Title

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

Running title

Dispersal of an invasive fish

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Summary

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

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

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

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

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

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

Introduction

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

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

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

The primary drivers of the range expansion of Ponto-Caspian gobies in Europe are equivocal. Anthropogenic changes to large European rivers have been proposed as factors facilitating their expansion, including alteration of river banks, flow regime (e.g. damming), water quality parameters (salinity and temperature) and intensification of boat traffic (reviewed by Roche et al., 2013). Invasive gobies are relatively small benthic fish, without a swim bladder and with poor swimming ability. Thus, their rapid, long-distance upstream dispersal has been explained through passive dispersal *via* shipping (Ahnelt, Banarescu, Spolwind, Harka, & Waidbacher, 1998; Wiesner, 2005; Roche et al., 2013). Their small size, cryptic behaviour and habit of spawning in cavities may facilitate their rapid transport in ballast waters or hull fouling outside their original range. This mechanism particularly explains their well-characterized dispersal in the River Danube system (Roche et al., 2013). An additional mechanism of dispersal is through downstream drift of juveniles, which has been documented in the round and tubenose gobies (Janáč, Šlapanský, Valová, & Jurajda, 2013). Long-distance dispersal with shipping or drift permits the foundation of new populations that serve as the source for secondary dispersal through short-distance movements. Thus, goby invasions appear to comprise a combination of passive and active dispersal mechanisms, both natural and human-mediated. This broad conclusion is supported by genetic data. For example, during the invasion of the round goby in North America there was no reduction in genetic diversity in adjacent upstream locations relative to the source lake population, suggesting continuous dispersal rather than a single, long-distance founding event (Bronnenhuber, Dufour, Higgs, & Heath, 2011).

The mechanism of dispersal has implications for the structure of phenotypes on the margins of an expansion (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Chapple, Simmonds & Wong, 2012; Chuang & Peterson, 2016). While passive dispersal through juvenile drift or accidental transport by shipping is predicted to select a random subset of the population, active dispersal by individuals may favour specific phenotypes (Chapple et al., 2012, Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Chuang & Peterson, 2016). Dispersing individuals must express a behavioural motivation to engage in persistent directional movement, particularly in species that typically display high site affinity. In the case of intraspecific competition, dispersal may also show density dependence. In Ponto-Caspian invasive gobies, males are highly territorial and aggressively defend their nesting shelters during the reproductive period (e.g. Miller, 1984; Meunier, Yavno, Ahmed, & Corkum, 2009; Błońska et al., 2016). In this situation, a high density in the core population may drive dispersal when small and subordinate individuals have a greater tendency to move.

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

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

Materials and methods

The racer goby was selected as the study taxon; this species is an important invasive species in a number of European river systems and is amenable to experimental work (Semenchenko, Grabowska, Grabowski, Rizevsky, & Pluta, 2013, Grabowska, Kakareko, Błońska, Przybylski, Kobak, & Copp, 2016). We obtained 48 males from the lower section of the River Vistula in Poland (52° 32’ 05” N, 19° 41’ 12” E), using a backpack electroshocker (EFGI 650, Bretschneider, Germany). Electrofishing was considered the least selective method of collection while also minimising injuries to fish. Racer gobies have occurred continuously at this location since 1999 (Kostrzewa & Grabowski, 2001) and can, thus, be considered as a relatively long-established population. Specimens were collected from the river bank along the shoreline from a depth of 0.3 - 0.7 m where the racer goby co-occurs with the western tubenose goby, with both species numerous (approx. ind 2 m^{-2}) and representing the most abundant species in the fish assemblage.

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

Experiments were conducted in two stages. In Experiment 1 fish were tested in groups of eight to determine their tendency to disperse. Individuals were assigned to groups based on comparable body size (TL) to minimise the effect of size differences on behaviour. Mean (sd) 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 respectively. In Experiments 2 and 3 fish were individually tested to evaluate tendency to explore a novel environment and to measure their predation efficiency.

