Round goby invasion of the Baltic Sea
The role of phenotypic variation

Magnús Thorlacius
To my family
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List of publications

This thesis is a summary of the following four papers which will be referred to in the text by their roman numerals.

I. Thorlacius. M., Hellström, G., Finn, F., Boman, N. and Brodin, T. Personality differentiation along the invasion succession of the round goby (*Neogobius melanostomus*) in the Baltic Sea. *In review.*


III. Thorlacius, M. and Brodin, T. Phenotypic differentiation of Round goby (*Neogobius melanostomus*) along a small-scale invasion succession. *Submitted manuscript.*

Author contributions

Paper I

TB designed the study. MT and NB tested and designed the methods, MT, NB and FF conducted the experiments, MT and FF analyzed the behavioral videos, GH analyzed the data, MT wrote the first draft of the paper and TB contributed with comments on the paper.

Paper II

MT, TB and GH designed the study. MT and GH set up the experiment. MT carried out the experiment, analyzed the data and wrote the first draft of the paper. GH advised during data analysis and TB contributed with comments on the paper.

Paper III

MT designed the study, carried out the experiment, analyzed the data and wrote the first draft of the paper. TB contributed with comments on the paper.

Paper IV

MT and MH designed the study and carried out the experiment. MT analyzed the data and wrote the first version of the paper. MH and TB contributed with comments on the paper.

Authors: Magnus Thorlacius (MT), Gustav Hellström (GH), Fia Finn (FF), Nils Boman (NB) and Tomas Brodin (TB).
Abstract

Biological invasions are a major threat to biodiversity worldwide with annual economic costs up to 1.4 trillion dollars. The round goby (*Neogobius melanostomus*) is a particularly fierce invader that threatens ecological function of the Baltic Sea. Individual variation in behavioral traits that remain constant through time and context have been identified as crucial factors for explaining different parts of the invasion process. For example, asocial behavior facilitates dispersal from high density populations and comes with fitness benefits in low conspecific density. The latter is especially relevant, in an invasion context, following the initial colonization of a novel environment when population density usually is low.

This thesis investigates the role of individual variation in phenotypic traits on species invasions. The main focus is on the effects of sociability, activity and boldness, but also including aggression and physiological stress tolerance, on dispersal tendency and selection at invasion fronts. To do this, we studied four round goby populations in the Baltic Sea, two of the most recently established and two of the oldest populations.

In 2012 we demonstrated that asocial, active and bold round gobies are overrepresented at invasion fronts. Two years later we showed that dispersal from the new populations was led by individuals with high activity levels, while in all populations larger individuals dispersed. We also determined the length of the so-called lag-phase, between colonization and spread, in both newly established populations. The end of the lag-phase is hypothesized being triggered by high population density in the harbors leading to dispersal and subsequent colonization of the surrounding areas by small asocial individuals. In our final experiment, we present evidence of stress coping styles in round gobies, in which more aggressive individuals are also more stress tolerant and *vice versa*. Though we found no connection between stress coping and population age, we found that mortality was unaffected by population density and that the gobies became more aggressive and stress tolerant when kept in high density.

To conclude, we have shown that: 1) individuals with high levels of activity, boldness and asociality are common at invasion fronts; 2) a lag phase occurs between colonization and spread in round goby invasions; 3) asocial individuals drive the spread from high density populations at the invasion front and; 4) round gobies adapt to high densities with high aggression and stress tolerance.

**Keywords:** Round goby (*Neogobius melanostomus*), behavior, animal personality, dispersal, species invasions, colonization, spread, sociability, activity, boldness, aggression, cortisol, coping-styles.
Introduction

The question why a species is present in one place and not in another is one of the simplest questions one can ask in ecology (Krebs 2001). Most or all species are bound to certain areas due to their physiological tolerance to temperature, salinity, weather, etc. However, within these areas species movement are often restricted by geographic barriers such as land, water or mountains, depending on the organism. As for animals that are less restricted (e.g. birds and many aquatic organisms), dispersal often takes place when the cost of staying outweighs the cost of venturing into the unknown (Cote et al. 2010a&b). Whether active or passive (human mediated), dispersal often serves as the starting point for species invasions (Mack et al. 2000; Bowler and Benton 2005; Hastings et al. 2005). As a consequence of increased globalization the frequency of unintentional introductions has increased. However, the majority of all introductions fail to establish and spread in the new environment (Williamson et al. 1986). Despite the low success-rate of introductions, species invasions are an ever-growing problem (Mack et al. 2000) with estimated economic costs of 1.4 trillion dollars, or about 5% of the global domestic product, already in 2009 (Yemshanov et al. 2009). Hence, a better understanding of the spatial ecology of invasive species is crucial, as it may prove helpful in constructing eradication or control programs (Jorgejans et al. 2008).

Dispersal and species invasions

The process of species invasion can be divided into 5 stages (departure, transit/transport, colonization, establishment and spread) (Bowler and Benton 2005; Lockwood et al. 2013), all of which may include different governing selection pressures (Clobert et al. 2009). The focus of this thesis is primarily on departure (II), colonization (I), establishment, and spread (III), in addition to one study that is indirectly connected to colonization, establishment and spread (IV). Starting with departure, leaving the safety of a familiar environment comes with the cost of uncertain availability of food and shelter, distance to nearest habitable patch, and the potential exposure to unfamiliar predators, congenerous and resources (Bowler and Benton 2005 Cote et al. 2010b). When dispersal takes place the costs of staying, usually a consequence of intra- and interspecific density and/or competition, low food availability, uneven sex ratio, relatedness, small patch size and/or patch isolation in the native range, tend to out-weigh the predicted costs of dispersing. Numerous studies have found evidence of increased emigration/dispersal propensity with increased density in various taxa such as insects (Otronen and Hanski 1983), reptiles (Cote and Clobert 2007), fish
(Cote et al. 2010) and mammals (O’Riain et al. 1996; reviewed by Bowler and Benton 2005) to name a few. With increasing population density the cost of staying can become greater than the cost of dispersing. This can arise either due to explorative competition, in which there are negative effects on resources, as a result of interference competition in which case individuals are simply competing for space (Harrison 1980; Herzig 1995) or due to the rapid spread of parasites that is common in dense populations (Sloggett and Weisser 2002). In contrast, for some species emigration has been connected to low densities in which the benefits of staying in a group are greater than the cost of competition (Kuussaari et al. 1996; Roland et al. 2000).

