Thea Bjørnsdatter Gullichsen

Do the invasive fish species round goby (*Neogobius melanostomus*) and the native fish species viviparous eelpout (*Zoarces viviparus*) compete for shelter?

Master's thesis in Biology
Supervisor: Gunilla Rosenqvist, Irja Ida Ratikainen, Isa Wallin
May 2019

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NTNU
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Abstract

Human-mediated introduction of species has increased drastically the last decades, with the increased connection across borders. The settlement of invasive species in a new environment can result in drastic changes in the ecosystem, and even result in local extinction of native species. One species that is currently regarded one of the most invasive species in the Baltic Sea is the round goby (*Neogobius melanostomus).* Round goby and the native species viviparous eelpout *(Zoarces viviparus)* are both benthic dwellers that inhabits the coast of Gotland in Sweden. With a shared habitat and the round goby being a highly competitive species, it can be expected that the viviparous eelpout is affected negatively by the round goby in some way. I performed a laboratory study to determine if round goby and viviparous eelpout compete for shelter when sharing a fish tank. I predicted that the round goby would guard the shelter by demonstrating aggressive behaviour when paired with the viviparous eelpout. I also examined if the level of aggressive interaction increased when shelter opportunities were limited. The prediction was that the aggressive interaction would increase in this case and that round goby would outcompete the viviparous eelpout. Contrary to my predictions, round goby did not guard the shelter by display of aggressive behaviour and viviparous eelpout used the shelter more frequently compared to the round goby. The low level of observed aggression differs from findings in several other studies investigating shelter competition with round goby.

Sammendrag

Introduksjon av arter forårsaket av mennesker har økt enormt over de siste tiårene, med økende transport og handel på tvers av landegrenser. Etablering av invasive arter i et nytt miljø kan resultere i drastiske endringer i et økosystem, og til og med resultere i lokal utryddelse av native arter. En art som for tiden blir sett på som en av de mest invasive artene i Østersjøen er svartmunnet kutling (*Neogobius melanostomus).* Svartmunnet kutling og den native arten ålekvabbe *(Zoarces viviparus)* er begge bunnlevende og holder til ved kysten av Gotland i Sverige. Med likt habitat og det faktum at svartmunnet kutling er en høyst konkurransedyktig art, kan det forventes at ålekvabben blir negativt påvirket. Jeg utførte et laboratoriestudium for å bestemme om svartmunnet kutling og ålekvabbe konkurrerer om skjulested når de deler fisketank. Jeg predikerte at svartmunnet kutling vil beskytte skjulestedet gjennom aggressiv adferd når den ble satt sammen med en ålekvabbe. Jeg undersøkte også om nivået av aggressive interaksjoner øker når skjulestedsmulighetene begrenses. I dette tilfellet var prediksjonen at aggressive interaksjoner ville øke og at svartmunnet kutling ville utkonkurrere ålekvabben. I motsetning til mine prediksjoner, beskyttet ikke svartmunnet kutling skjulestedet ved bruk av aggressiv adferd. Ålekvabben benyttet seg av skjulestedet mer enn svartmunnnet kutling. Det lave nivået av observert aggresjon er et ulikt funn sammenlignet med andre studier som undersøker skjulestedkonkurranse med svartmunnet kutling.

Acknowledgement

This master's thesis was written at the Department of Biology at the Norwegian University of Science and Technology (NTNU). It was funded by NTNU, the Country Administration Board at Gotland and Sparebanken Midt-Norge.

First of all, I would like to thank my supervisors: Gunilla Rosenqvist, for feedback, support and always positive words and encouragement. Thank you for introducing me to Gotland and I am very grateful that the fieldwork included bathing facilities (both The blue Lagoon and the Baltic Sea). I especially want to thank Irja Ida Ratikainen for lots of good and thorough feedback and also a lot of help with the data analysis. Last but not least, I want to thank Isa Wallin for always answering my questions as well as valuable feedback.

Thanks to Amanda Jansson, Anders Nissling and Ronny Höglund, who were of great help during the field work.

The data analysis in this thesis would not have been possible without the help of Agnes Holstad and Eirik Ryvoll Åsheim. I am eternally grateful for this help and you are my R-heroes. Also, thanks to Ioanna Gavriilidi for also helping me in the beginning with R.

I especially want to thank Katrine Andresen. This master period would have been really sad without you as my partner in crime. Thank you for being so patient at field, for all really enjoyable dinners and lunches and just for being so supportive and kind, even when I was stressed and tired.

A big thanks to all my friends for always supporting and cheering me up, and especially thanks to Camilla for being my friend but also all the help with proofreading. Thank you, Inger Moland Wahl for proofreading and tips. Lastly, I want to thank my parents for being a super team. My mom, this would not have been possible without your support, phone calls and hugs. My dad, thank you for your never-ending interest in what I am working with. Your proofreading, reading relevant material and always being available on the phone if I had any questions. Thank you for being my two biggest fans.

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Introduction

Invasive species

Increased globalization is one of many consequences of the expanding human population, which again has led to increased global trade and transport (Perrings *et al.*, 2010). This has simplified the connection across borders, but also led to a rapid increase of unintentional introductions of species in coastal waters around the world (Ruiz *et al.*, 1997, Carlton, 1989, Thorlacius, 2015). The frequency of human-mediated introduction has increased drastically, and therefore become an expanding threat the last decades (Hôrková and Kováč, 2014). A majority of all introduced species fail to establish and spread in the new environment, but there is a risk, both ecological and economic, that the introduced species settle (Williamson, 1996, Bax *et al.*, 2003, Ojaveer *et al.*, 2004). This may in the worst-case scenario lead to extinction of native species, and a decline in the total biodiversity (Dubs and Corkum, 1996).

The species invasion process can roughly be divided into three stages; transit/transport, establishment and spread (Lockwood *et al.*, 2013). This process, besides being initiated naturally by the species itself, can be caused by both direct and indirect human activities (L'avrinčíková *et al.*, 2005, Keller *et al.*, 2011). Direct actions include intentional release of organisms by facility owners of seafood industry and aquaculture, baitfish by anglers and stocking as food or game species (Fuller, 2003, Lockwood *et al.*, 2013). Indirect actions are non-intentional and include ballast water (Ruiz *et al.*, 1997) or propellers (Johnson *et al.*, 2001), the construction of canals, aquariums release and escapes from fish farms (Fuller, 2003). It is also expected that climate change will alter community composition, causing changes in phenology, genetic composition and species range, as well as affecting the structure and functioning of ecosystems (Root *et al.*, 2003, Walther *et al.*, 2002, Pörtner and Knust, 2007). All of these consequences could influence different parts of the invasion process. One example is former temperature constraints now enabling the spread of species to new suitable habitats (Hellmann *et al.*, 2008).

The invasion process is complicated and varies across ecosystems (Hirsch *et al.*, 2016). The study of invasion ecology has since the publication of the classical book "The ecology of invasions of plants and animals" (Elton, 1958) had an exponential growth the last decades (Richardson and Pyšek, 2008), and especially the interest for human-mediated species spread (Blackburn *et al.*, 2011). The invasion ecology requires a broad understanding within economics, evolution, population genetics, biogeography and ecology, and is therefore a multidisciplinary study. Each discipline has developed an individual terminology and, combined with the lack of a common definition, this has all led to a minimal overlap in language and terminology (Shrader-Frechette, 2001, Lockwood *et al.*, 2013). “Alien”, “exotic”, “non-indigenous” and “non-native” are only some of many names used in different research (Colautti and MacIsaac, 2004, Davis *et al.*, 2000). The definition of an invasive species will in this thesis be based on the definition from Keller *et al.* (2011): “A species is defined as invasive if it spreads widely and causes measurable environmental, economic, or human health impacts.” Non-indigenous, defined from Sergej Olenin (2017) will also be used to highlight the fact that “non-indigenous species (NIS) represents a biogeographical category, which also indicates human involvement in the introduction of a certain species to a particular ecosystem”. However, the definition is not only restricted to the bad influence.

