Master's thesis

Crayfish predation on mussels: an experimental approach

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ABSTRACT:

Noble crayfish *Astacus astacus* that is native to the Finnish lakes and signal crayfish *Pascifastacus leniusculus* that has been introduced to the Finnish lakes were used to test their impact on mussels. The noble crayfish predation was tested on the duck mussel *Anodonta anatina* while the signal crayfish predation was studied on both *A. anatina* and the endangered pearl mussel *Margaritifera margaritifera*. The laboratory experiments were carried in Konnevesi Research Station. Crayfish were placed individually in a 15 L flow-through tank without substrate. Male signal crayfish were the only successful predators of mussels eating 7 out of 42 *Anodonta* mussels while noble crayfish did not manage to open any mussels. Bites around the mussel edges were found in all *A. anatina* and *M. margaritifera* mussels exposed to signal and noble crayfish while none of the control mussel shells exhibited such bites. Most of the bites were located on posterior and anterior ends of the shell, close to the adductor muscles. The signal crayfish that has successfully eaten the mussel had damaged the posterior and anterior parts of shell, close to the adductor muscles. Small mussels were easier pray for crayfish. All successful predators were large male crayfish while small and female crayfish did not manage to open mussels. So, the results indicate that crayfish predation on mussels is possible, and that crayfish can also affect mussels by biting the shell edges.

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TIIVISTELMÄ:

Tässä työssä tutkittiin kokeellisesti rapujen simpukoihin kohdistuvaa predaatiota. Käytetyt rapulajit olivat jokirapu *Astacus astacus* ja amerikkalainen tulokaslaji täplärapu *Pascifastacus leniusculus*. Jokirapupredaatiota tutkittiin pikkujärvisimpukalla *Anodonta anatina* ja täplärapupredaatiota pikkujärvisimpukalla sekä jokihelmisimpukalla *Margaritifera margaritifera* Kokeissa ravut laitettiin yksittäin 15 litran läpivirtausaltaisiin simpukan/simpukoiden kanssa. Täplärapu osoittautui tehokkaammaksi predaattoriksi onnistuen aukaisemaan seitsemän 42:sta *Anodonta*sta. Jokirapu ei saanut avattua yhtään 37:stä *Anodonta*sta. Aukaisemisen ja pehmytosien syömisen lisäksi rapujen havaittiin nakertavan simpukoiden kuorten reunoja yrittäessään saada kuorta auki. Puremajälkiä todettiin kaikissa täpläravun kanssa yhteen laitetuissa *Anodonta*-simpukoissa, mutta ei yhdessäkään kontrollisimpukassa. Puremajälkiä esiintyi eniten kuoren etu- ja takapäässä, lähellä isoja kuorensulkijalihaksia. Puremajälkien määrä ja laajuus oli lähellä kuorensulkijalihaksia korkein juuri niissä tapauksissa, missä rapu oli onnistunut avaamaan simpukan, mikä kertoo mahdollisesti siitä, että kyky kohdistaa purenta näihin kohtiin on ravun kannalta edullista predaatiohetkellä. Predaatiotodennäköisyys kasvoi, kun ravun koko kasvoi suhteessa simpukan kokoon, eli pienet simpukat olivat ravuille helpompi kohde. Kaikki onnistuneet predaatiotapahtumat tulivat isokokoisten koirasrapujen taholta, kun taas pienet ravut tai naarasravut eivät onnistuneet avaaman yhtään simpukkaa. Täplärapujen ei annettu avata yhtään 17:sta jokihelmisimpukasta, mutta myös niillä kaikilla havaittiin puremajälkiä kuoren reunassa. Suoranaisen tappamisen lisäksi ravut voivat siis kiusata ja stressata simpukoita, mukaan lukien uhanalainen jokihelmisimpukka.

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1. INTRODUCTION

The freshwater pearl mussel *Margaritifera margarifera* used to occur at very high densities but has become endangered during the last 100 years (Bauer 1987). They have low motility, specialized habitat selection and a narrow host range. The Margaritiferidae belong to a very ancient family of the mussels that are thought to exist anywhere between the upper Paleozoic and upper Mesozoic periods and they formerly occurred at high densities until human activities has speeded up its declining (Bauer 1998).

Big Unionoida mussels provide important ecological values such as filter feeding were some mussels could filter up to 10 gallons of water per day (Mamun *et al.* 2011 The mussel shell is also used to measure the amount of pollutants found in lakes (Mamun *et al.* 2011). The uninoid musselsare valuable natural water purifiers, and at the same time they are creating good habitat for other aquatic organisms that are valuable for water environment (Spooner and Vaughn, 2006).

The *M. margaritifera* are valuable species both ecologically and economically. The *M. margaritifera* are referred to as 'keystone taxon' and are the main filter feeders in lakes and rivers were a single mussel can filter about 40 L per day improving water quality for animals and humans. Pearl aquaculture is used to remove pollutants from coastal waters while providing commercial value at the same time. However, once a very successful species, it is nowadays globally endangered and it is threatened by commercial exploitations such as pearl fishing and many other human induced factors such as eutrophication, siltation, damming of rivers, industrialization and many other reasons that are beyond our scope (Bauer and Wächtler 1953).

Muskrats have proven to be effective predators to unionoids and can take out thousands of unionoids from local population (Bauer and Wächtler 1953) and in streams and ponds could eliminate entire mussel population in a few years or less (Diggins and Stewart 2000). However, the impact of possible crayfish predation on freshwater mussels is less studied.

The aim of that study is to investigate the possible impact of the invasive signal crayfish species *P. leniusculus* and native noble crayfish *Astacus astacus* on mussels through predation, damaging or simply stressing the mussels. Crayfish have received little attention as a predator on mussels. Even though they have consumed large numbers of zebra mussels in laboratory tanks there has been no experiment that involves effect of crayfish on Unionids (Piesik 1974; MacIsaac 1994; Martin and Corkum 1994).

A comparative experiment took place in Ireland to test the predation effectiveness of crayfish on the invasive species *Dreissena polymorpha* that has caused much disruption both economically and ecologically around the world (Reynolds. & Donohoe 2001). Once zebra mussels were established they have been proven impossible to remove and therefore their removal was of considerable interest. Crayfish fed mostly on the small zebra mussels. However, some large mussels were also predated mainly by large-sized male crayfish. There is a correlation between the size and sex of the crayfish on the predation of the zebra mussels and size of zebra mussels predated. Other laboratory experiment was conducted with signal crayfish to test the potential of signal crayfish to control and regulate the threatening population of *D. polymorpha* (zu Ermagassen & Aldridge 2010). The results were similar to the above experiment which was carried out with zebra mussels (Reynolds & Donohoe 2001). In that experiment any feeding attempt was reported weather they were fully eaten or just damaged, shell chipped or observed manipulation. It is important to note that not only did the

size and sex of crayfish was related to the size of mussels consumed but the rate of consumption too with male crayfish consuming 3-51 mussels over 9 days (Reynolds & Donohoe 2001).

1.1 *Pascifastacus leniusculus* (Signal Crayfish)

The signal crayfish *P. leniusculus* is native species to the north-western North American which were transplanted to western states such as California around the nineteenth century (Abrahamsson and Goldman 1970), to supply food source for introduced fish species in sub-alipine, oligotrophic lakes. Signal crayfish provide economical values to the state of California and supports an important fishery in the delta of Sacramento River (McGriff 1983). Their most frequent size range is between 43 mm to 50 mm. Larger sized signal crayfish ranging from 51 to 72 mm do occur but at much lower frequencies (zu Ermagassen & Aldridge 2010).

It occurs in fast flowing shallow regions and deeper slow-flowing pools inhabits streams and rivers which offers refuges in the form of tree roots or rocks and juvenile stages prefers fast flowing shallow regions. The rivers mentioned above are well supplied with a variety of plant and animals and with leaf detritus which contribute to the food of this omnivorous species. Crayfish are omnivores and utilize wide range of food including attached algae and allochthonous detritus (Ruokonen 2012). As with all crayfish they require water with more than 5 mg/l of dissolved calcium (Holdich & Lowery 1988) *P. leniusculus* were not found on the step sides of Lake Tahoe, most probably because of its narrow littoral zone that makes it unsuitable for the existence of crayfish and on the contrary, they were found to be most abundant at depth 10 to 20 m. Signal crayfish prefers water temperature between 4-20^{o}C. Below 40 m the temperature rarely exceeds 8-10^{o}C and that is probably the limiting factor for signal crayfish distribution. Signal crayfish is a fresh water species that is also tolerant to brackish water and they live in eutrophic, nutrient abundant, and abundance of substrate types ranging from rock to sand (Holdich and Lowery 1988).

The signal crayfish is one of the most widely spread crayfish in Europe (Ruokonen 2012). The success of the signal crayfish in Europe is due to its tolerance of a wide range of habitats from the moderately oligotrophic lakes of Scandinavia which are the near the extremes of tolerance for pH and calcium concentrations until eutrophic flooded gravel lakes and streams that are rich in calcium in England (Holdich and Lowery 1988). They are tolerant of a range of habitats but they also do disturb these habitats. The signal crayfish occupies a wide range of littoral and profundal habitats in large lakes and prefers shallow water stony habitats (Ruokonen 2012).

