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Prey selection of the Red King Crab (*Paralithodes camtschaticus*) preying on lumpfish eggs (*Cyclopterus lumpus*), sea urchins (*Strongylocentrotus droebachiensis*) and scallops (*Chlamys islandica*)

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BIO-3910 Master's thesis in Biology

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Front page photos: Red king crabs consuming sea urchins, scallops and lumpfish eggs. All photos are taken by the author.

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Abstract

The red king crab, *Paralithodes camtchaticus*, is a new generalist predator in the Barents Sea and may have negative effects upon the commercially fished lumpfish eggs (*Cyclopterus lumpus*), sea urchins (*Strongylocentrotus droebachiensis*) and scallops (*Chlamys islandica*). Generalist predators consume an array of prey types, but have been shown to select certain prey over others. To obtain knowledge on how the king crab consume, select and actively select these prey, a laboratory experiment was performed. To detect active selection, the experiment was divided in two parts: first the crabs were given one prey item (no selection) and second they were given all three prey items (selection). Prey organisms consumed was evaluated after 22 hours. There was a significant selection for eggs and scallops and a significant active selection for scallops. The consumption, selection and active selection of prey appeared to be dependent on crab size and availability of alternative prey. With increasing crab size the amount of prey consumed increased and diet composition included a wider array of prey types. Due to the juvenile crabs residence in shallow waters for 5 years until maturation and the adult crabs annual migration to these areas during moulting/spawning, the red king crab predation could have a negative effect on all three prey types.

Key words: *Paralithodes camtchaticus*, *Cyclopterus lumpus*, consumption, selection, active selection, *Strongylocentrotus droebachiensis*, *Chlamys islandica*.

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1.1 Background

Since the industrialization and increase of human movement across continents there has been an increase in the introduction of new species to new non invaded areas (Lodge 1993, Mack et al. 2000). This has happened as a consequence of both deliberate introductions as well as by organisms accompanying humans when they travel to new areas (Lodge *op. cit*., Mack *op. cit*.). Some of these deliberately introduced species have proved to have a devastating and invasive effect on the ecosystem and environment; through predation, grazing, competition and alteration of the habitat (Mack et al. 2000). Introduced predatory species are hypothesized to have the most devastating effects on native prey populations by reducing and altering their numbers (Lodge 1993, Jørgensen 2005). One such introduced predatory species is the red king crab *Paralithodes camtschaticus* (Tilesius 1815). The red king crab was introduced to the Barents Sea from the North Pacific Ocean by Russian scientists in 1961 – 1969 (Orlov and Ivanov 1978). The intension of this introduction was to establish as a new harvestable species (Orlov and Ivanov *op. cit.*). However, the population has increased more than expected and since the early 1990s fishermen and scientists have seen a rapid westward spread. Today they have a distribution from Kapp Kanin (68° 38` North, 43° 23´ East) in the east to Sørøya (70° 36′ North, 22° 45′ East) in the west (Britayev et al. 2010, Jørgensen and Nilssen 2011). Some individual crabs have now been observed further west (Torstein Pedersen pers. comm. 2011). Along the coast of Finnmark in northern Norway they are spreading into the fjords and had an estimated total population of about 3 million individuals or about 3400 tons in 2010 (Anon. 2011a). These numbers, however, are lower than the actual population size because they include only crabs larger than 70 mm carapace length (CL) or are based on crabs weighing on average about 1.1 kg (Jan H. Sundet pers. comm. May 9, 2011). The Russian adult crab population was estimated to be about 40 – 50 million individuals in 2003 – 2005 (Britayev et al. 2010).