Studies of selection during invasion colonization are scarce, but traits commonly found among successful colonizers have been identified across taxa. These include short generation time, high growth rate and high fecundity (r-strategy) (Kolar and Lodge 2001). When successful, colonization of a habitat results in gene flow which then affects the population structure. The genes carried by the colonizers will be dominant in the new population and with greater number of colonizers comes more gene flow and a broader gene-pool. Additionally, initial dispersers are often followed by conspecifics that follow the chemical cues of the dispersers and consequently immigrate into the new population resulting in even more gene flow. However, if the individuals that initially managed to establish were a non-random sample of the source population founder effects may occur making the new population genetically distinct from the source population (Krebs 2001). When only a few individuals survive and/or manage to breed, gene flow can be very low (Slatkin 1987) and the likelihood of founder effects are relatively high.

Following successful colonization and establishment, a lag phase often occurs prior to further spread (Lockwood et al. 2007; Simberloff 2009); during which population growth is initially low due to limited size of the founding population (Krebs 2001). While densities are low, selection favors high reproductive rate (Burton et al. 2010), which may partly explain why successful invaders often are r-strategists (Kolar and Lodge 2001). Additionally, it has been hypothesized that during the early stages of invasion coevolved predators, parasites and pathogens are largely lacking (Colautti et al. 2004), thereby reducing negative effects on population growth. While generalist predators often are rather quick to change their diet using phenotypic plasticity, specialists are slower and adapt by means of natural selection, in many cases adapting their morphology to the new prey items size or shape (Smith and Palmer 1994). In newly invaded areas there may be numerous predators for which significant time often passes before discovering and starting to use the new prey item (Carlsson et al. 2009). As an example, round gobies leading the expansion of the distributional range
(invasion front) have been found to suffer 27% lower predation pressure when compared with individuals from well-established (older) areas (Brownscombe and Fox 2013).

At the end of the previously mentioned lag phase, populations adapted to low densities have been found to grow past their carrying capacity in the newly established area, resulting in either a crash in population size (Simberloff and Gibbons 2004) and/or the facilitation of density-dependent dispersal (Cote and Clobert 2007; Cote et al. 2010a). At this point the conditions and selection pressures at the invasion front often resembles those that initially triggered departure from the native range and dispersal is initiated. However sometimes, due to a founder effect caused by the limited number of colonizers often consisting of a specific phenotype, increased dispersal tendency may hasten further spread.

Certain phenotypic traits have been discovered to reduce the costs of dispersal (O’Riain et al. 1996; McCauley 2013). For example, dispersing individuals of the naked mole rat (Heterocephalus glaber), which lives in eusocial colonies, are larger and more energetic/active when compared to individuals that stay behind (O’Riain et al. 1996). Also, dragonflies that disperse greater distances have longer and slimmer wings than their residential conspecifics (McCauley 2013), though at the cost of reduced maneuverability (Svensson and Friberg 2007).

**The role of personality in dispersal and species invasions**

One important group of phenotypic traits is behaviors. The role of consistent individual differences in behavior, in for example dispersal and species invasions, has received increasing attention in the scientific community over the last decade leading to many new discoveries (Sih et al. 2004a&b; Reale et al. 2007; Juette et al. 2014). Before this recent development, behavioral variations within populations were treated as noise around an adaptive mean and their importance was thereby completely overlooked (Bolnick et al. 2003). In recent years however, behavioral traits with consistent individual variation have been identified as important factors in various ecological processes (Reale et al. 2007; Hudina et al. 2014; Juette et al. 2014). Sociability, activity, boldness-shyness, exploration and aggression have been identified being of particular importance and as a consequence are the most commonly studied behavioral traits in ecology (Réale et al. 2007). They have been referred to as temperament (Gosling 2001), coping style (Koolhaas et al. 1999) and personality (Réale et al. 2007), among other, and are also considered crucial for understanding the invasion process (Duckworth and Badyaev 2007; Cote et al. 2010a&b). These traits are often correlated and
form so called “behavioral syndromes” which preferably should be studied as a package (Sih et al. 2004a). When correlated traits are studied separately, false relationships can be found. For example, a correlation between male exploratory behavior and mating success was found, eventhough females selectively mate with bolder males and boldness was positively correlated with exploration (Sih et al. 2004a&b).

Sih et al. (2004a&b) described the theory of behavioral types in their review of the ecological aspects of behavioral theory. For example, an individual that is bold and/or active in different contexts (e.g. feeding, antipredator, dispersal etc.) has a bold and/or active behavioral type. Studies have shown that these traits can be expressed at maladaptive levels, in certain contexts, resulting in direct negative fitness consequences (Sih et al. 2003; Sih et al. 2004a&b; Sih and Watters 2005). For example, Arnqvist and Henriksson (1997) found female Raft spiders (Dolomedes fimbriatus), that normally consume the male after mating, living in areas where aggression is beneficial, to evolve aggressive behavioral types to such an extent that some females consume the males before mating. These maladaptive behavioral levels contradict previous theories in behavioral ecology stating that behavioral plasticity enables individuals to adapt to their present environment (Sih et al. 2004a&b).

The dispersal process is usually divided into three distinct stages (departure, transience and colonization) and is initiated when an individual decides to depart from the native range (Bowler and Benton 2005). Dispersal tendency and success have been connected to a wide range of behaviors such as asociality, boldness, activity, exploration and aggression (Fraser et al. 2001; Dingemanse et al. 2003; Duckworth and Badyaev 2007; Cote and Clobert 2007; Duckworth and Kruuk 2009; Cote et al. 2010a, Cote et al. 2011). In addition to dispersal tendency, which was affected in all of these studies, Cote et al. (2010a) found a negative correlation between individual sociability and dispersal distance in an artificial stream. In a subsequent study they also showed that personality-dependent dispersal was cancelled when predator cues were present (Cote et al. 2013), thereby revealing a context dependency of personality-dependent dispersal.

