final response consisted of summed up and averaged responses of these individuals.

Statistical analysis

We conducted the following types of statistical analyses: (i) comparison between the species within each pair in their single-species treatments (to test differences between the species); (ii) comparison between the species within each pair in the mixed-species treatment (to check which species has an advantage over the other when they are confronted in the same area); (iii) comparison of the behaviour of each species between the mixed vs. single species treatments (to test the impact of one species on the other). Dependent variables tested in the analyses were as follows: (i) the number of aggression events determined in six consecutive 10-min

periods during the exposure (analysed using a General Linear Mixed Model; the use of a Generalized Linear Model designed for count data was not possible due to non-integer data points averaged for single species pairs); (ii) the time spent in the feeder (analysed using a General Linear Mixed Model); (iii) the time to enter the feeder (analysed using a Cox proportional hazard regression to account for the individuals that did not enter the feeder at all). Independent variables were as follows: (i) species (in the comparisons between the species); (ii) treatment (in the comparison between the mixed vs. single species treatments for each species); (iii) temperature (17 and 25 °C); (iv) exposure time counted since the food introduction to the feeder (for the models testing the number of aggression events and time spent in the feeder, a continuous covariate: 10, 20, 30, 40, 50, 60 min), (v) individual pair ID as a random factor (to group repeated measurements for each pair of individuals). Species was a within-subject factor when the species tested in mixed-species treatments were compared to each other. The summary of all the models used in the study is shown in Suppl. material 4. In the above-mentioned models, we included all main effects and interactions and then applied backward simplification of the models by removing non-significant higher-order interactions. To meet the assumptions of the General Linear Model, we tested normality with a Shapiro-Wilk test as well as homoscedasticity with a Levene test. We log-transformed the exposure time, time spent in the feeder and number of aggression events to achieve normality. To disentangle significant interactions between exposure time and categorical factors, we used partial models to check: (1) significances of regression slopes for each categorical level; (2) differences between pairs of significant slopes for different categorical levels; (3) differences between the intercepts (means) of parallel or non-significant slopes for different categorical levels. We conducted all statistical analyses using the SPSS 29.0 statistical package (IBM Inc., USA).

Results

The number of aggression events (racer goby vs. European bullhead)

In all treatments, the number of aggression events exhibited by the racer goby and European bullhead decreased with time (a significant effect of exposure time), but was independent of temperature (Table 1, Fig. 1A–D). The number of intraspecific aggression events exhibited by these fish in the single-species treatments (Fig. 1A) depended on a significant main effect of species (Table 1): the racer goby revealed a significantly greater number of aggression events towards conspecifics (0.8 aggressive events on average during the entire 1-h exposure) than the European bullhead (0.1 events on average).

The numbers of interspecific aggression events displayed by the racer goby and European bullhead in the mixed-species treatment (Fig. 1B, 0.7 events on average) did not differ between the species (Table 1).

The racer goby showed similar levels of intra- and interspecific aggression (Fig. 1C), as shown by a non-significant effect of treatment (single vs. mixed-species) (Table 1). Whereas, the number of interspecific aggression events exhibited by the European bullhead was higher than that directed towards conspecifics (Fig. 1D), as shown by a significant effect of treatment (Table 1).

