Variation in behavior and the success of an invasive species

Comparison of sociability and activity between four populations of the Round goby (Neogobius melanostomus) in the Baltic Sea

Fia Finn
Abstract

Ecological invasion is a major global threat to biodiversity and behavioral studies could result in greater understanding for the mechanisms facilitating successful invasion. The theory of behavioral types is a notion that implies limited plasticity and makes it possible to predict behavioral responses to change. During an invasion, individuals from a population will come across different situations were different traits will be of more or less use. This will result in varying selection pressures along different stages of the invasion, and probably result in a non-random sample of behavioral types in the population successfully residing at an invasive front. At later stages of an invasion, behavior of the established group would probably shift to adapt into high-density tolerant behavioral types. The hypothesized theory of the study was that individuals at different stages of an invasion would differ in behavior. Specifically difference in sociability and activity were tested. The invasive round goby (*Neogobius melanostomus*) was sampled from four different locations in the Baltic Sea representing different stages of an ecological invasion. A behavioral essay was preformed were both sociability and activity was measured. The individuals from the populations representing a later stage of invasion (Hel and Swarzewo, Poland) were more sociable and less active than the individuals form the populations representing a earlier stage of invasion (Åland, Finland and Gotland, Sweden). The results show a difference in behavior between populations of the round goby and this further supports the theories about including behavior when explaining ecological phenomenon.

Key Words: Ecological invasion, behavior, *Neogobius Melanostomus*, sociability, activity
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1 Introduction
1.1 Background
1.1.2 Introduction to behavior in the context of ecology
One of the major global threats to biodiversity today is ecological invasion (Vitousek et al. 1997), a phenomenon where an alien species is successfully introduced and rapidly established in an ecosystem (Elton 1958). The invading individuals can affect the invaded ecosystem in a number of ways. For example, the invading individuals can carry parasites new to the ecosystem. Another possible effect is enhanced competition for the native species in the search for prey and habitat. Predation on native species is another way the invading individuals could affect the ecosystem (Elton 1958). These interactions and the degree to which the invasive species will affect the system are difficult to predict, but the effects have often been shown to have a negative impact on biodiversity of the invaded system (Elton 1958, Pimentel et al. 2001). Calculating the costs of ecological invasion is a complex task (Gren et al. 2007), but predictions have been made and one study showed that the global costs for invasive species was 5% of the total global budget (Ricciardi et al. 2011). Information about what makes a potential invader successful is therefore important, not only to increase awareness, but could also be used for stronger regulations of, for example, import and export. It could also contribute in the development of management programs (Shea et al. 2010).

The relevance of behavior as part of the explanation to why some individuals are more successful invaders can be understood by reviewing the different stages of dispersal. When dispersing, an individual will come across a set of different situations where different life history traits and behavioral traits will be of more or less use, and one can hypothesize a selection for or against different traits during dispersal (Freeman and Herron 2007). It has been shown that the dispersal success is influenced by interactions between species through predation, parasitism and competition (Freeman and Herron 2007). Focusing on the selection for different behavioral traits one can, for example, imagine the outer ranges of an aquatic species distribution and the advantages for a bold and exploring individual when searching for a new territory. A later stage, however, might select for a different behavior where e.g. a more social individual would be successful. Integrating animal personality with theories of ecological invasion is a method recently put to practice (Cote et al. 2010, Sih et al. 2012), and studies have shown that behavior affect an individual’s tendency to disperse (Fraser et al. 2001, Cote et al. 2010). To explain the mechanisms behind the success of invading individuals Fogarty et al. (2011) suggest combining spatial ecology, life history theory, network theory and animal personality.