The king crab migrate throughout their 20 year life span; the pelagic zoea larvae disperse passively with the sea currents and can be transported vast distances with ballast water in ships (Hjelset et al. 2003, Pedersen et al. 2006). Tagging experiments show that most crabs do short seasonal migrations from deep to shallow water, staying in the same costal areas and that only a few individual roe-bearing females migrate considerable distances (Sundet 2008b, Gjøsæter et al. 2010). A female crab can carry up to 300 000 eggs and can therefore potentially spread a large number of crabs to new uninhabited areas (Sherbakova et al. 2008). Juvenile crabs stay in shallow subtidal waters (5 – 50 m) until they reach maturity at a size of about 50 – 60 mm carapace width (CW) (66 – 105 mm CL) before moving into deeper water (Sundet 2008a, Falk-Petersen et al. 2011). Adult crabs choose their habitat according to feeding, molting and spawning behavior; migrating towards shore to spawn in late winter or early spring, while staying in deeper water to forage during wintertime (Jørgensen and Nilssen 2011, Falk-Petersen et al. 2011).

Due to their rapid spread and potential impact on the environment, management of the red king crab in Norwegian waters is increasing its focus on preventing them from spreading further west. Conflicting with this aim is the government's wish to promote the king crab as a harvestable species. According to the Central Bureau of Statistics the king crab fisheries generated approximately 88 million NOK in revenue in 2010 (Anon. 2011b). The management in Norway today is divided into two parts. West of Nordkapp at 26° East there is free fishery of crabs. The aim of the free fishery is to prevent them from spreading further west. In contrast, east of 26° East and up to the Russian border the population is regulated by a quota system (Anon. 2007). The quota for 2010/2011 in the regulated area was set to 900 tons male crabs and 50 tons female crabs with a minimum carapace length of 137 mm (Anon. 2010). The quota for 2011/2012 aims to prevent further spreading and reduce the population and has been increased to 1200 tons male crabs (the quota of 50 tons female crabs remains unchanged) and the minimum carapace length has been reduced to 130 mm (Anon. 2011c).

Research on the red king crab has for the most part been performed in their natural range in the North Pacific Ocean and the Bering Sea (Anon. 2007). However, some of the knowledge resulting from this research cannot be directly transferred to the population in the Barents Sea, due to a different bottom topography and different prey species available (Anon. 2007). Research on crabs in the Barents Sea has primarily been focused on population biology, ecological effects and distribution. There is only one case of long term monitoring of the bottom community in an area invaded with king crab. This monitor site is in the Motovsky Bay where the crab has been present for over 40 years and results show that there has been a steady decrease in biomass of echinoderms, bivalves and sipunculids (Anisimova et al. 2005). Russian researchers attribute this decrease to a combination of crab foraging and bottom trawling fisheries.

The red king crab is considered to be an opportunistic generalist predator that can eat a range of benthic prey (Cunningham 1969). Molluscs, crustaceans, echinoderms, polychaets, algae and fish remains are important food sources in both the Barents Sea and the Pacific Ocean (Jewett and Feder 1982, Sundet et al. 2000). The crab can have a negative effect on these species by decreasing these populations' densities and changing their structure (Pavlova 2009, Oug et al. 2010). In stomach samples from crabs collected in areas around Kodiak Island in Alaska, molluscs and arthropods were the dominant food groups (Jewett and Feder 1982). Bivalves were the most important mollusc accounting for 31.3% of the total food in wet weight. Bivalves were also the dominant prey item in the diets of juvenile crabs coming from the Varanger Fjord, Kola Bay and Dal'nezelenetskaja Bay (Britayev et al. 2010). In a laboratory experiment where adult crabs were presented with scallops (*Chlamys islandica*), sea urchins (*Strongylocentrotus droebachiensis*), horse mussel (*Modiolus modiolus*), sea star, common whelk and Astarte sp. for 48 hours, scallops made up 73 – 97% of the foraged prey in grams wet weight (Jørgensen 2005). The echinoderm species sea urchin has been found to have an occurrence frequency of about 25 – 55% in the stomachs of crabs larger than 60-70 CW in the Kola Bay (Pavlova 2009). The king crab can also serve as a new competitor for local species, competing with haddock (*Melanogrammus aeglefinus*) and troll crab (*Lithodes maja*) which have overlapping diets in the Barents Sea (Falk-Petersen et al. 2011).