1.2 *Astacus astacus* (Noble Crayfish)

Present day *A. astacus* is declining sharply in European waters, partially because of invasion of *P. leniusculus* (Westman *et al.* 2000) and others due to human impact through drainage of poisonous chemicals in the fields, meadows, forests surrounding crayfish waters and crayfish plague. They inhibit water bodies such as lakes and rivers that have a littoral zone 10-20 m wide and a space that amounts to 20-50% of total area in where they can find food and shelter They inhabit water with high oxygen content, neutral pH, summer water and water temperature 16-22^{o}C that has high calcium content.

Noble crayfish studies has revealed that a rise in water temperature and an increase in demand oxygen consumption and water temperature of 24^{o}C are critical that at higher temperature *A. astacus* will die due to the increase in oxygen consumption. The *A. astacus*

prefers dark and cold waters and juveniles chose a temperature zone with the range from 17-21^{o}C and a non acidic pH ranging from 5.0 to 10.0 and an optimum pH of 7.0-8.0.

The *A. astacus* is active at night and it spends the rest of its time motionless in a hiding place. Usually burrows dung in a suitable 7-36 cm long, 4-18 m wide substrate and 240 cm high.

In daytime the *A. astacus* usually sit in their burrows with their claws extending slightly outwards. When disturbed it takes a threat posture and spreads the claws upwards which is considered as a manifestation of a defense behavior. The noble crayfish *A. astacus* exhibit thigmotaxis, i.e it takes shelter in narrow hiding places from 3 sides. Territorial behavior of crayfish is connected with search for food and the majority of crayfish (82% of the population) would be found with 25 m of their hiding place when food is abundant. Females and males keep close to their burrows and the search for food using their antennae and antennules that move in circles (Passive search) and then they move towards the food in circular or straight live (Active search).

Noble crayfish display dominance and subordination when searching for food. The large males being usually dominant and it is expressed while occupying hiding-place in the threat 'posture' when nearing another individual and 'peck-order' when smaller specimen does not approach the food but yield it to larger individual.

The noble crayfish *A. astacus* collects and doesn't pursue food and they search food at bottom mainly at night. The *A. astacus* food differs depending on the period of its life. The plant component affirms 85% prevails in the diet of *A. astacus* while other reveal great preponderance of animal matter (98%) food of animal origin increase during reproduction, moulting which uses lots of energy and before moulting period and wintering when crayfish don't feed. Crayfish feed on plant matter and aquatic vegetation during spring due to its abundance and animal component in autumn increases again to ensure energy preservation during wintering. The *A. astacus* food niche and feeding spectrum is wide and they feed on various kinds of food and they adapt easily to new kinds of food and easily assimilate it.

The daily diet of *A. astacus* depends on age, sex and individual, physiological state, abundance and nutritive value of the food, the time of the year and environmental conditions. The daily diet is also affected by water temperature, the optimal temperature for mature specimens is 17-21^{o}C and for juveniles 18-23^{o}C but despite the low temperature their daily diet is higher in spring than in summer. They don't interfere with fish niches and they can breed successfully with fish presence except some predatory and bottom feeding fish such is eels and perches which consume juvenile *A. astacus* at time of reproduction.

The *A. astacus* starts with their pairing in October-November and juveniles are released on June-July of the following year. When females are carrying eggs they don't feed and leave their burrows and they move their abdominal appendages to supply the eggs with freshwater (Holdich and Lowery 1988).

2. BACKGROUND

In our experiment we used both Finnishspecies of crayfish; the native *A. astacus* and the introduced plague-resistant North American *P. leniusculus* (Westman *et al.* 2002) to have a clearance and understanding of the crayfish-mussel interaction and if crayfish does affect the mussel population weather it is through predation or damaging of mussels.

The signal crayfish *P. leniusculus* has been introduced to the Finnish lakes in efforts to halt the devastating crayfish plague *Aphanomyces astaci* that has devasted the most productive populations of native noble crayfish in Finland (Westman, *et al.* 2002). Between the year 1990 and 2006 nearly 2 million of the signal crayfish were introduced to several lakes and rivers in order to compensate for the disappearing native crayfish stock. As a result, the introduced crayfish become an economically valuable species in Finnish inland fisheries (Ruokonen 2012). For example, the crayfish *P. leniusculus* and *A. astacus* in a small in Lake Slickolampi in Finland were monitored from 1970 to 1990 and even though *P. leniusculus* witnessed a population increase. The size estimate in 1988 still showed that *A. astacus* was still the dominant species and therefore it was assumed that the situation in the lake was more or less stable (Westman *et al.* 1995).

Very few studies have been published on the interaction between *P. leniusculus* and *A. astacus* even though *P. leniusculus* has already been introduced to several thousand waters in the atleast 21 European countries (Holdich and Lowery 1988). Most of the introduction of *P. leniusculus* has been in plague-waters or stock specimens were carriers of plague. In Finnish Lake Slickolampi the *P. leniusculus* population grew steadily. Although in 1988 studies did show that *A. astacus* was the dominant species. Shortly afterwards the population of *A. astacus* unexpectedly began to decrease heavily and that of *P. leniusculus* began to increase suggesting that the new introduced species have been replacing the native species. For a species to do better than other it means that the invader must be performing better than the native species. Earlier studies show that the *P .leniusculus* did grow faster and reproduced better in Slickolampi giving the species a clear competitive advantage over *A. astacus* (Westman *et al.* 2002).

3. HYPOTHESIS

The aim of our experiment is to determine if the noble crayfish *A. astacus* and most importantly the introduced signal crayfish *P. leniusculus* can affect mussels through damage or predation. We test that through series of laboratory investigations.

It is easier and less energy consuming for most crayfish including signal crayfish to open the small mussel shell even though there were preferences and more attempts on bigger mussel. Large crayfish males are more likely to predate on more mussels and also bigger mussel shells compared to large female signal crayfish or juvenile signal crayfish (Perry *et al*. 1997). Therefore, we expect that bigger crayfish will feed on mussels that are easier to break their shells. However, zebra mussels are smaller in size compared to that of *A. anatina* and *M. margaritifera* were the *D. polymorpha* size hardly exceeds 18 mm, the *M. margaritifera* shell length are most frequent between 75 to 115 mm (Geist 2005) and since a big sized signal crayfish hardly predated on a large size zebra mussel makes it quite unlikely to predate on a *M. margaritifera* shell. Signal crayfish size can reach 70 and 72 mm. However, large sized crayfish are not very frequent. Most frequent size ranges from 43 mm-50 mm (Figure 2) and therefore, only assuming a frequent encounter of a large sized signal crayfish *P. leniusculu*s with small sized mussel than there might be a possibility of affecting on mussels. In that case even a very small sized *M. margaritifera* will be considered big for signal crayfish when compared to the largest sized zebra mussel. In any case, the likeness of signal crayfish to predate and destroy mussels is higher than that of the noble crayfish *A. astacus* since it is more dominant and bigger in size (Figure 2). The ones that will succeed in opening the muscle

should be able to break segment 4 and 14 (Figure 10) were the adductor muscles are located and especially segment 14 where the posterior adductor muscles are located (Figure 1). However, they are not expected to be able to break the hinge of the mussel.

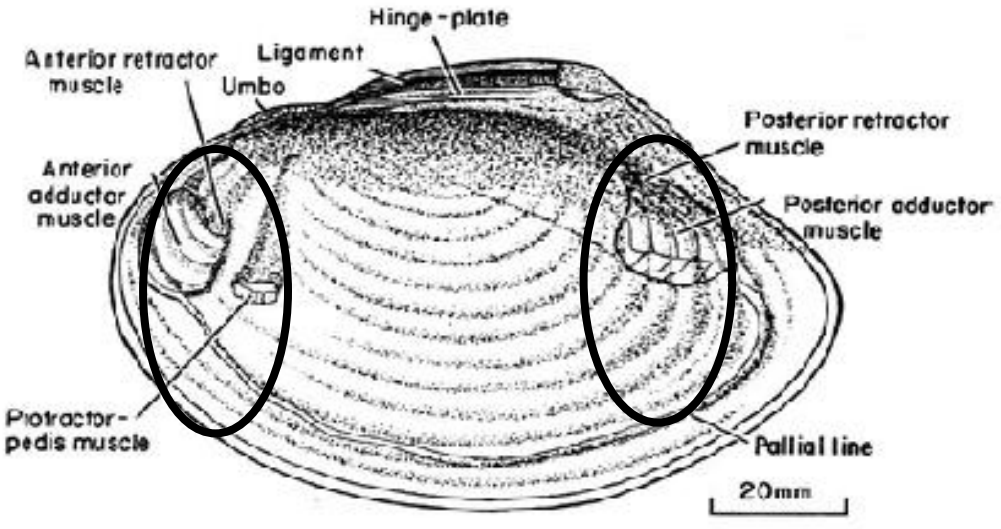

Figure 1. The successful predators of the mussel have usually broken the points of both anterior adductor muscle and the posterior adductor muscle (rounded areas) of the *A. anatina*. The point posterior adductor muscle is a more vital point for the crayfish to successfully open the mussel.Redrawn from Heikki Hämäläinen 'Identification of benthic invertebrates' lecture handouts.