Sih et al. (2004) review the applications of behavioral theory in an ecological context and describes the theory of behavioral types (BT). The notion of behavioral types is a concept which explains aspects of individual behavior and suggests that an individual with specific behavioral traits, for example aggression, tend to constantly exhibit these traits throughout many contexts, e.g. feeding and mating. One interesting aspect to this is that the behavior may “spill over” and are exhibited in situations where a less aggressive behavior would be favored (Sih et al. 2004). Yu and Pierce (1998) found that a plant (Cordia nodosa), that in south-east Peru are a common ant symbiont, sometimes suffered great damages on flowers, which is a form of castration, as a result individual ants being to bold. Another example of a behavior that “spill over” was observed by Arqvist and Henriksson (1997). They showed that female Raft spiders (Dolomedes fimbriatus) predated on possible mates prior to mating, leading them to not produce offspring. Normally the female mate with the male and consume
him after for extra energy, but here a behavior was seen which did not favor the female and considerably lowered her fitness. Arnqvist and Henriksson (1997) suggest that this less favorable behavior is a result of a selection favoring high aggression when feeding at earlier stages of the spider's life and when implemented the aggression level stays high. Important to note is that this theory implies limited behavioral plasticity. This notion is separated from earlier theories about behavior in ecology where it has been practice to assume that behavior is adapted to the present situation with its specific needs and can also adapt to new situations, so as to always display optimal behavior (Sih et al. 2004).

The hypothesis of this study is that variation in behavioral types should be detectable between different stages of an invasion succession. The study will focus on two out of five behavioral types suggested by Reale et al. (2007): sociability and activity.

1.1.2 Sociability
For a fish sociability might represent itself as tendency to shoal. The focal species of this study, however, is not a shoal forming species but rather an aggregating. This enables it to enjoy the advantages of being in a group but also undergo the same pressures of competition as individuals in a shoal might experience. An aggregating behavior may be selected for in a number of ways. It is an effective way to e.g. receive information about predator presence, available food resources and also to confuse a predator in pursuit (Freeman and Herron 2007). Living in groups does, however, also come with costs. The intraspecific competition is high, which means that the species does not only compete against other species for food and habitat, but competition is also high within the species (Freeman and Herron 2007). Considering sociability in the context of dispersal, dispersing might be a way of releasing competition by avoiding competition from intraspecifics. Cote et al. (2008) showed that common lizards (Lacerta vivipara) displaying different levels of sociability had varying success in high- versus low density populations. Social individuals had low survival rates in low density populations. Cote et al (2008) suggests adaptation to high density populations as an explanation for the low survival rates. An asocial individual on the other hand would avoid high density populations and therefore avoid the mental and physical stress of high competition. Considering this, one could predict a distribution of less social individuals on the outer ranges of an invasion succession, and more social individuals in an older, well established population of the invasion. Cote et al. (2010) found that sociability was an important factor for dispersal of the mosquitofish (Gambusia affinis). They also noted that asocial individuals displayed the greatest tendencies to disperse.

1.1.3 Activity
Being more or less active can be a determining factor for survival in several contexts. For example, being active during the presence of a predator can have a fatal outcome; however, being passive while competing for food can have the same effect (Freeman and Herron 2007). This tradeoff will suggestively, as in sociability, result in different levels of activity during the different stages of an invasion. This study hypothesizes higher activity in an early stage of invasion and lower activity levels in a later stage. In the early stages it is possible that an active behavioral type with high foraging rates and exploration would be successful. In a later stage however, predation risk could increase, due to, for example predators having discovered the new food source, and select against active individuals. However, increased predation risk for active individuals might also affect individuals in an early stage.
1.1.4 Behavioral syndromes
When a behavior type is present across contexts and also across a population it is referred to as a behavioral syndrome (Sih et al. 2004). For example, a behavioral type would be being social when feeding, in the presence of a predator and when facing a novel object. For the behavior to be a syndrome, a whole population would have high average social behavior across context, compared to other populations. Behavioral correlations are also a variable in the theory of behavioral syndromes. A syndrome could be a population being very social but also very active, compared to other populations (Dingemanse et al. 2007).

1.2 Aim
The aim of this study is to examine if there is difference in two dispersal associated behavioral traits, sociability and activity, between populations at two different stages of the invasion succession of the round goby in the Baltic Sea. It will also examine if there is a correlation between the two behavioral types

Framing of questions:
1. Is there a difference in sociability between the two different stages of invasion?
2. Do the four populations differ in sociability?
3. Is there a difference in activity between the two different stages of invasion?
4. Do the four populations differ in activity?
5. Can a correlation be seen between the two behavioral types in the different populations?