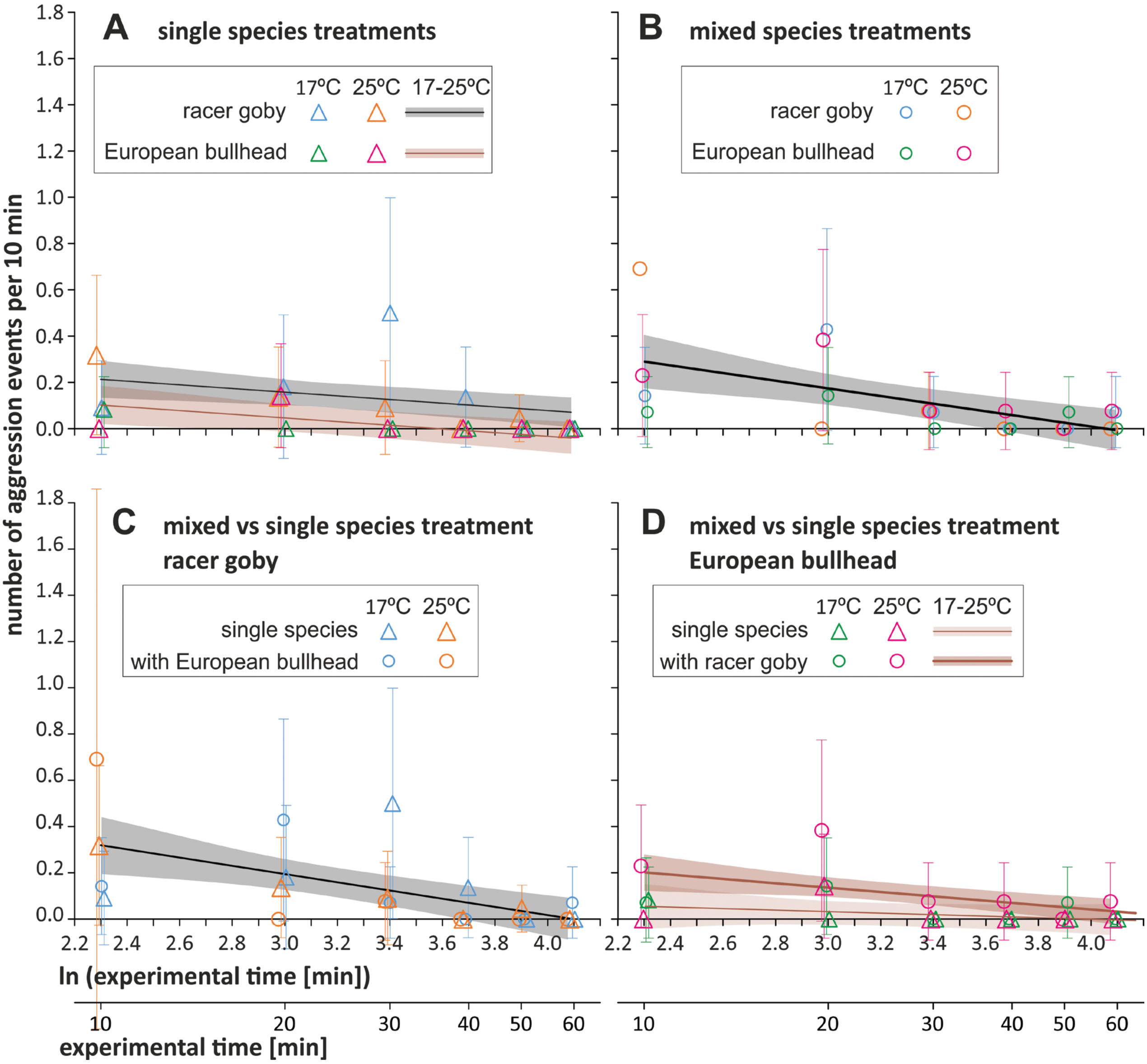

Figure 1. Numbers of aggression acts per 10 min (a single observation period) shown by the racer goby and European bullhead kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Panels **C, D** present comparisons of the behaviour of the racer goby and European bullhead, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models.

The number of aggression events (monkey goby vs. gudgeon)

In the single-species treatments (Fig. 2A), the monkey goby and gudgeon displayed similar levels of intraspecific aggression (0.3 aggression events on average during the 1-h exposure), irrespective of temperature, but decreasing with time (Table 2, Fig. 2A).

The number of interspecific aggression events displayed by these fish in the mixed-species treatment (Fig. 2B) depended on an interaction between species and exposure time, but was independent of temperature (Table 2, Suppl. material 5). This resulted from the significantly greater interspecific aggression of the gudgeon (1.8 aggression events on average during the entire 1-h exposure, including 0.8 events within the first 10 min) compared to that displayed by the monkey goby (0.1 events, all during the first 10 min) at the beginning of the exposure.

Table 1. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the number of aggressive events shown by the racer goby and European bullhead. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Racer goby vs European bullhead from single-species treatments	Species	1, 38	8.43	0.006*
	Temperature	1, 38	0.43	0.519
	Exposure time ^{C}	1, 204	7.85	0.006*
Racer goby vs European bullhead from the mixed-species treatment	Species^{WS}	1, 295	0.33	0.565
	Temperature	1, 25	0.75	0.395
	Exposure time^{C}	1, 295	13.78	<0.001*
Racer goby from mixed- vs single-species treatments	Treatment	1, 46	0.001	0.976
	Temperature	1, 46	0.09	0.766
	Exposure time^{C}	1, 244	13.40	<0.001*
European bullhead from mixed- vs single-species treatments	Treatment	1, 43	4.81	0.034*
	Temperature	1, 43	3.81	0.057
	Exposure time^{C}	1, 229	8.69	0.004*

^{WS} – within-subject effect, ^{C} – continuous covariate.

Table 2. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the number of aggressive events shown by the monkey goby and gudgeon. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Monkey goby vs gudgeon from single-species treatments	Species	1, 47	0.11	0.746
	Temperature	1, 47	0.06	0.806
	Exposure time^{C}	1, 249	13.73	<0.001*
Monkey goby vs gudgeon from the mixed-species treatment	Species^{WS} (Spec.)	1, 305	17.58	<0.001*
	Temperature	1, 26	1.06	0.313
	Exposure time^{C} (Time)	1, 305	17.28	<0.001*
	Spec.^{WS}*Time	1, 305	12.18	0.001*
Monkey goby from mixed- vs single-species treatments	Treatment	1, 50	1.88	0.177
	Temperature	1, 50	1.41	0.241
	Exposure time^{C}	1, 264	9.05	0.003*
Gudgeon from mixed- vs single-species treatments	Treatment (Treat.)	1, 279	9.42	0.002*
	Temperature (Temp.)	1, 279	1.56	0.212
	Exposure time (Time)^{C}	1, 261	19.98	<0.001*
	Treat.*Temp.	1, 279	6.06	0.014*
	Treat.*Time	1, 261	6.36	0.012*
	Temp.*Time	1, 261	1.28	0.259
	Treat.*Temp.*Time	1, 261	5.12	0.024*

^{WS} – within-subject effect, ^{C} – continuous covariate.

The monkey goby displayed similar levels of intra- and interspecific aggression (single vs. mixed-species treatments) irrespective of temperature (Fig. 2C), but decreasing with exposure time (Table 2).

On the other hand, the number of aggression events shown by the gudgeon (Fig. 2D) depended on an interaction between treatment (single vs. mixed-species), temperature and exposure time (Table 2). The aggression of gudgeon directed towards the monkey goby at 17 °C (2.2 events on average during the entire exposure, including 1.7 events within the first 20 min) was higher than that directed towards conspecifics (0.2 events, all within the first 20 min) at the beginning of the exposure, and decreased later, as shown by its significant slope (Suppl. material 5,

