

1 Title

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3 The role of intraspecific competition in the dispersal of an invasive fish

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5 Running title

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7 Dispersal of an invasive fish

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## 30 **Summary**

31 1. Ponto-Caspian gobies are among the most successful fish invaders in inland waters of Europe  
32 and in the Great Lakes of North America. Their invasions appear to comprise a combination of  
33 passive and active dispersal mechanisms, both natural and human-mediated. Despite the  
34 significance of Ponto-Caspian gobies as invasive species, there is little information about the  
35 mechanisms underpinning their dispersal. They are relatively small benthic fish, with high site  
36 affinity. Thus, actively dispersing individuals must express a behavioural motivation to engage  
37 in persistent directional movement.

38 2. Several recent studies have suggested that inter-individual behavioural differences in  
39 boldness, activity level and tendency to explore might underpin dispersal. In addition, because  
40 males are highly territorial, intraspecific competition may lead to density-dependent dispersal  
41 of subordinate individuals. To date, studies on this subject have focused mainly on comparisons  
42 between individuals from the core of established populations with those at the margins and,  
43 thus, address the outcome of dispersal rather than the mechanism itself.

44 3. We conducted a series of experiments on the racer goby *Babka gymnotrachelus* to address  
45 the question of what behavioural and physiological traits predict the tendency of an individual  
46 to perform dispersal behaviour, specifically considering the role of conspecifics in influencing  
47 the tendency to disperse. We used an artificial channel to measure dispersal tendency in this  
48 species in combination with behavioural trials.

49 4. Our results showed that fish with a greater tendency to disperse in an experimental channel  
50 grew slowly, were bolder; i.e. displayed a greater propensity to emerge from a cryptic  
51 background onto a white background, and performed worse in prey capture trials. As predicted,  
52 intraspecific competition played a primary role in the dispersal of the racer goby. Dominant

53 males showed a tendency to monopolize limited shelters with an outcome that subordinates  
54 were forced to disperse upstream. The specific growth rate of individuals appeared to be a good  
55 indicator of social position. Subordinate males expressed the lowest rates of growth, probably  
56 as a result of long-term deprivation of food in the presence of dominant conspecifics. They were  
57 also quicker to explore novel environments, possibly to search for food. Contrary to  
58 expectations, subordinate individuals performed relatively poorly in feeding trials when tested  
59 individually.

60 5. Our findings suggest that intraspecific competition in racer goby males is an important  
61 mechanism for active dispersal. It can also influence inter-individual variation in traits like  
62 boldness and tendency to explore novel environments. Similar responses to competitive  
63 interactions may have encouraged the invasive expansion of other Ponto-Caspian gobies  
64 following establishment in new environments, as well as other fish species that exhibit  
65 territorial behaviour.

66

## 67 **Introduction**

68 Biological invasions, where species are translocated to new geographical areas where they  
69 establish and spread, are a major cause of concern because of the potentially negative ecological  
70 and economic impacts of invading taxa (Blackburn et al., 2014). Global trade and  
71 communication directly contribute to the transport of wildlife across biogeographical  
72 boundaries and there is growing evidence of the negative effect of these movements on the  
73 integrity of native biota and even the irretrievable loss of some species; invasive species are  
74 recognised as one of the principal threats to global biodiversity (Simberloff et al., 2013).  
75 Freshwater species are declining faster than both marine and terrestrial species and appear  
76 particularly susceptible to the impact of invasions (Ricciardi & Rasmussen, 1999; Ricciardi &

77 McIsaac, 2011). Freshwater fish are among the most impacted group of animals affected by  
78 introductions of alien species (Vitousek, D'antonio, Loope, Rejmanek & Westbrooks, 1997),  
79 mostly from the introduction of species for aquaculture, recreational fishing, the aquarist trade  
80 and biocontrol (Casal, 2006). Invasive fish species are also associated with inadvertent transport  
81 in ballast waters, or from range expansion facilitated by the removal of geographic barriers,  
82 such as the connection of isolated sea basins by canals (Copp et al., 2005).