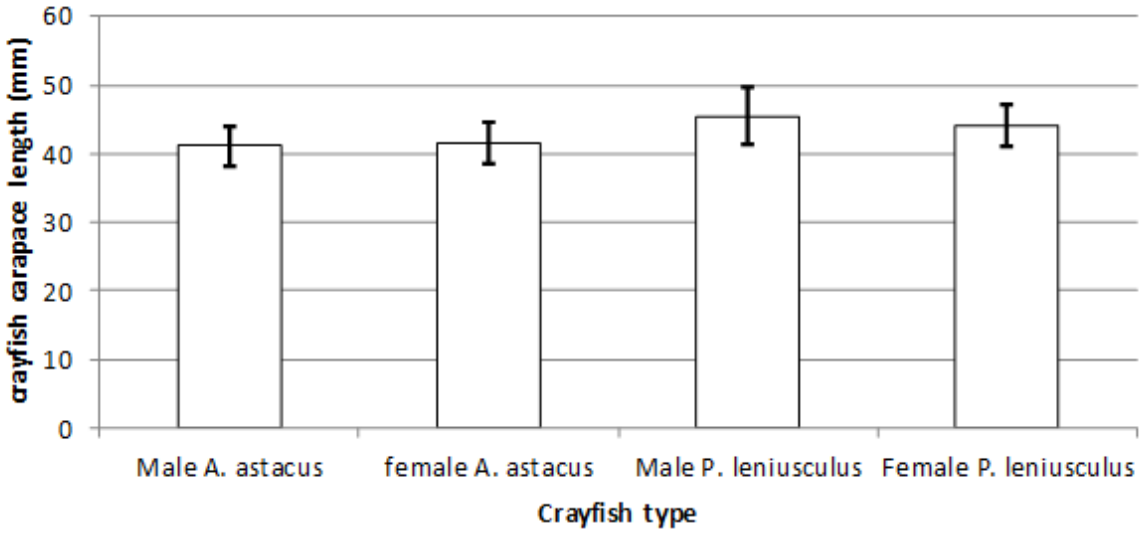

Figure 2. The mean carapace length (± s.d.) of both *P. leniusculus* and *A. astacus* that were used in the experiment. The signal crayfish the *P. leniusculus* are larger on average compared to the *A. astacus*. The size of male *A. astacus* is almost the same sized as the female *A. astacus*. While the male *P. leniusculus* is larger on average to than the female *P. leniusculus*. The female *P. leniusculus* is larger than both male and female *A. astacus*.

4. MATERIALS AND METHODS

4.1. Methods

Based on the experiments that were previously mentioned with crayfish and zebra mussels an experiment with similar principles was conducted between crayfish and different mussel species. The experiment was divided to two different periods. The first took place in spring 2011 to if the noble crayfish *A. astacus* do predate or does damage to the *A. anataina* and the second experiment took place in late summer 2011 in an enclosed laboratory in Konnevesi Research Station to test effect of signal crayfish *P. leniusculus* on both the pearl mussel *M. margaritefera* and the duck mussel *A. anatina*. The first part of the experiment was conducted with 37 boxes. Each box is 15 litres and is labeled. And in each box one individual noble crayfish *A. astacus* was added with an *A. anatina* mussel. The boxes were constantly supplied with water and connected to a water flow outlet for water regulation, aeration and cleansing. The experiment took place in April and lasted for 3 weeks. After transportation from a crayfish farm where the noble crayfish were stored over winter, the crayfish were placed in experimental boxes and fed with potatoes. One day before the experiment, the potatoes were removed and the crayfish is left without food for 24 hours, and then a mussel was added in each box. The noble crayfish behavior was then monitored and actions such as mussel manipulation, predation, and failed attempts were recorded. The age, sex and carapace length of the crayfish were recorded. The carapace length was measured to the tip of the rostrum with vernier calipers and sex was identified by the presence of modified gonopods in males (zu Ermagassen & Aldridge 2010). The mussel length was measured along their longest axis with a vernier caliper. After the first experiment in 2º C water temperature, the water temperature risen during the next two days to achieve 10º C. The increase in water temperature was to try to increase the activity of crayfish. Then the predation experiment procedure was repeated in 18 and 19 degree water temperature. Similarly, the feeding with potato (three days), starving (24 h), predations test (24 h) and gradual temperature increase (two days) rotated until the predation test was performed in the highest temperature, 19º C (Table 1).

In case no predation takes place, the mussels will be opened for the crayfish. The reason of opening the mussel is just to ensure if the crayfish didn't predate on the mussel due to failure opening the shells or because it doesn't feed on the mussel in the first place. Adding potatoes were to determine food preferences for crayfish. The experiment was carried at a 19 ^{o}C water temperature and a rough estimation was used to calculate the amount of mussel flesh consumed.

The experiment was repeated with signal crayfish *P. leniusculus* against both duck mussel *A. anatina* and the pearl mussel *M. margeritifera*. The experiment was carried with 49 boxes, each box is 15 liters. A crayfish was placed in each of the boxes. It is important to cover the boxes with a net since the signal crayfish had the ability to escape from its box. Nineteen crayfish were selected and were given *M. margaritefera* mussels. Two *A. anatina* mussels were added in seventeen of the boxes, one small mussel and other medium sized, and the eight remaining boxes had only one medium sized *A. anatina* since there were no more small-sized *A. anatina* mussels available. The five remaining crayfish were dead therefore, they weren't counted. The crayfish behavior, preferences and manipulation of the crayfish were recorded and its way of manipulation. Some of the small mussels were given to the largest male and female crayfish since hypothetically the large crayfish is more likely to feed on the small mussels. The crayfish were given mussels and left there for a week while

monitoring their behavior. In case there were no attempts or failed attempts on the mussel the crayfish were given maize to prevent starvation and then the maize is removed. The signal crayfish experiment was carried in 16^{o} C water temperature throughout the experiment.

Experiments were conducted with a natural photoperiod, i.e. 8h:14h light:dark for noble crayfish and 19h:5h light:dark for signal crayfish. After the end of each experiment the mussel was divided into 16 segments (Figure 3) and the number of bites in each segment was counted (Table 1).

Table 1. Experimental parameters used to conduct our research

Crayfish type	Number of crayfish used in the experiment	Crayfish sex	Water temperature ^{o}C	Amount of water per box	Amount of light (Natural photoperiod)	Number of *A. Anatina* / box	Number of *M. Margaritifera* / box
Noble crayfish *A. astacus*	37	20M/17F	2-19	15 L	8h:14h light:dark	1/37	0/37
Signal crayfish *P. leniusculus*	49	30M/19F	16	15 L	19h:5h light:dark	1/7, 2/19	1/18

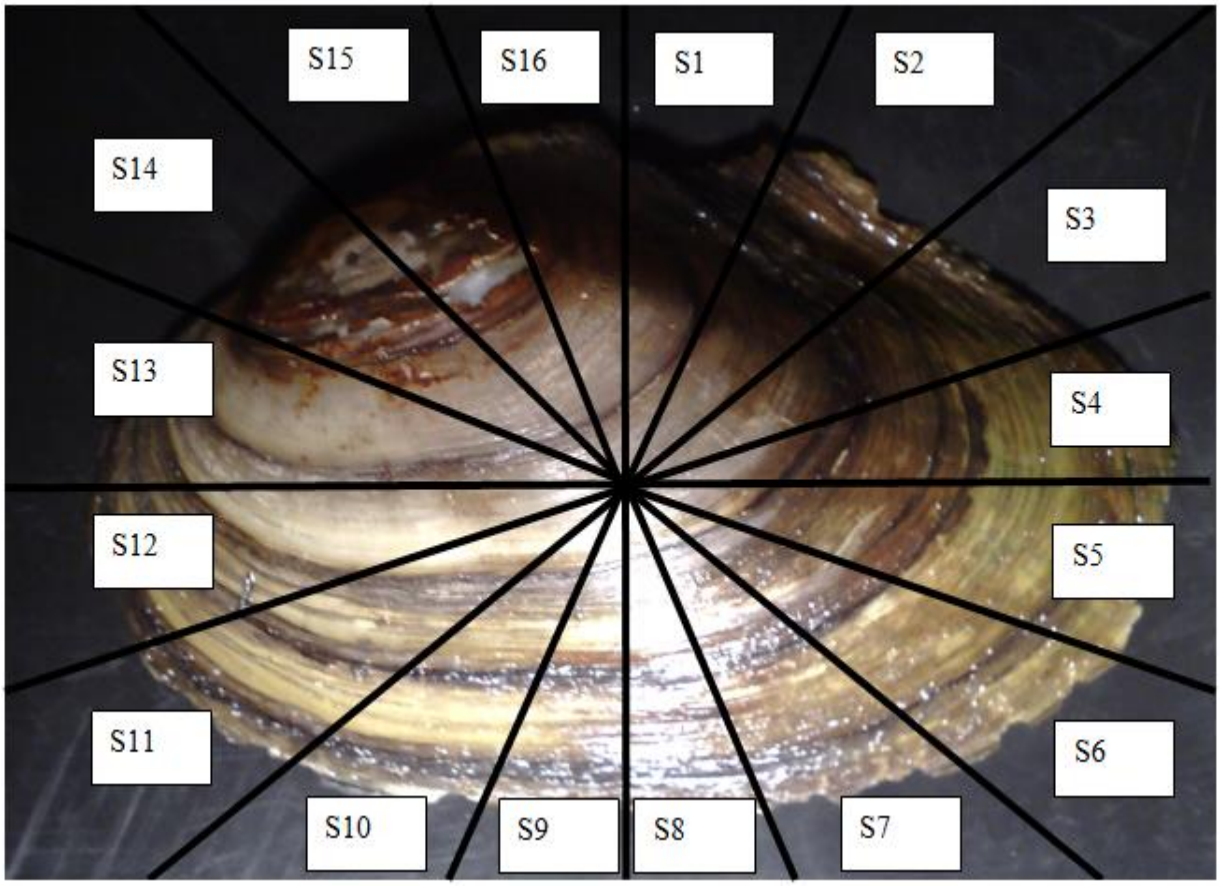

Figure 3. The mussels were divided into 16 sectors. The number of bites is counted in each sector of the mussel to indicate where the crayfish usually attacks.

