

Behavioral dependent dispersal in the invasive round goby *Neogobius melanostomus* depends on population age

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Abstract Biological invasions cause major ecological and economic costs in invaded habitats. The round goby *Neogobius melanostomus* is a successful invasive species and a major threat to the biodiversity and ecological function of the Baltic Sea. It is native to the Ponto-Caspian region and has, via ballast water transport of ships, invaded the Gulf of Gdansk in Poland. Since 1990, it has spread as far north as Raahel in Northern Finland (64°41'04"N, 24°28'44"E). Over the past decade, consistent individual differences of behavioral expressions have been shown to explain various ecological processes such as dispersal, survival or reproduction. We have previously shown that new and old populations differ in personality trait expression. Individuals in new populations are bolder, less sociable and more active than in old populations. Here we investigate if the behavioral differentiation can be explained by phenotype-dependent dispersal. This was investigated by measuring activity, boldness and sociability of individually marked gobies, and subsequently allowing them to disperse in a system composed of five consecutive tanks connected by tubes. Individual dispersal tendency and distance was measured. Our results revealed that in newly established populations, more active individuals disperse sooner and that latency of a group to disperse depends on the mean sociability of the group. This indicates the presence of personality dependent dispersal in this species and that it is maintained at the invasion front but lost as the populations get older [*Current Zoology* 61 (3): 529–542, 2015].

Keywords Personality, Activity, Dispersal, Round goby, *Neogobius melanostomus*, Species invasions

In modern ecology the expansion of a species range is often considered a starting point leading to species invasions (Hastings et al., 2005). This process tends to be rather slow in contrast to the rapid invasion that may follow when species dispersal is aided by human mediated or passive transport (Carlton, 1993). Biological invasions are rarely successful (Williamson et al., 1986), but phenotypic plasticity has been suggested as a crucial factor in facilitating invasion success (Holway and Suarez, 1999). Notably, differentiation between old and new populations in highly plastic traits will not necessarily mean that the new population is genetically different from the source population if the differentiation is the result of individuals changing phenotypes rather than a selection where the most adapted survive and reproduce (Price et al., 2003). By manipulating colonizer density and dispersal distance of individuals sampled randomly from the source population, Burgess and Marshall (2011) showed that individual specific phenotypic traits can be as or more important than colonizer number for reproductive output and subsequent genetic diversity. Barton et al., (2012) showed, by adding evolutionary dynamics to their model of invasive species

range expansion, that behavior increasing the expansion rate is selected for over behavior that minimizes mortality during the dispersal process.

Leaving the safety of a familiar environment comes with a high potential cost to the dispersers as travel distance, habitat quality, predators, and interspecific competitors are unknown (Stamps, 2001). This suggests that conditions in the native patch must be unfavorable for dispersing individuals in order to induce the dispersal process. Previous studies suggest that both physical and behavioral specialization for dispersal can reduce the cost/risk of dispersing (reviewed by Clobert et al., 2009). Furthermore, the notion that dispersers are a non-random sample of the source population has gained a lot of support in recent years (Cote et al., 2011). Individual patterns of behaving, feeling and thinking that remain constant in time and across different contexts (e.g. feeding, mating or, anti-predation) or situations (e.g. different levels of predation risk, food availability or during mating season vs. non-mating season) are referred to as personality (Gosling, 2001; Réale et al., 2007) or behavioral syndromes (Sih et al., 2004a, b). Though initially only studied in humans or primates, over the last decade

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personality has been the focus of numerous studies in various animal taxa (Gosling 2001) and has repeatedly been shown to be important for various ecological processes such as biological invasions (Réale et al., 2007; Hudina et al., 2014; Juetter et al., 2014). For example, although individual behavioral response to changes in the environment is plastic, an individual that is bolder than others in the absence of predators are still comparatively bolder than the other individuals in the population in the presence of a predator (Sih et al., 2004a; Magnhagen and Bunnefeld, 2009). One recent development in the study of animal personality is to investigate its role in dispersal. The increasing interest in personality dependent dispersal has, over the last decade, resulted in substantial advances in our understanding of the mechanisms behind dispersal success (Cote et al., 2010b). Personality dependent dispersal has been demonstrated in numerous studies (Belthoff and Dufty, 1998; Cote et al., 2007; Duckworth and Badyaev 2007; Cote et al., 2011; Thorlacius et al., in press) out of which, most have found dispersers to differentiate consistently from residents (O’Riain et al., 1996; Trefilov et al., 2000; Cote and Clobert 2007; Cote et al., 2010). As an example, Cote and Clobert (2007a) found personality dependent dispersal in the common lizard *Lacerta vivipara* to remain constant over a one year period. In 2010 at least 20 studies had found evidence of personality dependent dispersal (reviewed by Cote et al., 2010b) in which dispersal has been linked to asocial behavior (Cote and Clobert, 2007; Cote et al., 2010a; Cote et al., 2011), boldness (Cote et al., 2011), exploration (Korsten et al., 2010), activity (Holekamp, 1986; Ims, 1990) and aggressiveness (Duckworth and Badyaev, 2007).

Previous work thus suggests that asocial, bold, active and explorative individuals are prone to disperse (Holekamp, 1986; Ims, 1990; Cote and Clobert, 2007; Cote et al., 2010a, b; Cote et al., 2011). Of these traits, activity and exploration have most frequently been connected with dispersal tendency and are likely influential during all stages of the dispersal process (O’Riain et al., 1996; Belthoff and Dufty, 1998; de Fraipont et al., 2000; Fraser et al., 2001; Dingemans et al., 2003; Krackow 2003; Bonte et al., 2004; Aragon et al., 2006; Jokela et al., 2008; Cote et al., 2011). Cote et al. (2010a; 2011) demonstrated the importance of personality dependent dispersal in the invasive mosquitofish where asocial dispersed sooner and further in an artificial stream. These results suggest that when a population grows quickly to high numbers dispersal frequency should increase and be dominated by individuals with low social tolerance

(Cote and Clobert, 2007a; Cote et al., 2010a). From a sociability perspective, a similar effect may be expected from populations where densities have become very low, in which case social individuals are more likely to disperse in search for populations of higher density rather than avoiding competition (Cote and Clobert, 2007). Fogarty et al. (2011) produced a model demonstrating dispersal led by asocial dispersers with social followers that join the population when densities in the new area have reached a certain threshold. Additionally, bolder individuals are considered more likely to disperse than shy as population mean boldness scores have been found to facilitate dispersal (Cote et al., 2011). Contrastingly, in cases when dispersal is triggered by predation shy individuals may feel a greater need to disperse in order to avoid predation (Cote et al., 2010b) though Cote et al. (2013) found that increased predation-risk cancelled personality dependent dispersal in mosquitofish. Thus, invasion can be driven by dispersal of bold and asocial individuals, later followed by shy and social individuals.