Asocial individuals have lower fitness in high densities compared to low (Cote et al. 2008). As a result, asocial individuals commonly lead dispersal from densely populated areas (Cote and Clobert 2007a; Cote et al. 2010a). In contrast, fitness of social individuals is positively correlated to population density (to a certain point). Social individuals tend to hide in numbers when avoiding predators and disperse from low densities in search for higher densities by following chemical cues (Cote et al. 2007a).
In the context of species invasions, traits that are beneficial at different stages of the invasion process are also important to facilitate successful invasions (Moyle and Marchetti 2006). However, due to the variation in selection pressures during the different stages, it is unprobable that a single trait expression or behavioral type is the most successful during the entire invasion succession (Cote et al. 2009). Hence, successful invasions should require a combination of trait expressions or behavioral types in the founding population for the process to be completed (Sih et al. 2004a&b; Cote et al. 2010b; Fogarty et al. 2011). Studies relating personality with species invasions are scarce but not unheard of. As previously mentioned, dispersal tendency has been linked with asocial behavior (Cote et al. 2010a) and boldness (Cote et al. 2011) in the invasive mosquitofish (Gambusia affinis). Similarly, natal dispersal has been linked with exploration tendency in great tits (Parus major) (Dingemanse et al. 2003) and aggressive western bluebirds (Sialia mexicana) have been found to disperse and outcompete less aggressive mountain bluebird (Sialia currucoides) populations (Duckworth and Badyaev 2007). In recent years, inclusion of behavioral traits as important factors for the spread of invasive species has received increasing attention (Duckworth and Badyaev 2007; Groen et al. 2012; Myles-Gonzalez et al. 2015). In their study of the round goby in North America, Groen et al. (2012) found individuals captured at invasion fronts to outcompete individuals captured in older established areas when competing for a single shelter/nest. Similarly, Myles-Gonzalez et al. (2015) found individuals of the round goby from invasion fronts to be bolder and to disperse faster and further than those from older established areas.

**Stress coping styles**

Studies of physiological response to stressful events or conditions have revealed consistent individual specific response along the proactive-reactive axis. Proactive response is characterized by individuals reacting aggressively towards intruders, boldly and actively resume foraging and mating activities in risky situations. Proactive individuals also show a lower physiological stress response (e.g. release of glucocorticoid hormones). In contrast, reactive individuals exhibit high stress levels, are shy and more adaptable to change. These strategies are commonly referred to as stress coping styles (Koolhaas et al. 1999; Cockrem 2013; Castanheira et al. 2015). Under stable conditions, aggressive, bold and active (proactive) individuals generally have a competitive advantage, such as higher foraging efficiency (Smith and Blumstein 2008) and/or competition for shelter or resources (Duckworth and Badyaev 2007; Groen et al. 2012). However, in the presence of predation risk proactive individuals often express suboptimal levels of said behaviors which results in reduced survival (Sih et al. 2004).
As established in previous sections, activity, boldness and aggression have been recognized as crucial factors for the onset and success of dispersal and species invasions (O’Riain et al. 1996; Fraser et al. 2001; Duckworth and Badyaev 2007; Cote et al. 2011; Groen et al. 2012; Myles-Gonzalez et al. 2015). Nevertheless, not a single paper connecting stress coping styles with species invasions could be found, illustrating a major knowledge gap and a potentially fruitful research venue.

**Objectives**

The objective of this thesis is to investigate the role of consistent individual variation in behavioral traits and stress coping strategies for the spread of the invasive round goby (*Neogobius melanostomus*) in the Baltic Sea. Four study-populations were chosen, two of which are recently established whereas the remaining two are two of the oldest populations in the Baltic Sea. The specific questions for each paper (I-IV) are as follows:

I. (i) Is there a bias towards certain expressions of behavioral traits (sociability, boldness and/or activity) in newly established populations when compared with older populations in the invasion succession (phenotype dependent invasion success)? (ii) Is there a correlation between sociability, boldness and activity, revealing a dispersal syndrome, in which dispersers have lower social tolerance, are bolder and more active whereas residents show the opposite behavior?

II. (i) Do dispersers display phenotypic traits that are commonly overrepresented at invasion fronts (e.g. low sociability, high boldness and/or activity)? (ii) Do the effects of these traits on dispersal tendency differ between populations in early stages of the invasion process and older established populations? (iii) Are these behaviors (sociability, activity, boldness and dispersal tendency) consistent and repeatable?

III. (i) Is there a lag phase between establishment and spread in newly invaded areas? (ii) Are certain phenotypic traitexpressions more common at the extreme invasion front (surrounding the areas where round gobies were discovered 3-4 years earlier) compared to the newly established source population?

IV. (i) Are there stress coping styles in round gobies (high aggression and stress tolerant vs. low aggression and high stress in the presence of risk)? (ii) Are individuals from old and new populations different in aggression and stress tolerance?
Materials and methods

Model species

As a model species, we chose round goby (*Neogobius melanostomus*), which are small invasive fish with a benthic morphology and inhabit rocky substrates in shallow areas during the summer where they can reproduce several times per year (Wickett and Corkum 1998). The males fight for and defend nests into which several females may lay their eggs (Wickett and Corkum 1998; Sapota 2004). The males then stop feeding and guards the eggs (Wicket and Corkum 1998; Sapota 2004) and larvae (Hensler and Jude 2007). The round goby pose a threat to native fish in invaded areas by consuming eggs from other species (Steinhart *et al.* 2004) and by competing for space and resources (Dubs and Corkum 1996). The multiple reproductions combined with being highly competitive allow the round goby population to grow rapidly following an introduction. In the oldest population of the Baltic Sea (Hel), densities of up to 30 ind/m² were found only 14 years after first being discovered (Sapota 2004).

