Can the native shore crabs (*Carcinus maenas*) become a barrier to the invasion of the round goby (*Neogobius melanostomus*) in Öresund, southern Baltic Sea?

Nikolaos Papagiannopoulos

Department of Aquatic Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden

ABSTRACT

The round goby (*Neogobius melanostomus*) is a non-indigenous species to the Baltic Sea that has drawn the attention of many researchers in the last decade due to its rapid spreading and its impact on the local fauna. With recent concerns about the dispersal of the round goby towards the North Sea, the aim of this study was to determine if the native shore crab could compete with the invaders and prevent their advance. The ash-free weight and the handling time of four blue mussel size classes (7mm, 12mm, 17mm, 22mm) was measured for both predators in order to calculate their feeding efficiency on each size class. Selectivity experiments were conducted, in aquariums, to determine which size class was preferred by each predator. The results were in compliance with the optimal foraging theory; shore crabs consumed significantly more 17 and 22 mm mussels, while round gobies preferred significantly more 7 and 12 mm mussels. Competition experiments for a food source of ten mussels, with three treatments (goby vs. crab, goby vs. another goby, control), were also conducted. Round gobies were more dominant, consuming significantly more mussels than the crabs, indicating that the shore crab may not outcompete the invader in a limited prey situation.

Keywords: prey value, interspecific competition,

Introduction

Changes to local biodiversity, modification of the structure and functions of aquatic ecosystems, and alteration of ecosystem services can all be caused by non-indigenous species (Bax *et al*., 2003; Çinar *et al*., 2014). As a result, non-indigenous species are equally important as other anthropogenic drivers that have an effect on marine ecosystems, such as overexploitation of marine resources, habitat destruction and pollution. However, not all of those species are widespread or pose a major ecological and economical threat (Galil *et al*., 2014). There have been recorded over 100 non-indigenous species in the Baltic Sea (AquaNIS 2018), one fifth of which are widespread (Ojaveer & Kotta 2015). This smaller group of invasive species should be prioritized for post-invasion management actions (Ojaveer *et al*., 2015).

The round goby (*Neogobius melanostomus*, Pallas 1814), native to the Ponto-Caspian region, is a bottom-dwelling fish of the Gobiidae family. It is arguably one of the most invasive fish globally and has successfully invaded a wide range of habitats including the Laurentian Great Lakes, the Baltic Sea and numerous European rivers (Kornis *et al*., 2012). Numerous studies have reported the impact of the round goby invasion on the native fauna, especially in the Laurentian Great Lakes. The average size of dressenid mussels was found to be higher in areas with a round goby invasion than in areas without round gobies, due to predation on the smaller mussels (Djuricich & Janssen, 2001). A similar study reported that round gobies can significantly reduce the population of dressenid mussels (Lederer *et al*., 2006). In the absence of bivalves, larger round gobies may compete with native predator species for other benthic invertebrates (Skora & Rzeznik, 2001). Round gobies can outcompete a wide variety of native benthic fish species by dominating resources, even without possessing an inherent sensory advantage (Bergstrom & Mensinger, 2009).

In the Baltic Sea, round gobies were first reported in 1990 at Puck Bay, in the Gulf of Gdansk (Sapota & Skóra, 2005). Even though their populations were low and their dispersal slow in the beginning, round gobies have now expanded over vast areas and have reached densities high enough to have an impact on the native fauna (Karlson *et al*., 2007). Round gobies were estimated to disperse from the western coasts of the Baltic Sea towards the North Sea at an approximate rate of 30 km $year^{-1}$ (Azour *et al*., 2015). The accelerating rate of expansion can be attributed to multiple introduction events and the ability of round gobies to adapt rapidly to new habitats (Björklund & Almqvist, 2010). This raises an important question: how far can the round goby spread? A study that focused on the effects of salinity change, reported that survival rate was reduced by up to 34% in 30 PSU and concluded that the round goby's growth and ability to compete may be reduced in oceanic conditions, above 25 PSU (Behrens *et al*., 2017). Similar results were described by Hempel & Thiel, 2015; round goby growth was significantly lower in average at 30 PSU, but the growth patterns of some specimens showed that a further spread towards higher salinity regions is quite possible. Even though an increase in salinity may not completely prevent further round goby invasion directly, there is a possibility for an indirect effect in the form of marine species in the North Sea as predators or competitors.

In general, invasive species thrive when the new ecosystem lacks versatile competitors and natural predators to control their populations. One particular species, native to the Baltic Sea and the NE Atlantic, has the potential to outcompete other species in many cases. The European green crab (*Carcinus maenas*, Linnaeus 1758), or shore crab, is considered one of the 100 worst invasive species in the world (GISD, 2018). It has successfully invaded Europe (non-native areas), Africa, Atlantic North America, Pacific North America, Japan and Australia due to global shipping (Carlton & Cohen, 2003). Its preferred habitat and prey match those of the round goby, making it an excellent competitor.