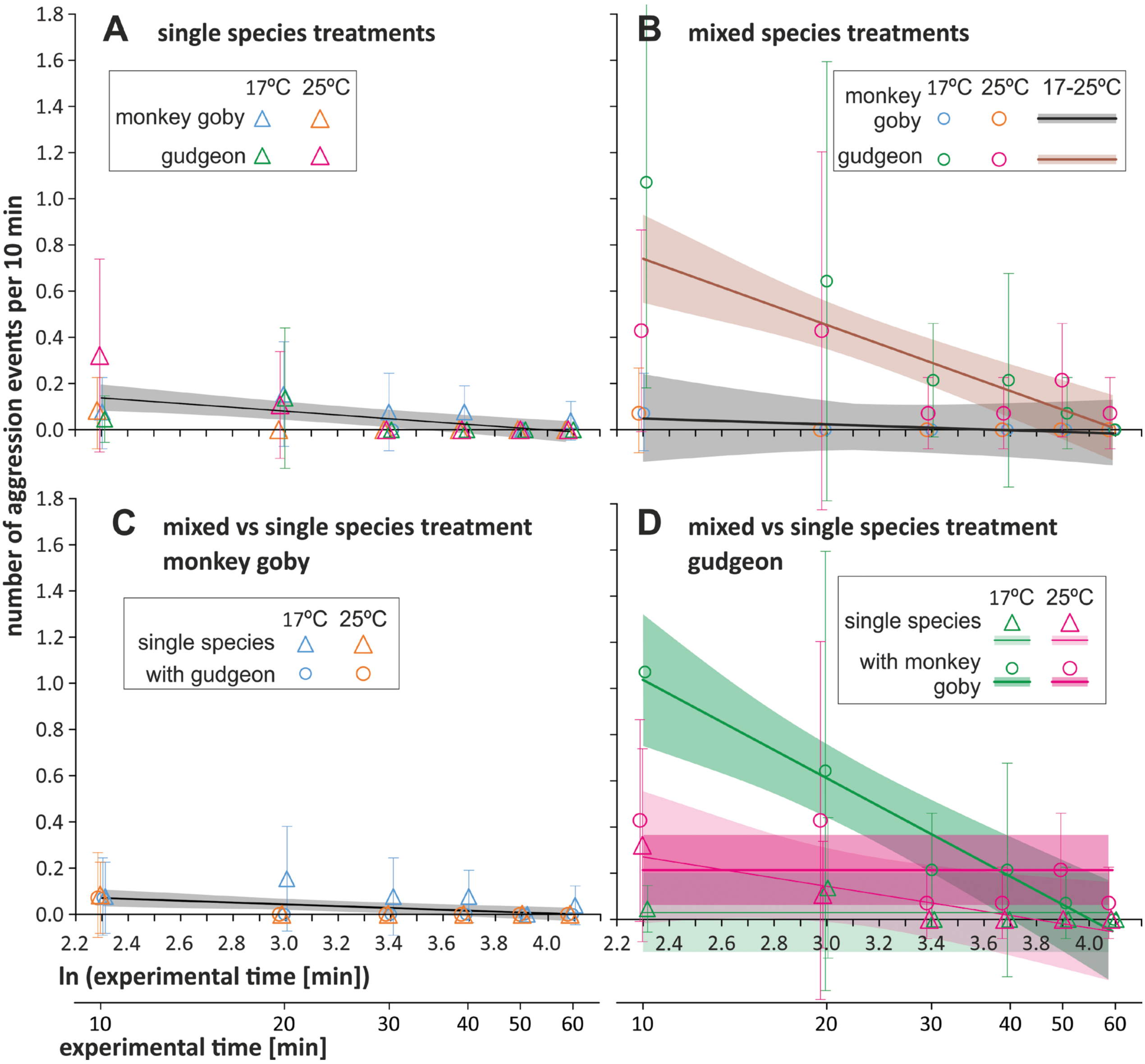

Figure 2. Numbers of aggression acts per 10 min (a single observation period) shown by the monkey goby and gudgeon kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Panels **C, D** present comparisons of the behaviour of the monkey goby and gudgeon, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models. Horizontal lines indicate non-significant slopes.

Fig. 2D). At 25 °C, the gudgeon showed similarly low levels of intra- and interspecific aggression (0.1 events, Fig. 2D).

Time to enter the feeder (racer goby vs. European bullhead)

In the single-species treatments (Fig. 3A) the racer goby entered the feeder earlier (after 2 min on average) than European bullhead (9 min), irrespective of temperature (Table 3).

In the mixed-species treatment (Fig. 3B), the racer goby entered the feeder faster (4.5 min and 13 min at 17 and 25 °C, respectively) than the European bullhead (22.5 min and 36.5 min, respectively), and both species appeared in the feeder faster at 17 vs. 25 °C (Table 3).

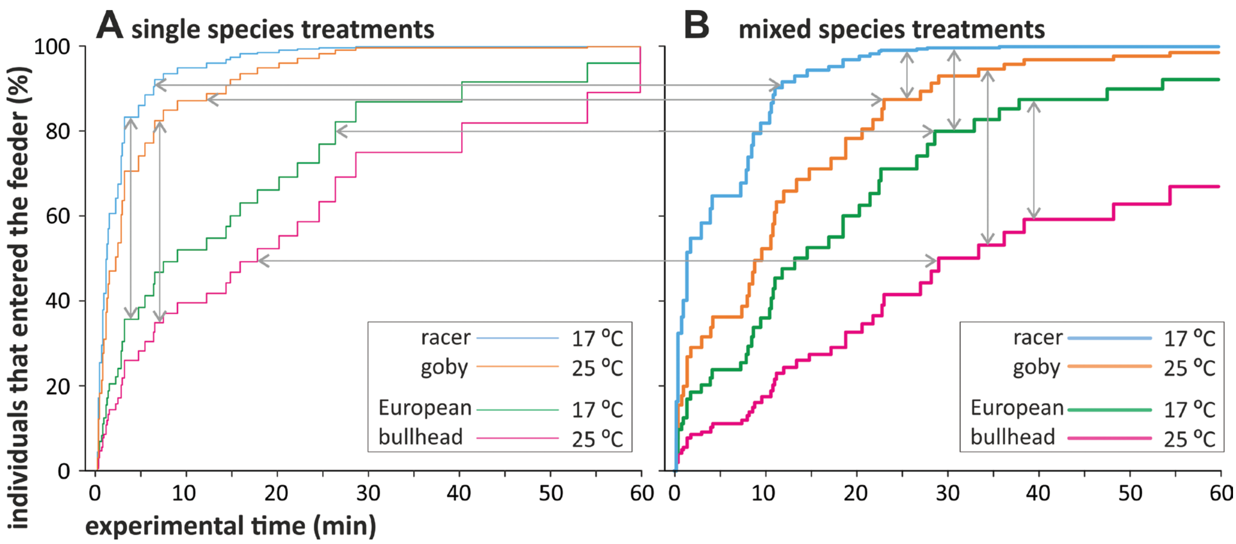

Figure 3. Times to enter the feeder by the racer goby and European bullhead kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Arrows indicate groups significantly differing from each other.

Table 3. Cox proportional hazard regression models to test the effect of treatment, temperature and species on the time to enter the feeder by the racer goby and European bullhead.