83         Five species of Ponto-Caspian gobies; round goby (*Neogobius melanostomus*), monkey  
84 goby (*Neogobius fluviatilis*), western tubenose goby (*Proterorhinus semilunaris*), bighead goby  
85 (*Ponticola kessleri*) and racer goby (*Babka gymnotrachelus*), are among the most successful  
86 fish invaders in inland waters of Europe, and two of these species (round and tubenose) are now  
87 also present in the Great Lakes of North America (Copp et al., 2005). These species have  
88 expanded from the Ponto-Caspian region to West and Central Europe through a system of  
89 artificial canals that connect the Black and Caspian Sea basins with the North and Baltic Sea  
90 basins (Bij de Vaate, Jazdzewski, Ketelaars, Gollasch, & Van der Velde, 2002). In many  
91 locations these invasive gobies constitute the most numerous component of fish assemblages  
92 (Roche, Janač, & Jurajda, 2013; Van Kessel, Dorenbosch, Kranenbarg, Van der Velde, &  
93 Leuven, 2016). The impact of these goby species on native fauna has yet to be fully  
94 characterised, but interspecific competition is one possible mechanism by which they may have  
95 an impact, which is supported by experimental studies (Błońska, Kobak, Kakareko, &  
96 Grabowska, 2016; Błońska, Kobak, & Grabowska, 2017; Jermacz, Kobak, Dzierżyńska, &  
97 Kakareko, 2015).

98         The primary drivers of the range expansion of Ponto-Caspian gobies in Europe are  
99 equivocal. Anthropogenic changes to large European rivers have been proposed as factors  
100 facilitating their expansion, including alteration of river banks, flow regime (e.g. damming),  
101 water quality parameters (salinity and temperature) and intensification of boat traffic (reviewed

102 by Roche et al., 2013). Invasive gobies are relatively small benthic fish, without a swim bladder  
103 and with poor swimming ability. Thus, their rapid, long-distance upstream dispersal has been  
104 explained through passive dispersal *via* shipping (Ahnelt, Banarescu, Spolwind, Harka, &  
105 Waidbacher, 1998; Wiesner, 2005; Roche et al., 2013). Their small size, cryptic behaviour and  
106 habit of spawning in cavities may facilitate their rapid transport in ballast waters or hull fouling  
107 outside their original range. This mechanism particularly explains their well-characterized  
108 dispersal in the River Danube system (Roche et al., 2013). An additional mechanism of  
109 dispersal is through downstream drift of juveniles, which has been documented in the round  
110 and tubenose gobies (Janáč, Šlapanský, Valová, & Jurajda, 2013). Long-distance dispersal with  
111 shipping or drift permits the foundation of new populations that serve as the source for  
112 secondary dispersal through short-distance movements. Thus, goby invasions appear to  
113 comprise a combination of passive and active dispersal mechanisms, both natural and human-  
114 mediated. This broad conclusion is supported by genetic data. For example, during the invasion  
115 of the round goby in North America there was no reduction in genetic diversity in adjacent  
116 upstream locations relative to the source lake population, suggesting continuous dispersal rather  
117 than a single, long-distance founding event (Bronnenhuber, Dufour, Higgs, & Heath, 2011).

118         The mechanism of dispersal has implications for the structure of phenotypes on the  
119 margins of an expansion (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Chapple,  
120 Simmonds & Wong, 2012; Chuang & Peterson, 2016). While passive dispersal through juvenile  
121 drift or accidental transport by shipping is predicted to select a random subset of the population,  
122 active dispersal by individuals may favour specific phenotypes (Chapple et al., 2012, Sih, Cote,  
123 Evans, Fogarty, & Pruitt, 2012; Chuang & Peterson, 2016). Dispersing individuals must express  
124 a behavioural motivation to engage in persistent directional movement, particularly in species  
125 that typically display high site affinity. In the case of intraspecific competition, dispersal may  
126 also show density dependence. In Ponto-Caspian invasive gobies, males are highly territorial

127 and aggressively defend their nesting shelters during the reproductive period (e.g. Miller, 1984;  
128 Meunier, Yavno, Ahmed, & Corkum, 2009; Błońska et al., 2016). In this situation, a high  
129 density in the core population may drive dispersal when small and subordinate individuals have  
130 a greater tendency to move.