Non-indigenous fish may have an increased difficulty invading an established assemblage structured by strong biotic interactions (Baltz & Moyle, 1993). This difficulty was mostly observed in native assemblages mainly structured by competition and predation (Ross, 1991). Blue mussels (*Mytilus edulis*, Linnaeus 1758), abundant in the area of Öresund, are consumed by both round gobies and shore crabs. There could be a possibility for the shore crab to become a dispersal barrier for the round goby if both species prefer the same prey size and the assemblage in this area is well established.

The aim of this study was to determine whether the presence of the shore crab could have an effect on the round goby invasion. In order to achieve that, the size of blue mussel prey that the shore crab and the round goby prefer was examined, and compared to identify any exploitative competition. Interaction and behaviour experiments were also conducted to determine if one of the species can outcompete the other when the food sources are limited.

Materials & Methods

Sampling

The round gobies used in the experiments were caught in April 2017 with fyke nets in a brackish water estuary in the southern Baltic Sea. The fish were tagged with passive integrated transponder tags (PIT tags; 12 × 2 mm; 0.1 g; Oregon RFID) after one week of acclimation. The gender and boldness of the fish were determined, as described by Ericsson 2018, and only male intermediate (neither bold nor shy) fish were later provided in September 2017 to avoid potential personality or gender-induced differences. Before each experiment, the length and weight of each individual was measured. The fish were kept in two 250 L tanks (salinity=18, T=10±1°C), enriched with sand and artificial eelgrass, with a 12 hour photoperiod and were fed to satiation with defrosted shrimp every second day.

Around 30 shore crabs were caught in September 2017 near the harbour of Ålabodarna with crab traps and ten of those were kept and used in the experiments. The length and weight of each crab was also measured before each experiment. The crabs were kept in separate 120 L aquariums (3/4 sides covered), with the same conditions as the fish, to avoid cannibalism and loss of claws due to territory defending.
Blue mussels, up to 30 mm long, were collected near the harbour of Ålabodarna using a small fishing dredge and were kept in a 150 L tank with the same salinity and temperature as the fish.

Measuring ash-free content

Different sized blue mussels were selected in order to establish a length to ash-free weight (AFW) relationship using a power function. The mussels were dried in an oven at 60 °C over 24 hours and the dry mass was measured. The mussels were burnt at 450 °C for one hour and the AFW was then calculated by subtracting the burnt weight from the dry weight. The power function was then used to calculate the average AFW for each mussel size class (MSC). Four size classes were used: 7mm (5-9mm), 12mm (10-14mm), 17mm (15-19mm), 22mm (20-24mm).

Prey value

The prey value of each MSC to each of the predators was calculated as prey energy content divided by the handling time. Energy content was derived from measuring AFW, assuming AFW was directly proportional to energy content. Mussel size and predator species specific handling times were determined from experiments. Each predator (round goby or shore crab) was placed in a 120 L aquarium and was given 48 hours to acclimate and starve. Several mussels of the same size class were positioned in the middle of the aquarium simultaneously in order to draw attention. The individuals were observed and were only timed during the consumption of the first mussel. The remaining mussels were then removed from the aquarium. This process was repeated for each MSC per individual and was replicated five times for both the crabs and the round gobies. The order which the different size classes of mussels were introduced to each individual were chosen randomly. The handling time was measured in seconds from the moment the individual attacked the mussel until the moment it was completely consumed. For the round gobies, it took several attempts to break the shell of the bigger mussels and that resulted in them giving up on the task temporarily, but resuming after a short period of time. This idle time was not included in the total handling time.

Prey selectivity

Ten 120 L aquariums were used and each had a 1 cm layer of fine sand and one ceramic in the middle for shelter. Twenty blue mussels from each size class were spread evenly in each aquarium and were given 30 minutes to acclimate. The treatment individual was then placed into the aquarium and was given 12 hours, from 20:00 to 08:00, to feed. This time was chosen due to the nocturnal feeding habits of both the round gobies and the crabs. The remaining mussels were sieved from the sand and were counted. The experiment was replicated ten times, for both the round gobies and the crabs, with a different individual each time.

Competition

These experiments were conducted in cooperation with Ottvall 2018. The same ten aquariums were also used for the competition and interaction experiments between crabs and round gobies. The environment, while still having a 1 cm sandy substrate, was altered so that one side was covered with artificial eelgrass while the other was fully exposed. Three treatments were selected for ten round gobies in order to observe any significant differences in their foraging behaviour: (a) presence of a crab, (b) presence of another goby, (c) control. Participating individuals were starved and placed in their corresponding aquarium 24 hours before each experiment to acclimate. A food source, ten blue mussels 10-15 mm long, was placed in the middle of the aquarium just outside the eelgrass area and the participants were given one hour to feed. Each treatment was recorded with a SONY HDR-CX405 camera and the videos were analysed for the number of mussels consumed by the focal fish. One of the treatment gobies died during acclimation, resulting in a total of nine replicates. It is important to note that the other round gobies that were used in treatment (b) were all unique individuals and not part of the treatment gobies.