Analysis	Effect	*df*	χ^2	*P*
Racer goby vs European bullhead from single-species treatments	Species	1	12.92	<0.001*
	Temperature	1	1.16	0.282
Racer goby vs European bullhead from the mixed-species treatment	Species	1	17.54	<0.001*
	Temperature	1	6.99	0.008*
Racer goby from mixed- vs single-species treatments	Treatment	1	4.96	0.026*
	Temperature	1	4.45	0.035*
European bullhead from mixed- vs single-species treatments	Treatment	1	10.58	<0.001*
	Temperature	1	0.63	0.429

The racer goby reached the feeder earlier in the presence of conspecifics than with the European bullhead (Table 3, Fig. 3A, B). The European bullhead also entered the feeder earlier in the presence of conspecifics than with the racer goby, irrespective of temperature (Table 3, Fig. 3A, B).

Time to enter the feeder (monkey goby vs. gudgeon)

In the single-species treatments (Fig. 4A), the monkey goby entered the feeder earlier (9 min and 3.5 min at 17 and 25 °C, respectively) than the gudgeon (21 min and 7.5 min, respectively), and both species appeared in the feeder faster at 25 vs. 17 °C (Table 4).

In the mixed-species treatment (Fig. 4B), the monkey goby entered the feeder earlier (8 min) than the gudgeon (19.5 min) irrespective of temperature (Table 4).

The entry time to the feeder shown by the monkey goby and gudgeon was independent of the species identity of the other individual in the pair (Table 4, Fig. 4A, B).

Time spent in the feeder (racer goby vs. European bullhead)

In the single-species treatments (Fig. 5A), both the racer goby and European bullhead spent more time in the feeder at 17 than 25 °C (3.4 vs. 1.9% of the total exposure time) throughout the exposure time as indicated by a significant main

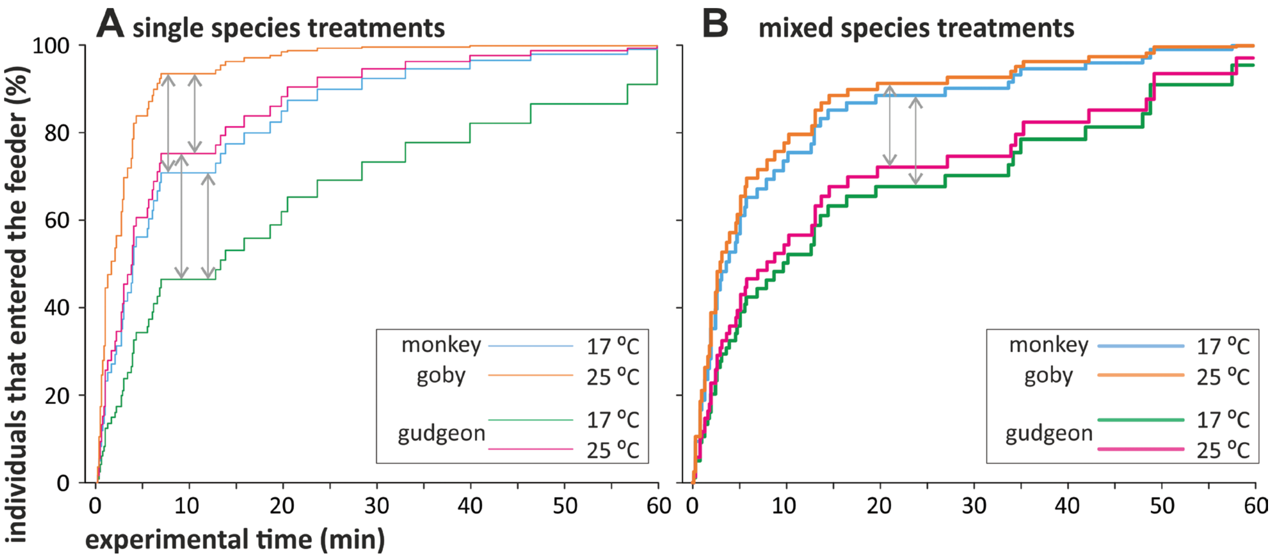

Figure 4. Times to enter the feeder by the monkey goby and gudgeon kept in separate single-species treatments (**A**) or together in the mixed-species treatment (**B**). Arrows indicate groups significantly differing from each other.

Table 4. Cox proportional hazard regression models to test the effect of treatment, temperature and species on the time to enter the feeder by monkey goby and gudgeon.

Analysis	Effect	*df*	χ^2	*P*
Monkey goby vs gudgeon from single-species treatments	Species	1	5.33	0.021*
	Temperature	1	6.42	0.011*
Monkey goby vs gudgeon from the mixed-species treatment	Species	1	4.74	0.029*
	Temperature	1	0.18	0.671
Monkey goby from mixed- vs single-species treatments	Treatment	1	0.56	0.454
	Temperature	1	0.10	0.754
Gudgeon from mixed- vs single-species treatments	Treatment	1	1.51	0.219
	Temperature	1	7.84	0.005*

effect of temperature (Table 5). Moreover, time spent in the feeder decreased with time (Fig. 5A, Table 5), but differently for each species, which resulted in a significant interaction between species and exposure time (Table 5, Suppl. material 6). The racer goby spent more time in the feeder than the European bullhead at the beginning of exposure (10.0 vs. 2.7% during the first 10 min of the exposure), but not at the end (Fig. 5A).

The presence of heterospecifics in the mixed-species treatment (Fig. 5B, C) did not affect the time spent in the feeder by the racer goby and European bullhead, compared to their behaviour in the single-species treatments, as shown by a non-significant effect of treatment (Table 5).