Generalist predators like the red king crab have a wide selection of prey types in their diet and often show some sign of preference or selection for certain prey when presented with multiple prey types (Wong and Barbeau 2005). Predators are considered to select a particular prey type if the proportion of that prey in the predators' diet is higher than the proportion found in the environment (Begon 2005). Selection can occur through both active and passive selection. If a predator consumes more than expected of one particular prey type when given a choice of multiple prey types compared to when they are not given a choice, they are considered to be doing an active selection (Underwood et al. 2004, Wong and Barbeau 2005). Predators often actively select food items that have a high energetic value or, may in some instances choose an array of prey types that help give a mixed and balanced diet (Begon 2005). Most predators, however, choose prey that give the most energy per unit time spent handling the prey (where time spent searching, attacking, opening, consuming and digesting prey is considered handling time), also called optimal foraging theory (Begon 2005, Wong and Barbeau 2005). This theory states that a predator should consume prey items that have a higher profitability (ratio of energy gain to handling time) and ignore prey of lower profitability to maximize energy intake per unit foraging time.

Passive selection of prey organisms, however, is based on the prey item itself or on the encounter rate between the predator and prey. Here the prey differ in their vulnerability to predators as they differ in predator avoidance mechanisms; the prey organism themselves therefore determine the outcome of the predator-prey encounter (Lang 2001). A generalist predator can display the following feeding behaviors based on encounter rates: opportunistic behavior or switching behavior. The former is where the predator catch prey based on the relative encounter rates in the environment. The latter is where the prey that is most abundant at any one time is most consumed (Lang 2001, Begon 2005).

The predators' size and their ability to capture and handle prey is also an important factor in prey consumption. The likelihood of encountering and successfully handling and consuming a prey item increases with size of the predator. Larger individuals will be capable of handling a larger array of difficult to handle prey and prey sizes compared to smaller individuals. This was the case in a laboratory experiment by Jørgensen (2005) who found that larger king crabs included more "difficult" prey in their diets than small crabs; they also had a wider array of prey in their diets when presented with different prey organisms. Field stomach analysis from king crabs found the same pattern (Pavlova 2009). The size of the prey items presented is another important factor in predator selection. Predators often show a selection for specific prey size groups. Small prey individuals are easier to open, but may contain very little energy, while large prey items are difficult to open, take a long time to handle, but often contain a large amount of energy (Wong and Barbeau 2005). The predators therefore often choose a prey size that is intermediate giving them the highest profitability (Osenberg et al. 1989, Wong and Barbeau 2005).

Through diving (video) and stomach samples from the field it has been observed that the king crab are capable of eating egg clutches from fish that spawn on the sea bottom (Nina Mikkelsen, pers. comm. 2010). These fish include capelin (*Mallotus villosus*) and lumpfish (*Cyclopterus lumpus*), both of which are important fish in Norwegian fisheries. There are a number of uncertainties surrounding how much effect the crab can have on these species. It is suggested that in years of low population size the crab predation on eggs could have a negative effect and lumpfish are believed to be especially vulnerable (Falk-Petersen et al. 2011). The commercial fishery for lumpfish in Norway is mainly based on their roe which is considered a delicacy and have been commercially harvested since the 1950s. In Norway this fishery takes place in northern Norway during the spring when the lumpfish come close to shore to spawn.

Lumpfish spawn in the spring in shallow subtidal waters, preferring hard rocky bottom areas that are covered by seaweed or kelp (*Laminaria* spp.) (Davenport 1985, Goulet et al. 1986). Male lumpfish defend territories where they entice the females to spawn their eggs. The eggs are always laid among rocks and *Laminaria* beds and never on exposed stones (Davenport 1985). In Norwegian waters, individual eggs are round and about 2.3 mm in diameter and the egg lumps can be as large as 26 cm × 10 cm × 10 cm (Davenport 1985). The males guard and give parental care to the egg lumps that contain eggs from several females, guarding them for about 6 – 10 weeks (Davenport *op. cit*.). Parental care consists of providing the eggs with good physical conditions such as increasing oxygen levels by pumping water over them, keeping them clean and guarding (Goulet et al. 1986). Males have been described removing predators like sea urchins and periwinkles (*Littorina* spp.), and chasing away individual fish such as wolfish (*Anarhichas lupus*) and conger eel (*Conger vulgaris*) (Davenport 1985, Goulet et al 1986). When attacked by groups of bigger fish like cunner (*Tautogolabris adspersus)* they have been shown to give up their guarding behavior (Goulet et al. 1986).