They are native to the Ponto-Caspian area (Jude *et al.* 1992), but invaded the Gulf of Gdansk in Poland, as well as the Laurentian Great Lakes in North America, in or just before 1990 (Corkum *et al.* 2004; Sapota and Skora 2005). They are known for passive long-distance dispersal by means of ballast water in freighters (Sapota and Skora 2005) and to disperse actively from established areas (Bronnenhuber *et al.* 2011; Gutowsky *et al.* 2011; LaRue *et al.* 2011), a process known as stratified dispersal (Björklund and Almqvist 2009). Its gradual spread throughout the southern Baltic Sea has been studied extensively from the very beginning (Sapota and Rzeznik 2001; Corkum *et al.* 2004; Sapota and Skora 2005; Björklund and Almqvist 2009&2010) and now there are established populations as far north as Mariehamn Åland (Kaj Ådjers, personal communication; I; II; III; IV). The fact that the round goby was discovered early in the invasion process and is currently spreading in the Baltic Sea, makes this a perfect study species for investigating the effects of individual variation in phenotypic traits on various aspects of the invasion process.
Study system

As previously mentioned, we used two of the newest and two of the oldest populations discovered in the Baltic Sea in all four papers except for paper III were we only used the newly established. The older populations were sampled in the Gulf of Gdansk in Poland, more specifically, in Hel (54°36´24”N, 18°47´53”E), where they were discovered in 1990 (Corkum et al. 2004; Sapota and Skora 2005), and in Swarzewo (54°45´24”N, 18°24´16”E), where they were discovered in 1994 (Sapota 2004; Sapota and Skora 2005) (Fig. 1). The newest populations were sampled in Visby (57°38´17”N, 18°17´13”E) which is located on the Swedish island of Gotland, where the gobies were discovered in 2010 (Rickard Gustafsson, personal communication), and in Mariehamn Åland (Finland) (60°06´01”N, 19°55´23”E), where they were discovered in 2011 (Kaj Ådjers, personal communication) (Fig. 1).

Capture methods, transportation and holding

Sampling in all locations was conducted using fyke-nets with mesh size 11-20 mm. The traps were left in the water for 24 hours on each catch site. In the harbor in Gotland, boat traffic and space-limitation sometimes precluded the use of traps. To compensate for this, two persons angled for one hour per site. For paper II, III and IV, round gobies were transported from their respective populations to a marine station (Umeå Marine Science Centre) in Norrbyn, 40 km south of Umeå. In the marine station gobies were kept in tanks containing 605 L of natural brackish water from the Bothnian Bay (0.4 % salinity) with a constant flowthrough. All tanks contained one shelter per individual and fish were fed ad libitum with pellets from Skretting Nutreco® three times per week.

Individual marking (pit-tag)

For paper I, the behavioral assays were conducted on site using the same aquarium and equipment. In subsequent experiments (II, III and IV) the gobies were marked individually with RFID tags, also known as Pit-tags, thereby enabling us to hold them in groups in the lab and still keep track of individual gobies. Prior to marking, each individual was sedated using ms-222 (Tricaine methanesulfonate) before inserting the tag into the body cavity.
Behavioral assays

In all studies and for all behavioral assays, each individual was allowed one hour of acclimatization in a 10 liter non-transparent container before sociability, activity and boldness and in the experimental aquarium for aggression. This was done to standardize stress levels that can vary between individuals depending on time taken to catch them in the tanks, but stress levels in round gobies have been found to peak 20 minutes after acute stress and return to normal levels after one hour (Marentette et al. 2013).

Figure 1. Round gobies were sampled in Hel and Swarzewo in Poland and in the harbors (dark grey areas) of Visby, Sweden and Mariehamn Åland for all studies, and additionally in the shorelines (light grey areas) surrounding Visby and Mariehamn. Modified from paper III.
**Sociability**

Sociability was measured in 80 L aquaria for paper I and 60 L for papers II, III and IV, which were divided into three compartments, using transparent glass walls. The middle compartment comprised 50% of the aquarium and the two side compartments 25% each (Fig. 2). At least one hour prior to each assay, two medium sized round gobies were placed in one end (chosen randomly) to allow them to acclimate before the focal individual was placed in the middle compartment. The position of each individual was digitally recorded for 25 minutes in paper I and one hour in papers II, III and IV. From the recordings, average distance to the wall separating the focal individual from the pair, during 10 (paper I) and 30 minutes (paper II, III and IV), was extracted and used as a sociability score. In all experiments, individuals that had not started moving during the first 15 (paper I) or 30 minutes (paper II, III and IV) were excluded from the analysis as sufficient data could not be extracted.

![Figure 2. Sociability aquarium used in paper II, III and IV.](image)

**Activity**

In I, II and III, activity was estimated during the sociability experiments as time spent moving (paper I) and number of moves representing a movement of more than one centimeter per six seconds (paper II and III) during the experimental period.

**Boldness**

In paper I, each individual was placed in a 40 L aquarium and left undisturbed for five minutes before a novel object (a 12 cm long, 10 cm diameter PVC pipe with one end closed) was introduced to the opposite side
of the aquarium. In paper II and III, we used 60 L aquarium and left the fish undisturbed for 10 minutes before presenting it with a simulated bird attack (a grey hard plastic plate formed in the shape of a beak attached to a thin PVC pipe). All trials were recorded to prevent any effect of human presence on fish behavior. In paper I, latency to move, swim one body length and approach the novel object were extracted from the videos and represented three different measures of boldness, while in paper II and III, latency to move following the “bird attack” was used as a boldness score.

**Aggression**

As previously mentioned, acclimatization prior to the aggression assays in paper IV, took place in the experimental aquarium. This was done to induce prior residence of the tank in the focal fish. Following acclimatization, recording was initiated and a mirror placed in one end of the aquarium. The fish was then recorded for one hour without disturbance. From the video, total number of attacks during a 15 minute period was extracted, starting when the fish first moved.