The model species in this study is the round goby *Neogobius melanostomus*. It is an invasive fish that originates in the Ponto-Caspian area and has spread to the Baltic Sea and the Laurentian Great Lakes, presumably via ballast water of freighters (Sapota and Skora, 2005; Björklund and Almqvist, 2009). It was first discovered in the Baltic Sea in the Gulf of Gdansk (Northern Poland) in 1990 (Sapota, 2004; Sapota and Skora, 2005) and has since spread as far north as the Bothnian Bay by means of stratified dispersal (passive transport over longer distances followed by natural dispersal) (Björklund and Almqvist, 2009). The round goby is an aggressive species (Groen et al., 2012), which may promote a competitive advantage for larger individuals in regard to intra- and interspecific competition (Brandner et al., 2013; Hudina et al., 2014). Previous studies have found more aggressive individuals at the invasion front compared to older populations (Duckworth and Badyaev, 2007; Groen et al., 2012; Juetter et al., 2014). Similarly, studies of the effect of body size and morphology have revealed larger individuals at the invasion front, likely due to higher food availability and lower intraspecific competition (Brandner et al., 2013). In contrast, smaller individuals might also end up at the invasion front as a result of being driven away by larger competitors (Brownscombe and Fox, 2012). The ongoing successful invasion of the round goby in the Baltic Sea constitutes a large-scale natural experiment for investigating personality dependent dispersal and ecological effects the-

reef in an invasion context. In a previous study we found round gobies *Neogobius melanostomus* in newly established populations (~4 years) to be bolder, more active and less social than older populations along the invasion succession (> 20 years) (Thorlacius et al., in press). However, we were unable to determine whether the differences in personality along the invasion succession were due to personality dependent dispersal or whether a random sample from the source population disperses to the novel areas and the bold, active and asocial individuals survived and reproduced (Thorlacius et al., in press). The goal of this study was to investigate the role of personality in active dispersal. More specifically, our hypotheses were (I) that bolder, more active and less social individuals disperse sooner, (II) that bolder and more active individuals disperse further, and (III) that dispersal is personality-dependent in young populations (at the invasion front) but not in older populations established over two decades ago.

1 Methods

1.1 Sampling locations and transport

During November 2013, two of the oldest round goby populations in the Baltic Sea were sampled in the Gulf of Gdansk, Poland (Fig. 1). More specifically 64 males from Hel (54°36'24" N, 18°47'53" E) and 64 from Swarzewo (54°45'24" N, 18°24'16" E) were captured with fyke-nets (mesh size = 15–20 mm) by Bartłomiej Arciszewski and associates at Hel Marine station of Gdansk University in Poland and subsequently shipped to Umeå on the 21st of November.

Sampling of the two newly established populations was conducted between 28th of April and 29th of May



Fig. 1 Round goby were sampled in the West harbor of Mariehamn in Åland (A) in and around the harbor of Visby on the island of Gotland in Sweden (G) and in the vicinity of Hel (H) and Swarzewo (S) in the Gulf of Gdansk in Northern Poland

2014. The first population was sampled in and around Visby Harbor on Gotland, Sweden (57°38'17" N, 18°17'13" E) (Fig. 1), where round gobies were first discovered in 2010 (Rickard Gustafsson personal communication) and the second in and around the West-harbor in Mariehamn, Åland (Finland) (60°06'01" N, 19°55'23" E) (Fig. 1) where they were discovered in 2011 (Kaj Ådjers personal communication). In Gotland, 23 males were sampled using eel-traps (mesh size = 11–17 mm) both in and around the harbor and by angling (6 individuals out of the 23) in the harbor where boat traffic precluded the use of eel-traps. Though the sampling methods differ, a study that was conducted in 2013 using 53 individuals from Gotland collected with the same methods revealed no difference in boldness between individuals captured by angling (32 individuals) and those caught in eel-traps (21 individuals) (ANOVA, $F = 0.092$, $P = 0.76$) (Thorlacius et al., unpublished data). In Åland all sampling was conducted using the same eel-traps as in Gotland and 46 males were caught. In all locations, the traps were kept in the water for approximately 24 hours before collecting caught fish. All sampled individuals were kept in holding nets for one to four days at the capture site before they were transported to Umeå Marine Science Center in Norrbyn, Northern Sweden. The fish were transported in 60 liter plastic fish transport bags, provided by Aneboda fish farm, filled with 33% water and 67% O₂-gas. The transport took approximately 30 hours for the Polish populations and 12 hours for the newly established populations. Only males were used in the experiment.

1.2 Holding conditions

At the marine station gobies were kept in square shaped tanks (110 × 110 × 100 cm) with a water level of 50 cm adding up to 605 liters per population (~26 L/individual for Gotland, ~13 L/individual for Åland and ~15L/individual for each of the Polish populations). Densities could not be standardized due to a lack of space. All tanks also contained one 12 cm long PVC pipe (diameter = 11 cm) per fish for shelter. The round gobies were provided a constant flow through of natural brackish water from the Bothnian Bay with about 0.4 % salinity. Temperature was not regulated, but followed the natural sea temperature ranging from 10.5°C in June to 15.4°C in August and down to 4.0°C in November. The fish were fed *ad libitum* with pellets from Skretting Nutreco® three times per week. As the round goby has not invaded the Swedish coast as far north as the marine station yet, all outlet water passed through both UV filters and mechanical filters to kill and/or stop all po-

tential pathogens, fertilized eggs and larvae.