Data analysis

In order to test if the differences between the mussels size classes were dependent on the species, a two-way ANOVA was conducted on the results of the handling time and feeding efficiency. A generalised linear model with a Poisson distribution was applied on the selectivity and competition results. Species and individuals were nested where appropriate to avoid pseudoreplication.

Permits

All the methods used in the experiments fully comply with the Malmö-Lund authority for ethics of animal experimentation (permit licence number: M36-14).

Results

There were no complications in the experiments with the exception of one fish mortality during the competition experiment. The average AFW for each MSC was calculated by using the length to AFW model of the mussels (Fig. 1). There was a significant difference in the handling times between the interaction of species and MSC ($p = 0.012$), the two predator species ($p < 0.001$) and the prey size ($p < 0.001$) (Table 1). The round gobies were handling mussels from size classes A, B and C faster than the crabs, while the crabs were handling size class D mussels faster. The larger the mussel the longer it took for both species to handle.
The average AFW was divided by the handling time for each species and MSC to create a prey value (Fig. 1).

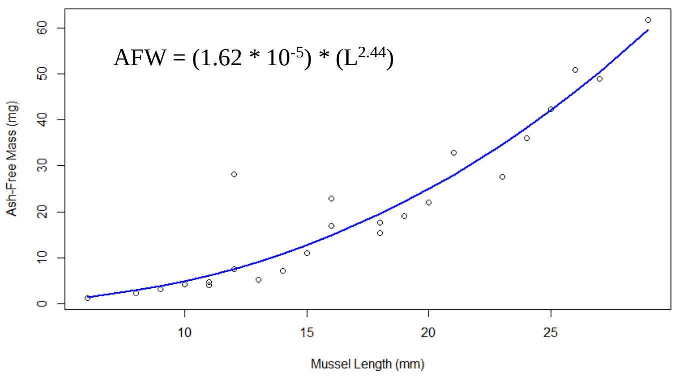

Fig. 1 – The length to AFW ratio for the Öresund blue mussels.

Overall, the round gobies were more efficient at consuming blue mussels ($p < 0.001$). There was a significant difference between the interaction of the species and the MSC ($p = 0.009$) but there was no significant difference between the MSC alone (Table 2). On average, the round gobies consumed a 7mm mussel in 11s, a 12mm in 40.6s, a 17mm in 142.8s and a 22mm in 261.8s. On the other hand, the crabs fully consumed a 7mm mussel in 75.2s, a 12mm in 144s, a 17mm in 193s and a 22mm in 238.2s.

Table 1 - Two-way ANOVA analysis on the handling time results.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Species	1	8962	8962	4.8	0.035
MSC	1	242417	242417	130.8	< 0.001
Species:MSC	1	12529	12529	6.7	0.014
Residuals	36	65449	1856		

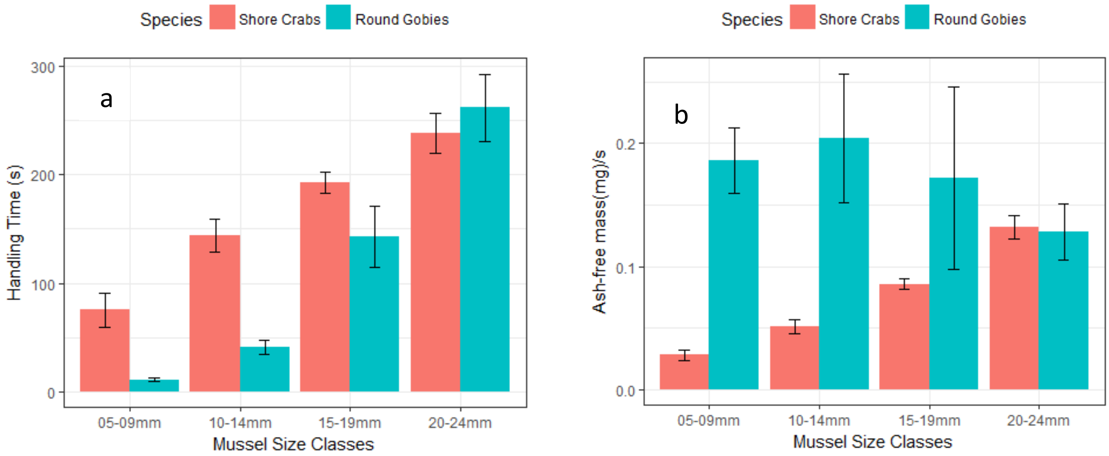

Fig. 2 – The average (a) handling time, in seconds, and (b) prey value, measured in AFW consumed per second (mg/s), of the four MSC for both species.

Table 2 - Two-way ANOVA analysis on the efficiency results.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Species	1	0.088	0.088	16.99	< 0.001
MSC	1	0.001	0.001	0.22	NS
Species:MSC	1	0.043	0.043	8.42	0.006
Residuals	36	0.18	0.005		

Table 3 – The level of significance for a generalized linear model with Poisson distribution on the selectivity results.