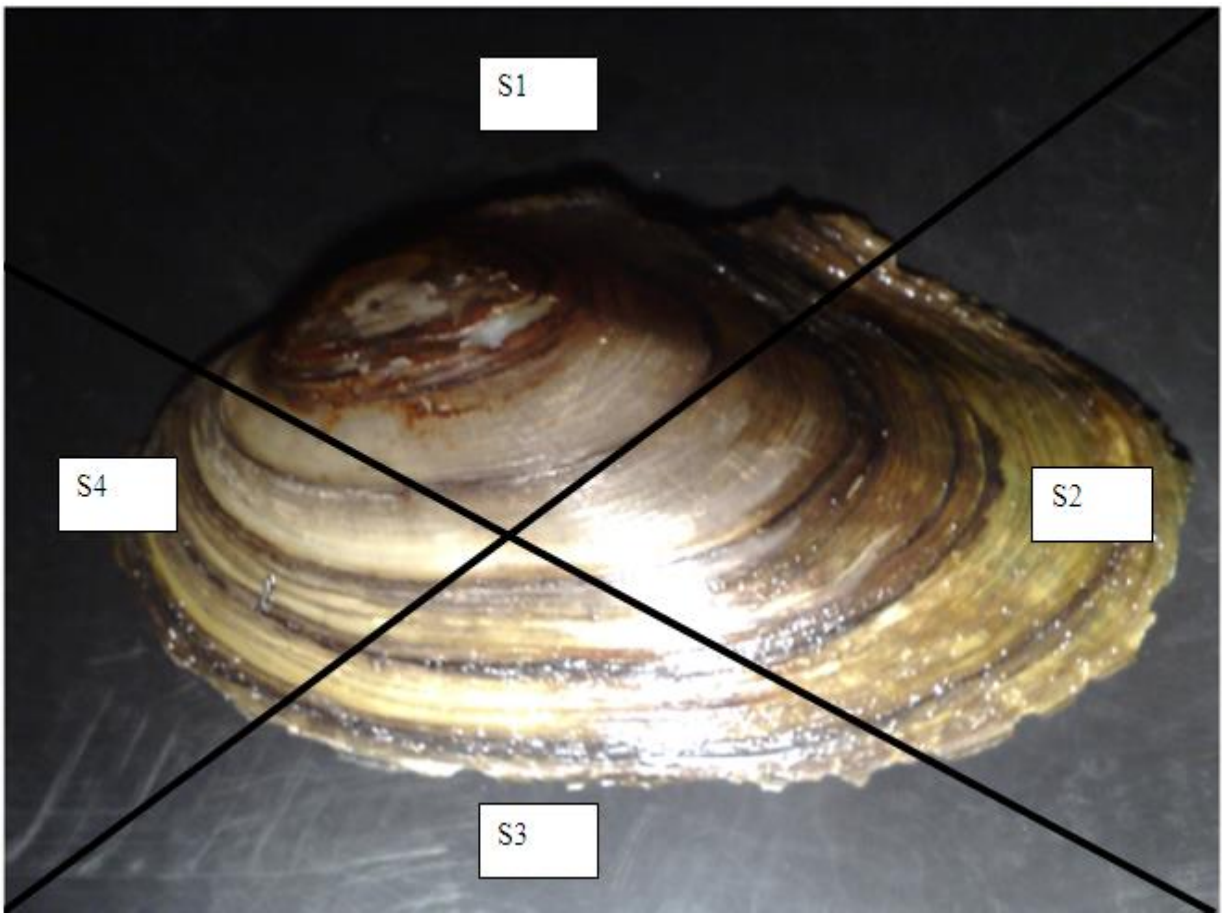

Figure 4. Since it was not possible to use ANOVA for analysis of individual sectors because of many zero bites (Friedman test). Sectors 2, 3, 4, 5 and 6 were combined and the average was counted representing sector 1 which is close to the posterior adductor muscle, ventral. Sector 7, 8, 9, 10 and 11 were combined and an average of them was referred to as sector 2. They are the bottom of the mussel far from the adductor muscles. Sector 12, 13 and 14 were combined on average to form sector 3 which is close to the anterior adductor muscle. Sector 1, 15 and 16 were combined to form the hinge.

4.2 Statistical methods for analysis

The analysis of covariance ANCOVA and analysis of variance ANOVA were applied as the data fulfilled the assumptions of variance analysis. First, ANCOVA was used to study the size-dependence of the signal crayfish predation by having the mussel size as the response variable, predation status (predated, non-predated) as a fixed factor and male crayfish carapace length as a covariate (females were excluded since no female crayfish has predated on the mussels). Because the effect of covariate was not significant ($F1.9 = 0.170$, $p = 0.692$) only predation status was included in the final analysis. The One-Way ANOVA was used also to analyze the size difference between male and female crayfish of both crayfish species. The ANOVA was used to test the difference in the size between the mussels that were successfully predated by signal crayfish and those that were not predated by the signal crayfish to analyze if the mussel size is a factor indicating whether or not it is likely to be eaten by crayfish. With the crayfish that were given 2 mussels, one small and the other bigger, which mussel was easier for the crayfish to predate on was analyzed using the Paired Samples T-test. ANOVA was also used to take size ratio (crayfish carapace length: mussel length) as the dependent

variable and the sex of crayfish as the factor to test the difference between the mussel size that was given to male and female crayfish. In addition, the ANOVA was used with crayfish carapace length as the response variable and predation statues (predated, not predated) as the factor (among the male crayfish) to analyze the effect of crayfish size on predation efficacy. In order to study the relation between the size of the crayfish and the mussel that is allocated to it, Pearson correlation analysis was used. In cases when two mussels were given for a crayfish, the statistical analyses were first performed by taking only the smaller mussel into account, and then the same procedure was repeated with the bigger mussel to find out if the results changed.

Both noble and signal crayfish impact was measured with the number of bites, or "biting score", representing the damage on of the 16 sectors of the mussel. Biting on the edge of mussel shell was scored manually. Small bite was scored as one point, the largest bites covered much bigger area, scoring up to 16 points. In the presence of two mussels with a crayfish only the small one was taken into account when counting the biting scores for individual sectors. However, it was not possible to use ANOVA for analysis of individual sectors because of many zero bites Sectors 2, 3, 4, 5 and 6 were combined and the average was counted representing sector 1 which is close to the posterior adductor muscle, ventral side. Sector 7, 8, 9, 10 and 11 were combined and an average of them was referred to as sector 2. They are the bottom of the mussel far from the adductor muscles. Sector 12, 13 and 14 were combined on average to form sector 3 which is close to the anterior adductor muscle. Sector 1, 15 and 16 were combined to form the hinge (Figure 4). To test if signal and noble crayfish have been biting the same sites a new variable was calculated by calculating the proportional biting frequency for each of the four main sectors. For instance sector 1 was calculated by calculating the percentage of number of bites in each sector to total number of bites on the mussel. The proportion was used as the response variable in MANOVA (Multivariate Analysis of Variance). When comparing the number of bites and their locations around the *A. anatina* and *M. margaritifera* mussels in the signal and noble crayfish, either MANOVA or ANOVA were used.

5. RESULTS

Both noble and signal crayfish starts moving towards the mussel within three to ten minutes and then they attack it by using the first and second pair of walking legs to orient the sharp edges of the shell so that it could chew it with the mandibles. Most mussel shells that were present with crayfish were chewed from the sides, explaining the high numbers eaten in segment 2 and 14 (Figure 10), in an attempt to facilitate opening the shell. The biting shows obvious attempt to open the mussel shells. Unlike the mussel shells of the control experiment which didn't have any clear sign of chewing on the edges.

At a 10^{o}C water temperature the noble crayfish were very idle and were mostly found lying in the corner of the experimental boxes thought, at times they were just moving slowly around the box. An interesting observation taking place is that only at 10^{o}C water temperature the crayfish was found to be predating on the potato using their chelae and signs of cuts on potato were found. On higher temperatures the crayfish were predating on the potato without any use of their chelae and only by chewing on the edges of the potato. At 10^{o}C water temperature one mussel was found partially opened and there has been a sign of content removal and a clear aggressive chewing of the sides of the mussels. However, it is not directly

witnessed how the mussel shells got opened and the crayfish wasn't found by its side. Besides, the shell wasn't fully opened and therefore, it wasn't counted among eaten mussels. The noble crayfish was a male with a carapace length of 41 mm and the mussel size was 52 mm which was quite large compared to the crayfish which is unexpected since the mussel is still considered to be relatively large compared to the crayfish itself defying most experiments carried on crayfish-mussel predation. It is still possible that the noble crayfish has successfully opened the mussel shell since the crayfish size was relatively big compared to other crayfish. However, no other successful attempts were observed at 10^{o}C even at higher temperatures despite the fact that the same noble crayfish was given a mussel of an almost exact same size and it has failed to open it, failed to damage it neither did it attempt to eat it and therefore we considered the mussel uneaten. In addition, same size and larger sized noble crayfish were given even smaller mussel shells and still they have failed to open or damage the shell. The only action that was recorded taking place at higher temperatures was the fact that the noble crayfish did move around inside the experimental boxes a little bit more.