The settlement of non-native species in a new environment can result in drastic changes in the ecology and may disturb the ecosystem, and even result in local extinction of native species (Bax *et al.*, 2003, Dubs and Corkum, 1996, Vanderploeg *et al.*, 2002). It is well-documented that invasive species can influence its new environment in multiple ways (Hirsch *et al.*, 2016). Direct influence includes predation, competition for resources, hybridization between closely related species or subspecies and transmission of diseases (Keller *et al.*, 2011). The more indirect way is by changing the pathway of nutrient, energy and contaminant flows in the food web by changes in the predator-prey relationship as well as through habitat modification (Vanderploeg *et al.*, 2002, Johnson *et al.*, 2005, Reyjol *et al.*, 2010).

Successful invasive species possess specific characteristics which promote their explosive growth and exploitation of their new habitat. These typically include aggressive behaviour, high fecundity, habitat plasticity, and a generalist feeding strategy (Keller *et al.*, 2011, Dubs and Corkum, 1996). In addition to these particular traits, the absence of specialized natural predators and parasites that usually would control their population growth is also often absent in the new habitat (Davis, 2009). The invasibility (the level of vulnerability a habitat is to invasions from outside species) gets influenced by the species composition, the functional groups present in the community and the strength of interaction among trophic levels (Lonsdale, 1999, Sakai *et al.*, 2001). All these factors may work as a buffer against invasion and competition for resources particularly may act as a frontline in defense against invasion. (Elton, 1958, Sakai *et al.*, 2001).

Round goby

One species that possesses characteristics of an invasive species and is currently regarded one of the most invasive non-indigenous species in the Baltic Sea is the round goby, *Neogobius melanostomus* (Pallas, 1814) (Ojaveer *et al.*, 2004). The round goby is native to the Ponto Caspian area (Charlebois, 1997), and the first reported spread was in the Kuybyshev Reservoir on the River Volga in 1968 (Balážová-L'avrinčíková and Kováč, 2007). It has continued to spread further after that, and in 1990 it was found in the Baltic sea and the Laurentian Great Lakes (Figure 1) (Sapota and Skóra, 2005, Jude *et al.*, 1992). The improvement of waterways and increase of commercial and recreational shipping across Europe and North American is stated to have increased the spread of round goby across the world's ocean (Hirsch *et al.*, 2016, Roche *et al.*, 2013). The round goby is known for passive long-distance spread often through ballast water and further actively dispersal from the established area, a process known as stratified dispersal (Sapota and Skóra, 2005, Bronnenhuber *et al.*, 2011, Lockwood *et al.*, 2013, Hengeveld, 1989). In 2008, a few individuals were found in Karlskrona, confirming presence of round goby in Sweden (FLORIN and KARLSSON, 2011). Two years later it was caught in Gothenburg and Visby (R. Gydemo, Gotland County Administrative Board, pers. comm.). Figure 1 shows the natural range of round goby, as well as their spread in Europe and North America. The species has little specialization to habitat, which can work in favour when encountering new ecological requirements in new environments (Jakubčinová *et al.*, 2017).

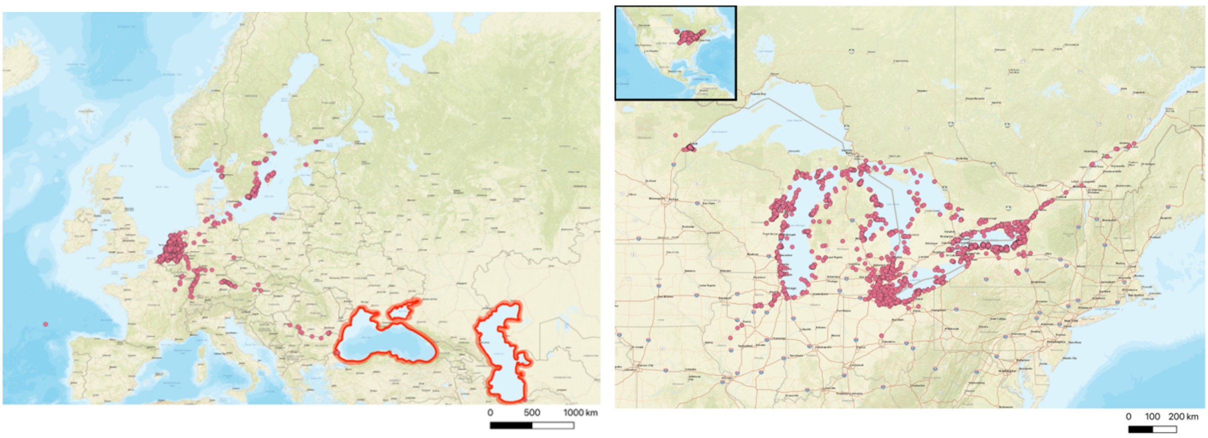

Figure 1: The native area of the round goby marked in solid red lines. The red marks represent the range of the round goby in Europe (left picture) as well as in the North-America Great Lakes (right picture). *(*Used with permission from Andresen (2019)).

The round goby is a demersal fish that occupies a variety of habitat types, from sandy/stony bottoms (Karlson *et al.*, 2007) to more substrate rich habitat such as stones and riprap (Kessel *et al.*, 2011). In the summer it often inhabits rocky substrate in shallow areas, where they can reproduce about every 20 days from April until September (Thorlacius, 2015, Corkum *et al.*, 1998). Males fight for and defend nests where several females may lay their eggs (Wickett and Corkum, 1998). When the males defend eggs, they stop feeding and guard the eggs and larvae (Wickett and Corkum, 1998, Thorlacius, 2015, Skabeikis and Lesutienė, 2015). The round goby represents a great part of the diet of great cormorants (*Phalacrocorax carbo*) and grey heron (*Ardea cinerea*) in the Baltic sea, so occupancy of shelters or refuges is a useful strategy to avoid visual predators (Belanger and Corkum, 2003, Jakubas, 2004). Its temperature tolerance is between -1 and 30°C, with an energetic optimum of 26°C, and the species can inhabit salinities between 0 and 40.5 psu. (Kornis *et al.*, 2012, Lee and Johnson, 2005). The round goby is a generalist feeder (Nurkse *et al.*, 2016). In addition to its high tolerance to environmental factors, short generation time and opportunistic diet preferences, aggressive behaviour and large size, compared to other species having similar benthic lifestyle, are all contributing to make the round goby the "perfect" invasive species (Verliin *et al.*, 2017, Corkum *et al.*, 1998).

Round goby's influence on native species

It is expected that round goby can (1) dominate and monopolize limited food supply by aggressive behaviour (Bergstrom and Mensinger, 2009) and/or compete for space (shelter or spawning substrate) and other resources (Dubs and Corkum, 1996, Balshine *et al.*, 2005), (2) negatively affect native fish through consumption of eggs and juveniles (Chotkowski and Marsden, 1999, Steinhart *et al.*, 2004) and (3) alter benthic communities by removal of invertebrates with cascading effects on benthic plants and nutrients cycles (Vélez-Espino *et al.*, 2010, Kuhns and Berg, 1999).