	Est. Std.	Error	z value	Pr (>|z|)
(Intercept)	-3.05	0.47	-6.5	< 0.001
Species	3.27	0.27	12.1	< 0.001
MSC	1.90	0.13	14.2	< 0.001
Species:MSC	-1.28	0.083	-15.3	< 0.001

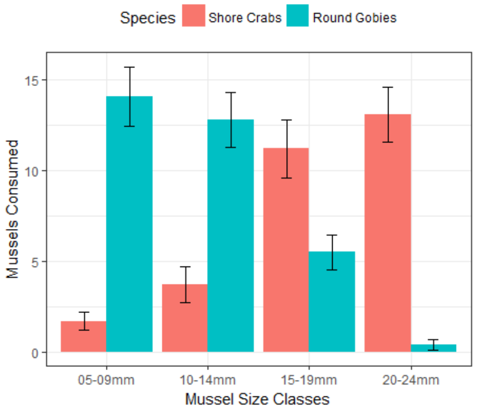

Fig. 3 – Number of blue mussels consumed from each size class by both species over a 12 hour period (20:00-08:00). A mussel was considered eaten if it was cracked open and there was no soft tissue left or if it was not collected by the 2mm sieve afterwards.

The selectivity experiment showed a significant interaction effect of species and mussel size (Table 3). Round gobies preferred the two smallest MSC while the crabs preferred the two largest ones ($p < 0.001$). On average the round gobies consumed 14.1 mussels of the 7 mm size class but only 0.4 of the 22 mm size class during the experimental period. Comparing the number of mussels consumed by the focal fish in each treatment during the competition experiment (Fig. 4) did not provide any significant differences (Table 4). The focal fish consumed significantly ($p < 0.001$) more blue mussels than the crabs in the crab treatment (Table 5). During this experiment, both the fish and the crabs aggressively defended the food source if they could, leading to some individuals consuming all ten mussels. The focal fish did not rush to the food source when there was no competitor present, and preferred to hide in the eelgrass. When another round goby was present, the focal fish spent more time in the open area compared to the other treatments. Ottvall 2018 further describes the behavioural interactions between the two species in this experiment.

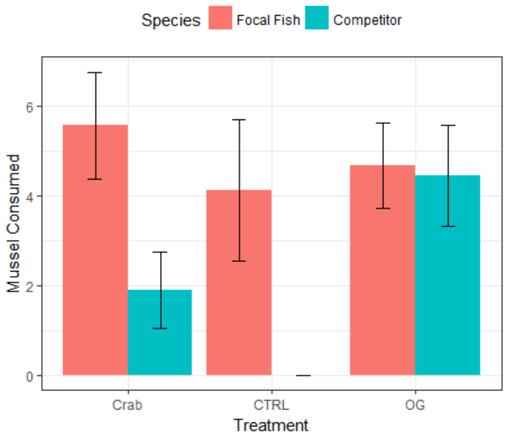

Fig. 4 – The number of blue mussels consumed in each competition treatment. Treatment "crab" corresponds to one focal round goby against one crab, "CTRL" to one focal round goby alone (thus no competitor to consume mussels) and "OG" to one focal round goby against another round goby (random non-focal). In some replicates, some of the blue mussels were not consumed so the total of the averages in each treatment is not exactly 10.

Table 4 - Generalized linear model with Poisson distribution comparing the average mussels consumed by the focal fish between the treatments.

Treatments	Estimate Std.	Error	z value	Pr (>|z|)
Crab & OG	-0.16	0.30	-0.53	NS
Crab & CTRL	-0.32	0.31	-1.02	NS
OG & CTRL	-0.44	0.53	-0.83	NS

Table 5 - Generalized linear model with Poisson distribution comparing the average mussels consumed by the focal fish and the crabs in the crab treatment.

	Estimate Std.	Error	z value	Pr (>|z|)
(Intercept)	1.71	0.14	12.1	< 0.001
Crabs	-1.08	0.28	-3.8	< 0.001

Discussion

After summarizing the results presented in this study, the hypothesis, that shore crabs could become a dispersal barrier, was rejected. The round goby proved to be a more efficient predator on average and dominated the limited food source in the competition experiments. No clear results were drawn by observing behavior during the competition experiments; domination varied among replicates, indicating that each specimen's personality played an important role. Bold shore crabs aggressively defended the food source while shy ones were forced to retreat to a hiding spot, allowing the round goby to forage undisturbed. The results from the selectivity experiment were in agreement with each species optimal foraging theory and with similar studies.