1.3 Marking

In order to identify each individual, the round gobies were marked with 22 mm Oregon RFID tags, also known as Pit-tags. Prior to marking, all fish were allowed at least one week to acclimatize to the holding environment and to make sure every individual had started to eat. Before marking, each individual was sedated using ms-222. The tag was inserted into the body cavity of the fish by making a small incision with a scalpel and pressing the tag inside. Only one fish, from Gotland, died following marking.

1.4 Behavioral and dispersal assays

One week after marking, assays of boldness, sociability and activity were conducted on 24 randomly chosen individuals per day until all fish were assayed. When all individuals had been tested in all assays they were divided into size-sorted groups of 10 individuals from the same population and run through a dispersal assay. This added up to a total of 12 dispersal groups. Both behavioral and dispersal assays were then repeated 4 months later. All behavioral assays (boldness, sociability and activity) were recorded from above using Logitech web-cameras connected to PC lap-tops (two cameras per computer) with Windows 7, using an open source software called iSpy (iSpyconnect.com).

1.5 Boldness

Boldness was measured as risk tolerance or latency to regain normal behavior after a risky encounter. Cormorants are one of the main predators for the round goby populations in the Gulf of Gdansk (Corkum et al., 2004). Not many cormorants were spotted in the newly invaded sampling locations, but a large number of common goosanders *Mergus merganser* and red-breasted mergansers *Mergus serrator* were observed foraging among the rocks where the gobies were observed and captured from the new populations. Based on this information, an artificial bird beak was built using a small PVC pipe and dark grey hard plastic sheet sawed into the shape of a beak. Each individual goby was isolated in a 10 liter container for one hour to standardize handling and stress levels before being placed in the experimental aquarium (60 L, 80 × 26.5 × 30 cm with non-transparent sides and a camera above). In the aquarium each individual was left to acclimate for 10 minutes before we remotely started the recording and pulled a string that released the beak making it penetrate the water surface approximately one body length from each fish. The beak was then immediately retracted. Round gobies responded in one of two ways to the bird attack:

1) they would freeze immediately, or 2) swim forcefully for a few seconds before freezing. Boldness was recorded from the videos as latency to first movement (seconds) in which a lower value would indicate higher levels of boldness or stress tolerance. After each trial the fish were returned to their individual 10 liter container for one hour before the sociability assay started. 75% of the water in the boldness aquarium was replaced between trials in order to reduce chemical cues carrying over between individuals/trials.

1.6 Sociability

Sociability was measured in 60 liter aquaria (80 × 26.5 × 30 cm) that were divided into three compartments using transparent hard plastic. The middle compartment comprised half of the volume and each end-compartment one fourth. Every day, one hour before beginning the experiments, two medium sized round gobies were placed in one end-compartment and the other was left empty. The focal individual was placed in the middle compartment and recorded without disturbance for one hour. One frame per six seconds was later extracted from each recording starting when the fish began to swim. Extracted frames were then used to analyze spatial use, average distance from stimuli pair (cm), of each fish with a lower value indicating higher sociability. Individuals that did not move during the first 30 min of the video were excluded from the analysis as sociability could not be recorded for a sufficient amount of time. Here, 75% of the water was also replaced between trials.

1.7 Activity

Activity was calculated from the sociability data as the sum of moves longer than one centimeter per six seconds (extracted frame). A high score indicates high activity.

1.8 Dispersal

The dispersal system was composed of five tanks (110 × 110 × 100 cm) connected with 50 cm long, 20 cm diameter PVC pipes (i.e. dispersal corridors) entering the tanks 5 cm above the bottom (Fig. 2). The top of each pipe connecting the tanks was removed to increase the perceived risk when moving through them and to ensure that gobies would not use them as shelter. The water level in the tanks was set to 23 cm to make sure that water did not overflow in the dispersal corridors. Each corridor was equipped with an antenna connected to an automatic Oregon RFID reader that records the time and identity (pit-tag number) of every fish that passes it. 24 hours before starting the experiment one group of 10 fish was introduced to the dispersal system

and were allowed to move freely for 20 hours to ensure that conspecific chemical cues would be present in the system also for the first experimental group. Following this one group at a time was placed in a tank at a randomized end of the system with the exit-corridor closed. This was done to ensure that no fish would swim through the dispersal corridor as a stress-induced escape response following the introduction into the tank. The dispersal corridor was remotely opened at the end of the acclimation period (120 min) giving the fish access to the entire dispersal system where they were left undisturbed for 21 hours. With only one antenna per dispersal corridor it is impossible to distinguish between movement through the corridor and movement into the range of the antenna and back. But with the antenna positioned in the middle of the corridor the fish had to move at least 15 cm into the corridor for a reading to occur. Using a corridor diameter of 20 cm ensures that more than one round goby easily can pass through simultaneously, but in such situations there is a risk that only one of the pit-tags is read correctly (Fisher et al., 2001). For each time a fish passed through a corridor a number of readings, starting and ending with low signal strength with a peak in the middle, were recorded. Before statistical analysis, all readings but the peaks were removed manually. From the data, dispersal tendency was measured in seconds as the latency to first enter antenna 1–4, and dispersal distance/exploration as the total number of readings multiplied with the distance from the center of one tank to the center of the next ($110/2 + 50 + 110/2 = 160$ cm). The fish always started in the tank at the opposite end to where the inflow of brackish water from the Bothnian Sea was. This water was more than likely free from round goby chemical cues, as this species has not yet invaded this area.

1.9 Repeatability

In October 2014, four months after the first behavioral trials, all behavioral experiments but dispersal, were repeated on a subsample ($n = 54$) using the same

methods and equipment as the first time. The dispersal experiment was repeated in November, four months after the first dispersal experiment. The fish were kept in natural brackish water pumped in from the Bothnian Sea, which was done to prevent round goby chemical cues from being already present in the water during experiments. This also meant that the average water temperature during the behavioral assays differed in accordance with the season, and was 10.3°C in June and 5.9°C in October while during the dispersal trials the average water temperatures were 12.7°C in July and 4.6°C in November.