2 Materials and methods
2.1 Study organism
The Round goby (Neogobius melanostomus) is a well suited organism to study when exploring the possible importance of behavior syndromes in the context of explaining the spread of an invasion. The bottom residing fish has its origins in the Ponto Caspian region (Charlebois et al. 1997), but has since the end of the twentieth century spread to a number of new locations. The first specimen of round goby in the Baltic Sea was found in 1990 at Hel Marine Station, Poland (Skóra and Stolarski 1993). The individual was estimated to be 3-4 years old, which points at an arrival date in the mid or late 1980s (Skóra and Stolarski 1993). It is commonly suggested that the fish arrived with ballast water from the Black- or Caspian Sea (Almqvist 2007). The round goby has been found in the Muugabay in Estland and also in the area around Helsinki (fig1). The first individual found in Swedish waters was caught in Karlskrona 2008 (Florin and Karlsson 2011) and have later been reported caught in Gothenburg and Visby. Invading populations of the round goby have been shown to grow to large densities over short periods of time and rapidly invoke large impact on the invaded system (Lederer et al. 2006). Reasons for the success of the round goby are probably a combination of several factors. The species is, for example, known to have male
parental care in the form of guarding and fanning the nest, and have high fecundity with the female being able to lay eggs up to six times in a season (Corkum et al. 1997). It has also been described as tolerant to variation in salinity (Corkum et al. 1997) and to have a broad diet (Charlebois et al. 1997).

2.2 Sampling and study site
A total number of 223 round gobies were sampled for this study. Sampling of round goby were done on four locations.

The two populations from an early stage of the invasion (2-3 years old) were sampled from Åland, Finland and Gotland, Sweden. The population from Åland was sampled in Mariehamn, (60° 6’ 0” N, 19° 56’ 0” E) between June 18th and 23rd using eel traps. Before being tested in the behavioral experiment, the individuals from Åland were kept in tanks with two individuals in each, for 24 days at Umeå University.

The population from Gotland was sampled two times using a combination of eel traps and angling in Visby Harbor (57° 38’ 30” N, 18° 17’ 45” E). The first took place on the 24th and 25th of May. The individuals were kept at Umeå University for 54 days in separate tanks. The second sampling was performed between Juli 30th and August 4th and the fish was only sampled using angling with fishing rods. These individuals were kept overnight and where then tested in the behavioral experiments on location.

The populations representing a late stage of the invasion (24-27 years old) were sampled from Hel (54° 36' 30.17"N, 18° 48' 2.88"E) and Swarzewo (54° 45' 42.11"N, 18° 23’ 51.68"E) in the Bay of Gdansk, Poland between August 27th and September 10th. The sampling was done using fyke nets and gill nets and the individuals where kept for 2-15 days in two tanks before being tested.

2.3 Measuring sociability and activity
Sociability and activity where measured in the same experimental essay (Ward et al. 2004). It was conducted in an aquarium 35 cm high × 30 cm wide × 100 cm long (fig. 2). The aquarium was partitioned by transparent walls into three compartments, one big in the middle (50cm) and two smaller on each side (25cm). The three compartments were filled with sea water from each location, with a 5 mm deep layer of gravel. The focal individual was placed in the middle compartment and two fish from the same population were placed in the left compartment. With the walls being transparent but solid, it was possible for the focal individual to see the conspecifics but not to sense any chemical cues. The behavior of the focal fish was videorecorded for 30 minutes. The individuals in the left compartment were the same for all individuals tested in the same population. Most sociability-groups consisted of one male and one female fish to minimize biased behavior. However, when this could not be done, the limitation were having too few males and choosing to use them as focal individuals and having two males as group individuals.

Figure 2. A sketch of the experimental set up for measuring sociability and activity.
2.3.1 Behavioral analysis
To quantify sociability and activity ten of the 30 min recording was analyzed in OBSERVER 2.01., starting 15 min into the recording. This 15-min acclimation period was included to decrease the risk that the observed behavior would be affected by stress. The middle compartment of the aquarium was separated into ten equally wide zones (1-10) by vertical lines. The location of the fish (1-10) was recorded for the full ten minutes and activity was recorded as total time spent active for the ten minutes.