The average handling time of *M. edulis* was significantly different between the interaction, the two predator species and the MSC (Table 1). The round gobies were more efficient at consuming smaller, 7 and 12 mm, blue mussels while the crabs were more efficient at consuming larger, 22 mm, blue mussels. The shore crabs appeared to have difficulties to get the required grip to crack the mussels because they were not attached to any hard surface like they would normally, resulting in very long handling times (Fig. 2a). For the same reason, the round gobies were able to consume the smaller mussels much faster, swallowing them whole, and crack the larger ones inside their mouth. The usage of attached blue mussels in the handling experiment was evaluated as highly impractical (more than double the observation and preparation time) and would bring an additional factor to the table, the efficiency of each individual to find the mussels in a rocky substrate that might have very few similarities to its original habitat, overcomplicating the results. Shore crabs have a reduced handling time on blue mussels when a competitor is introduced (Chakravarti & Cotton, 2014), and the round gobies used in our experiments showed a similar tendency. So despite the fact that unattached mussels were used, the approximate handling time of each size class is balanced by the fact that each trial included only one specimen at a time. Round gobies struggled to crack larger mussels open and, in many cases, had to spit out the mussel and try again. Once they succeeded in cracking the mussel, it was a matter of seconds until they swallowed it. The crabs seemed to have no difficulties cracking the larger mussels; around 90% of their handling time was about separating and eating the soft tissue. During these experiments, it took much longer for the shore crabs than the round gobies to find the prey items (especially the smaller mussels) but that search time is not included in the results.

The MSC used in this experiment, were chosen after observing both species and their feeding habits, and comparing to size classes chosen by similar studies. After both species being fed with mussels up to 45 mm long for several days, it was concluded that only the largest of the gobies, >165 mm, could consume mussels with a length of >25 mm; possibly due to gape limitation. On the other hand, the crabs were able to crack open blue mussels up to 40 mm length in a reasonable amount of time. Shore crabs can also adopt a slower attack method which is effective against all larger sizes but the prey value decreases rapidly at much larger mussels due to the long handling times (Elner & Hughes 1978). In a similar experiment using Baltic Sea round gobies, Schrandt *et al*. 2016 also used four prey options, but in the form of two species (*M. balthica* and *M. trossulus*) and two size classes (6-9 mm and 10-13 mm). Having a limit of 25 mm in the prey size that both predators could compete for and in order to allow comparison between the two studies, the four size classes chosen for this study were the most relevant.

The high standard deviation in the round gobies efficiency value (Fig. 2b) can be attributed to just one factor; size. The larger the round goby is, the more efficient it becomes at consuming bigger mussels (Karlson *et al*., 2007). As expected, crabs were more efficient at consuming larger mussels, since the time needed to crack a small mussel open is almost the same as the time required for a bigger and more nutritious one. Elner & Hughes, 1978, concluded that the optimal prey mussel size increases with the crab size. The MSC used in the current study may not include the optimal sizes of mussels compared to the mean size of crabs used (54.3 ± 7.9 g), but were chosen in order to compare the two predator species. It is important to note that the efficiency of the round gobies at consuming larger mussels may in fact be lower than presented in this study if the mussels are strongly attached on a hard surface. Although, when round goby individuals encounter a clump of small mussels, which is fairly common in the southern Baltic Sea, they are able to consume several mussels at once (Naddafi & Rudstam, 2013), as long as the gape size allows it, further increasing their efficiency. This was not the case in the selectivity experiments that followed; all of the mussels were randomly spread on a sandy bottom so no mussel clusters were formed.

According to the optimal foraging theory, predators will choose to consume the prey type that provides the highest amount of energy for the time required to find and handle it (Hughes 1980). In the selectivity experiment, it was expected that round gobies would prefer mussels below 12 mm length, whereas the crabs were expected to have a preference for larger mussels, above 17 mm length. In a similar study, round gobies from Mariehamn, Finland, preferred 6-9 mm Baltic Sea blue mussels over 10-13 mm blue mussels and 6-13 mm Baltic clams when either the density or the biomass of prey was constant, suggesting that encounter rates were not a driving force for the selectivity (Schrandt *et al*., 2016). In the current study, there was no significant difference between the number of 7 and 12 mm mussels consumed but there was a significant preference towards those two size classes over the bigger ones. A possible explanation for this difference between the two results may be the fact that the fish used in Schrandt *et al*. 2016 were smaller (mean length = 143.9 ± 2.8 mm) than the ones used in the current study (mean length = 157.9 ± 0.5 mm). In a study conducted with specimen from the Great Lakes, which were also smaller than the ones used in our experiments, it was reported that round gobies always preferred mussels <10mm (Ray & Corkum, 1997). Nevertheless, the common ground between the results is the tendency that the round gobies have a preference towards the smaller blue mussels when they are given a choice.

The selectivity results for crabs were in agreement with their efficiency values, and completely opposite from the gobies results, since they consumed significantly more 17 and 22 mm mussels compared to other two size classes. When the prey availability is unlimited, crabs will choose mussel sizes close to the predicted optimum but will also include suboptimal mussel sizes in their diet depending on their encounter rates (Elner & Hughes 1978). In a similar study, shore crabs consumed mussels from each size class in proportion to the rates at which they were encountered and picked up (Jubb *et al*. 1983). This contradicts with the results presented in the prey selectivity experiment, indicating that the prey density chosen was high enough to allow selectivity among the MSC. The same study also suggested that crabs reject smaller mussels due to low energetic value and larger mussels due to their resistance to crushing, after briefly manipulating them. Shore crabs in some cases may also prefer slightly smaller mussels, even when it would not have the most beneficial prey value, in order to minimize the risk of claw damage and maximize long-term feeding (Smallegange *et al*., 2008).