Resource competition with native species

When focusing on the direct competition for space and resources, it is expected that round goby will affect most small benthic fish that have a similar niche requirement (Balshine *et al.*, 2005, Janáč *et al.*, 2016). In the Baltic Sea this concerns the flounder, *Platithys flesus*, some species of the Gobiidae family (the sand goby, *Pomatoschistus minutus*, the common goby, *Pomatoschistus microps,* and the black goby, *Gobius niger),* as well as the viviparous eelpout, *Zoarces viviparus* (Balážová-L'avrinčíková and Kováč, 2007). Refuges and preference for shelter are influenced by the fish lifecycle and the time of day. During daylight hours (including dusk and dawn) piscivorous fish are active and prey species increase their use of shelter (Dubs and Corkum, 1996, Kessel *et al.*, 2011). Both native benthic species and round goby in the Baltic sea has preference for shelter in some part of their lifecycle, so competition for shelter when shelter is a limiting factor is likely in a shared habitat (Kessel *et al.*, 2011).

Viviparous eelpout

Viviparous eelpout and round goby share habitat in the Baltic Sea (ArtDatabanken, 2015a, 2015b) and resource competition between the two is not previously been investigated. These two species have a similar diet and both species are benthic dwellers, so there is a potential for one of them outcompeting the other (Ronisz *et al.*, 2005, Charlebois, 1997).

The eelpout is a euryhaline blenny and inhabits coastal waters of Northern Europe, as well as the Baltic Sea (Gercken *et al.*, 2006). The wide distribution makes the species tolerant to a various range of salinities and temperature (Hedman *et al.*, 2011). It is considered a cold-water species, and the survival is lower during warmer summers due to reduced growth and fecundity with increasing water temperature (Pörtner *et al.*, 2001, Helcom, 2013). Viviparous eelpout is a stationary species, with its main habitat in shallow water and up to 40 m depth. The habitat is often vegetated sandy sediment or stony bottoms. The species is a nocturnal feeder on invertebrates and small fish (Langhamer *et al.*, 2018, Ojaveer *et al.*, 2004, Helcom, 2013).

Viviparous eelpout is often used in experimental studies, which explore the effect of contaminant exposure on individual health and as a bioindicator of pollution in the field (Gercken *et al.*, 2006, Voigt, 2007). This species has many characteristics suited for this type of study and has also been proposed by HELCOM and OSPAR as a sentinel species (Asker *et al.*, 2016). Further, the HELCOM red list states that also competition, predation and alien species pose threats to this species (Helcom, 2013). Unfortunately, there are very few published articles about interaction between viviparous eelpout and other species. Therefore, my thesis aims to fill a bit of this knowledge gap.

Hypothesis

The focus of this study was to investigate how round goby affect the native viviparous eelpout. My main hypothesis was that round goby will outcompete viviparous eelpout for shelter.

The predictions were; 1) round goby will guard the shelter by display of aggressive behaviour, and 2) aggressive interaction between the species will increase when shelter is limited and 3) the round goby is the more successful competitor and will outcompete viviparous eelpout.

Materials and methods

The field study was conducted from the 21st of May to 19th of June 2018 at Ar Research Station located on northern Gotland in Sweden (57.916920°N, 18.937566°E).

Fish collection and husbandry

A total number of 64 round gobies and 23 viviparous eelpouts were caught for the experiments conducted in the period of the field work. The catch was carried out at three different spots in Fårösund harbour (Figure 2) in three different days to ensure adequate amounts of fish. In all sampling rounds, the fish were caught by fishing net traps of different sizes, fishing overnight. 2-4 prawns were used as bait in each trap on each sampling occasion.

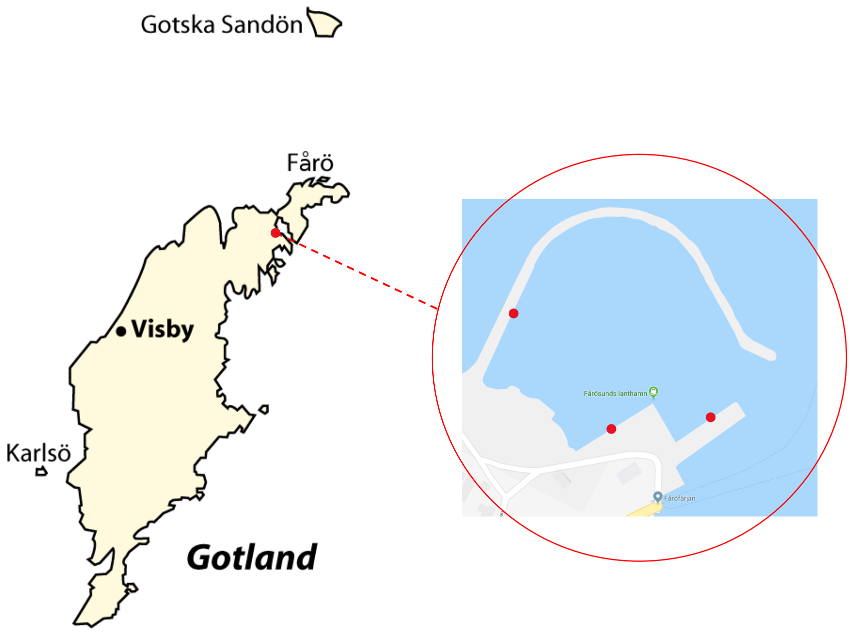

Figure 2: A map of Gotland showing where Fårösund is situated. The map segment in focus is Fårösund harbour, and the marked red dots are locations of net traps (Mic, 2003, Google, 2019)

On the 23rd of May, five bait traps were placed at the quay (57.866062°N, 19.05930°E), three on the mole (57.866667°N, 19.056533°E) and three inside the mole (57.865961, 19.057916). The second and third sampling was carried out on the 10th and 11th of June, in which the traps were placed out in two different spots, five at the quay (57.866062°N, 19.05930°E), and four inside the mole (57.865961, 19.057916). Fish caught in the net traps were sampled the morning after and transported back to Ar Research Station in cooler bags filled with seawater with air pumps attached, cool packs and small plants. On the 11th of June, one of the round gobies brought back showed signs of sickness and was euthanized. At the Ar Research Station, the different species were sorted into stocking tanks (90x90cm), after they had acclimatized in 10 L buckets with seawater from the tanks. Every round goby was further sorted in two total length categories (7-14cm and >14cm) and according to sex (table 1). Sex was determined by the description given in Kornis *et al.* (2012). Table 1 is a complete overview of the catch.

Table 1: A complete overview of species and number caught on each sampling occasion in the experiment together with the sex and length division. Viviparous eelpout could not be sexed based on appearance and is therefore not classified according to sex.

Species	**Number**			**Comments**
	24th of May	**11th of June**	**12th of June**	
Round goby	20	2	2	Male, 7-14 cm
Round goby	16			Male, >14
Round goby	15	1		Female, 7-14 cm
Round goby	6	1		Female, >14 cm
Round goby	1			Unknown sex - 10 cm
Viviparous eelpout	22		1	Unknown sex

Tanks used to store fish outside of the experiment period (stocking tanks) had artificial plants, terra cotta pipes, grey plastic pipes and bricks for the fish to hide in. The tanks were provided with constantly flowing water from the Baltic Sea and also several air stones. The water temperature in these tanks followed natural water temperature at this time of the year, ranging between 5.4 - 15.5°C. The tanks were rinsed every day, and the fish were fed a mix of mysids, Artemia ssp. and krill twice a day when they were not used in experiments. The day before onset of the experiment, the fish to be included were not fed, to enhance interaction (Dubs and Corkum, 1996). On the 25th of May, the water in one tank was changed to freshwater for a short time by accident, but this was adjusted immediately after discovery. This tank contained males of round goby >14 cm. None of the fish showed signs of change in behaviour due to this mistake.