Time spent in the feeder (monkey goby vs. gudgeon)

In the single-species treatments (Fig. 6A), time spent by the monkey goby and gudgeon in the feeder depended on species*exposure time and temperature*exposure time interactions (Table 6). Time spent in the feeder by both species decreased with time at different rates, depending on species and temperature (Suppl. material 6). At the beginning of the exposure, both species spent more time in the feeder at 25 °C than at 17 °C (4.9 vs. 2.1% of time during the first 20 min of the exposure),

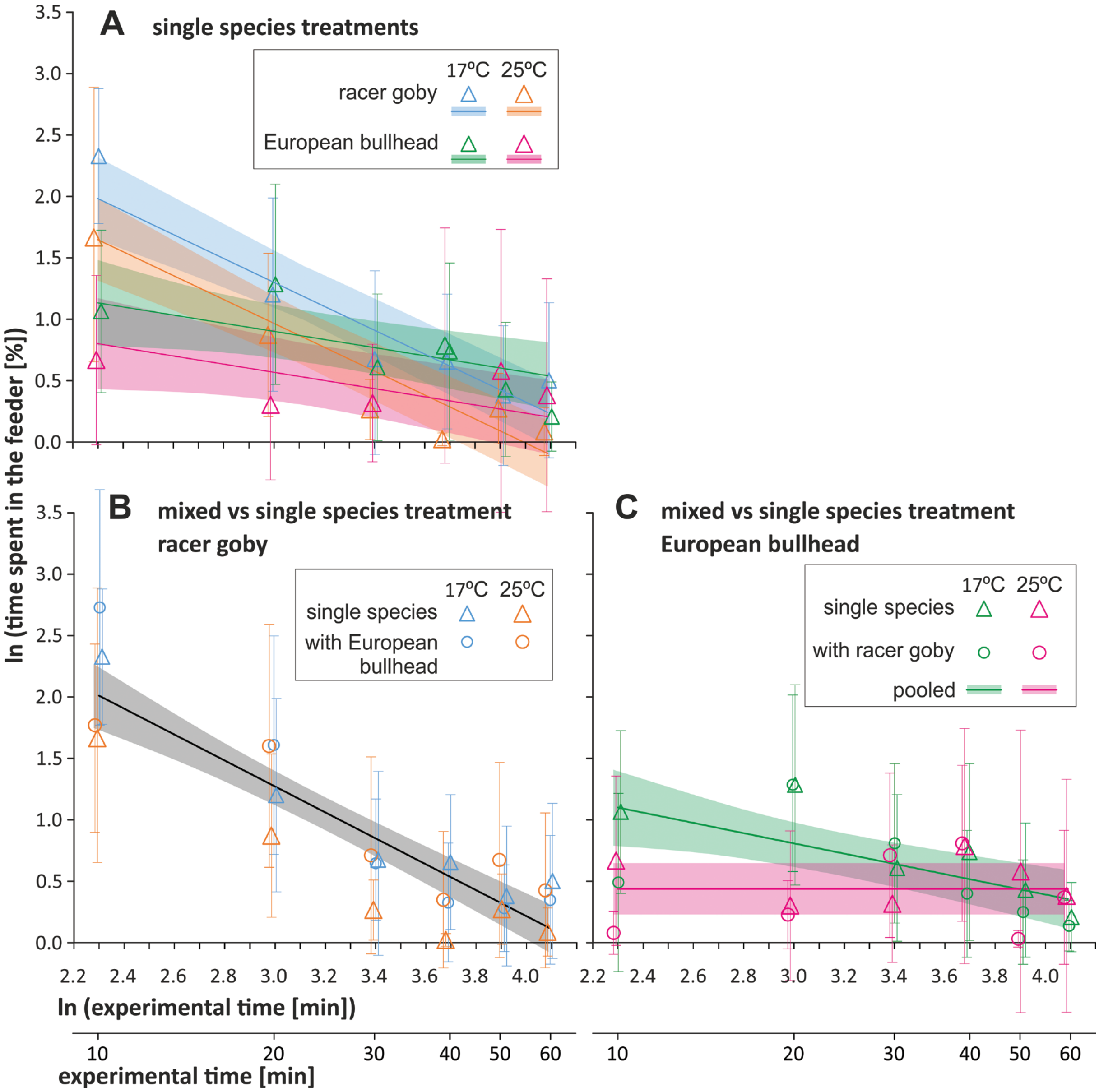

Figure 5. Times spent in the feeder (as percentage of the total exposure time) by the racer goby and European bullhead kept in separate single-species treatments (**A**). Panels **B, C** present comparisons of the behaviour of the racer goby and European bullhead, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models. Horizontal lines indicate non-significant slopes.

and the monkey goby spent more time in the feeder than the gudgeon (4.7 vs. 2.3% of time during the first 20 min of the exposure).

The feeder was occupied for a longer time by the monkey goby in the presence of the gudgeon in the mixed-species treatment (6.9% of the total exposure time, Fig. 6B) than in the single-species treatment (2%) throughout the exposure duration, as shown by a significant main effect of treatment (Table 6).

Whereas the gudgeon spent more time in the presence of conspecifics than with the monkey goby, but only at the beginning of exposure at 25 °C (6.7 vs. 4.0% of time during the first 20 min of the exposure, Fig. 6C), as shown by a significant interaction between treatment (single vs. mixed-species treatment), temperature and exposure time (Table 6, Suppl. material 6).

Table 5. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the feeder occupancy time shown by the racer goby and European bullhead. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Racer goby vs European bullhead from single-species treatments	Species (Spec.)	1, 220	14.44	<0.001*
	Temperature	1, 38	6.74	0.013*
	Exposure time (Time)^C	1, 203	55.08	<0.001*
	Spec.*Time	1, 203	13.30	<0.001*
Racer goby from mixed- vs single-species treatments	Treatment	1, 46	2.43	0.126
	Temperature	1, 46	2.95	0.093
	Exposure time^C	1, 244	103.98	<0.001*
European bullhead from mixed- vs single-species treatments	Treatment	1, 43	1.32	0.258
	Temperature (Temp.)	1, 246	9.10	0.003*
	Exposure time (Time)^C	1, 228	3.19	0.075
	Temp.*Time	1, 228	7.59	0.006*

^{C} – continuous covariate.

Table 6. General Linear Mixed Models to test the impact of treatment, temperature, exposure time and species on the feeder occupancy time shown by the monkey goby and gudgeon. Non-significant higher order interactions were removed from the models in a simplification procedure.