The soft tissue dry weight of blue mussels differs depending on the season as described by Wolowicz *et al*. 2006, but due to time constraints sampling was restricted to autumn only. There is an elevation in the soft tissue dry weight of blue mussels in the Southern Baltic Sea during late spring and early summer, when the mussels maintain mature gametes, due to the spring phytoplankton bloom (Wolowicz *et al*. 2006). The blue mussels used in this experiment were collected during October, after the reproduction period, when the soft tissue dry weight reaches its lowest values. This might have slightly increased the consumption of the blue mussels in general since they provided considerably fewer calories, and decreased the average handling time since there was less soft tissue to consume. Nonetheless, it is assumed that these differences would not have altered the results, if the mussels had been sampled during late spring.

The round gobies were significantly more dominant at consuming blue mussels during the competition experiments (Fig. 3); consuming more mussels than the crabs in 7 out of the 9 replicates. Even though there were no significant differences between the mussels consumed by the focal gobies at the control treatment and at the other two treatments, they seemed to become more active and increase their consumption rate when a competitor was introduced. The round gobies might become stimulated by the presence of a competitor thus reaching for the food source faster than when being alone.

Since each trial only lasted for 60 minutes, not every prey item was consumed. This may have slightly benefited the gobies because they have far lower handling times for the mussel sizes that were used (12 mm) but the aim of this experiment was to assess competitiveness on a common prey species and size.

Another aspect to the shore crab presence is an indirect effect, inducing phenotypic plasticity in blue mussels. According to Leonard *et al*., 1999, blue mussels produce more byssal threads, increasing their attachment strength, and produce thicker more robust shells at the presence of shore crabs. Another study confirmed this claim when Baltic Sea blue mussels were introduced to shore crab cue water and initiated a similar phenotypic plasticity response (Reimer & Harms-Ringdahl, 2001). This can have a significant effect on their prey value for the round goby by increasing the handling time thus making it more profitable to choose a different prey. It has been documented that round gobies may shift their diet when the preferable size mussel abundance drops below a certain level, usually at a greater depth, and consume more shrimps than mussels (Walsh *et al*., 2007). Another study found that when offered an equal amount of mussels and amphipods round gobies preferred the latter as they could ingest substantially more biomass by excluding mussels, due to their shells, from the diet (Diggins *et al*., 2002).

The difference between the mussel size preferences of the round gobies and the crabs may have a negative effect on blue mussel beds when both predators are abundant since all mussel sizes will be vulnerable to predation. Areas dominated by smaller blue mussels appear to be more susceptible to a round goby invasion due to its high feeding efficiency on those size classes (Fig. 2b) and the lack of competition for this food source from the shore crabs. It is expected that a round goby invasion in the North Sea will increase the average size of blue mussels and significantly decrease the populations overall, similarly to the dreissenid populations in the Laurentian Great Lakes (Djuricich & Janssen, 2001; Lederer *et al*., 2006). Shore crab populations will not be affected immediately by a round goby invasion, but might decline in the long run, if the availability of other prey is insufficient, when the abundance of bigger blue mussels declines.

The dispersal rate did not get affected by the abundance and density of parasites as expected in the Danube River (Brandner *et al*., 2013). The same study also suggested that a shift may occur in the invaded ecosystem, increasing the populations of prey species that are more resistant to round goby predation thus reducing the invasion's dispersal rate. Wetlands were found to be more resistant to round goby invasion in coastal areas of Lake Michigan (Cooper *et al*., 2007), but it is unclear which trait is increasing this resistance and whether it could be found in a marine ecosystem. In a different study, a model showed that, between the arrival and establishment phases of an invasion, even if the numbers of new adult individuals entering an area is low, there is a high probability of establishment; but a high concentration of juvenile round gobies are needed to pose a significant risk of invasion (Vélez-Espino *et al*., 2010). The same study concluded that preventative measures aiming to minimize the propagule pressure are the most effective management option to reduce the risk of future invasions. In the case of the North Sea, it is nearly impossible, without extreme methods, to control the propagule pressure, which is adult round gobies entering a new region, so learning more about the interactions between round gobies and native species is important. For example, increasing fishing effort in areas that the round goby has not been established yet could have a reverse effect than the intended if it also affects species that counter the invasion in some way. With the current dispersal rate of 30 km year^{-1}, it is estimated that the round goby could reach the North Sea by 2019; meaning that some risks will have to be taken when deciding what measures should be implemented, due to the lack of data currently on the interactions between the round goby and the species native to the North Sea (or other marine ecosystems).