Experiment design

Competition for shelter

The experiment was carried out in 12 90x90cm grey fiberglass tanks with a water depth of ca 50 cm. The tanks were provided with constantly flowing water from 40m depth from the Baltic Sea. The water temperature reflected the temperature in the sea, ranging between 9.0 - 11.8 °C and salinity level at 7.0-7.1 ‰. Each tank was divided into two parts (A, B) with yellow tape (Fig. 3). The experiment ran for six days in total (5^{th} – 8^{th} of June and 14^{th} -15^{th} of June). The first two days of the experiment (5^{th} and 6^{th} of June) the provided shelter was 30 cm long terracotta pipes with an inner diameter of 9 cm (Fig. 3a). The last four days of the experiment (7^{th}-, 8^{th}-, 14^{th}- and 15^{th} of June) the shelter was changed to three terracotta bricks with holes stacked together to create a cavity (Fig. 3b). The reason for the change of shelter was that some of the individuals were bigger and I wanted to ensure similar sheltering opportunities regardless of size. The tanks were also provided with 8-12 artificial plants symmetrically placed on both sides of the yellow tape (Fig. 3). All experiments were conducted during the daytime as shelter use then may be greater due to increased predation risk (Dubs and Corkum, 1996, Church *et al.*, 2017, Stammler and Corkum, 2005).

Fish were put in the experiment tanks from around 08:00 and the experiment ended around 18:00. The experimental setup with two shelters ran from 09:00 to 13:00, hereafter referred to as Shelter_2. Then one pipe (Fig. 3 a2) or one stack of bricks (Fig. 3 b2) was removed, and the other one was placed in the middle of the tank for the rest of the experiment that day, hereafter referred to as Shelter_1. Otherwise, the tank remained unchanged.

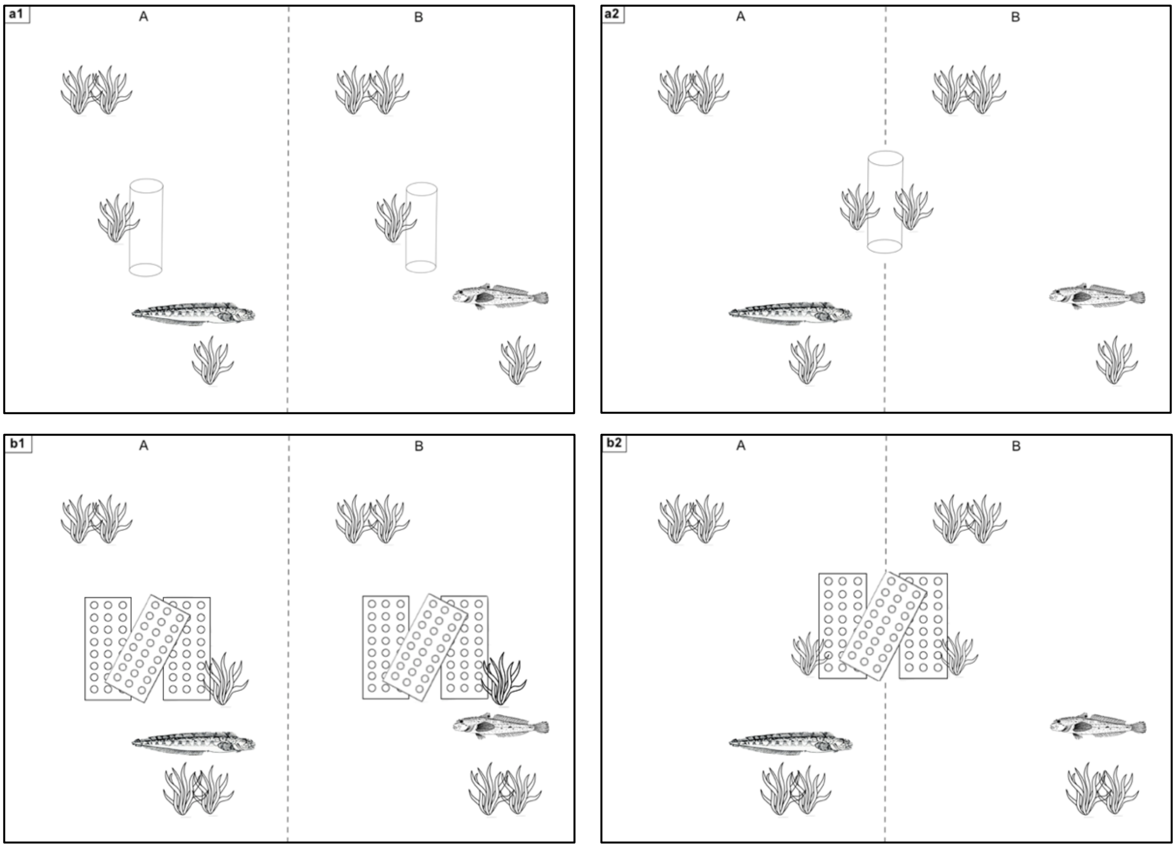

Figure 3: Experimental set up to test for shelter competition between viviparous eelpout and the round goby. Each 90x90cm grey tank contained a set of artificial plants set symmetrical on each side of the tape and either (a) pipes or (b) bricks as shelter. Figure (a2) and (b2) is the experimental setup after 13:00 with only one pipe or one stack of brick as shelter. (Round goby, viviparous eelpout and the plant: (Poos *et al.*, 2010, Juulijs, 2019, Ultra Coloring Pages, 2019)

Selection of experimental fish

Ten round goby males (7-14 cm) were reused from an experiment carried out the 29th of May and the 2nd of June. I tried to avoid fish already used in an experiment for as long as possible and made sure that no individuals were used on two consecutive days.

Each of the 12 tanks contained one individual of round goby and one viviparous eelpout. Six round goby males were paired with six viviparous eelpouts of approximately the same size. Size was based mostly on the anterior part, since round goby and viviparous eelpout are different in shape. The viviparous eelpout was always larger in total length compared to round goby. The setup was the same for round goby males and females. The first four days of the experiment the males were held in the six tanks nearest to the windows and the females nearest to the wall, and during the two last days of the experiment I switched sides, so the females were closest to the window with the brightest light condition.

At the start of each experimental day, a total number of 24 10 L white buckets were rinsed and filled with water from 40m depth from the Baltic Sea. Before the experiment started, I randomly distributed the different size classes for round goby (7-14 cm and >14) between the twelve tanks. Individuals of the desired sizes, sexes and species were caught with a hoop net from the tank they were held in and placed in a bucket. The fish were then carefully transferred to the experimental tanks by two people, starting at each end (tank 1 and 12) over a time interval of 5 minutes. On day 2 - 4 of the experiment, the water in the 10 L buckets the fish were held in shortly before the experiment, might have accidentally been replaced with fresh water. The fish appeared unaffected by this potential incident.

Observational protocol

The observations started after the fish had been in the experimental tanks for approximately one hour to acclimatize. Acclimation was included to reduce the risk of observing stress-induced behaviour (Finn, 2012). The observations of behaviour were conducted by two people every fifteen minutes between 09.00-18.00. Approximately one-hour acclimation time was also added after the removal of one shelter at 13.00. The two first readings at the start of the day as well as after the acclimation time when switching to one shelter were always performed together with another observer. This was decided in order to rule out potential differences in observing the behaviour and position of the fish.