131 Despite their significance as invasive species, there is little information about the  
132 mechanisms underpinning Ponto-Caspian goby dispersal. To date, studies on this subject have  
133 only considered the round goby with most research focused on comparisons between  
134 individuals from the core of established populations with those at the margins (Brandner,  
135 Cerwenka, Schliewen, & Geist, 2013; Thorlacius, Hellström, & Brodin, 2015; Thorlacius &  
136 Brodin, 2017). Thus, these studies address the outcome of dispersal rather than the mechanism  
137 itself.

138 Here we address the question of what behavioural and physiological traits predict the  
139 tendency of an individual to perform dispersal behaviour, particularly considering the role of  
140 conspecifics in influencing the tendency to disperse. Our goal was to identify the traits that  
141 differentiated individuals that dispersed the greatest distances and specifically whether it was  
142 intraspecific competition that resulted in the displacement of subordinate individuals or instead  
143 whether it was dominant individuals, in better condition, that had the greater propensity to  
144 disperse.

145

## 146 **Materials and methods**

147 The racer goby was selected as the study taxon; this species is an important invasive species in  
148 a number of European river systems and is amenable to experimental work (Semenchenko,  
149 Grabowska, Grabowski, Rizevsky, & Pluta, 2013, Grabowska, Kakareko, Błońska, Przybylski,  
150 Kobak, & Copp, 2016). We obtained 48 males from the lower section of the River Vistula in  
151 Poland (52° 32' 05" N, 19° 41' 12" E), using a backpack electroshocker (EFGI 650,

152 Bretschneider, Germany). Electrofishing was considered the least selective method of  
153 collection while also minimising injuries to fish. Racer gobies have occurred continuously at  
154 this location since 1999 (Kostrzewa & Grabowski, 2001) and can, thus, be considered as a  
155 relatively long-established population. Specimens were collected from the river bank along the  
156 shoreline from a depth of 0.3 - 0.7 m where the racer goby co-occurs with the western tubenose  
157 goby, with both species numerous (approx. ind 2 m<sup>-2</sup>) and representing the most abundant  
158 species in the fish assemblage.

159 Fish were collected on the 2<sup>nd</sup> September 2016, which is outside the reproductive season  
160 for the species (Grabowska, 2005). Dispersal rates were predicted to be higher outside the  
161 spawning period (Brownscombe & Fox, 2012). Fish were transported to the laboratory in  
162 aerated containers and after one day were weighed (to the nearest 10 mg), measured for total  
163 body length (TL, nearest mm) and individually marked with two visible subcutaneous elastomer  
164 tags (Northwest Marine Technology, Inc., USA), following the procedure of Marentette, Wang,  
165 Tong, Sopinka, Taves, Koops, & Balshine, (2011). Fish were assigned to six groups of eight  
166 individuals and allowed to acclimatize for one week in 70-liter experimental aquaria connected  
167 to a recirculation system. Fish were daily fed *ad libitum* with frozen bloodworm.

168 Experiments were conducted in two stages. In Experiment 1 fish were tested in groups  
169 of eight to determine their tendency to disperse. Individuals were assigned to groups based on  
170 comparable body size (TL) to minimise the effect of size differences on behaviour. Mean (sd)  
171 TL of groups 1-6 was 81.9 (6.1), 68.3 (1.5), 67.3 (2.9), 60.4 (2.6), 89.1 (4.6), 74.8 (3.3) mm  
172 respectively. In Experiments 2 and 3 fish were individually tested to evaluate tendency to  
173 explore a novel environment and to measure their predation efficiency.