Since no important behavioral observation was noticed at any water temperature a comparative experiment was carried out with noble crayfish to test preferences between mussels and potatoes and therefore mussel and potatoes were used in each second box with the mussel in order to make preferences observation. Once the mussel shell was opened the crayfish did seek it immediately and in a very short period of time a huge number of the mussel flesh was eaten. The percentage was just a rough estimation of how much of the mussel flesh was consumed. As shown in the graph, it is obvious that within 12 hours 23 crayfish have consumed most of the mussel content (Table 5) and 10 did fully consume the mussel and within 4 days 35 crayfish predated on most of mussel flesh and 30 did fully consume the mussel (Table 6). It is also worth noting that the mussel's flesh was fully consumed unlike the potatoes that were predated by taking several bites from the potato edge and no sign of strong consumption was observed. Some of the mussels were fully consumed and others have left only the anterior and posterior muscle of the mussel unconsumed (Figure 1). When the potato was placed few of the crayfish did go initially for the potato and shifted later towards the mussel. However, it was observed that most have preferred feeding on the mussel than feeding on the potato. It is important to note that mussels were not successfully predated. They all have exhibited bites on their sides. In the meanwhile, other mussels in tanks that did not include crayfish and served as a control didn't exhibit any of those bites.

As for the signal crayfish the results among the 49 signal crayfish, 7 *A. anatina* mussels were opened and eaten fully (Table 4). On the other hand, there wasn't any success predating a *M. margaritefera* except the *M. margaritefera* sides were slightly chewed (Figure 14). Two of the signal crayfish did succeed to predate on both mussels shells while the others 3 predated only on the small mussel while leaving the bigger mussel (Figure 5). The two that have predated on both mussels ate the smaller ones first and it was confirmed by the T-test that indicated that all signal crayfish preferred the smaller mussel individual ($t = -4.490$, $df = 2$, $p = 0.046$). The mean size (length ± s.e) of predated mussels and non-predated mussels was 35.5 ± 7.2 mm and 53.0 ± 1.0 mm respectively.

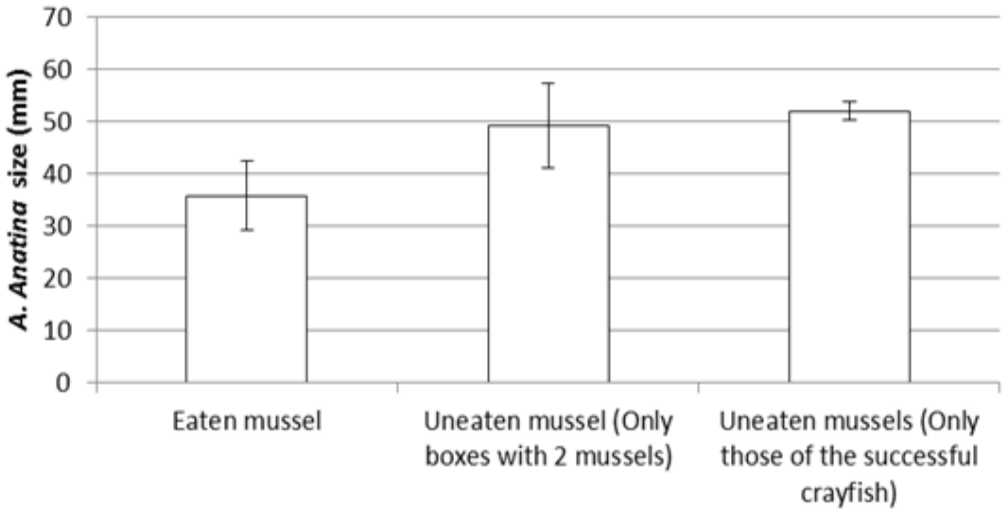

Figure 5. Comparison of mean size of *A. anatina* mussels (± s.d) sizes between those that were eaten by the *P .leniusculus*, those that were unconsumed by the crayfish that has successfully eaten the mussel and all other *A. anatina* (Only boxes with 2 mussels were taken into account). The average size of eaten mussel is clearly smaller that its peers.

The difference between the carapace length of those who predated on the mussels and those which didn't were not statistically significant (One-Way ANOVA, $F_{1,9}$ = 1.390, p = 0.272) where the average length of those who predated on mussels was 49.0 ± 1.8 mm and those which didn't predate were 46.2 ± 1.6mm.

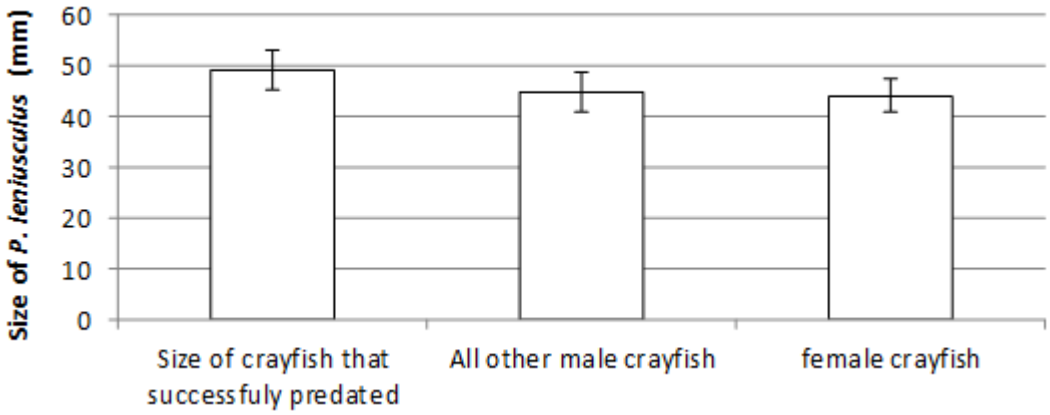

Figure 6. Mean size (± s.d) of the *P. leniusculus* that had successfully predated on the mussels and all other male and female crayfish of both species. The *P. leniusculus* that have predated on small mussels larger sized on average compared to its peers.

The results of the ANOVA have also indicated that the size difference between the predated small mussel and the larger mussel that were placed with the crayfish that has successfully predated on the mussel, since all the successful crayfish had 2 mussels in their box. The results were statistically significant (F1,9 = 8.183, p = 0.021) and the mean size (length ± s.e.) of the predated (n = 5) and non-predated mussels (n = 5) was 32.4 ± 2.5 mm and 42.4 ± 2.5 mm, respectively (Figure 5). That means that the length of the predated mussels was on average 10 mm smaller compared to the larger mussel that was given to the crayfish

that has successfully predated on the mussel. When the crayfish-mussel size ratio was calculated, the crayfish carapace length: mussel length was 1.6 on average while when we compared the length of the crayfish: length of the non-predated mussel the ratio varied from 1.25 to 2.04 while the ratio of the crayfish length to predated large mussels it was 0.87 to 1.21.

All successful attempts were male signal crayfish while noble crayfish and the female signal crayfish didn't succeed in opening any mussel. Therefore, we tested the length significance of male and female signal crayfish using the One-Way ANOVA. The minimum/maximum lengths for males and females were 41/54 mm and 39/50mm, respectively. The result was that the carapace length wasn't statistically significant (One-Way ANOVA, $F_{1.21} = 4.296$, $p = 0.051$) and though on average the male carapace length was slightly larger than that of the female crayfish 47.6 ± 1.2 mm while the female average length was 44.4 ± 1.0 mm. Since none of the female crayfish predated on the mussels therefore, studying the length of predated and un-predated mussels can't be studied in the case of female crayfish and the ANOVA results indicated that the size differences between males and females were not statistically significant even though that the males were relatively a bit larger (mean ± s.e.) crayfish carapace length: mussel length ratio (0.962 ± 0.059) than females (0.885 ± 0.054). When the ANOVA was used again this time to distinguish between the mean size of mussel allocated to male and female signal crayfish the results were not statistically significant ($F1,21 = 0.448$, $p = 0.511$). The mean size (length ± s.e) of the mussels given to male ($n = 10$) and female ($n = 5$) crayfish was 50.0 ± 2.7 mm and 52.4 ± 2.4 mm, respectively.

Table 2. Sex-differences in predation. In cases when there were two mussels in the box, only the smaller mussels were included in the data. Numbers and proportions (%) of male and female signal crayfish that predated on *Anodonta anatina* mussels are calculated.

Sex	N of individuals	N of those which predated	Proportion of those which predated
Male	10	5	50.0 %
Female	12	0	0 %
Tot.	22	5	22.7

Half of the male signal crayfish predated on the mussels, whereas no female signal crayfish predated on the mussels (Table 2) and the difference was statistically significant for the male crayfish according to (Fisher's Exact Test, $p = 0.01$) which means that males can affect small mussel. The same experiment was repeated with the larger mussels. Two out of 10 male signal crayfish predated on mussels representing 20% success in males while 0% in females (Table 3). The difference was not statistically significant (Fisher's Exact Test, $p = 0.195$). Therefore, when the larger mussels were taken into account there was no significance between males and females as predators on mussels.

Table 3. Sex-differences in predation. In cases when there were two mussels in the box, only the bigger mussels were included in the data. Numbers and proportions (%) of male and female signal crayfish that predated on *A.anatina* mussels were calculated.