Observations were conducted from tank 1 to 12, and the first fish to be observed was chosen in that moment (by chance). The observation was a snapshot of the position and the behaviour of the fish. The behaviour was divided into four categories: swimming, resting (when the fish lay still), hiding (either hiding in the pipe/bricks or inside the plants with some parts of their body) and interaction. The type of interaction was noted when the two fish interacted with each other in some way. The expected interactions between the two species included chasing, biting, approaches and "blowing up" the body to look scary. The interaction between fish were first divided into five different categories (category 0-4). Category 0 was when the fish did not interact at all, in category 1 they were laying close but not touching, either face to face or side by side, 2: when they were laying so close that they were touching with any part of the body, 3: swimming on each other so they were touching and, 4: when they were biting or showed some other type of aggressive behaviour.

At 18:00 the last observation was done, and after that, all the 24 fish were taken out and the total length (cm) was measured with the help of a measuring board. Measured fish was put back into storage tanks and kept separate from the fish that was not recently used in the experiment. This experiment was carried out under the Ethical permit S27-15 by the Swedish Board of Agriculture.

Data analysis

Interaction between fish

There were very few observations in the last two categories of interaction (Appendix A). Based on this the four categories (1-4) were combined into one category, so the measured interaction was now either classified as 0 (no interaction) or 1 (interaction). Due to the lack of clear signs of aggression between the fish, combined with the debatable grade of competition. I will from here forward refer to this measure as "interaction" rather than "competition".

Changes in the interaction between fish and hiding behaviour over time

Models were used to test if time influenced the variance before the analysis of the interaction between fish and hiding behaviour was conducted. The variation in the interactions between the fish was analysed with a generalized linear model with binomial distribution of the error and time and number of shelters as fixed factors. Variation in hiding behaviour was analysed in a similar way, with time, number of shelters, species and length as fixed factors. In both analyses, time was not significant, i.e. time did not explain a significant amount of the variance in neither interaction between fish nor the hiding behaviour. Based on this I decided not to include the effect of time in subsequent analyses.

The probability of "interaction" between fish

The analysis.

The effect of number of shelters on the interaction between the fish was analysed using a generalized linear mixed-effect model with a binomial distribution of the error. Random effects were included to account for the non-independence of observations within a tank on different days, due to, e.g. the positioning of the tanks. The analysis was conducted in R 3.5.1 (R Core Team, 2018), with the *glmer* function from the *lme4* package (Bates *et al.*, 2015). The response variable in this analysis was the interaction between fish. The total interaction, which was calculated by adding the observed interaction per day in each treatment (Shelter_2 or Shelter_1). The model included the size difference in cm between the two fish, number of shelters (two or one), sex of the round goby and used (if the fish was used before) as fixed factors and tank was included as a random factor.

The interpretation of the parameters in terms of probability of interaction was calculated using the equation for the inverse of the logit function (Equation 1).

$$\mu = \frac{\exp{(X\beta)}}{1+\exp{(X\beta)}} = \frac{1}{1+\exp{(-X\beta)}} \qquad \text{(Equation 1)}$$

The probability of hiding

The analysis

To investigate which of the species generally won the competition for shelter I analysed the variation in hiding behaviour between species and if the amount of shelter affected this, again using a generalized linear mixed-effect model with a binomial distribution of the error. The analysis was conducted in R 3.5.1 (R Core Team, 2018) with the *glmer* function from the *lme4* package (Bates *et al.*, 2015). The response variable was hiding, calculated as total number of observations of hiding for each species in each treatment (Shelter_2 or Shelter_1) on each day. Species (round goby and viviparous eelpout), length (length of the fish measured as total length), number of shelters and if the fish were used before was included as fixed factors. The interaction between species and number of shelters and species and length were also included. To account for the non-independence of the observations in the tank each day, tank was included as a random factor.

Hiding analysis with shelter type

The type of shelter provided for the fish was changed after two days of experiments because the shelters were used less than expected. In the analyses of hiding behaviour above, both bricks and pipes were defined as the same. With the restricted amount of data collected in the presented experiment I was not able to include all potential explanatory variables in one model, so the effect of species on hiding with shelter type was analysed separately. The analysis had species, length, number of shelters, used and shelter type as fixed factors, and tank as a random factor. The interaction between species and shelter type was also added in the model, to know if shelter type influenced the interaction between species and amount of shelter. One similar analysis without used as fixed factor and the interaction between species and length in addition was also conducted.

Results

The probability of interaction between fish

Figure 4 shows the increase in probability of interaction with the size difference between the fish. The model the figure is based on is a simplified model without "used" and "sex" as fixed factors. This change had minimal effect on the parameter estimates. The probabilities presented are based on the full model (table 2).

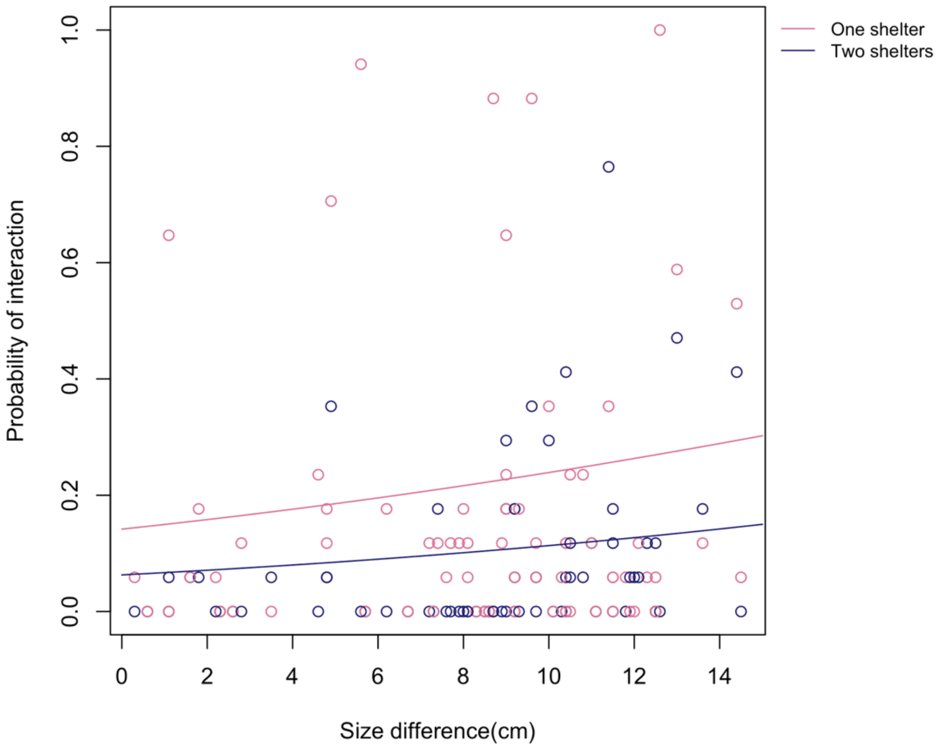

Figure 4: Logistic regression of the probability of interaction on the size difference between the fish using a GLMM with a binomial distribution of the error. The blue colour represents two shelters, and the pink colour when there is one shelter in the tank. The lines are the estimated probability for each treatment (Shelter_2 or Shelter_1) from the model. Each point equals the total amount of interaction over the total amount of observations in one tank, one day at one treatment (Shelter_2 or Shelter_1).