**Dispersal**

The dispersal system, used in paper II, was constructed from five square shaped tanks (110 x 110 x 100 cm) connected with 50 cm long dispersal corridors 5 cm above the bottom (Fig 3). The corridors were constructed from 20 cm diameter PVC pipes of which 1/3 was laterally removed creating a shallow dispersal corridor exposed skywards to increase perceived risk. The corridors were equipped with antennas (one antenna/corridor) connected to an automatic pit-tag reader which recorded the time and pit-

![Image](image-url)

**Figure 3.** The dispersal system was composed of five square shaped tanks (110 x 110 x 100 cm) with a water level of 23 cm. Dispersal corridors with a diameter of 20 cm, equipped with pit-tag antennas, enabled the round gobies to disperse freely for 21 hours. An automatic pit tag reader recorded the time, ID of the fish and the antenna number each time an individual passed through a dispersal corridor (Figure from paper II, Thorlacius et al. 2015).
tag number of every fish passing through. Each trial was initiated by placing the dispersal group, consisting of ten individuals sorted by population and similarity in size, in one end of the dispersal system (starting tank). The first corridor was always closed for two hours (for acclimatization) following introduction of each dispersal group to prevent dispersal due to stress-induced escape response. At the end of the two hour period the corridor was remotely opened, allowing the fish undisturbed access to the entire dispersal system for 21 hours.

Dispersal tendency was measured as latency to enter antenna 1-4 (seconds) and dispersal distance (or exploration) was measured as the total number of readings multiplied with the distance from the center of one tank to the center of the next \((110/2 + 50 + 110/2 = 160 \text{ cm})\).

**Population abundance and catch per unit effort**

In paper III population abundance and catch per unit effort was compared between the harbors and surrounding shorelines of Åland and Gotland (Fig. 1). Population abundance was estimated using a mark-recapture method at four (Gotland) and five (Åland) occasions over two breeding seasons (2013-2014). On each trapping occasion and station, all gobies caught were weighed to nearest 0.1 g (wet weight), measured for total length to nearest mm, sex-determined and marked (individual marking (pit-tag)).

Estimation of population abundance was done using Program Mark (White 2007), more specifically the POPAN function of the Jolly Seber model. Out of 1029 marked individuals in Åland and 531 in Gotland, only one was recaptured in Åland and two in Gotland, making estimates of abundance imprecise (large confidence interval). It took 5 days to complete catching in all sites at each sampling occasion, and days were pooled in order to improve mean precision (Cooch and White 2007).

Due to lack of recaptures, population growth was estimated exclusively by calculating catch per unit effort. Within area, occasion and type/size of trap, total number of round goby caught per 24 hours per trap was calculated (captures of zero included). In addition, sex ratio was calculated as the proportion (%) of males per area and occasion.

**Estimation of stress response to different densities**

In paper IV, we investigated individual stress tolerance along a succession of population age. 36 individuals from Åland, 18 from Gotland, 54 from Hel and 54 from Swarzewo, which had been held in different densities (Åland:
38/m²; Gotland: 19/m²; Hel: 26/m²; Swarzewo: 26/m²) for the previous five months. In January 2015 all individuals were weighed, measured for length and placed in groups of 18 (15/m²) (9 groups in total) with one shelter each. After 45 days in the standardized density (15/m²), shelters were removed from all but two groups (one from Hel and one from Swarzewo) that were used as control. After a week without shelters, 10 out of the 18 individuals in each group were euthanized and blood was extracted. After another week, in densities of 6.5/m², the remaining 8 individuals were sampled.

Using a heparinized syringe, blood was drawn from the caudal vein and stored on ice until all individuals in the respective sample-event had been sampled. The blood was then centrifuged for 2 minutes at 5000 rpm’s to obtain plasma which was stored at -20°C until it could be analyzed. The sampled plasma was later analyzed for cortisol concentrations using a commercial enzyme linked immunosorbent assay (ELISA) kit as described in the manufacturer’s instructions (product # 402710, Neogen Corporation, Lexington USA).

**Consistency and Repeatability**

In paper II and III, sociability, activity and boldness, as well as dispersal tendency and distance/exploration for paper II, were repeated on a subsample (54 individuals) after four months for paper II and (61 individuals) after three months for paper III. During this period, temperature of the water, pumped in from the Bothnian Bay, was not regulated which resulted in a difference in temperature between the initial and repeated trials. In June 2014 the mean temperature was 10.3°C while when repeated in October it was only 5.9°C. For the dispersal assays, the temperature in July 2014 was 12.7°C but only 4.6°C in November when the trials were repeated. The potential effects of these discrepancies in temperature are discussed in detail further down.

**Data analysis**

**Mixed models**

The effect of population age (large scale in paper I and small scale in paper III) on sociability, activity and boldness were modeled using separate mixed effects models for each behavior with population as random factors (Pinheiro et al. 2013). Poisson errors were used for the boldness model in paper I in which overdispersion was corrected for using an observational level random effect (Zuur et al. 2012). Gaussian errors were used for all other models. In paper II, effect of sociability, activity, boldness, body size,
condition (calculated as $100^\ast(weight/length^3)$ (Nash et al. 2006)) and within group size range on dispersal tendency and distance/exploration was modeled. Population and group were added as random factors in all of the models (Pinheiro et al. 2013) and a variance function that allows for different variances between dispersal groups added to the sociability and boldness models due to heteroscedasticity revealed by residual plots.

In paper IV, the effect of blood sampling cohort, treatment densities, holding densities, aggression, total body length, wet weight and within group variation in length on cortisol concentrations were modeled, without control groups, separately with population, treatment density and blood sampling cohort as random factors (Pinheiro et al. 2013). Due to heteroscedasticity revealed in residual plots for the models for previous holding densities and aggression, a variance function that allows for different variances between populations was included. The effect of total body length and weight on aggression was modeled using population age as random effects and a variance function that allows for different variances between the populations added to correct for heteroscedasticity.

In all four papers, optimization of model structures was conducted following the outline by Zuur et al. (2009), using AIC-based model selection (Burnham and Andersso 2002), and determining significance by comparing the models with and without the fixed factor in question as a fixed effect, using a likelihood ratio test.

**Correlations**

In paper I, Spearman’s rank correlations were used to test for correlations between behavioral traits and between behavior and body size. In papers II and III however, the behavioral traits were log transformed and Pearson’s correlations could be used.

**ANOVA**

In papers I, II and IV, differences in body size (length and weight) between the populations were analysed using ANOVA followed by Tukey’s multiple comparison of means with 95% confidence interval.