2.4 Statistics
Sociability was calculated by adding the total time spent in the ten different zones (1-10, 1 being closest to the compartment containing the group individuals) in the aquarium multiplied with a sociability-factor from 8 to -8:

\[ t_{zone1} \times 8 + t_{zone2} \times 4 + t_{zone3} \times 2 + t_{zone4} \times 1 + t_{zone5} \times (-1) + t_{zone6} \times (-1) + t_{zone7} \times (-1) + t_{zone8} \times (-2) + t_{zone9} \times (-4) + t_{zone10} \times (-8) \]

The higher the score the more sociable the individual was and the results will be referred to in this report as weighted sociability. Possible difference in weighted sociability and activity was analyzed using Two Sample T-test when testing for difference between the mean weighted sociability and activity of the old populations (Hel and Swarzevo) and the new (Gotland and Åland). An alternative way of testing the first and third hypothesis is by using a Generalized Linear Mixed Model with population as random factor. When difference in sociability and activity was tested between all four populations the Independent-Sample Kruskal-Wallis Test was used. After testing, four outliers were found and removed from the Hel and Swarzevo populations (annex1, fig 1). Possible behavioral differences between females and males in each population were also tested. A spearman correlation test was performed for weighted sociability and activity, for the two stages of invasion.

3 Results
3.1 Sociability
The individuals from the older populations (Hel and Swarzevo) were more sociable than the recently established (Åland and Gotland) \((3015.43 \pm 372.55, 1705.08 \pm 197.76; \text{mean} \pm \text{S.E.}\) respectively, fig 3). The difference was close to confirmed after removing four outliers (annex 1 fig. 1), (T-test; \(df_{2,4}, p = 0.055\)). However, since it was not possible to rule out effect of population on the results, population was added as random factor and difference was confirmed statistically (Generalized Linear Mixed Model; \(df_{1,139}, p = 0.00\)).
Figure 3. Mean weighted sociability ± standard error for the newly established (Åland Gotland) and the older populations (Hel and Swarzevo).

When the four populations were compared the individuals from Hel were most sociable followed by Swarzevo and Åland, leaving Gotland being least sociable (3229.42 ±460.91, 2779.48±338.48, 1895.99±460.92, 1409.17±635.49; mean±S.E respectively, fig 4). The difference was marginally significant (Independent-Sample Kruskal-Wallis; df$_{1,130}$, p = 0.065). Four apparent outliers were found in the test (annex 1, fig 1) and when removed, the difference was confirmed (p=0.02, fig. 4). When comparing male and female sociability it was found that the males were more sociable in Hel and Swarzevo. The difference was confirmed (Independent-Sample Mann-Whitney; df$_{1,130}$, p = 0.042, fig 4). No difference was found in male and female sociability between Åland and Gotland.

Figure 4. Mean weighted sociability ± standard error for females and males from Åland, Gotland, Hel and Swarzevo. The four outliers have been removed.
3.2 Activity
The individuals sampled from the newly established populations (Åland and Gotland) were significantly more active than the individuals sampled from the older populations (Hel and Swarzewo) (135.08±12.78, 81.44±6.28; mean ± S.E respectively). The difference was not confirmed statistically (T-test; df_{2.4}, p = 0.15). However, similar to the results for sociability it was not possible to rule out the effect of population on activity. With population as random factor difference was confirmed statistically (Generalized Linear Mixed Model; df_{1,130}, p = 0.045, fig. 5)

![Figure 5. Mean activity (s) and standard error for the newly established populations (Åland and Gotland) and the older populations (Hel and Swarzewo).](image)

Individuals from Åland were most active followed by Gotland, Hel and Swarzewo (147.55±15.66, 115.76±21.51, 96.50±9.12, 64.82±7.85; mean ± S.E respectively, fig 6). The difference in activity between populations was confirmed statistically (Independent-Sample Kruskal-Wallis; df_{1,130}, p = 0.00). No difference in activity was found between the sexes (Independent-Sample Mann-Whitney; df_{1,130}, p = 0.975, fig. 6)
Figure 6. Mean activity (s) ± standard error for female and male individuals from Åland, Gotland, Hel and Swarzewo.

3.3 Correlation between behavioral types
No significant correlation was found between the behavioral types in either of the two stages of invasion ($r_s = -0.16, p = 0.26, r_s = 0.06, p = 0.62$, correlation coefficient and p-value for the early and the late stage of invasion respectively).