Analysis	Effect	*df*	*F*	*P*
Monkey goby vs gudgeon from single-species treatments	Species (Spec.)	1, 264	27.41	<0.001*
	Temperature (Temp.)	1, 264	20.27	<0.001*
	Exposure Time (Time)^C	1, 247	91.76	<0.001*
	Spec.*Time	1, 247	24.71	<0.001*
	Temp.*Time	1, 247	17.78	<0.001*
Monkey goby from mixed- vs single-species treatments	Treatment	1, 50	8.28	0.006*
	Temperature	1, 50	0.03	0.871
	Exposure time^C	1, 264	108.14	<0.001*
Gudgeon from mixed- vs single-species treatments	Treatment (Treat.)	1, 290	0.06	0.803
	Temperature (Temp.)	1, 290	8.10	0.005*
	Exposure time (Time)^C	1, 261	14.47	<0.001*
	Treat.*Temp.	1, 290	3.58	0.060
	Treat.*Time	1, 261	0.02	0.889
	Temp.*Time	1, 261	6.28	0.013*
	Treat.*Temp.*Time	1, 261	4.00	0.046*

^{C} – continuous covariate.

Discussion

Present work supported the first hypothesis that the non-native gobies are more successful food competitors than their native counterparts. Although the invaders did not consistently outperform the natives in terms of higher aggression, they revealed faster and longer food access compared to the natives. However, the second hypothesis was not confirmed. The effect of an elevated temperature on interspecific competition did not translate into a more apparent dominance of the gobies over the native fish.

Aggression

In single-species treatments, the racer goby was more aggressive than the European bullhead. In contrast, the gudgeon and monkey goby did not differ in level of aggression in the second pair of co-existing species. This finding suggests that aggressive

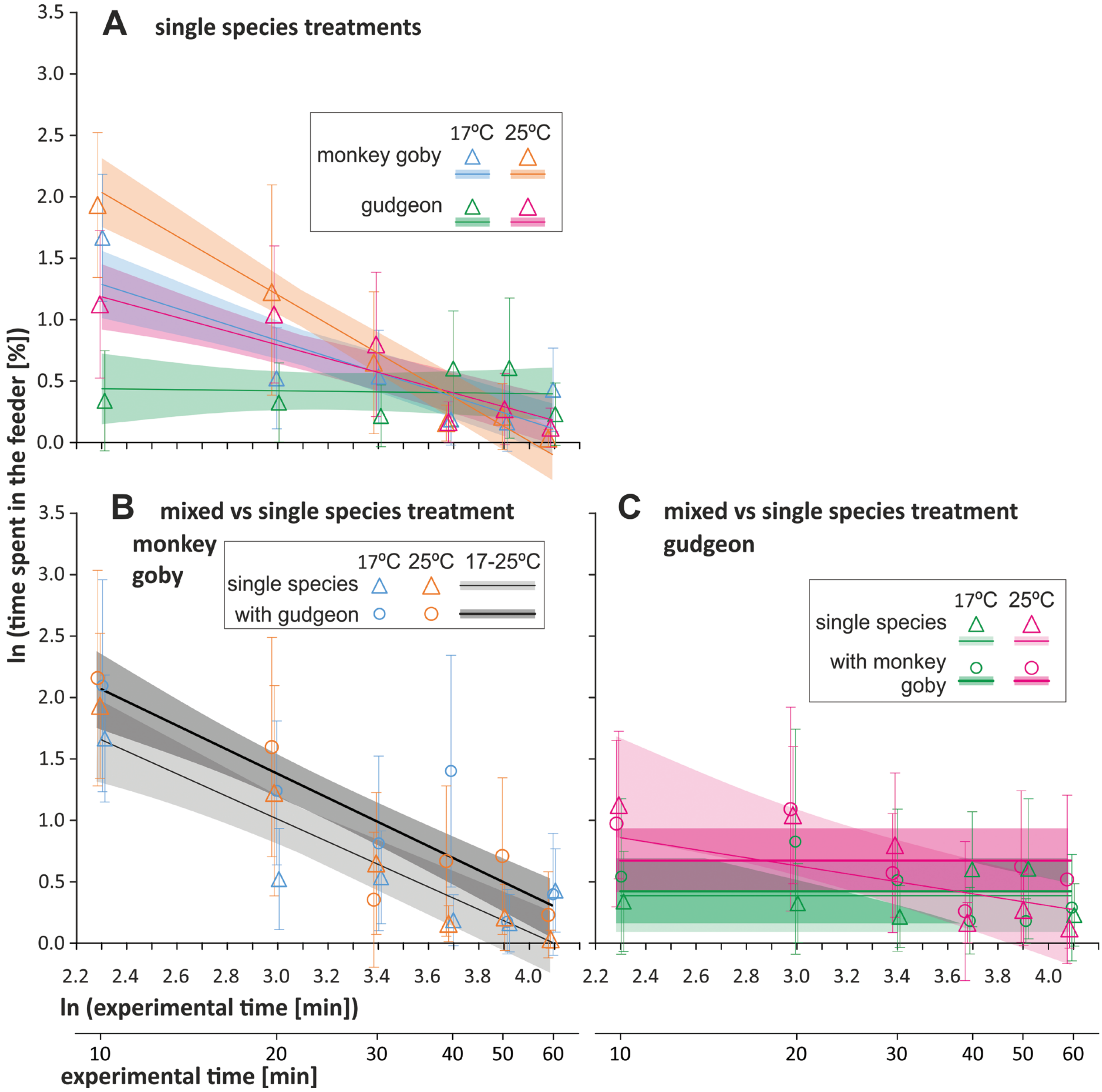

Figure 6. Times spent in the feeder (as percentage of the total exposure time) by the monkey goby and gudgeon kept in separate single-species treatments (**A**). Panels **B, C** present comparisons of the behaviour of the monkey goby and gudgeon, respectively, between the single- and mixed-species treatments. Symbols represent raw data (means ± 95%CI) for each species, temperature and period. Lines are predicted by the models (with 95%CI as shaded areas). Common slopes were predicted for groups of data that did not differ significantly from each other in the models. Horizontal lines indicate non-significant slopes.