In conclusion, it is evident that shore crabs may not prevent further round goby invasion towards the North Sea directly, but could in cooperation with other factors, such as higher salinity and keystone predators including round gobies in their diet, contribute towards a more invasion-resilient ecosystem. Future studies should focus on other marine prey species that may be an important part of the round goby diet in the North

Sea, on the feeding habits of juvenile round gobies since size is an important factor, and on the effectiveness of some marine predators to adopt round gobies in their diet. Conducting experiments in a marine environment (30 PSU) is also recommended since it has been proven to reduce round goby growth, survival rate and the ability to compete (Hempel & Thiel, 2015; Behrens *et al*., 2017).

Acknowledgements

I thank O. Ottvall for his help during sampling, setting up the aquariums and conducting the competition experiments. I also thank P. Carlsson, for his help during the sampling of blue mussels, and my supervisors A. Nilsson and A. Persson for their invaluable advisement throughout the experiments and data analysis. This study was funded by Lund University as a master's degree project.

REFERENCES

AquaNIS (2018) Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. http://www.corpi.ku.lt/databases/index.php/aquanis Version 2.36+ (Accessed 24 April 2018)
Azour, F., van Deurs, M., Behrens, J., Carl, H., Hüssy, K., Greisen, K., & Møller, P. R. (2015). Invasion rate and population characteristics of the round goby *Neogobius melanostomus*: effects of density and invasion history. *Aquatic Biology*, 24(1), 41-52.
Baltz, D. M., & Moyle, P. B. (1993). Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications*, 3(2), 246-255.
Bax, N., Williamson, A., Aguero, M., Gonzalez, E., & Geeves, W. (2003). Marine invasive alien species: a threat to global biodiversity. *Marine policy*, 27(4), 313-323.
Behrens, J. W., van Deurs, M., & Christensen, E. A. (2017). Evaluating dispersal potential of an invasive fish by the use of aerobic scope and osmoregulation capacity. *PloS one*, 12(4), e0176038.
Belanger, R. M., & Corkum, L. D. (2003). Susceptibility of tethered round gobies (*Neogobius melanostomus*) to predation in habitats with and without shelters. *Journal of Great Lakes Research*, 29(4), 588-593.
Bergstrom, M. A., & Mensinger, A. F. (2009). Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. *Transactions of the American Fisheries Society*, 138(5), 1009-1017.
Björklund, M., & Almqvist, G. (2010). Rapid spatial genetic differentiation in an invasive species, the round goby *Neogobius melanostomus* in the Baltic Sea. *Biological Invasions*, 12(8), 2609-2618.
Brandner, J., Cerwenka, A. F., Schliewen, U. K., & Geist, J. (2013). Bigger is better: characteristics of round gobies forming an invasion front in the Danube River. *PLoS One*, 8(9), e73036.
Carlton, J. T., & Cohen, A. N. (2003). Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. *Journal of Biogeography*, 30(12), 1809-1820.
Chakravarti, L. J., & Cotton, P. A. (2014). The effects of a competitor on the foraging behaviour of the shore crab *Carcinus maenas*. *PloS one*, 9(4), e93546.
Çinar, M. E., Arianoutsou, M., Zenetos, A., & Golani, D. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions*, 9(4), 391-423.
Cooper, M. J., Ruetz III, C. R., Uzarski, D. G., & Burton, T. M. (2007). Distribution of round gobies in coastal areas of Lake Michigan: are wetlands resistant to invasion?. *Journal of Great Lakes Research*, 33(2), 303-313.
Diggins, T. P., Kaur, J., Chakraborti, R. K., & DePinto, J. V. (2002). Diet choice by the exotic round goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. *Journal of Great Lakes Research*, 28(3), 411-420.