3.4 Male female ratios
The sex-ratio was male biased at all locations. In Gotland male:female ratio was 15:5, Åland 22:9, Hel 36:7 and Swarzewo 37:2 (fig. 4, fig. 6).

Since individuals from Gotland and Åland were kept for different periods of time before the behavioral essays were performed, and that might affect the results, we tested for possible differences between the populations. However, when tested, no difference was found between the different time treatments (ANOVA; sociability: $F_{9,19} = 2.19, p = 0.16$, activity: $F_{9,19} = 0.67, p = 0.42$).

4 Discussion
The results presented in this study support the hypothesis that the individuals from the older stage (Hel and Swarzewo) were more sociable than individuals from an early stage of the invasion (Gotland and Åland). Cote et al. (2008) found that social individuals of the common lizard were less successful in low density populations, and suggested that it could be a result of high aggressiveness in social males. This theory might also be part of the explanation why asocial behavior types are dominant in the early stages of the invasion by the round goby. Populations at early stage of an invasion would be of lower densities than populations at an older stage. Male round goby are known to aggressively compete for and defend their nests. If social males put a lot of energy into being aggressive in a low density population it might be a waste of energy. Asocial individuals in the same situation might put energy into foraging for food or avoiding predators and therefore be the stronger competitor in a low density...
population. The fact that the early stages were less sociable might also be a result of a different selection pressure during invasion. The individuals from Åland and Gotland have probably been transported by ship from the Bay of Gdansk and even though it might be a random sample caught in the ballast water, individuals surviving and managing to establish are most likely not random. If survival is nonrandom, it can be hypothesized that these individuals have phenotypical traits suited for this invasion front. Such traits would most likely be adapted to an environment where interspecific competition is low, as individuals at the invasion front are populating empty habitats. It is also possible that predation could be low as there might be a time lag before predators discover the new resource (Sih et al. 2010). The individuals that manage to establish and reproduce would be those that are not high-density depending (i.e highly sociable). If they are not dependent on high densities this means that they might be successful without aggregating. Considering the fact that individuals, at both parts of the invasion, might face different growth/predation risk trade-offs this might mean that the traits that make them successful in an invasive front make them less suited in a high-density population. The correlation between sociability and dispersal has earlier been found in mosquitofish (Cote et al. 2010) where asocial individuals tended to disperse longer distances.

Difference in activity between individuals from old and new populations was even more pronounced, with individuals from new populations being more active than those from older. Considering the conditions when operating at an invasive front, with possible lower predation pressure, high activity could be favored for example when feeding (Sih et al. 2012). A trait involving a high grade of exploring tendency should also be a trait favored at an invasive front as the individuals would have to move and search for nesting spots and exploring novel food items. In contrast, at a later stage of invasion, predators would have adapted to this new resource and high activity would put individuals at high risk. This would possibly lead to lower levels of activity displayed by individuals from a later stage of the invasion, as displayed in this study. A factor to add about activity measurements is that individuals from the old populations were sampled in September and the younger populations were sampled earlier (May through July). This could possibly affect activity as males might exhaust themselves during spawning. The majority of the sampled individuals from the older populations where males (73/81) and the results might therefore be affected. However, this explanation seems unlikely as no difference in activity between males and females was found. The fact that the females were considerably fewer might have affected the accuracy of this result.