behaviour is of primary importance for establishing intra-species dominance in the racer goby, while it is not so in the other species tested. Interestingly, relatively higher aggression was revealed in inter-species interactions in these species in our study (Ladich 1988, 1990, 1997; Hadjiaghai and Ladich 2015; Horvatić et al. 2016, 2021; Fattorini et al. 2023). According to the resource overlap hypothesis (Connell 1983; Britton et al. 2010; Peiman and Robinson 2010), intraspecific aggression is usually stronger than interspecific one because of the greater niche similarity between conspecifics compared to heterospecifics (Kornis et al. 2014). While, in the present work, the native species increased their aggression in the presence of their invasive counterparts. Moreover, the gudgeon was more aggressive towards the monkey goby

than the other way round. These findings are also surprising in the light of the fact that, in general, invasive fish species have been found to display higher levels of aggression than native fish species (Blanchet et al. 2007; Martin et al. 2010; Kakareko et al. 2013), which is considered an important behavioural mechanism determining the competitive superiority of successful invaders (Pintor et al. 2008; Hudina et al. 2014; Silva et al. 2019). Although the opposite situations can be found e.g., in native cichlids: the Kariba tilapia *Oreochromis mortimeri* (Chifamba and Mauru 2017) and the Mexican mojarra *Cichlasoma istlanum* (Archundia and Arce 2019), these are rather rare. In the case of the Ponto-Caspian gobies, earlier laboratory experiments on adult individuals have demonstrated that the higher aggressiveness allowed them to gain an advantage over native species (Kakareko et al. 2013; Jermacz et al. 2015; Grabowska et al. 2016). Nevertheless, relatively high aggression of invasive gobies in those experiments could depend on their larger size (associated with older age and maturity) than that of the gobies tested in the present work (Logue et al. 2011; Funghi et al. 2015; Beltrão et al. 2021; Diatroptov and Opaev 2023), especially during the spawning period (Grabowska et al. 2016). On the contrary, we showed that juvenile specimens of the invasive gobies exhibited lower aggression against their native counterparts (except the gudgeon at 25 °C). It is worth noting that aggression can depend on metabolic traits (Seth et al. 2013; Killen et al. 2014). Species with relatively high standard (resting) metabolism displayed more aggression (Metcalfe et al. 1995; Cutts et al. 1998). Indeed, our findings are supported in this respect by the results of Kłosiński et al. (2024), who showed that the native species from the same populations and similar in size to those studied in this work exhibit a higher resting metabolism compared to the invasive gobies. This indicates that juveniles of native gudgeon and European bullhead have a potential to expend energy on activities associated with aggressive behaviour. Although such behaviour, as mentioned earlier, is not displayed by the natives in intra-population interactions, it is activated when confronted with juvenile gobies (less aggressive than older individuals). This suggests that the native fish treat juvenile gobies as weaker opponents than conspecifics when assessing the risk of defeat before deciding to start fighting. Nevertheless, in our study, despite the aggression displayed by the natives, the invasive gobies could reach the feeder more efficiently than their native competitors. Thus, the aggression of the native fish turned out to be ineffective against the alien competitors.

The relationship between temperature and aggression acts can be variable. Elevated temperature can either increase (Wilson et al. 2007; Seebacher et al. 2013) or decrease aggression level (White et al. 2019), or cause no changes in aggression (White et al. 2020). In our study, the gudgeon was less aggressive against the monkey goby at 25 °C than at 17 °C. This inability to maintain the constant level of aggression could be accounted for by the temperature elevated beyond its physiological tolerance (Kłosiński et al. 2024), causing a relatively high energy demand. Thus, the gudgeon might have suppressed costly aggressive acts in favour of reaching the feeder earlier to compensate for metabolic costs associated with elevated temperature (Morgan et al. 2001). From the metabolic point of view, aggressive behaviours are associated with relatively high energetic expenditures (Briffa and Sneddon 2007; Seebacher et al. 2013; Fisher et al. 2021), which are expected to have adverse consequences for fitness in the natives.

Regarding the first pair of fish studied, we found that the aggression shown by the European bullhead and racer goby was independent of temperature. This indicates the potential of the European bullhead to survive in warming waters, assuming they have

access to abundant food resources and meet increased energy needs under such conditions. According to Killen et al. (2013), the greater the metabolic scope, the faster the recovery after the effort, and the lower probability that aggressive behaviour is constrained by maximal metabolic capacity. A higher aerobic scope shown by the European bullhead compared to the racer goby, both at 17 and 25 °C (Kłosiński et al. 2024), can allow it to show a greater flexibility in energy allocation (Maazouzi et al. 2011; Killen et al. 2016). On the other hand, allocating too much energy in aggression can lead to the depletion of energy resources for other life activities, such as anti-predatory defences or foraging (Sneddon et al. 1999; Seebacher et al. 2013; Chifamba and Mauru 2017). Therefore, aggression can be beneficial if food resources are possible to defend (Peiman and Robinson 2010). However, our study suggests this is not the case for juvenile European bullhead facing the racer goby invasion in the wild. This is because, in our experiment, the bullhead aggression was insufficient to effectively defend the food resource against the invasive competitor (see the subchapter below).

Foraging

We posit that the time to enter the feeder and the time spent in the feeder should be considered together. These two behaviours are likely to act together in the same direction to enhance the probability of success in food resource competition. Both gobies tended to reach the feeder before their native counterparts. This was likely to limit foraging of their native competitors and provided the invasives with better access to the richest food resources (directly after the food application), which has also been shown for larger (adult) European bullhead and racer goby (Kakareko et al. 2013). Thus, competition between invasive gobies and their native counterparts is likely to depend on the exploitation of resources by the invaders, successfully reducing the foraging time of the natives (Keiller et al. 2021). This has been demonstrated in our study for the monkey goby-gudgeon pair. Alternatively, even if the native species spent the same time in the feeder as their invasive counterparts, the food could have already been eaten by the gobies, being earlier visitors in the feeder. This has been shown in the racer goby-European bullhead pair in our study.