In Experiment 1 the propensity to disperse in an artificial channel was tested. The experiment was conducted in a semi-natural mesocosm in the Botanic Gardens of the University of Łódź (Fig. 1). The artificial channel was 8 m long and 0.5 m wide and was supplied with water from an adjacent holding tank of 75 m^3. Water was circulated through the channel by a pump with a capacity of 25 m^3 h^{-1}, providing constant water flow and aeration, and mimicking river flow. Mean (sd) water temperature was 17.8 (±1.47) °C over the course of the experiment. The channel was divided into 17 sectors, each 0.5 m long (except for sector D-1), separated by plastic netting baffles (mesh size 5 mm) that allowed fish to move up or down the channel between adjacent compartments through 100 mm wide gaps. Gaps between baffles were offset alternately to the left and right, which prevented fish from moving from the bottom to the top of the channel in a straight line and effectively increased the length of the channel to just over 12 m (Fig. 1). The first sector (S1) was 1.5 m long and could be isolated from the rest of the channel with a door. The last sector (S17) was separated from the adjacent sector with a non-return funnel to prevent fish that entered it from re-entering the lower sections of the channel. In each of the other sectors (S2-S16) there was a single shelter, while sectors S1 and S17 each had 4 shelters. Water flowed from S17 to S1.

Fish movement was tested during the day and overnight. For night trials eight randomly selected individuals were placed in S1 at 1800 h, allowed 2 hours to acclimatize to conditions, after which the door connecting S1 and S2 was opened. Fish were able to remain in S1 or move up the channel, through successive sectors, to S17. Fish were left in the channel for 12 hours to provide them with the opportunity to redistribute themselves over the entire period of darkness. At 0800 h on the following day, the sector into which each individual had moved was recorded. The same procedure was performed to test daytime movement, with the experimental procedure starting at 900 h and continuing until 1700 h. The order in which night and day trials was conducted was randomized for each fish group. After completion of both trials, all fish were removed from the outdoor channel and transferred to experimental aquaria. We conducted six replicate observations on each test group of eight fish (three night-time trials and three day-time trials) with 3-day intervals between trials. In the period between trials, fish were housed together in experimental aquaria. Trials were conducted between 10/09/16 and 29/10/2016. Sunrise and sunset at the start of trials was between 0609 h and 1907 h and between 07.31 h and 1719 h at the end. While in the experimental channel fish were not fed to minimize the risk that food distribution influenced dispersal. While held in aquaria between trials, experimental fish were fed *ad libitum*. The total number of sectors through which each individual fish moved across all 6 replicate observations was taken as a measure of their propensity to move upstream away from the starting sector, S1.

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

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

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

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

Data analysis

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

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

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

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

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

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

Where $Distance_{ij}$ is the distance moved by fish in the experimental channel (Experiment 1), scored as the total number of sectors through which fish *i* passed in experimental group *j*, which was assumed to follow a Poisson distribution with mean μ_{ij} and variance μ_{ij} with an identity link function. The model contained a linear effect for fish specific growth rate (*SGR*), latency to emerge from cover in Experiment 2 (*emergence*), and number of prey eaten in Experiment 3 (*prey*). An optimal fixed structure of the model was identified with a backward selection procedure using Watanabe-Akaike Information Criterion (WAIC) (Vehtari, Gelman, & Gabry, 2017). The random intercept *group* was included in the model to introduce a correlation structure between observations for fish tested together in the same experimental group with variance σ^2, distributed normally and equal to 0.

Results

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

Discussion

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

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

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

Assuming that dispersal distance and latency to emerge were a response to individual state of satiation, mediated by social position, a prediction was that subordinates would eat more prey in trials to compensate, or at least their consumption rates should not differ from dominant individuals. However, contrary to expectations, subordinate individuals performed relatively poorly in feeding trials. In experiments in which fish had a limited food supply the initial response was increased activity, indicative of food searching behaviour (Méndez & Wieser, 1993; Sogard & Olla, 1996). However, following a protracted period of starvation they reduced activity, possibly as a mechanism to save energy (Méndez & Wieser, 1993; Sogard & Olla, 1996; Van Dijk, Staaks & Hardewig, 2002). In the present study, racer gobies were given the opportunity to feed on gammarids. Capture of such mobile prey is energy demanding, which may have had the effect of further worsening their condition resulting in the observed poor growth performance. In contrast, dominant individuals, which did not leave the donor sector to disperse in the artificial channel, were more efficient at capturing gammarids in trials, presumably because they were in better condition.

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

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

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

Conflicts of Interest

The authors declare no conflicts of interest.

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

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

Figure Captions

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

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

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

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