**Consistency and repeatability**

The behavioral assays, along with the dispersal trials in paper II, were repeated using the same methods and equipment on a subsample after four months. Consistency was estimated using correlations (Spearman’s rank for
paper II and Pearson’s for paper III) and repeatability, or the Intraclass correlation coefficient (Sokal and Rohlf 1995), was estimated using the package ICC (Wolak et al. 2012) in the statistical program R (R Development Core Team 2012).

Non-normally distributed variables were log-transformed to achieve normality. Also, for sociability, boldness and dispersal tendency, lower scores represented higher sociability/boldness/dispersal tendency. This was corrected for by subtracting the score from the maximum distance to conspecifics for sociability and time for boldness and dispersal tendency.

All statistical analysis were conducted in the statistical program R (R Development Core Team 2012), using the packages “nlme” (Pinheiro et al. 2009) and “lme4” (Bates et al. 2011) for the mixed models and “ICC” (Wolak et al. 2012) for repeatability.

Results and discussion

Phenotypic differentiation along a large scale invasion succession

In 2012, round gobies from Åland and Gotland (one-two years from first being discovered) were found less social, more active and bolder than their conspecifics from the older populations in Poland (18-22 years) (I, Fig. 4a, b & c). All three of these traits have previously been connected with dispersal tendency (Cote et al. 2010b) and/or distance (Ims 1990), in among others, the invasive mosquitofish (Cote et al. 2010a; Cote et al. 2011). Only two other studies, conducted in the field, comparing populations at invasion fronts with older established populations could be found (Groen et al. 2012; Myles-Gonzalez et al. 2015). Groen et al. (2012), connected aggressive behavior of individuals captured at invasion fronts, with superior competitive ability while Myles-Gonzalez (2015), found round gobies at invasion fronts to be bolder, have greater dispersal tendency and higher resting metabolic rate when compared with individuals in older populations.

Paper I is the first study to find differences in sociability between individuals at an invasion front and conspecifics in older populations, and even studies connecting sociability and dispersal or species invasions are scarce (Cote et al. 2010b). Based on previous studies of sociability, two scenarios may cause the apparent differentiation. One possibility is that a random sample from the source population was carried passively to the novel environment and that selection for asocial behavioral in low densities (Cote et al. 2008) has
caused the observed differences. Social individuals often rely on safety in numbers as a means of predator avoidance, which may be ineffective for a period following colonization as densities are too low (Lewis and Kareiva 1993). The other possibility is that asocial individuals dispersed from the older populations due to high population densities (Cote and Clobert 2007; Cote et al. 2010) and since older invasive populations of round gobies have been found in densities of up to 30 ind./m² (Sapota 2004) this explanation seems plausible. Both scenarios would in turn be expected to increasingly dampen population growth in the older populations as densities increase (Cote et al. 2008; Fogarty et al. 2011).

Colonization of novel environments presumably start with a smaller than optimal population resulting in slow population growth due to limited genetic diversity (Allee-effect) (Lewis and Kareiva 1993). This could limit the diversity of behavioral types in the population to the most capable of surviving the dispersal and the initial conditions when establishing. Bold and active individuals have been found to resume foraging activities and exploration of the environment relatively fast in the presence of predation risk (Smith and Blumstein 2008) and to have greater reproductive success (Reale at al. 2000; Smith and Blumstein 2008). In this context, novel environments are often perceived as risky by the disperser due to lack of knowledge concerning shelter, predation, food resources, etc. (Stamps 2001). Another potentially important factor benefiting bold and active individuals is connected to the enemy release hypothesis, which suggests that

Figure 4. Mean values of sociability (a), activity (b) and boldness (c) in the newly established populations (New) one-two years after they were first discovered and the older populations (Old) 18-22 years from first being discovered. Error bars denote ± CI. Modified from I.
invasive individuals may leave coevolved predators, parasites and pathogens behind resulting in reduced predation risk (Colautti et al. 2004).

In paper II, we investigated the effect of population age on dispersal tendency using individuals captured in 2014 from the same four populations as in I. As expected, active individuals, in the newly established populations, had a higher dispersal tendency in the dispersal system (I, Fig. 5a). This matches previous findings of active individuals in natural populations having a higher emigration rate than less active individuals (O’Riain et al. 1996; Bonte et al. 2004; Aragon et al. 2006). Additionally, populations often experience selection for higher growth and reproductive rate in low densities (Burton et al. 2010), and high activity is known to facilitate foraging levels and growth (Brodin and Johansson 2004). The benefit of increased activity is particularly relevant in newly colonized areas due to the previously mentioned enemy release hypothesis (Colautti et al. 2004). Also, activity is commonly measured in the same, or very similar, way as exploration (Reale et al. 2007) and/or boldness (Brodin and Drotz 2014) which have also been connected with dispersal tendency (Fraser et al. 2001; Cote et al. 2011).

No connection was found between behavior and dispersal in the old populations (II). Though surprising, it is possible that behaviors increasing dispersal tendency is selected for at invasion fronts but that selection changes with increasing population age. This type of selection pressure for increased dispersal, often generating spatial sorting of phenotypes, is referred to as “the Olympic village effect” (Phillips et al. 2008a; Shine et al. 2011) and is withheld through assortative mating by dispersal ability at the forefront of invasive spread. Given time this process may lead to runaway selection for increased rate of spread (Travis and Dytham 2002; Hughes et al. 2007). With time, local population densities grow (here 3-5 years (III)), which increases the cost of staying until it, for certain phenotypes, surpasses the cost of dispersing. At that point density-dependent selection no longer favors disperser phenotypes but shifts towards other trait combinations that are more successful in high densities and intraspecific competition. It is possible however, that this shift in selection pressure may have already taken place in the newer study populations, which were already 3-5 years old and very abundant at the time of sampling. In addition, such a scenario would explain the lack of correlation between dispersal tendency and either of sociability and boldness. We did however find a connection between mean sociability of dispersal group and dispersal, in which groups with high mean sociability dispersed sooner (Fig. 5b). As a possible explanation for these contradicting results, aggression may to some extent have confounded our sociability scores as aggressive interactions were observed during our
sociability trials. In aggressive species it is very difficult to isolate sociability from aggression (Hudina et al. 2014).