174 In Experiment 1 the propensity to disperse in an artificial channel was tested. The  
175 experiment was conducted in a semi-natural mesocosm in the Botanic Gardens of the University  
176 of Łódź (Fig. 1). The artificial channel was 8 m long and 0.5 m wide and was supplied with

177 water from an adjacent holding tank of 75 m<sup>3</sup>. Water was circulated through the channel by a  
178 pump with a capacity of 25 m<sup>3</sup> h<sup>-1</sup>, providing constant water flow and aeration, and mimicking  
179 river flow. Mean (sd) water temperature was 17.8 (±1.47) °C over the course of the experiment.  
180 The channel was divided into 17 sectors, each 0.5 m long (except for sector D-1), separated by  
181 plastic netting baffles (mesh size 5 mm) that allowed fish to move up or down the channel  
182 between adjacent compartments through 100 mm wide gaps. Gaps between baffles were offset  
183 alternately to the left and right, which prevented fish from moving from the bottom to the top  
184 of the channel in a straight line and effectively increased the length of the channel to just over  
185 12 m (Fig. 1). The first sector (S1) was 1.5 m long and could be isolated from the rest of the  
186 channel with a door. The last sector (S17) was separated from the adjacent sector with a non-  
187 return funnel to prevent fish that entered it from re-entering the lower sections of the channel.  
188 In each of the other sectors (S2-S16) there was a single shelter, while sectors S1 and S17 each  
189 had 4 shelters. Water flowed from S17 to S1.

190 Fish movement was tested during the day and overnight. For night trials eight randomly  
191 selected individuals were placed in S1 at 1800 h, allowed 2 hours to acclimatize to conditions,  
192 after which the door connecting S1 and S2 was opened. Fish were able to remain in S1 or move  
193 up the channel, through successive sectors, to S17. Fish were left in the channel for 12 hours to  
194 provide them with the opportunity to redistribute themselves over the entire period of darkness.  
195 At 0800 h on the following day, the sector into which each individual had moved was recorded.  
196 The same procedure was performed to test daytime movement, with the experimental procedure  
197 starting at 900 h and continuing until 1700 h. The order in which night and day trials was  
198 conducted was randomized for each fish group. After completion of both trials, all fish were  
199 removed from the outdoor channel and transferred to experimental aquaria. We conducted six  
200 replicate observations on each test group of eight fish (three night-time trials and three day-time  
201 trials) with 3-day intervals between trials. In the period between trials, fish were housed together



202 in experimental aquaria. Trials were conducted between 10/09/16 and 29/10/2016. Sunrise and  
203 sunset at the start of trials was between 0609 h and 1907 h and between 07.31 h and 1719 h at  
204 the end. While in the experimental channel fish were not fed to minimize the risk that food  
205 distribution influenced dispersal. While held in aquaria between trials, experimental fish were  
206 fed *ad libitum*. The total number of sectors through which each individual fish moved across  
207 all 6 replicate observations was taken as a measure of their propensity to move upstream away  
208 from the starting sector, S1.

209 Experiment 2 tested the propensity of fish to explore a novel environment by moving from  
210 a relatively secure environment in which they were concealed, represented by a dark field, to  
211 one with negligible concealment, represented by a white field (Strand, Alanära, Staffan, &  
212 Magnhagen, 2007). To conduct trials, fish were placed individually in a 70 l experimental  
213 aquarium (500 × 400 × 360 mm) with a digital video camera suspended directly above it. To  
214 limit the impact of external cues on fish behaviour, the sides of the aquarium were screened.  
215 The aquarium was divided in a 2:1 ratio with a movable vertical baffle made of plastic netting  
216 separating the larger dark field from the white field area. Each field was created by placing a  
217 piece of either black or white card underneath the respective section of the aquarium. A single  
218 fish was placed in the dark field section for 30 min. and allowed to settle. After this time the  
219 baffle was raised for 90 min., permitting the fish to explore the white field. Camera recordings  
220 were subsequently analysed and scored for: 1. latency to emerge from the dark field (time after  
221 which an individual left the dark field by a full body length, 2. the frequency of departures from  
222 the dark field, 3. the total time spent on the white field. Trials were conducted during daytime,  
223 between 1000 h and 1600 h. Mean (sd) water temperature was 21 ( $\pm 1.10$ ) °C over the course of  
224 the experiment. Aquarium water temperature and photoperiod were adjusted to match  
225 prevailing conditions outdoors.