1.10 Physical measurements

Each individual was weighed and measured for length during the marking process. From the data, Fulton's condition factor was calculated for each individual using the formula: $100 \times (\text{Weight}/\text{Length}^3)$ (Nash et al., 2006). The fish were weighed and measured again after the second round of behavioral experiments.

1.11 Statistics

Transformations

The behavioral and dispersal variables were not normally distributed. Boldness was measured as latency to first movement, revealing a lower value for higher levels of boldness. These were log-transformed and subtracted from the logarithm of the total time recorded (3,600 sec) to achieve a normally distributed positive value for higher levels of boldness. Activity was also log-transformed and sociability log-transformed and subtracted from the maximum distance from the pair (40 cm) to get a higher value for higher sociability. Not all individuals moved during the behavioral experiments, and the completely immobile were excluded from the analysis (Appendix I: Table A1). Latency to disperse for antenna one through four also generated non-normally distributed negative value for higher dispersal tendency (in seconds) and were thus log-transformed and subtracted from the logarithm of the total time ($21 \times 60 \times 60$ seconds). Distance travelled was also log-trans-

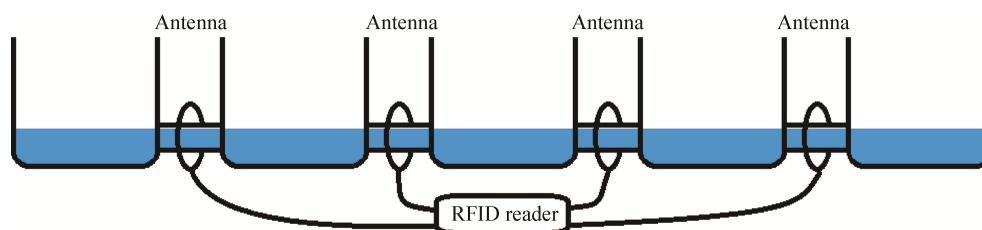


Fig. 2 The dispersal system was composed of five 1210 liter tanks connected with dispersal corridors equipped with pit-tag antennas. 10 round gobies were placed in one end of the system and allowed to spread for 21 hours undisturbed. Each time an individual passed through a dispersal corridor the time, ID of the fish and antenna number was recorded automatically

formed to achieve normal distribution.

Behavioral and physical comparisons

Testing for correlations between the behavioral traits were done, for the new and old populations separately, using Pearson's correlations of the transformed variables as were correlations between behaviors and body length and condition followed by power tests. Additionally, total body length and weight were compared between all four of the populations using ANOVA followed by a Tukey's multiple comparison of means with 95% family-wise confidence level.

Behavior, physical parameters and dispersal

The effects of boldness, activity and sociability on dispersal tendency and exploration in the dispersal system were modeled using a mixed effect model. More specifically, we included random intercepts for population and group to account for within-population pseudo-replication (Pinheiro et al., 2013). Gaussian errors were used for all models. Residual plots revealed heteroscedasticity in the models for boldness and sociability due to differences in variance between the dispersal groups. This was corrected for by using a variance function that allows for different variances between the dispersal groups.

Optimization of the model structure on both fixed and random components was done using AIC-based model selection as suggested by Zuur et al. (2009) which lead us to include the behavioral traits only as fixed effects, and population and dispersal group as random effects. Significance of behavioral traits was determined using a likelihood ratio test comparing the models with and without a certain behavior as a fixed effect.

Consistency and repeatability

Consistency was estimated using Pearson's correlation of the data for all behavioral, dispersal and physical parameters. The intraclass correlation coefficient (Sokal and Rohlf, 1995) or repeatability was estimated using the package "ICC" (Wolak et al., 2012) in the statistical program R (R Development Core Team, 2012).

All statistical analysis were conducted using the statistical program R (R Development Core Team, 2012)

2 Results

2.1 Behavioral correlations and body size

There were no significant correlations between boldness, activity and sociability (Table 1), nor were any of these traits correlated with total body length or condition (Appendix I: Table A2). Power analyses revealed that due to high variation and relatively low sample size,

statistical power ranged from 0.056 to 0.16 for the correlations between behavioral traits and from 0.048 to 0.31 for correlations between behavior and body size and condition. This means that the required sample size for a power of 0.8 would be very high for most correlations between behavioral traits ($n = 158-4,561$) and for the correlations between behavior and body length or condition ($n = 129-136,961$). Based on this we cannot, due to our sample size, confirm or refute the presence of behavioral correlations in these populations. Total body length, however, differed between all populations except Åland (mean length = 17.49 and weight = 89.00) and Hel (mean length = 18.68 and weight = 113.48) (Appendix I: Table A3) which contained the largest individuals followed by Swarzewo (mean length = 15.48 and weight = 67.47) and finally Gotland (mean length = 13.61 and weight = 45.91).

2.2 Phenotype dependent dispersal

In the newly established populations, more active individuals dispersed sooner (Appendix I: Table A4, Fig. 3A). Boldness and sociability were not connected with dispersal tendency or distance when analyzing the data for all individuals in the dispersal groups. None of the behavioral traits were correlated with dispersal in the older populations. However, mean sociability score for each dispersal group affected individual dispersal tendency, with individuals from newly established populations in groups with a higher mean sociability score dispersing sooner (Appendix I: Table A3, Fig. 3B). Group mean boldness and activity did not affect dispersal tendency in any of the populations (new or old), nor did group mean sociability in the old populations (Appendix I: Table A3).