The probability of interaction between the fish increased with 0.054 when one shelter was removed (given a size difference of zero), and this difference increased slightly with increasing size difference. We also see in the model (Fig. 4) that there was a higher probability of interaction between the fish when there is a greater size difference (Fig. 4). The probability of interaction at mean size difference (8.39cm) with one shelter was 0.149 and per cm increase in size difference the probability increased with 0.008. The model results further emphasize that if the fish were used or not before as well as the sex of the fish did not influence the probability of interaction between the fish significantly.

Table 2: Model output from the generalized linear mixed-effect model of the variation of interaction between the two treatments (shelter_2 or shelter_1) and the random effect estimates to the model.

	Estimate	Standard error	P-value
Intercept	-3.144	0.291	<0.001
Size difference	0.064	0.021	0.002
One shelter	0.899	0.132	<0.001
Male	0.022	0.134	0.871
Used before	-0.059	0.130	0.653

		Variance	Standard deviation
Tanks	Intercept	0.296	0.544

The probability of hiding

The activity level differed between the two species. Figure 5 shows that viviparous eelpout hides double the amount of round goby. In addition, round goby rest more outside of shelter than viviparous eelpout.

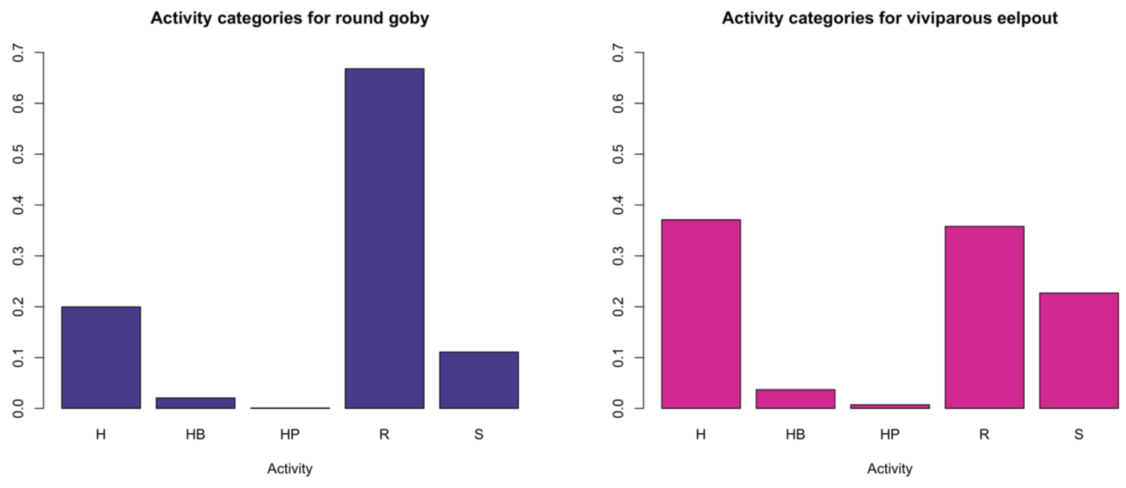

Figure 5: The amount of activity in the different activity categories for both species. H are hiding, HB are when the fish was hiding between the wall and another object and HP was hiding in plant. R stands for resting and S for swimming. HB and HP were not included in the analysis.

The results of the analysis of hiding for species will only include the model without shelter type. A simpler model is presented due to convergence problems in the estimation of the most complex model. Shelter type has a strong effect but including this do not change the parameter estimates for the other effects in the model. This applies for both version of analyses of shelter type (both the model with species and shelter type interaction, and the model without used and species and length interaction) (Appendix B1 and B2).

Figure 6 illustrates the decrease in probability of hiding with total length (cm) for both species. The probability of hiding also decreases when one shelter is removed in the tank for both species. The probability of hiding for round goby at minimum length (9.8 cm) was for two shelters 0.436 and the probability decreased with 0.106 when one shelter was removed. For the maximum length (18.1cm) of round goby the probability of hiding was 0.090 and decreased with only 0.031 when one shelter was removed. The same trends apply for the viviparous eelpout regarding the probability of hiding. At minimum length (10.9cm) in two shelters the probability is 0.734 and decrease with 0.092 when one shelter was removed. Maximum length (29.0cm) had a probability of 0.262 in Shelter_2 and decrease with 0.075 to Shelter_1. All the calculations presented are based on the model output (table 3) and calculated with the help of equation 1. Round goby has also a lower probability of hiding than the viviparous eelpout (figure 6 and table 3). Also, the fact that the fish had been used before influenced the variance and made the fish more prone to hide (table 3).

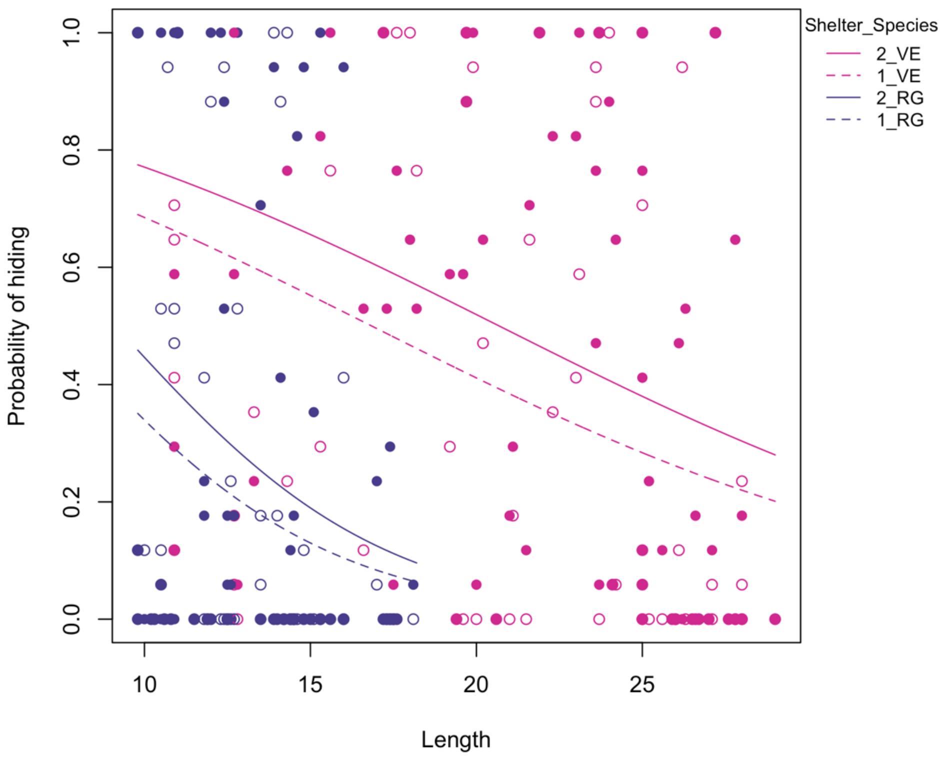

Figure 6: Predicted probabilities of hiding based on logistic regression with the length of the fish included as explanatory variable (see main text for details). The purple colour represents the round goby, and the pink colour represents viviparous eelpout. The solid lines represent when there are two shelters in the tank (Shelter_2), and the dashed line is when there is one shelter in the tank (Shelter_1). Each point is the total amount of hiding for one species, one day at one treatment (Shelter_2 or Shelter_1). Filled points represent Shelter_2 and the open points represent Shelter_1. The total length of round goby is maximum 18.1 cm.

Table 3: Model output from the generalized linear mixed-effect model of the variation of hiding between the two species and the random effects estimate to the model.