Djuricich, P., & Janssen, J. (2001). Impact of round goby predation on zebra mussel size distribution at Calumet Harbor, Lake Michigan. *Journal of Great Lakes Research*, 27(3), 312-318.
Elner, R. W., & Hughes, R. N. (1978). Energy maximization in the diet of the shore crab, *Carcinus maenas*. *The Journal of Animal Ecology*, 103-116.
Ericsson P. (2018) Is bolder better? The influence of personality on competitive success and predation susceptibility in the invasive round goby (*Neogobius melanostomus*). *Lund University Publications Student Papers*.
Galil, B. S., Marchini, A., Occhipinti-Ambrogi, A., Minchin, D., Narščius, A., Ojaveer, H., & Olenin, S. (2014). International arrivals: widespread bioinvasions in European Seas. *Ethology Ecology & Evolution*, 26(2-3), 152-171.
Global Invasive Species Database (2018). Downloaded from http://www.iucngisd.org/gisd/100_worst.php on 27-04-2018.
Hayden, T. A., & Miner, J. G. (2009). Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: diel vertical migration of early juvenile round goby. *Biological Invasions*, 11(8), 1767-1776.
Hempel, M., & Thiel, R. (2015). Effects of salinity on survival, daily food intake and growth of juvenile round goby *Neogobius melanostomus* (Pallas, 1814) from a brackish water system. *Journal of Applied Ichthyology*, 31(2), 370-374.
Hughes, R. N. (1980). Optimal foraging theory in the marine context. *Oceanogr. Mar. Biol. Ann. Rev*., 18, 423-481.
Jubb, C. A., Hughes, R. N., & Ap Rheinallt, T. (1983). Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* (L.) *Journal of Experimental Marine Biology and Ecology*, 66(1), 81-87.
Karlson, A. M., Almqvist, G., Skóra, K. E., & Appelberg, M. (2007). Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. *ICES Journal of Marine Science*, 64(3), 479-486.
Kornis, M. S., Mercado-Silva, N., & Vander Zanden, M. J. (2012). Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of fish biology*, 80(2), 235-285.
Lederer, A., Massart, J., & Janssen, J. (2006). Impact of round gobies (*Neogobius melanostomus)* on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. *Journal of Great Lakes Research*, 32(1), 1-10.
Lee, V. A., & Johnson, T. B. (2005). Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). *Journal of Great Lakes Research*, 31(2), 125-134.
Leonard, G. H., Bertness, M. D., & Yund, P. O. (1999). Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology*, 80(1), 1-14.
Marsden, J. E., Charlebois, P., Wolfe, K., Jude, D. J., & Rudnicka, S. (1996). *The round goby (Neogobius melanostomus): a review of European and North American literature*. INHS Center for Aquatic Ecology.
Moskal'kova, K. I. (1996). Ecological and morphophysiological prerequisites to range extension in the round goby *Neogobius melanostomus* under conditions of anthropogenic pollution. *Journal of Ichthyology* 36, 584–590.
Naddafi, R., & Rudstam, L. G. (2014). Predation on invasive zebra mussel, *Dreissena polymorpha*, by pumpkinseed sunfish, rusty crayfish, and round goby. *Hydrobiologia*, 721(1), 107-115.
Ojaveer, H., Galil, B. S., Lehtiniemi, M., Christoffersen, M., Clink, S., Florin, A. B., & Behrens, J. W. (2015). Twenty five years of invasion: management of the round goby *Neogobius melanostomus* in the Baltic Sea. *Management of biological Invasions*, 6(4), 329-339.
Ojaveer, H., & Kotta, J. (2015). Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: literature survey evidences major limitations in knowledge. *Hydrobiologia*, 750(1), 171-185.
Ottvall (2018). Uninvited guests in troubled waters: Interspecific interactions between the non-indigenous round goby, *Neogobius melanostomus*, and the native benthic community of Öresund. *Lund University Publications Student Papers*.

Ray, W. J., & Corkum, L. D. (1997). Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environmental Biology of Fishes*, 50(3), 267-273.
Reimer, O., & Harms-Ringdahl, S. (2001). Predator-inducible changes in blue mussels from the predator-free Baltic Sea. *Marine Biology*, 139(5), 959-965.
Ross, S. T. (1991). Mechanisms structuring stream fish assemblages: are there lessons from introduced species?. *Environmental biology of Fishes*, 30(4), 359-368.
Sapota, M. R., & Skóra, K. E. (2005). Spread of alien (non-indigenous) fish species *Neogobius melanostomus* in the Gulf of Gdansk (south Baltic). *Biological Invasions*, 7(2), 157-164.
Schrandt, M. N., Stone, L. C., Klimek, B., Makelin, S., Heck, K. L., Mattila, J., & Herlevi, H. (2016). A laboratory study of potential effects of the invasive round goby on nearshore fauna of the Baltic Sea. *Aquatic invasions*.
Skóra, K., Olenin, S., & Gollasch, S. (1999). *Neogobius melanostomus* (Pallas, 1811). In *Case Histories on Introduced Species: Their General Biology, Distribution, Range Expansion, and Impact* (Gollasch, S., Minchin, D., Rosenthal, H. & Boight, M., eds), pp. 69–73. Berlin: Logos-Verlag.
Skora, K. E., & Rzeznik, J. (2001). Observations on diet composition of Neogobius melanostomus Pallas 1811 (Gobiidae, Pisces) in the Gulf of Gdansk (Baltic Sea). *Journal of Great Lakes Research*, 27(3), 290-299.
Smallegange, I. M., Hidding, B., Eppenga, J. M., & van der Meer, J. (2008). Optimal foraging and risk of claw damage: how flexible are shore crabs in their prey size selectivity?. *Journal of Experimental Marine Biology and Ecology*, 367(2), 157-163.
Vélez-Espino, L. A., Koops, M. A., & Balshine, S. (2010). Invasion dynamics of round goby (*Neogobius melanostomus*) in Hamilton Harbour, Lake Ontario. *Biological Invasions*, 12(11), 3861-3875.
Walsh, M. G., Dittman, D. E., & O'Gorman, R. (2007). Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. *Journal of Great Lakes Research*, 33(1), 83-92.
Wołowicz, M., Sokołowski, A., Bawazir, A. S., & Lasota, R. (2006). Effect of eutrophication on the distribution and ecophysiology of the mussel *Mytilus trossulus* (Bivalvia) in southern Baltic Sea (the Gulf of Gdańsk). *Limnology and Oceanography*, 51(1part2), 580-590.