The king crab distribution in northern Norway now overlaps hard bottom communities in spawning season and adult crabs are known to migrate to shallow water during spring time, where there are eggs from lumpfish and other species of fish available (Gjøsæter et al. 2010). An underwater video from the Varangerfjord shows a large king crab easily pushing away a defending male lumpfish while eating the egg lump (Nina Mikkelsen pers. comm. 2010). In a field investigation, stomach content analysis showed that there were only a few crabs that had a lot of lumpfish eggs in their stomach while a significantly larger share had few eggs in their stomach (Nina Mikkelsen pers. comm. 2010). King crab is evolutionarily a “new” predator on lumpfish eggs and other bottom spawning fish, and may have an effect on these fish species reproduction success.

1.2 Objectives and approach

There is no knowledge surrounding how the king crab would select fish eggs such as the lumpfish eggs or how much they would consume and damage them. To obtain more knowledge regarding the selection and consumption of lumpfish roe, I wanted to examine how much eggs they consumed and test experimentally how the eggs would be selected when presented together with alternative prey. This was done through a laboratory experiment where the crabs were presented with lumpfish eggs and the alternative prey items: sea urchins and scallops. To detect active selection, the experiment was divided in two parts. In the first part, crabs were presented with only one prey item at a time to see if they could and would eat the prey. In the second part, the same crabs were presented with all the prey items together to see if there was any prey that were selected or not selected.

Questions investigated were:

- Will the lumpfish eggs be actively selected when the crabs are given a choice of prey items?
- Do the king crabs demonstrate selection or active selection for the three prey items presented?
- Does the consumption of the prey items change when there is choice of alternative prey compared to when there is no choice?
- Could selection and active selection of prey be due to a variability in the size of the crab, handling time or/and prey size?
- What effects could the king crab have on these prey species in their natural environment?

2. Materials and methods

2.1 Experimental design

The crabs were caught in the Porsangerfjord at Holmfjord (70° 1′ 7″ North, 25° 1′ 25″ East) in April 2010, using commercial crab traps that were left out overnight. Only male crabs were used due to Norwegian law and to prevent potential mating or release of eggs west of 26° East.

The crabs were transported to the laboratory (Faculty of Bioscience, Fisheries and Economics) at the university campus in Tromsø, Norway on April 30, 2010 and kept in storage tanks. Two round storage tanks of 2 m diameter with rounded bottoms, natural seawater flow (6 – 9 l/min) and an ambient temperature of 5 – 7°C were used. The tanks contained 16 and 17 crabs. Every crab was weighed and measured from the eye cavity to the back of the carapace (CL) and across the carapace (CW). The size of the crabs ranged from 300 – 2220 g, 84 – 133 mm CL and 94 – 154 mm CW (Table A1). They were individually numbered to tell the crabs apart by using plastic colored strips in different combinations on the legs. The crabs were fed 0.5 – 1 kg thawed capelin each day, which was distributed to each tank before and between experiments.

The prey species sea urchin and scallops used in the experiment were caught with a triangular scrape in Balsfjord (69° 18′ 17″ North, 19° 12′ 13″ East) in May 2010 and kept in two 1 m^2 square tanks with a water depth of 30 cm (Figure 1). They were provided with natural sea water flow (0.9 l/min for scallops and 4 l/min for sea urchins) at an ambient temperature of about 5 – 7°C.

a) b)

Figure 1. a) one of the 1×1 m^2 experimental tanks used. The crab here is undergoing test one where lumpfish eggs are presented alone. b) crab undergoing test two where all prey types are presented together.