226 In Experiment 3 fish were individually tested for their prey capture ability. The experiment  
227 was conducted in 10 L aquaria (290 × 190 × 170 mm) at 21 °C between 1000 h and 1600 h.  
228 Prey used in trials were gammarids, which are highly mobile. No substrate was added to aquaria  
229 to deprive prey of refuges. Ten individuals each of two gammarid species, *Dikerogammarus*  
230 *haemobaphes* and *D. villosus*, were added to aquaria prior to the addition of fish to allow the  
231 prey to acclimate to aquarium condition. Both species of gammarid are native to the Ponto-  
232 Caspian region but have invaded the River Vistula and are the most common prey item in the  
233 diet of the racer goby at the collection site (Grabowska & Grabowski, 2005). After 1 h a single  
234 racer goby was gently released into an experimental aquarium and allowed to feed for 3 h. Pilot  
235 studies had shown that this length of time was sufficient for the capture of all the gammarids  
236 by a single goby. At the end of each trial, the fish was removed and any surviving gammarids  
237 were counted.

238 Over the course of all three experiments, the integrity of each group of eight males was  
239 maintained throughout, except for short intervals during Experiments 2 and 3 when single  
240 individuals were removed for testing. Experiments 1-3 were completed for all fish over a three-  
241 month period. At the end of this time all fish were again measured (TL) and weighed (W). The  
242 Fulton index was calculated for each fish at the start of the experiment as a measure of initial  
243 body condition and their specific growth rate, based on length, was calculated over the whole  
244 period of the experiment (Wootton 1998).

245 Experimental procedures were carried out under permits (28/ŁB61/2017) and  
246 (27/ŁB60/2017) from the Local Ethical Committee of the University of Łódź.

247

## 248 **Data analysis**

249 We fitted a Generalised Linear Mixed Model (GLMM) to data with the goal of identifying those  
250 variables that predicted the number of sectors in the experimental channel that individual fish

251 traversed in Experiment 1. Before fitting a model, a data exploration was carried out following  
 252 the protocol of Zuur, Ieno & Elphick (2010). Data were examined for outliers in the response  
 253 and explanatory variables, homogeneity and zero inflation in the response variables, collinearity  
 254 between explanatory variables and the nature of relationships between the response and  
 255 explanatory variables were also examined. Two behavioural covariates (number of emergences  
 256 and time spent on a white background) were dropped from the model due to collinearity. Data  
 257 were modelled using R (version 3.5.0; R Development Core Team 2018) with models fitted in  
 258 a Bayesian framework using Integrated Nested Laplace Approximation (R-INLA; Rue, Riebler,  
 259 Sørbye, Illian, Simpson, & Lindgren, 2017). Data were fitted with a Poisson Generalized Linear  
 260 Mixed Model (GLMM), specified as:

261

$$Distance_{ij} = \text{Poisson}(\mu_{ij})$$

262

$$E(Distance_{ij}) = \text{var}(Distance_{ij}) = \mu_{ij}$$

263

$$\mu_{ij} = \eta_{ij}$$

264

$$\eta_{ij} = \beta_1 + \beta_2 \times SGR_{ij} + \beta_3 \times emergence_{ij} + \beta_4 \times prey_{ij} + group_j$$

265

$$group_j \sim N(0, \sigma_{group}^2)$$

266

267

268 Where  $Distance_{ij}$  is the distance moved by fish in the experimental channel (Experiment 1),  
 269 scored as the total number of sectors through which fish  $i$  passed in experimental group  $j$ , which  
 270 was assumed to follow a Poisson distribution with mean  $\mu_{ij}$  and variance  $\mu_{ij}$  with an identity link  
 271 function. The model contained a linear effect for fish specific growth rate ( $SGR$ ), latency to  
 272 emerge from cover in Experiment 2 ( $emergence$ ), and number of prey eaten in Experiment 3  
 273 ( $prey$ ). An optimal fixed structure of the model was identified with a backward selection  
 274 procedure using Watanabe-Akaike Information Criterion (WAIC) (Vehtari, Gelman, & Gabry,  
 275 2017). The random intercept  $group$  was included in the model to introduce a correlation

276 structure between observations for fish tested together in the same experimental group with  
277 variance  $\sigma^2$ , distributed normally and equal to 0.