Total body length was positively connected with dispersal tendency for antenna one, two and three for the newly established populations (Appendix I: Table A3, Fig. 4A) and marginally significant for antenna two and four for the old populations (Appendix I: Table A3, Fig. 4B). Though the dispersal groups were sorted by size, a significant correlation between within group body length size-range and time of dispersal was found, but

Table 1 Pearson's correlation between the behavioral traits (activity, boldness and sociability) in newly established and older populations separately using the transformed variables (transformations described in Methods)

		Newly established	Older
Activity	Boldness	$r = 0.22, P = 0.17$	$r = -0.16, P = 0.28$
Sociability	Boldness	$r = 0.041, P = 0.76$	$r = -0.040, P = 0.76$
Sociability	Activity	$r = -0.15, P = 0.32$	$r = -0.066, P = 0.66$

Table 2 Consistency (Spearman’s rank correlation) and repeatability (intraclass correlation coefficients) of individual behavior calculated separately for newly established and old populations

		Rank consistency	Repeatability
Newly established populations	Boldness	$\rho = 0.61, P = 0.00064^{***}$	$F_{65,30} = 0.005, P = 0.94, ICC = 0.48$
	Activity	$\rho = 0.025, P = 0.92$	$F_{53,26} = 0.059, P = 0.81, ICC = 0.077$
	Sociability	$\rho = -0.078, P = 0.74$	$F_{54,26} = 0.023, P = 0.88, ICC = -0.18$
	Dispersal tendency (antenna1)	$\rho = 0.36, P = 0.0053^{**}$	$F_{60,57} = 8.35, P = 0.0046^{**}, ICC = 0.35$
	Dispersal tendency (antenna2)	$\rho = 0.29, P = 0.028^*$	$F_{59,59} = 9.095, P = 0.00315^{**}, ICC = 0.29$
	Dispersal tendency (antenna3)	$\rho = 0.38, P = 0.0053^{**}$	$F_{58,55} = 13.53, P = 0.00036^{***}, ICC = 0.29$
	Dispersal tendency (antenna4)	$\rho = 0.38, P = 0.0046^{**}$	$F_{59,55} = 7.87, P = 0.0059^{**}, ICC = 0.32$
	Exploration in a novel environment	$\rho = 0.19, P = 0.14$	$F_{60,59} = 0.63, P = 0.43, ICC = 0.19$
Old populations (>20 years)	Boldness	$\rho = 0.059, P = 0.79$	$F_{30,30} = 0.25, P = 0.62, ICC = -0.21$
	Activity	$\rho = 0.094, P = 0.71$	$F_{46,20} = 6.44, P = 0.014^*, ICC = -0.67$
	Sociability	$\rho = -0.024, P = 0.92$	$F_{61,20} = 1.82, P = 0.18, ICC = 0.20$
	Dispersal tendency (antenna1)	$\rho = -0.033, P = 0.81$	$F_{60,59} = 0.25, P = 0.62, ICC = -0.045$
	Dispersal tendency (antenna2)	$\rho = 0.12, P = 0.33$	$F_{60,59} = 0.22, P = 0.64, ICC = 0.073$
	Dispersal tendency (antenna3)	$\rho = 0.088, P = 0.13$	$F_{60,59} = 0.54, P = 0.46, ICC = -0.015$
	Dispersal tendency (antenna4)	$\rho = 0.21, P = 0.21$	$F_{60,59} = 0.79, P = 0.38, ICC = 0.11$
	Exploration in a novel environment	$\rho = 0.18, P = 0.17$	$F_{60,59} = 0.12, P = 0.73, ICC = 0.20$

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$

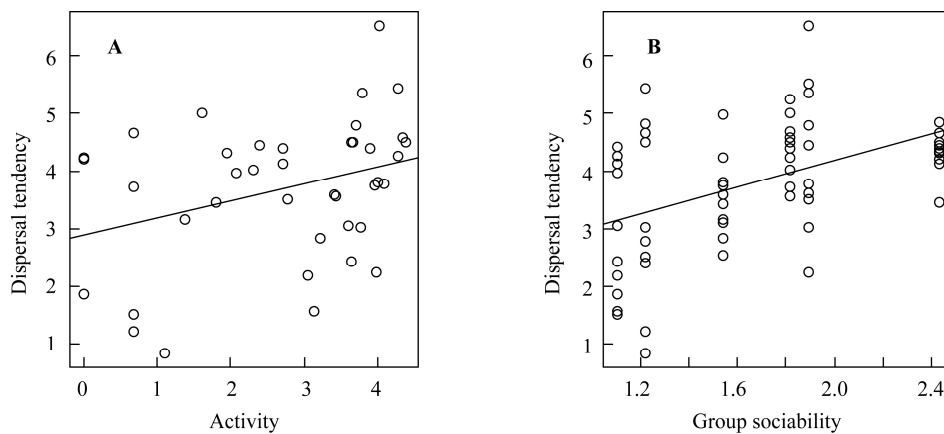


Fig. 3 Individuals in the newly established populations that are more active have higher dispersal tendency (disperse sooner) (A) and individuals in populations with high mean sociability also disperse sooner (B)

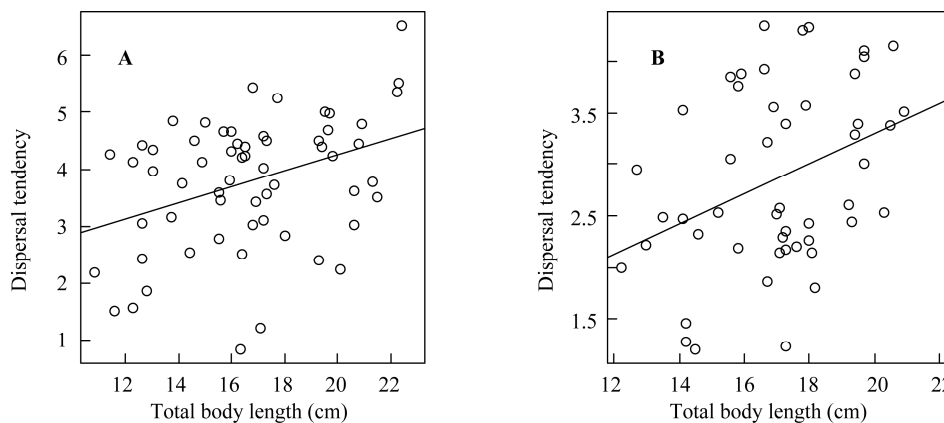


Fig. 4 Larger individuals dispersed sooner in both the new (A) antenna 1) and the older populations (B) antenna 2).

only in the older populations. Individuals in groups consisting of more similar sized gobies (small size-range) dispersed sooner (Appendix I: Table A3).