To collect eggs from lumpfish, 20 females and 4 males were caught in May 2010 by a fisherman at Sommarøy, Tromsø using gillnets. They were distributed to 3 storage tanks; two large tanks at Troms Marin Yngel on Kvaløya and one at the university laboratory (Faculty of Biosciences, Fisheries and Economics). The tank at the university laboratory had 2 m diameter rounded bottoms. The lumpfish were kept under as natural conditions as possible with weak light, rocks with seaweed for spawning and with 6 – 9 females and one to two males in each tank. About 10 egg lumps of fertilized eggs were collected over the course of the experiment and kept in egg incubators supplied with natural seawater flow (4 l/min), rich air flow and an ambient temperature of 5 – 7°C.

Before the experiment, the crabs were moved from the storage tanks to one experimental tank (only used for starvation) where they were deprived of food for 48 hours to initiate hunger and an immediate feeding response (Jørgensen 2005). Three grey, square 1x1m experimental tanks with natural seawater flow, a water depth of about 30 cm and an ambient temperature of 5 – 7°C were used during the experiment (Figure 1). One crab was placed in each of the three experiment tanks during testing. The square outflow grates at the bottom of the tanks were covered with a fine mesh fabric to prevent prey pieces being transported out. To prevent the crab opening the outflow grate, a large rock was placed on top of it. To keep the light dim and prevent stress from activity in the room a green tarpaulin was placed over all the storage and experimental tanks.

An infrared video camera was set up over one of the tanks to record feeding activity during the experiment. It was turned on at the beginning and turned off at the end of each experiment. The video recordings were divided into 30 minute video clips and stored on an external PC hard disc.

The videos were later investigated to estimate the average handling time for the three prey types. This was done by watching the videos and taking the time from the crab encountered, grabbed and handled the prey until it was finished eating and had discarded it. Some general behavior such as movement, feeding behavior and feeding techniques was also noted. There were 21 test rounds filmed (923 videos) and a total of 446 hours and 12 minutes of videos were watched and analyzed (Figure 2). The average handling times for each crab and the different prey types was analyzed and calculated. It was possible to estimate the average handling time for eggs from 12 videos based on 103 egg eating events. Average handling time for sea urchins was estimated from 5 videos based on 19 predation events and the average handling time for scallops was based on 9 videos with a total of 35 feeding events (Figure 6, Table A4). The 95% confidence intervals for the average values were calculated using bootstrapping with 1000 resamplings. To determine if there was a correlation between two variables e.g. size of the crab and handling time, Spearman rank correlation coefficient (ρ) was used.