278

## 279 **Results**

280 The distance moved by experimental fish was negatively associated with their growth rate, with  
281 fish that grew slowly tending to disperse further in the experimental channel (Fig. 2; Table 1).  
282 Similarly, those that showed a greater propensity to emerge from a cryptic background onto a  
283 white background dispersed further than those that took longer to emerge (Fig. 3; Table 1).  
284 Finally, fish that performed poorly in prey capture trials also showed a greater tendency to  
285 disperse in the experimental channel (Fig. 4; Table 1). Thus, fish that grew slowly, emerged  
286 from a refuge quickly and performed poorly in prey capture trials were predicted to disperse  
287 the greatest distance, while those that grew quickly, were reluctant to emerge from safety and  
288 performed best in prey capture trials were predicted to move least.

289

## 290 **Discussion**

291 We predicted that subordinate individuals that were smaller and in poorer condition would  
292 move a greater distance in an experimental stream in the case that intraspecific competition  
293 plays the primary role in dispersal of the invasive racer goby. These predictions were satisfied,  
294 with males that dispersed the greatest distance in the experimental channel showing the poorest  
295 growth and feeding performance and with a reduced latency to enter a novel environment. As  
296 anticipated, we infer that the social position of an individual after a prolonged period in the  
297 same shoal of fish permitted the establishment of a stable hierarchy that influenced growth rate,  
298 with subordinate males expressing the lowest rates of growth.

299 In the experimental channel dominant males monopolized shelters in the donor section  
300 of the experimental stream, which represented a key limiting resource, with an outcome that

301 subordinates were forced to disperse upstream. Previous research on the racer goby has shown  
302 that dominant males occupy shelters within the first 15 minutes of stocking in experimental  
303 aquaria (Grabowska et al., 2016). There are other clues that shelter availability can be limiting,  
304 resulting in competition in this species. Racer gobies show cryptic behaviour and express a  
305 preference for habitats with hiding places, both under natural conditions and in the laboratory  
306 (Kakareko, 2011; Jermacz et al., 2015; Grabowska et al., 2016). This species is also  
307 crepuscular/nocturnal, spending daylight hours inside a shelter that they leave to forage during  
308 darkness (Grabowska et al., 2016); feeding activity is largely nocturnal (Grabowska &  
309 Grabowski, 2005; Kakareko, Kobak, Grabowska, Jermacz, Przybylski, Poznańska, & Copp,  
310 2013). The affinity of racer gobies for shelter is especially pronounced during the reproductive  
311 season (Jermacz et al., 2015; Grabowska et al. 2016; Błońska et al., 2016), when shelters serve  
312 as nest sites. Because care is exclusively paternal in this species, males occupy shelters for  
313 longer than females (Błońska et al., 2017). While nesting, males show a reduced probability to  
314 disperse (Marentette et al., 2011), presumably because care of eggs and larval stages reinforces  
315 site fidelity. Outside the breeding season, males are more likely to leave refuges and disperse,  
316 consequently the current study was conducted during autumn to maximise the likelihood of  
317 dispersal, though our results suggest that dominant males show restricted dispersal even outside  
318 the breeding season. The limited availability of shelters can lead to both inter- and intraspecific  
319 competition, with aggressive interactions observed among goby species, including racer gobies,  
320 in laboratory settings (Jermacz et al., 2015; Grabowska et al., 2016; Błońska et al., 2017).  
321 During competitive contests fish exhibit overt aggressive behaviour involving biting and  
322 chasing rivals, as well as threat behaviour involving flaring the opercula, gaping and fin raising  
323 (Jermacz et al., 2015; Grabowska et al., 2016).