2.3 Consistency and repeatability

Boldness was both consistent and repeatable in the newly established populations, but not in the older populations (Appendix I: Table A4). Activity was not consistent over the four month period and showed low repeatability in the newly established populations, and sociability was neither consistent nor repeatable (Appendix I: Table A4). Dispersal tendency, or latency to first pass antenna 1 through 4, was both consistent and repeatable for the newly invaded populations but neither consistent nor repeatable for the older populations (Appendix I: Table A4). Exploration, or distance travelled, in the dispersal system was not consistent and showed low levels of repeatability.

3 Discussion

Here we showed that, in newly established populations of the round goby from the ongoing invasion of the Baltic Sea, more active individuals had a greater dispersal tendency (lower latency to pass through dispersal corridor 1) and larger individuals dispersed sooner than smaller individuals. Also, individuals from new populations dispersed sooner when in groups with a high mean sociability, whereas no such correlation was found for individuals from old populations. In addition, the size range within dispersal group was positively correlated to dispersal tendency in the older populations where individuals in bad condition also dispersed sooner.

3.1 Personality-dependent dispersal

In one of our previous studies (Thorlacius et al., in press) individuals from newly established populations were bolder, more active and less social than individuals from older populations along an invasion succession (same populations as used in this experiment). Here we found, as expected, that active individuals dispersed sooner than less active individuals in the newly established populations. This is in accordance with previous studies in which active individuals were found to have higher emigration rates and a greater dispersal tendency in natural populations (Bonte et al., 2004; Aragon et al., 2006). High activity could be adaptive in novel areas as higher activity levels can result in higher foraging rates and faster growth (Brodin and Johansson, 2004). This is especially true under low predation-risk and since dispersers colonizing novel areas often are released from the pressure of coevolved predators and enter low-risk

environments (Colautti et al., 2004). Additionally, activity levels are often correlated with and sometimes measured in the same way as exploration (Réale et al., 2007) and/or boldness (Brodin and Drotz, 2014), which repeatedly has been connected with dispersal tendency (Fraser et al., 2001; Cote et al., 2010a) and found to be heritable through numerous generations (Korsten et al., 2013).

Surprisingly no correlation was found between behavior and dispersal tendency in the old populations. It seems probable, however, that a high frequency of individuals with behavioral adaptations to dispersal only is present in a population for a few years following the invasion and colonization of an area. Over time the adaptive value of a disperser phenotype fades out as selection instead grows stronger on other trait combinations favored by increasing population density and competition. This has been found for aggression in western bluebirds in which highly aggressive individuals were found at the invasion front but only for a few generations (Duckworth and Badyaev, 2007). This change in selective regime is called the Olympic village effect, or spatial sorting (Phillips et al., 2008a; Shine et al., 2011), and results in assortative mating by dispersal ability at the invasion front, which then leads to runaway selection for increased rate of dispersal and spread (Travis and Dytham, 2002; Hughes et al., 2007). Populations that have successfully invaded a novel environment often experience a lag phase before spreading further throughout the region (Lockwood et al., 2007; Simberloff 2009). At that stage, densities are usually low in comparison to the native or source population, and thus there should be selection for reproductive rate (Burton et al., 2010) instead of dispersal rate. And as densities grow, it can be expected that tolerance for high densities will be selected for. At this stage the dispersal phenotypes, favored at the invasion front, will be present at low frequencies in the population compared to newer populations at the new range-margin. Additionally, this process is possibly connected with the enemy release hypothesis which states that by dispersing to a novel environment, individuals leave behind specialized predators, parasites and pathogens (Colautti et al., 2004). With time and growing densities the “enemies” likely catch up with the population or alternatively new enemies specialize in the new prey/host, thereby changing the quality of the habitat and the selective regime which might facilitate further dispersal. Based on our results one might suspect that this gradual change in selection pressure potentially already started in our study popula-

tions since we found no correlation between sociability, boldness and dispersal tendency or distance travelled. Sampling for our earlier study was done 1–2 years after the round gobies first were discovered in the newly invaded areas (Kaj Ådjers personal communication; Rickard Gustafsson personal communication). This enabled us to study founder-individuals of new populations at the very invasion front with all the characteristics that made them successful invaders. In this study however, the new populations were at least 3–4 years old and round goby density was already high in the core areas.

In contrast to earlier studies, we found no correlation between individual sociability and dispersal tendency (Cote and Clobert, 2007; Cote et al., 2011). This was surprising as dispersal tendency has been connected with asocial behavior in both invasive (Cote et al., 2010a) and non-invasive species (Cote and Clobert, 2007), but with the important difference that densities were not manipulated in this study. When analyzing how mean sociability of groups affects dispersal tendency, the results are in opposition to earlier studies as individuals in groups with high mean sociability disperse sooner than individuals in low sociability groups. As previously mentioned, the round goby is an aggressive species and aggression can be very hard to isolate from sociability (Hudina et al., 2014) and can therefore to some extent confound sociability measures. Hence, one explanation for the positive correlation between mean group sociability and dispersal could be that the sociability score was confounded by aggression as aggressive individuals have been found to drive away less aggressive individuals (Duckworth and Badyaev, 2007). Based on the potentially confounding factors for sociability and the lack of repeatability in our sociability measures we can neither confirm nor discard the possibility that levels of sociability also plays a role for dispersal tendency in round gobies. Additional studies, and well developed tailor-made methods, are required in order to better measure and understand the social behavior of this aggressive species.