Considering the results from this study, where a variation in behavioral types have been found over different stages of an invasion, a possible explanation could be that variation in behavioral types is important for invasion success. Variation in behavior might facilitate a quicker adaptation than other phenotypical adaptations, especially considering that behavior could be rooted in experience (Hellström 2012), and facilitate a successful invasion. An example where behavior has been shown to facilitate range expansion, which could be a component in an invasion, was found by Duckworth and Badyaev (2007). They observed an adaptive integration of aggression and dispersal in western bluebirds (Sialia mexicana) on the outer ranges of an invasion. Being aggressive, the birds were able to replace the mountain bluebird (Sialia currucoides) in the nesting areas. Once this competing species was gone, the behavior of the birds in the invaded area got less aggressive over a few generations. These results can be compared with the results of this study where, similarly, a difference in
behavioral type is found between different stages of the invasion of the Baltic Sea. My results might therefore add to the literature about variation in behavioral type being a facilitator for rapid dispersal. The variation in behavioral type, with one dominating the outer ranges of dispersal and another taking over at an already colonized patch, can also be applied to phenotypic traits that are not behavioral. An example could be a possible release of predator pressure in a new patch which would make room for individuals that grow faster and reproduce more being that they don’t have to invest in defensive morphology. After some time, predators would possibly discover this new resource and the individuals who arrived to the patch first will no longer have the optimal phenotype. They would probably be replaced by phenotypically adapted individuals and possibly spread to a new patch further facilitating invasion (Freeman and Herron 2007). Change in phenotype has been seen in an invasion front of the round goby were individuals have been growing faster, maturing faster and being bigger in size (Gutowski and Fox 2011). Individuals at the invasive front also seem to benefit from higher quality foods that take less energy to collect (Gutowski and Fox 2011). Considering that variation in other phenotypical traits being important factors for a successful dispersal this further strengthens the theories about behavior being an important factor in explaining dispersal success.

The results from this study could be implemented when trying to decrease the amount of Round goby being spread through ballast water. If we know which individuals have a higher likelihood of being facilitators of invasion, and how they behave, special efforts could be made to make sure that these specific individuals, for example, do not get into ballast water of ships. Another application of these results could be predicting how a species would response to an environmental change, especially rapid change caused by human activity. When climate changes abnormally fast evolution might be too slow of a process and the possibility of adaptation would be depending on behavior. This is why prediction of population's response to environmental change without considering variation in behavior could be misleading. Another implication of intraspecific variation in behavior is that one species could fill the ecological roles off several species and, depending on phenotype, affect its ecosystem in different ways. Also, including the theory of behavioral types and syndromes adds another dimension to predicting invasive species impact on an ecosystem.

The skewed sex-ratio, with males being much more common than females, that was found in this study have been found throughout Puck Bay and in the Great Lakes, where the Round goby is also an invasive species (Corkum et al. 2004). An even higher male to female ratio, of 6:1, were found in the Western Basin of Lake Erie and in Detroit River (Young et al. 2010). Collections have been made by beem trawl from the round gobies native range and the results were 1:1 (Kovtun 1979). This could suggest that invasive populations might differ from native populations in sex-ratio. Males being dominant in invasive populations might be a result of release from density-dependent male competition, a possible controlling factor in populations from the native areas. The greatest difference between males and females, which was found in Hel and Swarzewo, could also be explained by females starting to migrate to deeper parts of the sea in preparation for winter.

An inevitable aspect to add is the different conditions that the experiments were conducted in. One part of the sampled individuals from the population from Gotland had been held pairwise in aquariums in the lab at Umeå University for 54 days. The other individuals sampled from Gotland were only kept overnight. The populations from Åland were also kept
at Umeå University, but for 24 days. The essays preformed on the individuals from Gotland and Åland was conducted in a tent and the essays preformed on the individuals from Hel and Swarzevo was conducted in the lab at Hel marine research-station. This could have an effect in the sense that during a day of experiments the light conditions might vary. The wind was also a factor which could have affected the results as it ripped in the tent canvas during some of the experiments. For the populations from Poland however, the essays were preformed indoors and at equal conditions for both populations. These differences in methods might affect the strength of my results. However, when effects of the different methods were tested, none were found which indicates limited effects at worst.

5 Summary
The results show a difference in behavior between populations of the round goby and this further supports the theories about including behavior when explaining ecological phenomenon. Including knowledge about difference in individual behavior can contribute to a greater understanding for mechanisms in both ecology and evolution. The combination of different behavioral syndromes and different ecological conditions should make for a number of possible results, but consistency in individual behavior and correlations between behavioral syndromes might take us steps closer to assess and create good model predictions about the impact invasive species could have on an ecosystem.

These results are an indication that contributes to the authenticity of a recent but important insight about behavior in ecology: the behavior and impact of an invasive species should not be measured as a mean for the species. But rather mean behavior for a population, or even individual difference in behavior.

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Annex 1

Fig. 1. Result from the Independent-Sample Kruskal-Wallis test where difference in weighted sociability was tested for the four populations (Gotland(1), Åland(2), Hel(3), Swarzewo(4)) in which the four outliers are displayed.