324         Dominant individuals may also monopolize food resources through aggressive  
325 interactions (reviewed in Ward, Webster, & Hart, 2006). In the present study, the slowest

326 growth rates were seen in males that tended to disperse the greatest distances in the artificial  
327 channel, supporting the prediction of a role for social interactions in driving dispersal. The  
328 formation of stable social dominance is one of the consequences of variation in the relative  
329 competitive ability of an individual (Huntingford & Turner, 1987). Dominant individuals tend  
330 to obtain a disproportionate share of food resources compared to subordinates (reviewed in  
331 Ward et al., 2006). Thus, reduced growth rates observed in our studies among subordinates  
332 resulted from limited feeding opportunities during the three months the fish were kept together  
333 in social groups. Huntingford, Metcalfe, Thorpe, Graham, & Adams (1990) concluded from  
334 studies on Atlantic salmon that greater body size is an effect of dominance in social group rather  
335 than a cause. Food deprivation is a common stimulus for dispersal (Lidicker & Stenseth, 1992).  
336 Hungry fish emerge from shelters and explore novel environments sooner than satiated  
337 individuals, even if it involves risk taking (Gotceitas & Godin, 1991; Godin & Crossman, 1994).  
338 Thus, in the present study the food deprivation experienced by subordinate males, rather than  
339 specific “personality traits”; i.e. boldness or tendency to explore, appears to be the reason why  
340 they had reduced latency to leave a refuge (cryptic background) and enter a novel environment  
341 (white background) when they were tested individually. An outcome was that subordinate  
342 males deprived of food were more willing to engage in risky behaviour and explore novel  
343 environments, possibly to search for food; the proximate cue for this behaviour possibly  
344 stimulated by individual physiological state. The likelihood of emerging from safety can also  
345 be influenced by a number of demographic factors including age and sex, as well as  
346 environmental variables, such as predation risk (Krause, Loader, McDermott, & Ruxton, 1998;  
347 Krause, Loader, Kirkman, & Ruxton, 1999).

348         Assuming that dispersal distance and latency to emerge were a response to individual  
349 state of satiation, mediated by social position, a prediction was that subordinates would eat more  
350 prey in trials to compensate, or at least their consumption rates should not differ from dominant

351 individuals. However, contrary to expectations, subordinate individuals performed relatively  
352 poorly in feeding trials. In experiments in which fish had a limited food supply the initial  
353 response was increased activity, indicative of food searching behaviour (Méndez & Wieser,  
354 1993; Sogard & Olla, 1996). However, following a protracted period of starvation they reduced  
355 activity, possibly as a mechanism to save energy (Méndez & Wieser, 1993; Sogard & Olla,  
356 1996; Van Dijk, Staaks & Hardewig, 2002). In the present study, racer gobies were given the  
357 opportunity to feed on gammarids. Capture of such mobile prey is energy demanding, which  
358 may have had the effect of further worsening their condition resulting in the observed poor  
359 growth performance. In contrast, dominant individuals, which did not leave the donor sector to  
360 disperse in the artificial channel, were more efficient at capturing gammarids in trials,  
361 presumably because they were in better condition.

362         The role of inter-individual behavioural variability in biological invasions has received  
363 growing attention (e.g. Holway & Suarez, 1999; Rehage & Sih, 2004; Chapple et al., 2012).  
364 These previous studies have linked dispersal tendency to behavioural traits such as boldness,  
365 aggression, exploratory tendency, activity level, and sociability (e.g. Sih, Bell, & Johnson,  
366 2004; Duckworth & Badyaev, 2007; Cote et al., 2010), including ‘dispersal syndromes’  
367 (Stevens, Whitmee, Le Gaillard, Clobert, Böhning-Gaese, Bonte, et al., 2014). Notably, studies  
368 on other Ponto-Caspian gobies, such as the round goby, have also demonstrated variation  
369 among populations at different stages of invasion (Myles-Gonzalez et al., 2015, Thorlacius et  
370 al., 2015; Thorlacius & Brodin, 2017), implicating a spatio-temporal component to behavioural  
371 variation. However, the results from the above mentioned studies show striking inconsistencies  
372 and evidence for a common behavioural profile for dispersing individuals is lacking. Thorlacius  
373 et al., (2015) suggested that while the likelihood of inter-individual behavioural differences  
374 might determine dispersal in newly established populations, in source populations dispersal  
375 appears to be a function of competition.