Sex	N of individuals	N of those which predated	Proportion of those which predated
Male	10	2	20.0 %
Female	12	0	0 %
Tot.	22	5	9.1

Since no female crayfish predated on the mussels (Table 4), than the length of predated vs. non-predated mussels cannot be analyzed for female crayfish. However, the ratio of carapace length: mussel length can be compared to both males and females. The males carapace length: mussel length ratio was larger (1.33 ± 0.09) compared to the females (0.912 ± 0.084) and therefore the ratio difference was statistically significant (ANOVA, $F_{1,21} = 11.327$, $p = 0.003$). It is worth noting that the comparison between males and females as predators might have some bias since the results of ANOVA has indicated that the means size of mussels allocated to male and female was statistically significantly different ($F_{1,21} = 13.106$, $p = 0.002$). The mean size of the mussel (length ± s.e) of the mussel given to male (n = 10) and female (n = 5) crayfish was 37.4 ± 2.7 mm and 50.8 ± 2.5 mm, respectively. So, when only the smaller mussels were included the size of mussels given to male crayfish was on average 13.4 mm smaller than those given to female crayfish. When testing the relationship between crayfish length and mussel size there was a significant negative correlation (Spearman r = -0.439, p = 0.041, n = 22). In other words, smaller mussels were allocated to larger crayfish (Fig. 7).

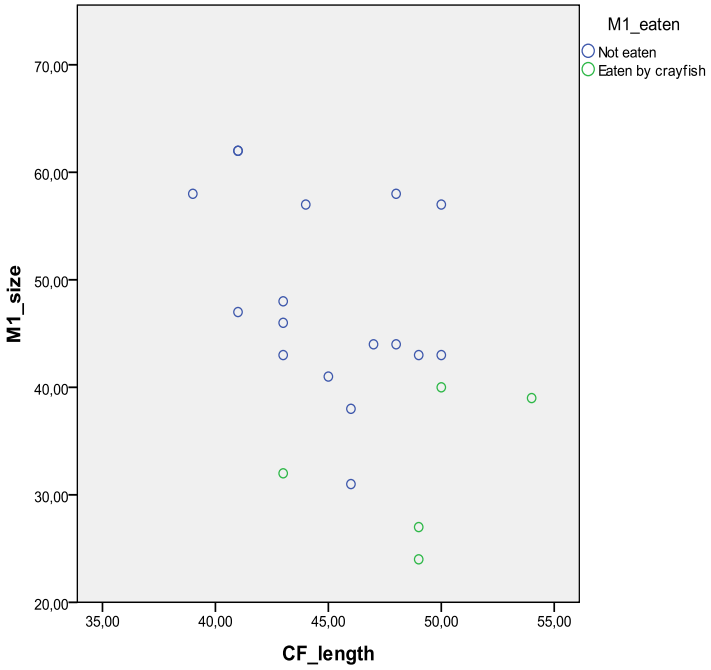

Figure 7. The relationship between signal crayfish size (CF_length) and mussel size (M1_size) when only the smaller mussels were taken into account in those ten crayfish cases where two mussels were given to crayfish. The figure indicates that the smaller mussels were intentionally given to the larger crayfish.

When the same procedure was used to study the relation between the crayfish and the large mussel size there was no significant correlation between crayfish size and mussel size (Spearman r = -0.007, p = 0.974, n = 22) (Figure 8).

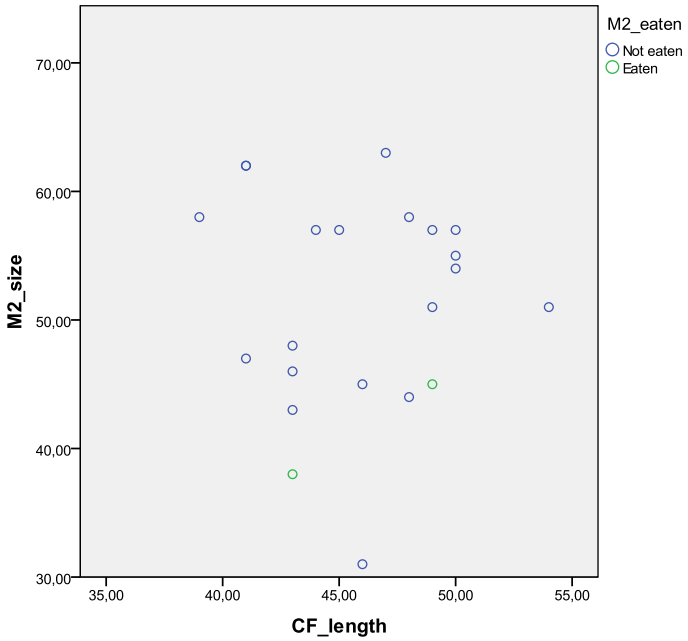

Figure 8. Relationship between signal crayfish size (CF_length) and mussel size (M2_size) when only the larger mussels were taken into account in those ten crayfish cases where two mussels were given to crayfish. Still some of the smaller ones were given to the larger crayfish.

Surprisingly among the only 2 successful signal crayfish, one had the smallest length 43 mm while the rest were 49 mm and over. The way they opened the mussels was by chewing the sides and breaking the fragile side lines with their chelaes and gain access to the mussel's flesh, which explains the high bites in sectors 4 and 14 (Figure 10). The largest eaten mussel was 45 mm length and it was eaten by a 49 mm crayfish male which is unusual since most mussels eaten during or experiments were usually slightly more than 30 mm or less. When comparing the size of the predated mussels (n = 7) to those of the non-predated mussels (n = 25) using the One-Way ANOVA it indicates that the difference in the size of the mussel was highly significant ($F_{1,31}$ = 18.819, $p < 0.001$) and that the predated mussel size that lies in the length of 35.0 ± 3.1 mm happens to be smaller than those non-predated mussels which lies in the length of 50.2 ± 1.6 (Table 2) and (Table 3). When testing the impact of both signal and noble crayfish on mussel sectors it was found that signal crayfish had more impact on sector 1, 2, 3, 4, 5, 6, 12, 13, 14, 15 and 16. While, there was more attempts on sector 7, 8, 9, 10 and 11 from noble crayfish. Once the mussel sectors were combined to only 1, 2, 3 and 4 (Figure 4), it was indicated using the Friedman test for signal crayfish that the bites were not randomly distributed around the shells (Friendman Test, n = 22, χ^2 = 22.472, df = 3, $p < 0.001$). With the Wilcoxon Signed Rank test used to continue testing differences between paired combination of sectors it was found that there were more bites in sector 1 than in sector 2 (Wilcoxon Signed Rank Test, exact $p < 0.001$). When sector 1 and sector 3 were compared there was almost no significant difference, even though there is a bit more bites on sector 1 than sector 3 (Wilcoxon Signed Rank Test, exact $p < 0.058$). There were more bites in sector 1 compared to that of sector 4 (Wilcoxon Signed Rank Test, exact $p < 0.001$). There was no significance difference between sector 2 and 3 (Wlicoxon Signed Tank Test, exact 0.126). There was found no significance differences either between sector 2 and sector 4 (Wilcoxon Signed Rank Test,

exact $p < 0.701$). However, sector 3 had more bites than sector 4 (Wilcoxon Signed Rank Test, exact $p = 0.008$).

The Friendman test, results indicate that bites are not randomly distributed around the shell (Friedman Test, $n = 31$, $\chi^2 = 47.004$, $df = 3$, $p < 0.001$). We continue using the Wilcoxon Signed Rank Test to compare the impact of the noble crayfish on different sectors of the mussel. The noble crayfish did have more bites in sector 1 than in sector 2 (Wilcoxon Signed Rank Test, exact $p = 0.006$). There were also more bites in sector 1 than in sector 3 (Wilcoxon Signed Tank Test, exact $p < 0.016$), more bites in sector 1 than in sector 4 (Wilcoxon Signed Rank Test, exact $p < 0.001$), more bites in sector 2 than sector 4 (Wilcoxon Signed Rank Test, exact $p < 0.01$) and more bites in sector 3 than in sector 4 (Wilcoxon Signed Rank Test, exact $p < 0.001$). However, there was found no significance between sector 2 and sector 3 (Wilcoxon Signed Rank Test, exact $p < 0.615$). Interestingly, there was no statistical significance between signal and noble crayfish in the total number of bites on the shell of *A . anatina* (Mann-Withney U-test, $Z = -1.147$, $p = 0.251$). The multivariate test of MANOVA indicates that the signal and noble crayfish differ from each other with respect to biting sites (Wilk's Lambda = 0.810, $F_{3,49} = 3.833$, $p < 0.015$). Signal crayfish has shown statistical significance proportion of bites on sector 1 when compared to noble crayfish ($F_{1,51} = 4.531$, $p = 0.038$) and a significance higher proportion of bites on sector 2 in noble crayfish than in signal crayfish ($F_{1,51} = 5.207$, $p = 0.027$). However, there were no significant differences between noble and signal crayfish with respect to proportional bites on sector 3 and 4. When testing the impact of signal crayfish on both *A. anatina* and *M. margaritifera*, it was found that the *A. anatina* had more bites in sectors 1, 2, 3, 4, 5, 6, 13, 14, 15 and sector (Sector 1 and Sector 4). On the contrary, the signal crayfish had attacked sector 7, 8, 9, 10, 12 (Sector 2 and 3) in the *M. margaritifera*. The *M. margaritifera* had an exceptionally high bite frequency on sector 12 while the *A. anatina* had an exceptionally high frequency on sector 4. In other words the signal crayfish had attacked more sector 1 (posterior end) in the *A. anatina* mussel while on the other hand it had preferred to attack sector 3 (anterior end) in the *M. margaritifera*. So, the question is if there is statistical significance between both *A. Anatina* and *M. margaritifera*. Using logarithm-transformed total number of bites as a response variable (Log_{10}(tot n of bites + 1)) to compare the total number of bites on both *A. anatina* and *M. margaritifera* mussel it was found that there was no difference between *A. anatina* and *M. margaritifera* in total number of bites (One-way Anova, $F_{1,37} = 0.203$, $p = 0.655$). Higher proportions of bites in sector 1 in *A. anodonta* than in *M. margaritifera* (Mann-Withney U-test, $Z = -4.264$, $p < 0.001$). The *M. margaritifera* had higher proportions of bites in sector 2 compared to the *A. anodonta* (One-way Anova, $F_{1,37} = 11.365$, $p = 0.002$). The higher proportion of bites in sector 3 in *M. margaritifera* than in *A. anodonta* (One-way Anova, $F_{1,37} = 15.546$, $p < 0.001$). In sector 4 there were higher proportion of bites in *A. anodonta* than in *M. margaritifera* (Mann-Withney U-test, $Z = -4.320$, $p < 0.001$).