**Phenotypic differentiation along a small scale invasion succession**

Using mark-recapture (Fig. 6a&b) and catch-per-unit-effort (CPUE), the harbor populations were found much more densely populated than the surrounding shorelines, but with a major increase in CPUE along the shorelines in 2014 (3-5 years from colonization of the harbors) (III, Fig. 7). This population increase of the naturally dispersing front-population probably marks the end of the lag-phase that is often observed between introduction and spread (Sakai et al. 2001). However, judging by the size of the harbor populations in 2013, we might have expected the lag-phase to end already then (III). During the first years following a new colonization limited spread is often observed. This can be explained by the costs of dispersing from newly established, low density (low competition and often low predation) populations are higher than the costs of staying (Sakai et al. 2001). Hence, the rapid increase in CPUE in surrounding shorelines is presumably the result of increased costs of staying due to high population densities and as a consequence high intraspecific competition within the harbors. This is also supported by the fact that the colonization of

![Figure 5. In newly established populations, active individuals (a), and individuals in groups with high mean sociability (b), had lower latency to disperse. Modified from II.](image)
surrounding shorelines is driven by asocial individuals (III, Fig. 8a). As discussed earlier, density dependent dispersal is commonly led by asocial individuals (Cote and Clobert 2007; Cote et al. 2010a) as they have higher fitness in lower densities (Cote et al. 2008). Hence, our results indicate an ongoing behavioral sorting with asocial behavioral types overrepresented at invasion fronts.

As boldness has been connected to dispersal tendency in previous studies of the round goby (Myles-Gonzalez et al. 2015) and other fish (Fraser et al. 2001; Cote et al. 2011), over-representation of bolder individuals along the shorelines was expected. However, a previous study comparing invasion fronts with older established areas, as we did here (Fig. 8c), did not find any differentiation of boldness between the populations (Groen et al. 2012; III). More importantly, as individual dispersal tendency has been connected with activity in these very populations (II), among others (O’Riain et al. 1996), the lack of differentiation in activity between individuals along the newly colonized shorelines and the harbors is surprising (Fig. 8b). Based on this the conclusion is that sociability is the most important factor facilitating spread from high conspecific densities in natural populations.

Body size has been identified as a key trait for population dynamics, as well as an important fitness determinant (Banks and Thompson, 1987; Werner

**Figure 6.** The mark-recapture data analysis revealed substantially higher round goby abundance in the harbors in both Åland (a) and Gotland (b) when compared with the surrounding shorelines. Error bars indicate ±95% confidence interval. From paper III.
and Gilliam, 1984). This is especially true for an aggressive species, like the round goby, in which males fight for and defend nests during the warmer half of the year (Wickett and Corkum 1998; Stammler and Corkum 2005; Sopinka et al. 2010). For example, a three percent difference in body size has been found sufficient to determine the outcome of a competitive interaction for a shelter/nest in favor of the larger individual (Stammler and Corkum 2005). In the dispersal assays, larger individuals were found to disperse sooner (II), while the colonizers of the shorelines were smaller than average individuals within the harbors (III). In neither study was behavior correlated with body size (II, III). These seem like contradicting results, but when considering the fact that reproductively active males in nature stay within their home range, limited to 5 meters (Stammler and Corkum 2005), once they have established residency it is not surprising that large males stay in the cavity-rich harbors. Smaller individuals however, have little chance of acquiring a nest in abundant areas like the harbors (III) and should therefore benefit more from venturing out-side the harbor areas (Brownscombe and Fox 2012). During the dispersal assays however, all fish had been removed from their home territory, forcing them to restart the process of locating a

![Figure 7](image-url)  
**Figure 7.** Catch per unit effort (CPUE) along the shoreline outside of the harbor in Mariehamn, (Åland) and Visby (Gotland) during the different sampling occasions. Error bars indicate ±95% confidence interval. Modified from III.
suitable nest (e.g. cavity). In nature, larger individuals have been found overrepresented at invasion fronts when conditions are better there than in older parts of the established range (Brandner et al. 2013). Due to absence of food and shelter, our dispersal system may have been perceived as low-quality habitat from which dispersal led by larger and presumably dominant individuals would be predicted (Brandner et al. 2013). In the older populations, dispersal was also negatively correlated with size range within dispersal groups and physical condition (II). With increasing size range, hierarchy is predicted to be established faster and with less aggressive interactions. However, with decreasing size difference between aggressors’s both uncertainty of competitive superiority and frequency of aggressive encounters increases. To reduce the cost of aggressive interactions, in particularly for individuals with low energy reserve, dispersal might have been induced. Also, individuals with low energetic state (low condition) are more pressed to find food which also could lead to higher dispersal tendency. Judging from our results, there appears to be behaviorally driven dispersal in newly established populations while competition is more important inducing dispersal in older populations.

**Stress coping styles**

In paper IV we showed, for the first time, evidence for the presence of stress coping strategies in the round goby (Fig. 9a). Proactive individuals that have a low stress-response to high conspecific density also display high levels of
aggression while reactive individuals display high stress-response and low aggression.

Stress coping styles are well described in fish, though especially in farmed fish (Castanheira et al. 2015). Individuals are categorized along a proactive-reactive axis where proactive individuals are more aggressive, stress tolerant, bold and active than reactive individuals (Koolhaas et al. 1999). Despite the intuitive connection between stress and biological invasions we have not found a single study on how stress coping strategies, or stress tolerance,
affect species invasions. This is surprising since an individual’s way of dealing with various biotic and abiotic challenges (stressors) during the invasion process may profoundly affect which individuals that succeed or fail to complete the process. Apart from physiological stress, several studies have connected activity, boldness and aggression with dispersal tendency (O’Riain et al. 1996; Fraser et al. 2001; Duckworth and Badyaev 2007) and/or invasions (Cote et al. 2011; Groen et al. 2012; Myles-Gonzalez et al. 2015; I; II; III). Boldness and activity, components of individual coping strategy (Koolhaas et al. 1999), were in paper I found to be expressed in high levels at the invasion front and to correlate positively with dispersal (II). Based on this we expected proactive individuals to be more successful in the newly established populations. Even though reactive individuals are supposedly better at dealing with environmental change (Koolhaas et al. 1999; Cockrem 2013; Castanheira et al. 2015) we hypothesized that the positive correlations priorly found between dispersal/invasion success and aggression (Duckworth and Badyaev 2007; Groen et al. 2012), boldness (Cote et al. 2011) and activity (II) respectively, would be more important for the phenotypic sorting along invasion gradients.