376 Competitive interactions are typically density dependent and can lead to dispersal when  
377 population size is elevated. However, density-dependent effects are context dependent with a  
378 range of proximate factors driving dispersal behaviour. Thorlacius et al., (2015) suggested that  
379 the trigger for dispersal in the round goby in its invasive range may vary with the age of the  
380 population. In newly-established populations individual variation in ‘personality’ traits may be  
381 the main driver of dispersal of some individuals, while in its native range density-dependent  
382 competition may be a more important mechanism underpinning dispersal (Thorlacius et al.,  
383 2015). Thorlacius et al., (2015) concluded that in newly-established populations more active  
384 individuals disperse sooner and that boldness was not connected with dispersal tendency or  
385 dispersal distance. Strikingly, they also showed that behavioural traits were uncorrelated with  
386 individual propensity to disperse in the native population, but there was also a negative  
387 correlation between body size and dispersal tendency, as well as individual condition  
388 (Thorlacius et al., 2015). Thus, like the present study, individuals in poorer condition dispersed  
389 sooner from the experimental flume. The findings of Thorlacius et al., (2015) lend support to  
390 the concept that competition drives dispersal in native populations, where difference in size and  
391 body condition determine the outcome of conflict, with subordinates forced by larger, dominant  
392 individuals to move. In the present study, experimental fish came from a source population that  
393 was founded at least 15 years ago and was relatively well-established. Thus, our findings are  
394 largely in agreement with the predictions of Thorlacius et al. (2015); i.e. that subordinate males  
395 dispersed the greatest distance. Later studies by Thorlacius & Brodin (2017) have demonstrated  
396 phenotypic differentiation between dispersing and resident individuals with dispersers smaller  
397 and expressing less frequent social interactions than in the source population. This finding  
398 suggests that, at least in species that achieve high population densities rapidly, social  
399 interactions may play a more important role than some behavioural traits.



400 We conclude that competition among male gobies drives dispersal outside of the breeding  
401 season, at least in the study population. The broader applicability of our findings in different  
402 reproductive contexts, to females and juveniles, to fish from different source populations, and  
403 to other taxa remains to be demonstrated. However, a comparable mechanism for active  
404 dispersal may underpin dispersal in other Ponto-Caspian gobies, and other fish species that  
405 exhibit dominance associated with territorial behaviour and may facilitate their expansion  
406 outside their native range.

407

#### 408 **Conflicts of Interest**

409 The authors declare no conflicts of interest.

410

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589 **Table 1.** Posterior mean estimates of distance moved in an experimental channel by male racer  
590 gobies modelled using a Poisson GLMM fitted using INLA. CrI is the 95% Bayesian credible  
591 interval. Credible intervals that do not contain zero indicate a statistically important effect.

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Model parameter	Posterior mean	Lower CrI	Upper CrI
Intercept	3.330	3.072	3.587
Specific growth rate	-0.304	-0.385	-0.222
Emergence	0.101	0.035	0.168
Prey capture	-0.203	-0.273	-0.134

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592  
593

594 **Figure Captions**

595 **Figure 1.** Sketch of experimental set-up used to determine distance moved by experimental  
596 racer gobies in an artificial channel (see Materials and methods for description and dimensions).  
597 Fish were released in sector D-1. Water was pumped through the channel continuously. Sectors  
598 were separated by baffles that were offset alternately to the left and right.

599 **Figure 2.** Fitted values of distance moved in an experimental channel (solid line) and 95%  
600 Bayesian credible intervals (shaded area) against specific growth rate ( $\% \text{ day}^{-1}$ ) for racer gobies  
601 modelled using a Poisson GLMM fitted using INLA. Black circles are observed values.

602 **Figure 3.** Fitted values of distance moved in an experimental channel (solid line) and 95%  
603 Bayesian credible intervals (shaded area) against time to emerge (s) from a dark field onto a  
604 white field for racer gobies modelled using a Poisson GLMM fitted using INLA. Black circles  
605 are observed values.

606 **Figure 4.** Fitted values of distance moved in an experimental channel (solid line) and 95%  
607 Bayesian credible intervals (shaded area) against number of prey captured ( $3 \text{ h}^{-1}$ ) in  
608 experimental trials for racer gobies modelled using a Poisson GLMM fitted using INLA. Black  
609 circles are observed values.