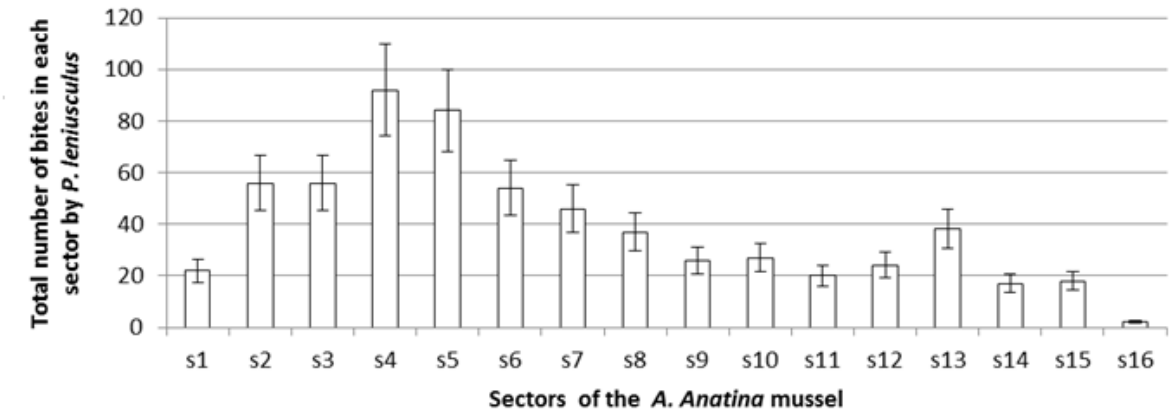

Figure 9. (Mean ± s.d) of number of bites in each sector of the *A. anatina* mussel by the *P. leniusculus.* Total bites were counted by counting the number of bites by each individual crayfish in each individual sector and then summing it all up. The graph indicates where the *P. leniusculus* were dominantly attacking the small mussels. The graph includes all the *P. leniusculus.*

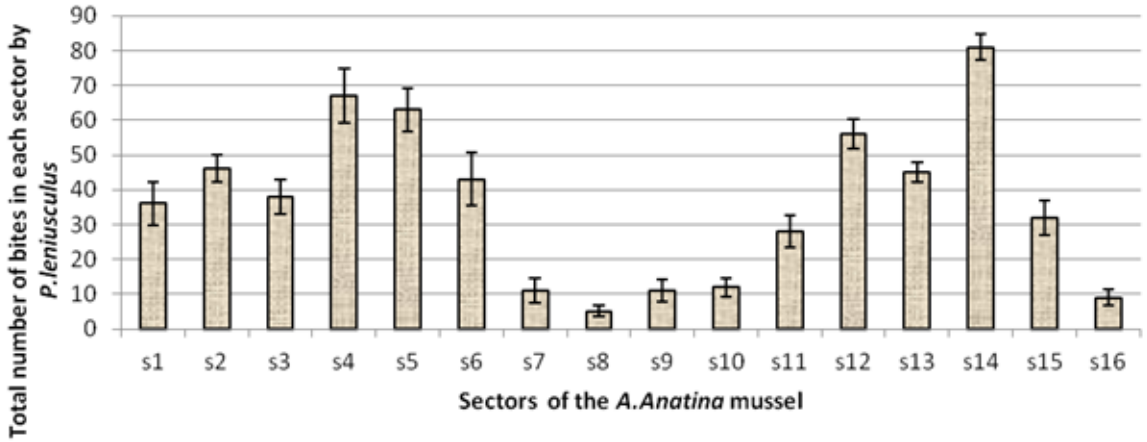

Figure 10. Average number of bites (± s.d) in each sector of the *A. anatina* mussel by the *P. leniusculus.* Total bites were counted by counting the number of bites by each individual crayfish in each individual sector and then summing it all up. The graph includes only crayfish that have successfully predated on *A. anatina* mussels. The graph indicates that the successful crayfish has been attacking mainly sector 4 and sector 14. Due to their fragility these sectors were strongly fractured.

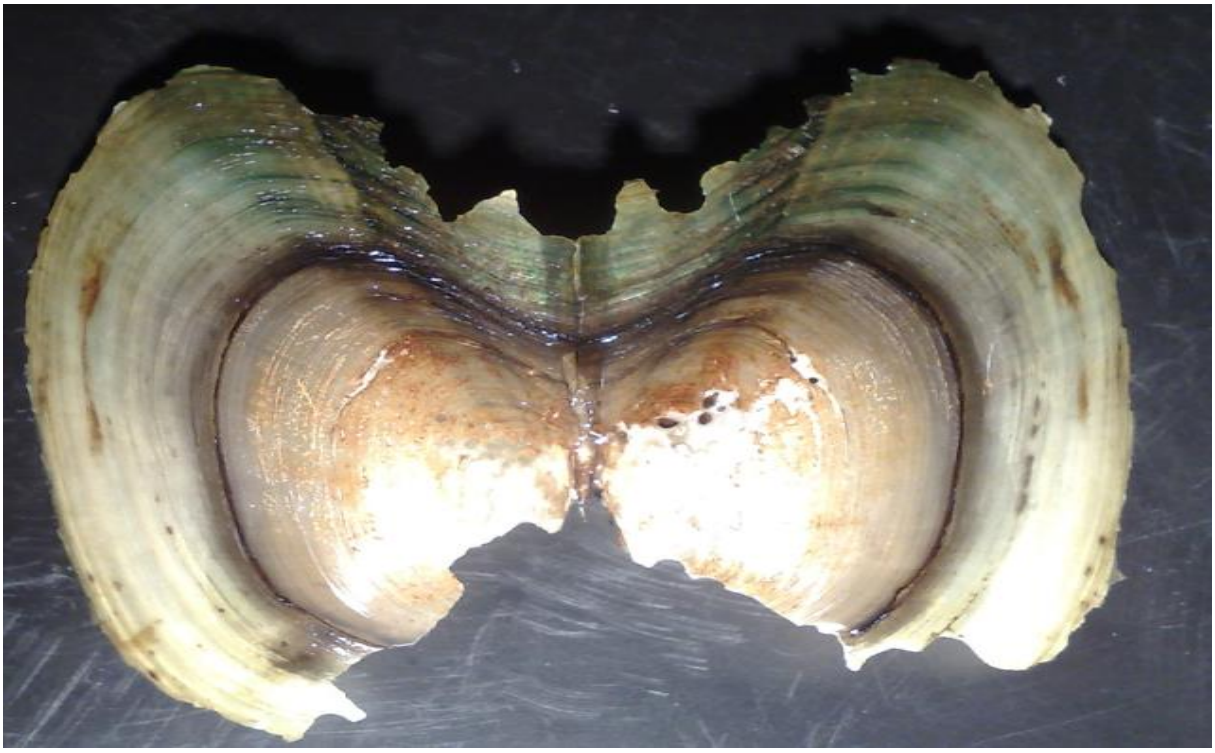

Figure 11. An *A. anatina* mussel over 32 mm eaten by a *P. lenisculus* with a carapace length equal to 43 mm. Sides totally chewed and their fragile side broken.

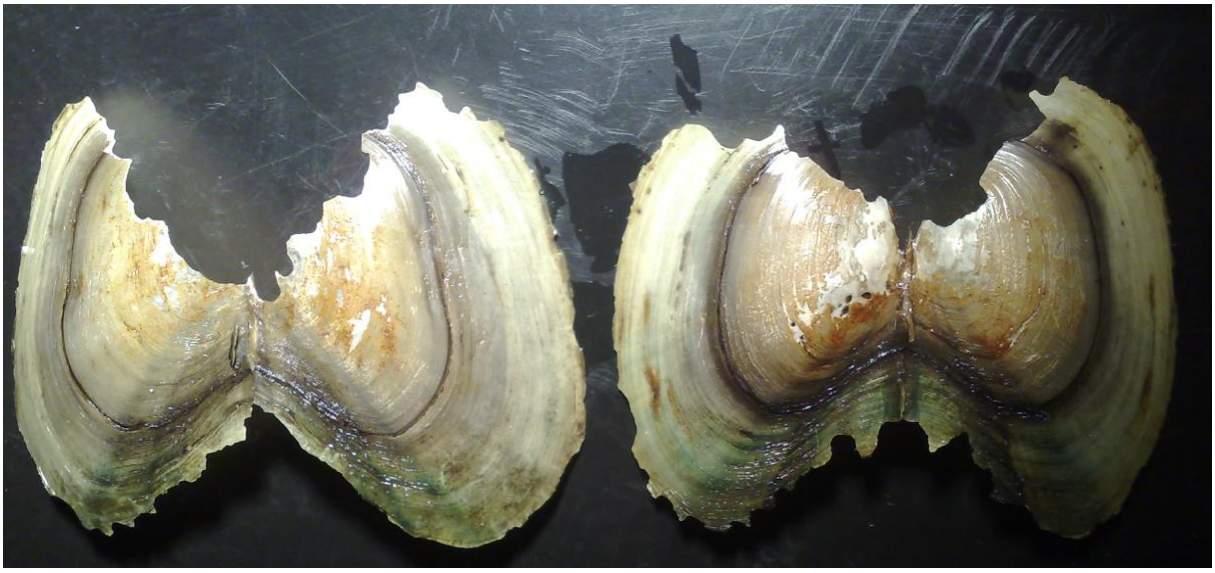

Figure 12. The two *A. anatina* that were eaten by a small sized *P. leniusculus* individual with a 43 mm carapace length, which was the smallest crayfish to feed on mussels The first mussel size was slightly over 32 mm (Left) and the other slightly over 38 mm (Right).