However, our results revealed no effect of population age on aggression, stress response or body size (IV, Fig. 9b,c&d). Instead we found a direct effect of holding densities prior to the experiment on both aggression (Fig. 10).
10a) and stress response (Fig. 10b). Individuals in the population that was held at the highest densities during the period prior to the experiment (Åland) were the most aggressive (Fig. 9a) and least stressed, though only significantly different from Gotland (Fig. 9c).

**Repeatability of behavioral traits**

Most studies of personality traits report rather low but significant repeatability (Bell et al. 2009). In paper II and III, we investigated repeatability of sociability, activity and boldness over a period of three (III) to four (II) months. Unfortunately, due to a flow through of natural brackish water, temperature differed significantly between the trials (behaviors - 4.4°C and dispersal - 8.1°C) which more than likely affected repeatability.

Our results revealed consistency and repeatability in boldness and dispersal tendency and distance/exploration in the new populations only. Previous studies have found bold individuals to be more consistent than shy (Magnhagen and Bunnefeld 2009) which is in line with our results of bolder individuals in the new populations (I). Similarly, repeatability in dispersal tendency has been found significant in several studies and across taxa (spiders: Bonte et al. 2009; birds: Doligez et al. 2009; fish: Cote et al. 2010a). The presence of consistency and repeatability, despite the temperature difference, suggests that boldness, and dispersal tendency are robust traits with high predictable value.

When it comes to sociability and activity there are several explanations for the lack of repeatability. The first assays were conducted in the peak of the breeding season, while the repeated trials were conducted in September (III) and October (II). Apart from obvious behavioral alterations across this temperature gradient and differing stages of the mating season, the round goby also migrate to deeper areas in the fall (Jude et al. 1992). Hence, it is possible that free-living gobies would have already left the breeding areas at the time of our repeated trials. It is therefore impossible to say, judging from our results, whether sociability and activity are repeatable within breeding seasons or not.

**Conclusions**

In paper I, we showed that individuals in newly established round goby populations are not a random sample from the source population. They are less social, more active and bolder than the average individual in the older
populations. With three traits, that have all been connected with dispersal tendency, overrepresented in these populations, a high rate of invasive spread is to be expected.

In paper II we found evidence suggesting that the driver of invasive spread might change with population age. In new (3-5 year old) populations, dispersal was positively correlated to individual levels of activity, while in older populations dispersal was not correlated with any behavior. In both cases, larger individuals dispersed sooner which may partly be explained by the urge of reproductively active males to establish nests/territories.

In paper III, we demonstrated the presence of a lag-phase of 3-5 years between colonization and spread. Then, at the end of the lag-phase, our results suggest that spread was performed by asocial individuals of smaller than average body size probably as a response to increasing conspecific density. Asocial individuals have lower fitness in high densities and stand a much better chance of successfully defending a nest away from the abundance of larger competitors that are found in the harbors. This information is important for management purposes and monitoring studies, as action should be taken within 3-5 years from first discovery of this species in order to prevent further spread.

And finally, in paper IV, we found the first evidence of stress coping strategies in the round goby in which individuals with greater stress-tolerance are also more aggressive. The round goby tolerate long periods in very high densities without an increase in mortality. During this time, our results suggest that, they adapt to high intraspecific competition by reducing stress responsiveness and increasing aggression.

**Future studies**

Most studies of the effects of individual behavioral traits on invasion spread are limited to laboratory studies which indirectly make assumptions of their relation to natural events. More studies of behavior in nature are needed to shed light on these effects. Mark recapture studies have been attempted for these purposes, in paper III among others. Due to the high abundances commonly found of many invasive species, low recapture-rates and unknown factors such as migration patterns, studies not dependent on recaptures, such as acoustic telemetry, may be a better alternative.
When it comes to long-distance dispersal of the round goby, evidence suggests that ballast water transport is the most common method of dispersal. However, the lack of information regarding seasonal migratory patterns and whether all individuals return to the same area every year makes predicting dispersal patterns and distances difficult. We have shown that certain behavioral types have greater dispersal tendency during the reproductive season, but whether these behavioral types disperse undetected in deeper waters before emerging to shallow breeding areas is not known. A greater understanding of these processes would greatly improve predictions of invasive spread as well as being useful for construction of control programmes.

Round goby larvae migrate vertically to feed by the surface during night time (Hayden and Miner 2009). In rivers and marine areas with high currents, this may be an important dispersal vector which appears largely overlooked in marine environments. Following currents from areas with already established round goby populations and applying capture methods suitable for larval and juvenile stages could shed some light on the importance of this dispersal vector. In addition, it would also provide useful information for predictions of rate of spread, invasion routes and construction of control programs.

Additionally, for relating dispersal tendency with individual behavior at invasion fronts, populations more recent than 3-5 years should be studied. All evidence suggests that there is a selection for asocial, active and bold behavioral types at invasion fronts but that it fades out locally as populations get older. Additionally, the harbor environment differs to a large extent from that found along the shore line. Whether the same processes influence spread from the harbors as will facilitate spread along the shore or in rivers is a subject for future studies.

Sociability seems to play an important role in dispersal and species invasions. In aggressive species however, such as the round goby, separating aggression from social interactions is a challenge. Studies of sociability in different context or possibly social network experiments might shed a light on how to separate the effects of these behavioral traits in ecological processes like dispersal and species invasions.

As mentioned in the thesis, relating individual stress response with invasion success appears to be completely overlooked. The majority of all introductions do not lead to invasions due to the varying obstacles that individuals are faced with along the way. Hence, it seems intuitive that stress
tolerance, or stress coping styles, are an important factor during species invasions and should be investigated further.

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