An elevated temperature delayed the time to enter the feeder by the invasive racer goby, despite the fact that this species originates from a warmer climate than that in its invaded range. Hence, increased temperature may have a disruptive effect not only on natives, but also on invasive species. However, the native species, being less adapted to elevated temperatures, can use even more energy or even limit their foraging (thus causing difficulties with obtaining energy) at 25 °C. Therefore, in the longer term, indirect (exploitation) competition (Vonshak et al. 2012; Newman et al. 2020) may adversely affect native species more than invasives as waters become warmer. It is worth emphasising that of the Ponto-Caspian Gobiidae, the round goby (*Neogobius melanostomus*) has received the greatest attention in terms of successfully competing for food with native fish (Grabowska et al. 2023). Janssen and Jude (2001) proposed that interference competition, rather than exploitation competition, was the primary mechanism for declines in the mottled sculpin populations following the round goby invasion. Less attention has been given to the other goby species from the Ponto-Caspian region, which have expanded to many European inland waters. For the first time, we showed that interspecific competition between juvenile individuals of these gobies and their native counterparts is based on the ability to gain better (faster and longer) access to food resources

rather than on direct aggression. Moreover, the ability to assess their chances and avoid a direct conflict with an opponent allows animals to minimize their energy loss and risk of injuries (Parker and Rubenstein 1981; Moretz 2003; Poulos and McCormick 2014), which is consistent with the non-aggressive (fight-avoiding) behaviour of juvenile invasive gobies in our experiment.

Final remarks

Our study has shown that, regardless of summer temperatures (normal or elevated) that occur in Central European rivers, the juvenile invasive gobies are more effective than their native counterparts in competing for access to limited food resources. This finding broadens the knowledge of the threat posed by the Ponto-Caspian gobies towards native European freshwater fishes (see a review by Grabowska et al. 2023), although it does not support the growing evidence for the negative influence of elevated temperatures on native fish species in competitive interactions with invasive species (Taniguchi et al. 1998; Oyugi et al. 2012; Ramberg-Pihl et al. 2023). In our study, the native fish, although more aggressive, could not effectively compete with the juvenile individuals of the gobies irrespective of temperature. This suggests that, in the wild, the juveniles of the invasive gobies have a competitive advantage over natives, gaining better access to food without the cost of aggression, and will maintain this advantage as waters get warmer. It is worth bearing in mind that the gobies have been proven to outperform the natives in other aspects of global warming. They have lower living costs by keeping a lower resting metabolism at the elevated temperature (Kłosiński et al. 2024) and show a greater physiological tolerance to hypoxia (Kłosiński et al. 2025), which is considered another effect of global warming in fresh waters (Ficke et al. 2007; Jane et al. 2021). Therefore, the future invasion success of the alien gobies owing to efficient food competition may be even enhanced by warming waters, although further studies are needed to confirm this.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

We sampled and used the fish by the permit of the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland, statement no. 30/2022 from 22 June 2022. In addition, the capture and use of the European bullhead, which is protected by law in Poland, was accepted by the Regional Directorate of Environmental Protection in Bydgoszcz, Poland (approval number: WOP.6401.4.52.2022.MO). The procedures conducted within the study met the ASAB/ABS guidelines for the use of animals in research (ASAB Ethical Committee and ABS Animal Care Committee 2019). The housing conditions guaranteed a high level of animal welfare, which was manifested by the overall activity and food intake of the fish throughout the research period. The fish had no external signs of stress or disease. Each specimen was used only once. After the experiments, the European bullhead and gudgeon were released into the wild from which they were caught. In turn, racer goby and monkey goby, as invasive species were euthanized by an overdose of buffered Tricaine Methanesulfonate (MS-222) and disposed of according to the Regulation of the Polish Minister of the Environment from 9 September 2011 (Journal of Laws No. 210, item 1260). Killing was conducted by a qualified, certified person (certificate No. 2355/2015 issued by the Polish Laboratory Animal Science Association).

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Author contributions

PK: Conceptualisation, Resources, Methodology, Investigation, Formal analysis, Data interpretation, Visualisation, Writing-Original draft preparation. JK: Conceptualisation, Resources, Formal analysis, Data interpretation, Visualisation, Writing-Review & Editing. TK: Conceptualisation, Resources, Methodology, Data interpretation, Writing-Review & Editing, Supervision.

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Data availability

The data that support the findings of this study are available from the corresponding author, PK, upon reasonable request.

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Supplementary material 1

Experimental setup

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: tif

Explanation note: Experimental setup (all the dimensions are given in mm).

Link: https://doi.org/10.3897/neobiota.97.134566.suppl1

Supplementary material 2

Experimental procedure

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: tif

Explanation note: Experimental procedure.

Link: https://doi.org/10.3897/neobiota.97.134566.suppl2

Supplementary material 3

Numbers of replicates and individual size differences in particular experimental treatments

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: Numbers of replicates (*n*) and individual size (total length, TL) differences in particular experimental treatments (pairs of fish in particular species configurations tested at specific temperatures). Individual sizes were compared between the species within each species pair in each experimental treatment using t-tests for dependent samples.

Link: https://doi.org/10.3897/neobiota.97.134566.suppl3

Supplementary material 4

The summary of all the models used in the study

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: The summary of all the models used in the study.

Link: https://doi.org/10.3897/neobiota.97.134566.suppl4

Supplementary material 5

Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the number of aggression events shown by the monkey goby and gudgeon (see Table 2)

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the number of aggression events shown by the monkey goby and gudgeon (see Table 2).

Link: https://doi.org/10.3897/neobiota.97.134566.suppl5

Supplementary material 6

Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the time spent in the feeder by the racer goby and European bullhead (see Table 5), as well as by the monkey goby and gudgeon (Table 6)

Authors: Piotr Kłosiński, Jarosław Kobak, Tomasz Kakareko

Data type: docx

Explanation note: Tests of slope significance for particular levels of categorical factors interacting with exposure time in their effects on the time spent in the feeder by the racer goby and European bullhead (see Table 5), as well as by the monkey goby and gudgeon (Table 6).

Link: https://doi.org/10.3897/neobiota.97.134566.suppl6