Figure 13. A damaged *A. Anatina* that was chewed mainly from the sides and at the side it was cut and its flesh eaten. The *A.Anatina* was eaten by a 49 mm *P.leniusculus* and the mussel is 45 mm long which is considered to be a large mussel for the average *P.leniusculus*.

Figure 14. An *A. anatina* like the majority or other Anadonta mussels that was not eaten but were chewed from their sides the same way the potatoes were chewed from the sides. That is a 58 mm *A. Anadonta* which is considered to be a large size mussel and was chewed by a 39 mm *P. leniusculus* which is considered to be small size.

Figure 15. An unsuccessful attempt on *M. margeritifera* musel. However, there is a small sign of *P. leniusculus* crayfish bites around the mussel shell.

Table 4. General statistics on the number of trials and successful predation attempts on *A. Anatina* and *M. margaritifera* by both *A. astacus* and *P.leniusculus*.

Description	Number of crayfish	Number of occurences
Number of male *P. leniusculus* that has predated on the *A .anatina* mussel	14	5
Number of *A .astacus* that has successfully predated on *A. Anatina* mussel	16	0
Female crayfish of both species that has predated on mussels	39	0
Total number of male crayfish that successfully predated on mussels	5	5
Successful attempt on *M. margaritifera* mussels	19	0

Table 5. The number of *A. astacus* that have predated 90% of the *A. anatina* mussel content, less than 90% of the *A. anatina* mussel content and the entire mussel content in 12 hours period.

Percentage of mussel flesh consumed by *Astacus astacus*	Number of *Astacus astacus* that has fed on the mussel
Less than 90% of the mussel flesh consumed	15
More than 90% of the mussel flesh consumed	12
All flesh is consumed	10
Total	37

Table 6. The number of *A.astacus* that have predated 90%, less than 90% and the entire mussel content in 4 days period.

Percentage of mussel flesh consumed by *Astacus astacus*	Number of *Astacus astacus* that has fed on the mussel
Less than 90% of the mussel flesh consumed	4
More than 90% of the mussel flesh consumed	3
All flesh is consumed	30
Total	37

6. DISCUSSION

The noble crayfish attacked the *A. anatina* mussel in the present study a similar manner to that of signal crayfish on zebra mussels zu Ermagassen & Aldridge 2010). It seems that the strength of the mussel shell forces the crayfish to slowly chew the sides so that in the long-term it will break the mussel shell and get access to the mussel flesh. In most cases, the noble crayfish would prefer the mussel to the potato and consuming most of the mussel content in 12 hours (Table 5) and nearly the entire content in 5 days period (Table 6). The reason why crayfish would prefers mussels to potatoes are not known but they will definitely choose food that is easier to access. In the end, the experiment proves that the effects of noble crayfish on mussels is extremely limited if at all.

According to (Westman, *et al.* 2002) study, the invasive signal crayfish was able to take over the noble crayfish. Therefore, hypothetically the signal crayfish was more likely to be a more effective predator and they were far more effective than their noble crayfish counterparts and had more significant results. The ability of the signal crayfish to escape from their boxes is sufficient to prove that they are stronger and more aggressive compared to noble crayfish. The large-sized male crayfish were able to destroy and predate on small sized mussel shells just as was hypothetically predicted while leaving the medium sized unharmed or slightly damaged. In case of small predated mussel, the crayfish carapace length: mussel length ratio varied from 1.25 to 2.04, indicating that the crayfish carapace length should be around 1.25 times longer than the mussel length in order to achieve a successful predation. One of the small signal crayfish did succeed predating on one of the larger mussels that was even larger than the average mussel length and that was hypothetically unlikely to be eaten by a small crayfish (43 mm carapace length). It is not surprising that all attempts on the pearl mussel ended up in failure, even though there were signs of chewing on the sides of the mussels and that is because the pearl mussel shell is quite strong and also because the pearl mussel average

size is quite huge. compared to other mussels. The smallest pearl mussel was 55 mm and the largest was 101 mm. According to (zu Ermagassen & Aldridge 2010) crayfish aren't usually able to break and feed on mussels that are above 30 mm. The largest mussel eaten in our experiment was 45 mm. Thence, pearl mussel is just too large for crayfish to break. Besides, pearl mussels will close their shells and remove their exposed feet back into the shell immediately after detecting any threat. The signal crayfish was able to open mussel shells that were around 20 to 30 mm in length. As shown in the graph above (Figure 5) most of the pearl mussel population length ranges from 65 to 115 mm which are too large for crayfish to consume. The biggest recorded mussel that was predated by a signal crayfish is 45 mm. Sometimes it took the crayfish a week or 2 and sometimes 3 weeks to open a mussel shell that was same box. It is therefore, not practical to claim that the crayfish in its normal environment will wait for weeks to open a mussel shell. Therefore, it could be concluded from that experiment that the invasive male signal crayfish do have significance on small *A. anatina* mussel since half of the males that were given small *A. anatina* have successfully predated on the mussels (Table 2). However, there is no proof that the crayfish will be willing to attempt to break a mussel for weeks and try to open a mussel shell especially, if they have an easy access to other food resources unless they are in an environment full of mussels with extremely limited food source options. For instance, the signal crayfish did predate first on the mollusks and maize for nutrition since it was easier to access mollusks and maize than to access a mussel shell. Thirdly, the smallest mussels were intentionally given to some of the largest crayfish since they were hypothetically the crayfish were more likely to break these mussels (Figure 7). It is seems that the crayfish do have a preference to the mussel and it is proven by the fact that they are mussel flesh was fully consumed once they had access to it (Table 5) and (Table 6). Also all signal crayfish without exception, have made attempts to manipulate the mussel including mussel shell. The female signal and noble crayfish had zero success opening mussels proving, they don't have significance opening mussels. The noble crayfish preferred the opened mussel shell compared to the potatoes and they did predate fully on the smaller mussels while they consumed most of the bigger mussels over a longer period of time (Table 5) and (Table 6).

7. CONCLUSION

Similar experiments have been performed using the invasive mussel species *D. polymorpha* and *P. leniusculus* as a potential predator that could control the abundance of the zebra mussel *D. polymorpha*. However, the present study is the first experiment that tests noble crayfish as potential predator on Unionids. The similarity between these experiments carried with zebra mussel, unionids and margaritiferids support the hypothesis because it was found that the large crayfish are most likely to predate on mussels, especially the small mussels since they are the easiest to break.

It is obvious that the predation on the mussel does cost the crayfish lots of energy and it is very difficult to open the mussel shell. Therefore, the reason the impact of crayfish on mussels is limited was due to fact that mussel shell are rather difficult to break and it has nothing to do with food preferences, which was proven by the high consumption of mussel flesh by both signal and noble crayfish. Large male signal crayfish was proven to have significant impact on small mussels (Table 2) while noble crayfish possess very limited threat to mussels if at all. Not a single pearl mussel was found opened except maybe a few bites to

the sides of the mussel which might cause stress to the pearl mussel. However, it is difficult to determine whether the threat to the pearl mussel is absolute because there wasn't any juvenile pearl mussel with a size less than 40 mm in the experiment and we don't know if the small pearl mussel shell occurs in abundance in an environment filled with crayfish population. From the samples it is obvious that most of the pearl mussel size ranges from 70 to 115 mm (Geist 2005) Anyhow, pearl mussels with size less than 40 mm are not very common and therefore, the crayfish have no real threat except maybe causing a bit of harmless damage to the mussel shell. Even though the large majority of crayfish didn't directly consumer or break the mussel it is possible they my stress the mussel by biting its edges or simply trying to manipulate it.

Therefore, in the future experiments, I suggest to have several tanks filled with water or placing the crayfish in cages and putting them in to their natural environments. These cages and tanks are segregated where one tank has only large male crayfish with a mixture of several mussels with different sizes. The second is filled with female crayfish and several other mussels of different sizes. Finally, the same is repeated with juvenile crayfish and if it is possible to have a small juvenile pearl mussel and water tank without crayfish as a control. Then the numbers of mussels eaten or damaged are recorded and the percentage is calculated for comparisons and in this way it might be more efficient strategy to determine the effects of crayfish on mussels. The chelae length should be taken into account because they do provide information about the effectiveness of crayfish as a predator (see Garvey & Stein 1993).

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