3.2 Body size, condition and dispersal tendency

Body size has been identified as an important fitness determinant in many animals as well as a key trait for population dynamics (Banks and Thompson, 1987; Werner and Gilliam, 1984). In all of our four study populations larger individuals dispersed sooner than smaller individuals did. This result is in accordance with a study showing that larger individuals lead the spread of the round goby upstream along the Danube River in Austria and Germany possibly facilitated by lower intraspecific

competition and higher food availability at the invasion front (Brandner et al., 2013), although the opposite pattern has been found in another population (Thorlacius et al., in prep). When it comes to intraspecific competition, a three percent difference in body size has been found enough to determine dominance in favor of the larger individual (Stammler and Corkum, 2005). In our study, body size difference between the smallest and largest individual in each dispersal group vary between 6 and 46 percent. This may partly explain why we found within dispersal-group size range to be negatively correlated to dispersal tendency as disputes may have settled more quickly in groups with large size range. Though, one would expect smaller individuals to disperse sooner than larger since smaller individuals have higher metabolic rate and lower reserves (Krause et al., 1998). As such, the lack of food in the starting tank of the dispersal system might have induced dispersal in smaller individuals before larger ones. Our results, along with the above information, suggest that there is dispersal driven movement at the invasion front and that competition driven movement could be more important in older populations. In addition, there was a negative correlation between individual condition and dispersal tendency showing that individuals in good condition dispersed later. This seems intuitive since individuals in “bad” condition have less resources saved and must hence search more actively for food (Mikolajewski et al., 2004). Another potential reason for this correlation is that individuals in good condition usually have a competitive advantage and as a consequence the individuals in bad condition might have been driven away from patches with good condition individuals.

3.3 Consistency and repeatability

In many studies, repeatability scores of behavioral traits have been low but significant (Bell et al., 2009). Bolder individuals have been found to be more consistent in their behavior across different context than shyer individuals (Magnhagen and Bunnefeld, 2009). Low levels of boldness in the older populations might explain the lack of consistency and low repeatability of boldness in the older populations. Contrastingly, boldness was both repeatable and consistent in the new populations that displayed higher levels of boldness.

Dispersal tendency has been found to be repeatable in spiders (Bonte et al., 2009), birds (Doligez et al., 2009) and fish (Cote et al., 2010a). This is in accordance with our finding that dispersal tendency of individuals from new populations are repeatable. Admittedly, repeatability was rather low but, considering a water

temperature difference of 8.1°C between the two dispersal trials the fact that it was repeatable at all suggests dispersal being a very robust trait. Should the movement between tanks be driven by competition in the old populations and by dispersal in the new, then that might explain why dispersal was consistent and repeatable only in the new populations. The groups were mixed before the second dispersal assay and in a different group competition driven movement might be different as it is dependent on the individuals currently in the group.

In this study we add to current knowledge of what drives the dispersal process in different stages of an ongoing biological invasion. However, in order to fully understand the role of personality in the spread of this invasive species more studies are needed. The newly established populations are 3–4 years old which may be too old and dense to represent the invasion front, as catch per unit effort has increased in these areas since 2012 (Thorlacius et al., in prep). Additionally, our methods for measuring sociability are likely confounded by aggression which calls for further analysis, possibly in colder temperatures outside of the reproductive season. It is clear however, that dispersal strategies differ between new and old populations. Dispersal seems to be driven by activity, body size and possibly aggression in newly established populations, while in old populations dispersal seems to be driven by competition where larger individuals invest a lot of energy competing aggressively for space and nesting opportunities (Wickett and Corkum, 1998; Corkum et al., 2004; Meunier et al., 2009).

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Appendix I

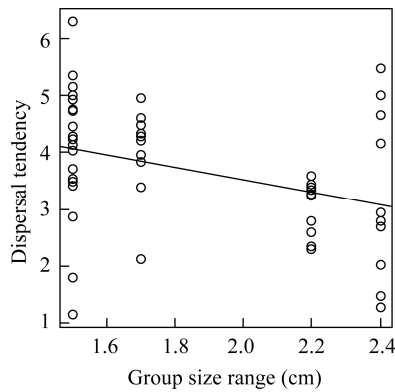


Fig. A1 Dispersal tendency of individuals from the old populations were negatively correlated to within group difference in body length (antenna 1)

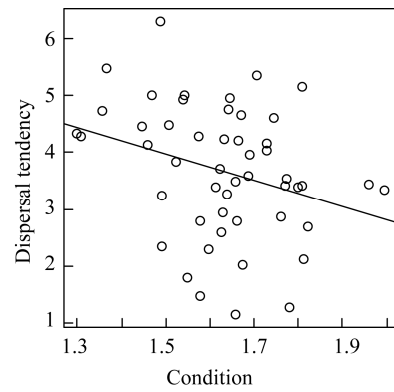


Fig. A2 Dispersal tendency (antenna 1) was negatively correlated to condition in the older populations

Table A1 Individuals that did not move during a behavioral trial were excluded from the corresponding analysis

Population	Activity	Sociability	Boldness
Åland	20 (43%)	4 (9%)	5 (11%)
Gotland	8 (35%)	3 (13%)	0 (0%)
Hel	13 (41%)	1 (3%)	2 (6%)
Swarzewo	8 (25%)	2 (6%)	0 (0%)

Presented are number of excluded individuals per population in each behavioral trial and the percentage of the total sample size it represents.