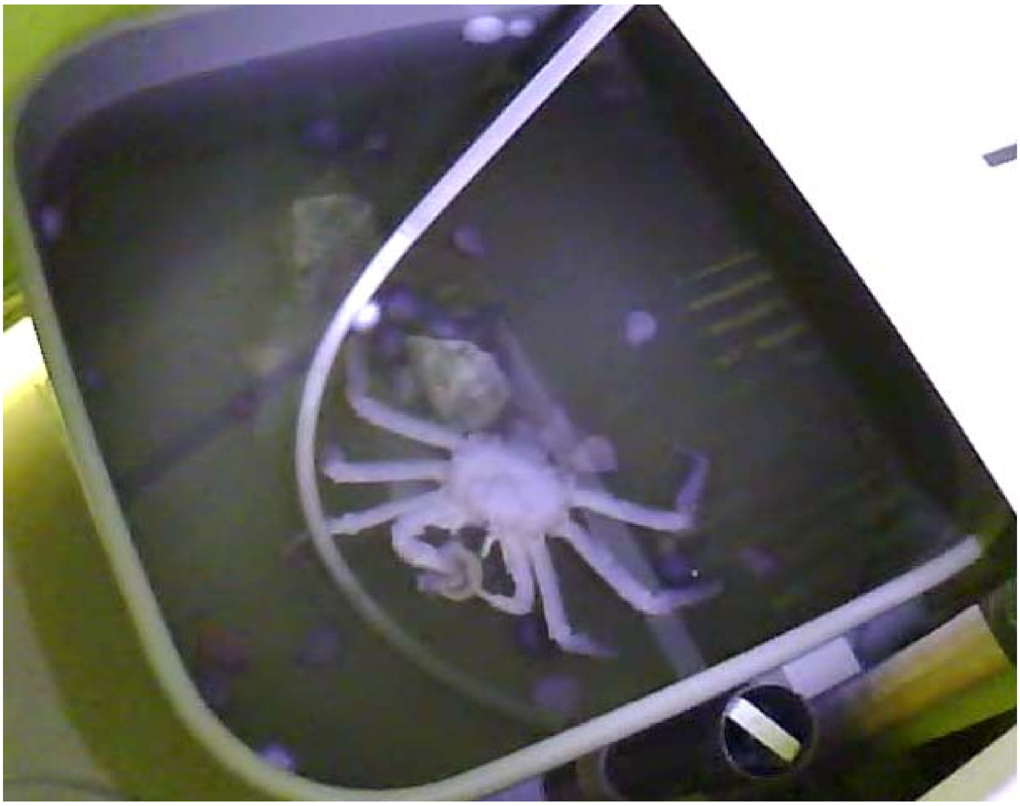

Figure 2. Photo from the video analysis. The photo shows crab nr 21 handling a scallop during test 2.

2.2 Treatment design

The experiment was divided in two parts (Table 1). In test one, the crabs were presented with one prey type at a time (for densities see Table 2 and Figure 1a). This was done to investigate if they actually could and would eat the prey item presented. The same crabs were tested with three prey types over a course of five days. The crabs were starved for about 48 hours in an empty experiment tank, before being placed in the experiment tank with one of the prey types for about 22 hours. The crabs were then starved for about 26 hours before being placed in the experiment tank with the second prey type. This followed by another starvation period of about 26 hours and a feeding period of about 22 hours (Table 1 and Figure 1a).

In test two, the same crab individuals from test one were presented with all the prey types together, at the same density of each prey as in test one (Table 2 and Figure 1b). This was done to investigate if there is an active selection on the prey types presented.

Table 1. Treatment design used during the experiment. Day number, test number, duration of activity and activity.

Day	Test nr.	Duration (hours)	Activity
1	1	24	Starvation
2	1	24	Starvation
3	1	22	Prey item 1
4	1	26	Starvation
5	1	22	Prey item 2
6	1	26	Starvation
7	1	22	Prey item 3
8	2	26	Starvation
9	2	22	All 3 prey items

In the experiments, the crabs were presented with 15 scallops and/or 15 sea urchins of various sizes and/or about 150 grams of lumpfish eggs (Table 2). Before starting the tests, the groups of scallops and the groups of sea urchins were wet weighed using a digital gram lab scale. Individuals were measured from the umbo to the back of the shell (shell height, scallops) or across the body (diameter, sea urchins) using a caliper. The sea urchins and scallops were randomly distributed in the experiment tank, while the lumpfish eggs were fastened by string to a large rock and placed at random in one of the tanks corners. A total of 18 kg of scallops, 22 kg of sea urchins and 2.2 kg lumpfish eggs were used during the whole experiment. There was one crab per experiment tank and they were allowed to feed on the prey for 22 hours after which they were placed in the starving tank or back in one of the storage tanks. The prey items remaining in the experimental tank were counted, measured and wet weighed. Undamaged prey was placed back in their holding tanks for later use. All damaged prey items were wet weighed to the nearest 0.1 g and put in plastic bags and stored in a freezer at -18°C.

Table 2. The average wet weight of eggs (g), average wet weight sea urchins (g), average sea urchin size (cm), number of sea urchins, average wet weight scallops (g), average scallop size (cm) and number of scallops, together with ± standard deviation presented to the crabs during test one and test two.