	Estimate	Standard error	P-value
Intercept	1.696	0.391	<0.001
Species viviparous eelpout	0.090	0.401	0.823
Length	-0.247	0.027	<0.001
One shelter	-0.450	0.107	<0.001
Used before	0.472	0.075	<0.001
SpeciesVE: One shelter	0.014	0.139	0.920
SpeciesVE: Length	0.134	0.028	<0.001

		Variance	Standard deviation
Tanks	Intercept	0.314	0.561

Shelter type

Shelter type affect the probability of hiding for both species (Appendix B). The proportion of observations where the fish were hiding for both species in both treatments (two shelter or one shelter) and shelter types are presented in figure 6. Viviparous eelpout uses the shelter, regardless of type, more than round goby. The same tendency was shown for both bricks and pipes, but both species preferred the bricks as shelter (Appendix B).

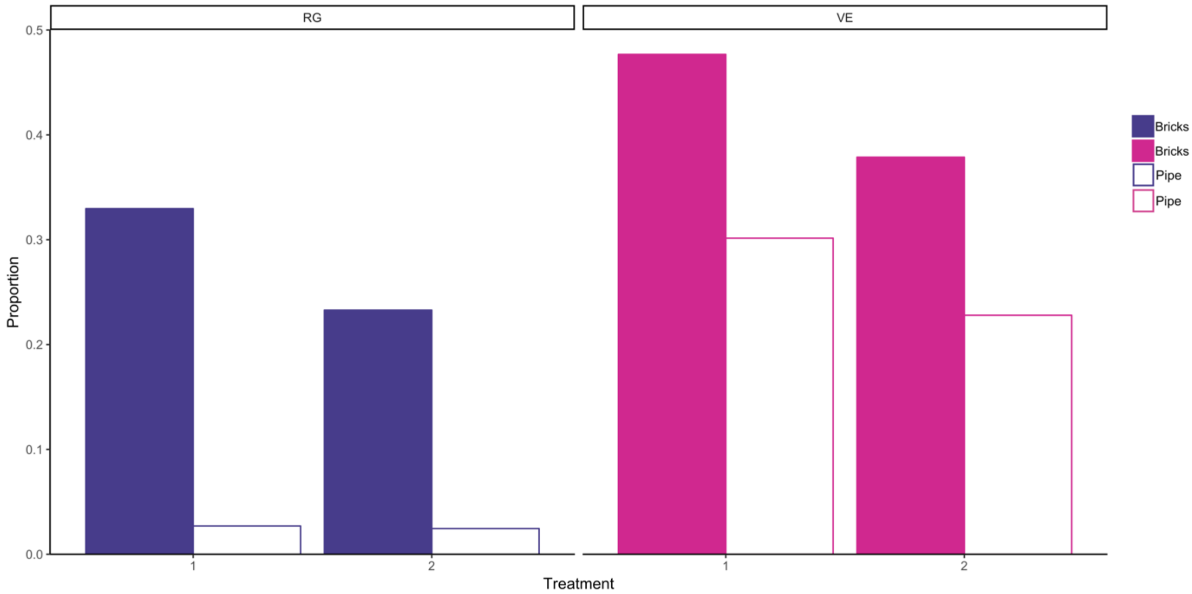

Figure 7: The proportion of observations where the fish were hiding in both species (RG: round goby and VE: viviparous eelpout) in each treatment (treatment 1: two shelters or treatment 2: one shelter) and for each shelter type (bricks or pipe). The purple colour represents round goby and the pink colour represents viviparous eelpout.

Discussion

I detected an increase in the interaction between the fish when one shelter was removed. Despite this increase, there were no clear signs of aggression. I only registered two incidents out of 2532 observations where I saw clear aggressive behaviour. No aggression was observed during the acclimation time either. The observed lack of aggression by the round goby is in contrast to several other studies, which state that round goby is a highly aggressive species (Groen *et al.*, 2012). Balshine *et al.* (2005) found that round goby exhibited overall more aggressive behaviour than the common logperch *(Percina caprodes)* when investigating territorial defence and behavioural interaction. Dubs and Corkum (1996) concluded that the aggressive display and approaches of round goby would likely result in the demise of mottled sculpins *(Cottus bairdi)* and that round goby will drive them from their present nearshore habitat. These two studies, as well as Church *et al.* (2017) have all found evident aggressive behaviour of the round goby in shelter competition. These are all laboratory studies and examine intruder/resident behaviours (Church *et al.*, 2017, Balshine *et al.*, 2005, Dubs and Corkum, 1996). Their approach was to add one of the species (resident) in the tank before the other, giving them a head start in the establishment. However, in my study the fish were placed into the tanks at the same time, and the dynamics between them may be different because of this difference in the experimental design.

I predicted that the round goby would guard the shelter in the presence of viviparous eelpout by display of aggressive behaviour. The findings in the analysis of the probability of hiding for the two species were unanticipated, as the outcome was low signs of clear aggression of the round goby. Furthermore, it was found that the viviparous eelpout has a much higher probability of shelter use compared to the round goby. Round goby does not monopolize shelter in this experiment. One may think that the lack of aggression displayed from the round goby is a sign of low competition for shelter between the two, but it could also have other possible explanations. One plausible explanation is that the round goby feel more secure around the viviparous eelpout than the other way around, so the experienced need for shelter is lower for the round goby. The probability of shelter use for both fish is also significantly decreasing in Shelter_1 when there is only one shelter in the tanks. One plausible explanation for this could be that viviparous eelpout and round goby are equivalent competitors, so they both reduce the other species use of shelter.

The use of shelter also differs between these two species during the breeding season. Round goby are known to use a shelter as nest (Corkum *et al.*, 1998), while viviparous eelpouts give birth to fully developed fry and have no clear use of shelter throughout the reproduction (Hedman *et al.*, 2011). Round goby are highly aggressive in their defence behaviour against intruders and approach, bites and chase intruders when defending their nest (Corkum *et al.*, 1998). Therefore, if the shelter in this study had been used as a nest by the round goby, more clear aggressive behaviour would have been expected.

The shelter type was shifted after two days of experiment, and shelter use significantly differs between the shelter types. The use of pipes is less for both species compared to the use of bricks. The use of pipes by the round goby is almost non existing (Fig. 7). For the viviparous eelpout the difference is not quite that severe. These relationships may partly be explained by the difference in morphology of the two species, with viviparous eelpout having a slim body compared to the stouter round goby with a wider head (Charlebois, 1997, ArtDatabanken, 2015a). Because of this, the pipe would seem to be more convenient for the viviparous eelpout to use than for the round goby.

I found a decrease in the probability of hiding with increasing length of the fish. Accordingly, the small fish of both species were hiding the most. For the round goby this behaviour is consistent with what Belanger and Corkum (2003) found out when investigating the susceptibility of round goby to predation in sandy habitats with and without shelters. When there was a greater potential risk of predation in open habitats, small individuals were removed more often than larger individuals and should therefore use shelter when possible. However, my finding of an increase in interactions between fish with increasing size differences does not fully agree with the findings of Balshine *et al.* (2005). They found that when the size difference between resident – intruder pairs was small, significantly more aggressive acts were exhibited compared to when the size difference was large. The result of my study does not contradict with their result because the aggression level I found was low, but it could indicate a different trend.

There are two distinct ways to interpret the results of the increasing probability of interaction with increasing size difference between the fish. The first interpretation is based on the assumption that competition is strongest when the fish are close, and if this is the case I find more competition when size difference is large. However, it is also possible that distance between individuals indicates competition, and thus that my measure of interaction between the fish relates inversely to competition. If this is the case, we can understand why similarly sized fish are observed to interact less often, as this would fit the prediction of higher competition between fish of similar size as stated by Balshine *et al.* (2005). It is important to remember that the difference in size difference between the fish can be hard to interpret, based on the fact that these two species are of very different shapes. This means that a size difference of 0 cm does not automatically mean that they are equal competitors.