Table A2 The behavioral variables were compared with total body length and condition (Fulton’s condition factor) for newly established and older populations separately using Pearson’s correlation

	Newly established		Older	
	Body length (cm)	Condition	Body length (cm)	Condition
Activity	$r = 0.19, p=0.23$	$r = 0.065, P = 0.68$	$r = 0.24, P = 0.11$	$r = 0.028, P = 0.85$
Boldness	$r = 0.085, p=0.50$	$r = 0.11, P = 0.40$	$r = 0.22, P = 0.078$	$r = 0.13, P = 0.31$
Sociability	$r = 0.0076, p=0.95$	$r = 0.17, P = 0.18$	$r = 0.041, P = 0.76$	$r = 0.082, P = 0.53$

Table A3 Length and weight comparisons between the study populations using ANOVA and Tukey’s multiple comparison of means with 95% family-wise confidence level

	Population	Åland	Gotland	Hel	Swarzewo
Length	Åland		> 0.001***	0.13	0.0019**
	Gotland			> 0.001***	0.016*
	Hel				0.001***
	Swarzewo				
Weight	Population	Åland	Gotland	Hel	Swarzewo
	Åland		> 0.001***	0.024*	0.026*
	Gotland			> 0.001***	0.082
	Hel				0.001***
					Swarzewo

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$

Table A4 Effects of behavior, total body length, within dispersal group size range and condition on dispersal parameters was tested using a mixed effects model with population and group as a random factor. Dispersal tendency 1–4 denotes latency to pass through dispersal corridor 1–4

Response variable	Fixed variable	Statistical test	
		Newly established	Older
Dispersal tendency 1	Activity	$F_{1,33} = 4.62, P = 0.039^*$	$F_{1,31} = 2.71, P = 0.11$
Dispersal tendency 2	Activity	$F_{1,32} = 1.82, P = 0.19$	$F_{1,31} = 1.73, P = 0.20$
Dispersal tendency 3	Activity	$F_{1,29} = 1.56, P = 0.22$	$F_{1,31} = 0.73, P = 0.40$
Dispersal tendency 4	Activity	$F_{1,32} = 1.85, P = 0.18$	$F_{1,31} = 3.33, P = 0.078$
Distance/Exploration	Activity	$F_{1,33} = 0.23, P = 0.63$	$F_{1,31} = 0.044, P = 0.84$
Dispersal tendency 1	Boldness	$F_{1,50} = 0.24, P = 0.62$	$F_{1,44} = 0.33, P = 0.57$
Dispersal tendency 2	Boldness	$F_{1,49} = 0.63, P = 0.43$	$F_{1,43} = 0.032, P = 0.86$
Dispersal tendency 3	Boldness	$F_{1,46} = 0.17, P = 0.68$	$F_{1,43} = 0.014, P = 0.91$
Dispersal tendency 4	Boldness	$F_{1,49} = 0.0077, P = 0.93$	$F_{1,43} = 0.22, P = 0.64$
Distance/Exploration	Boldness	$F_{1,50} = 2.36, P = 0.13$	$F_{1,44} = 0.97, P = 0.33$
Dispersal tendency 1	Sociability	$F_{1,49} = 1.050, P = 0.31$	$F_{1,43} = 3.18, P = 0.082$
Dispersal tendency 2	Sociability	$F_{1,48} = 2.82, P = 0.10$	$F_{1,42} = 0.085, P = 0.77$
Dispersal tendency 3	Sociability	$F_{1,44} = 1.18, P = 0.28$	$F_{1,42} = 1.64, P = 0.21$
Dispersal tendency 4	Sociability	$F_{1,48} = 0.76, P = 0.39$	$F_{1,42} = 0.30, P = 0.59$
Distance/Exploration	Sociability	$F_{1,49} = 0.87, P = 0.36$	$F_{1,43} = 0.15, P = 0.70$
Dispersal tendency 1	Within gr. mean activity	$F_{1,53} = 0.10, P = 0.75$	$F_{1,52} = 1.11, P = 0.30$
Dispersal tendency 1	Within gr. mean boldness	$F_{1,53} = 1.046, P = 0.31$	$F_{1,44} = 0.025, P = 0.88$
Dispersal tendency 1	Within gr. mean sociability	$F_{1,57} = 7.94, P = 0.0066^{**}$	$F_{1,44} = 1.018, P = 0.32$
Dispersal tendency 1	Body length (cm)	$F_{1,53} = 5.54, P = 0.022^*$	$F_{1,44} = 0.57, P = 0.45$
Dispersal tendency 2	Body length (cm)	$F_{1,52} = 4.53, P = 0.038^*$	$F_{1,43} = 3.20, P = 0.081$
Dispersal tendency 3	Body length (cm)	$F_{1,48} = 5.96, P = 0.018^*$	$F_{1,43} = 1.38, P = 0.25$
Dispersal tendency 4	Body length (cm)	$F_{1,52} = 2.089, P = 0.15$	$F_{1,43} = 2.98, P = 0.091$
Distance/Exploration	Body length (cm)	$F_{1,53} = 0.46, P = 0.50$	$F_{1,44} = 0.15, P = 0.70$
Dispersal tendency 1	Within gr. size range	$F_{1,3} = 0.081, P = 0.79$	$F_{1,47} = 7.28, P = 0.0097^{**}$
Dispersal tendency 2	Within gr. size range	$F_{1,3} = 0.73, P = 0.40$	$F_{1,46} = 17.09, P < 0.0001^{***}$
Dispersal tendency 3	Within gr. size range	$F_{1,3} = 0.11, P = 0.76$	$F_{1,46} = 11.83, P = 0.012^*$
Dispersal tendency 4	Within gr. size range	$F_{1,3} = 0.13, P = 0.75$	$F_{1,46} = 15.23, P < 0.0001^{***}$
Distance/Exploration	Within gr. size range	$F_{1,3} = 0.60, P = 0.50$	$F_{1,47} = 0.074, P = 0.79$
Dispersal tendency 1	Condition (Fulton's)	$F_{1,53} = 1.19, P = 0.28$	$F_{1,44} = 4.85, P = 0.033^*$
Dispersal tendency 2	Condition (Fulton's)	$F_{1,52} = 0.62, P = 0.43$	$F_{1,43} = 6.46, P = 0.015^*$
Dispersal tendency 3	Condition (Fulton's)	$F_{1,48} = 0.21, P = 0.65$	$F_{1,43} = 4.34, P = 0.043^*$
Dispersal tendency 4	Condition (Fulton's)	$F_{1,52} = 0.38, P = 0.54$	$F_{1,43} = 6.12, P = 0.017^*$
Distance/Exploration	Condition (Fulton's)	$F_{1,53} = 1.25, P = 0.27$	$F_{1,44} = 0.21, P = 0.65$

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$