The main purpose of this study was to investigate if there was shelter competition between viviparous eelpout and round goby. Competition for shelter as a resource between the two species was neither confirmed nor rejected in this experimental study. Williamson (1996) state that competition is considered challenging to demonstrate, define and to analyse, and that this may be why competition is considered to be a less severe consequence of invasion. Despite this, competition is an essential factor in the structure of communities and the different use of resources is a critical factor in the coexistence of species (Piet and Guruge, 1997, Karlson *et al.*, 2007). Studies on the exact mechanism by which the round goby outcompete or exclude the viviparous eelpout have not been conducted before, but round goby has the potential to outcompete native species. Although this study is not able to show this, there is an underlying importance to do more research on this topic.

A greater understanding of the behaviour behind these mechanisms will be essential for motivating decision makers (Hirsch *et al.*) and give a greater understanding of the mechanisms facilitating a successful invasion (Finn, 2012). As stated by Hirsch *et al.* (2016): "The safest way to know whether a non-native species will have impacts in a new ecosystem is knowledge about impacts in already invaded ecosystems". Despite the Eelpout not having a substantial commercial value, it is useful for us humans as an indicator species with regards to pollution. It is also an important prey for birds and larger fish species, which means that a decline in its prevalence could have future negative consequences (Lehikoinen, 2005, Hedman *et al.*, 2011).

One more aspect that may be of importance for the future of the interaction between viviparous eelpout and round goby, is the fact that the ocean temperature is increasing. Sorte *et al.* (2010) predict a shift in community composition with a decrease in native species abundance as well as an increase in introduced species with ocean warming. Round goby thrives in warmer water than typically found in Sweden, as opposed to the viviparous eelpout that has reduced survival during warmer summers (Pörtner *et al.*, 2001, Lee and Johnson, 2005). An increase in temperature could therefore influence the interaction between these fish further, with increased stress inflicted on the eelpout. This could have negative consequences in the competition for resources. In the wild, an eviction from shelter may result in the use of less preferred habitats where food is less abundant, and predation is more frequent (Kessel *et al.*, 2011).

Conclusion

It is often stated that round goby is an aggressive species that often monopolize resources (either food or shelter) (Charlebois, 1997, Groen *et al.*, 2012). This study aimed to shed more light on the potential competition between the round goby and a native species of the Baltic Sea viviparous eelpout. From this experimental study I find quite low competition for shelter between the two species. However, based on the fact that these species share habitat and that some part of their diet overlap competition over resources should be expected. There is therefore still a need for further investigation of the behavioural interactions between these species. One interesting aspect would be to see how the interaction between the species is with different size combinations, for example when the round goby is larger in size compared to the eelpout. This may impact the interaction and enhance competition for shelter. In this laboratory study, abiotic and biotic factors that could also affects the interaction between the fish are ruled out. Field studies are therefore needed to quantify the degree of interaction further.

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Appendix A: Histogram of competition

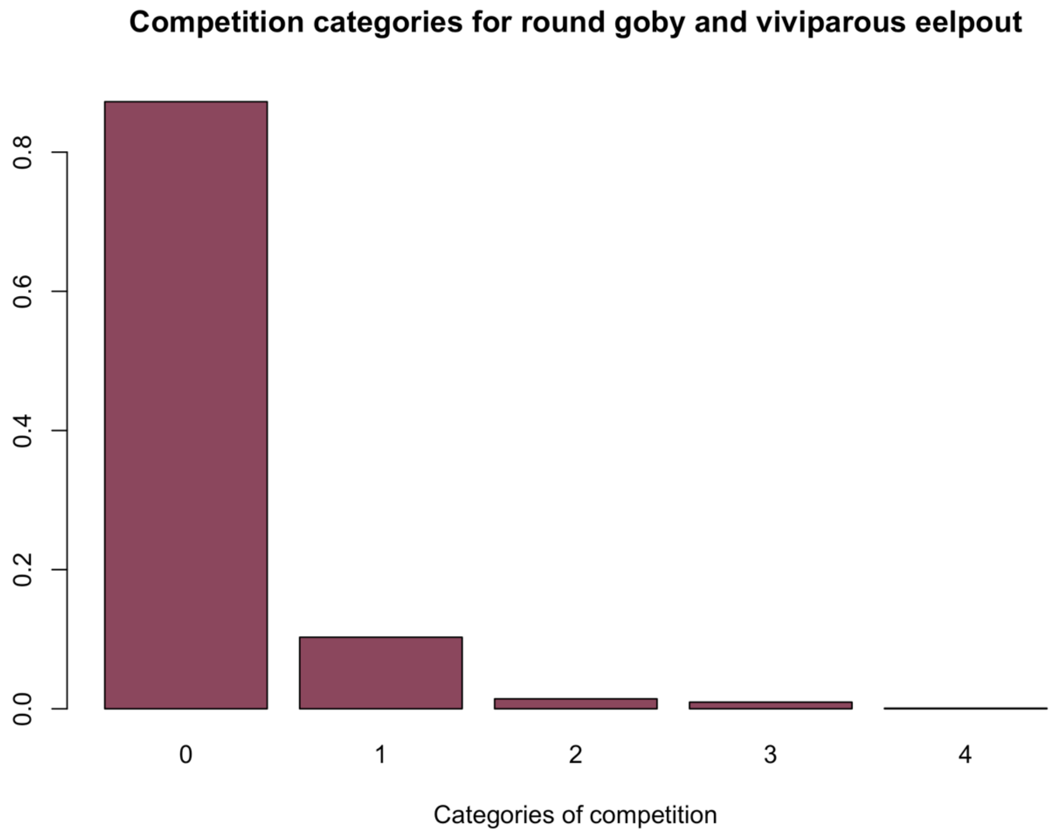

Figure A: Histogram over the 5 different categories of competition(interaction) registered for both species. Category 0 was when the fish did not interact at all, category 1: they were laying close but not touching, either face to face or side by side, 2: when they were laying so close that they were touching with any part of the body, 3: swimming on each other so they were touching and, 4: when they were biting or showed some other type of aggressive behaviour.

Appendix B: Model output – analysis with shelter type

B1: Model output for the model with species and shelter type interaction

Table B1: Model output from the analysis of probability of hiding between the two species with shelter type included. This model had the interaction between species and shelter type. Random effects estimate to the model are also included

	Estimate	Standard error	P-value
Intercept	1.462	0.229	<0.001
Species viviparous eelpout	1.928	0.118	<0.001
Length	-0.121	0.009	<0.001
One shelter	-0.468	0.071	<0.001
Used before	-0.901	0.121	<0.001
Pipe shelter	-3.244	0.243	<0.001
SpeciesVE: Pipe	1.693	0.252	<0.001

		Variance	Standard deviation
Tanks	Intercept	0.3002	0.5479

B2: Model output for the model without used and species and length interaction

Table B2: Model output from the analysis of probability of hiding between the two species with shelter type included. This model was without "used" and the interaction between species and length was included. Random effects estimate to the model are also included

	Estimate	Standard error	P-value
Intercept	1.603	0.390	<0.001
Species viviparous eelpout	0.732	0.404	0.070
Length	-0.183	0.027	<0.001
One shelter	-0.461	0.070	<0.001
Pipe shelter	-2.619	0.230	<0.001
SpeciesVE: Pipe	1.883	0.251	<0.001
SpeciesVE: Length	0.071	0.028	0.013

		Variance	Standard deviation
Tanks	Intercept	0.296	0.544

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