	Average grams of eggs ± SD	Average grams of sea urchin ± SD	Average sea urchin size cm ± SD	Nr. of Sea Urchins	Average grams of Scallops ± SD	Average scallop size cm ± SD	Nr. of Scallops
Test one	153.9 ± 2.1	754.7 ± 107.4	4.56 ± 0.39	15	585.8 ± 71.4	6.38 ± 0.39	15
Test two	154.0 ± 1.9	760.7 ± 28.3	4.67 ± 0.24	15	612.2 ± 62.9	6.53 ± 0.38	15

To prevent any experiment tank biases, the crabs were tested in all three tanks using a random block design called Latin Square design (Table A3). A rock was also added to a random corner of all the experimental tanks that were not tested for egg predation in test one; therefore all the tanks were physically very similar.

2.3 Statistics

Consumption

Consumption data was calculated by taking prey item weight before test start minus prey item weight after the test (uneaten prey items and prey remains). This data on proportion of food consumed per individual did not show a normal distribution; therefore, non-parametric tests were used. The Wilcoxon non – parametric sign test was used to determine if the food consumption data for the different prey types was significantly different from each other (Zar 1974, Løvås 2005). In the results section, the Wilcoxon test results are denoted by W. Spearman rank correlation coefficient (ρ) together with bootstrapping with 1000 resamplings was used to determine if there was a significant correlation between consumption of prey and crab size (g wet weight). For the correlation coefficient the 95% confidence interval is denoted as CI with lower and upper significance level respectively. The critical level for ρ was 0.521 with 95% significance level and $n = 15$. If the 95% confidence level did not overlap with zero, this was taken as indication a statistical significance.

Selectivity

To investigate if the crabs were selecting particular prey types, Manly's alpha (α_i) also known as Chesson's index (Chesson 1978, Wong and Barbeau 2005) was used:

$$\alpha_i = \frac{\ln(ni0 - ri/ni0)}{\sum_{j=1}^{m} \ln(nj0 - rj/nj0)} \quad i = 1,....,m \qquad \text{(eq. 1)}$$

Where *i* and *j* stand for prey type, *ri* and *rj* is the weight of prey *i* and *j* consumed, *ni0* and *nj0* is the weight of prey *i* and *j* available in the environment at the start of the experiment and *m* is the number of prey available for consumption at the start of the experiment. This measure is scaled between 0 and 1, where α_i = 1 when only prey *i* is consumed, α_i = 0 when no prey type *i* is consumed and α_i = 1/i when there is no selection. This version of the Chesson index is adapted for the experimental situation where the prey abundance is reduced due to feeding during the experiment. This is a good method because it can be used when several prey are eaten without replacement of prey consumed. The 95% confidence interval for α_i for the different prey types in each size group was determined using bootstrapping with 1000 re-samples. To make the analysis and presentation simpler the crabs were divided into three size groups, consisting of small crabs (< 740 g), medium/middle crabs (750 – 1490 g) and large crabs (> 1490 g) (Figure 4).

Active selection

To investigate if there was active selection of prey, we compared the amount of prey eaten when all three prey types were present (choice is available, observed frequencies) to the amount of prey eaten when there is only one prey item present (no choice available, expected frequencies).

$$E_m = \frac{R \cdot S_m}{(S_i + S_m + S_j)} \qquad \text{(eq. 2)}$$

$$E_i = \frac{R \cdot S_i}{(S_i + S_m + S_j)} \qquad \text{(eq. 3)}$$

$$E_j = \frac{R \cdot S_j}{(S_i + S_m + S_j)} \qquad \text{(eq. 4)}$$

where E_m, E_i and E_j is the expected weight (grams) of eggs, sea urchins and scallops eaten in test two; R is the total weight (grams) of eggs, sea urchins and scallops eaten when presented together in test two; S_i, S_m, and S_j is the weight (grams) of eggs, sea urchin and scallops eaten when presented alone in test one (Wong and Barbeau 2005). There is active selection if the test values of E_m, E_i and E_j are significantly different from the observed values of prey consumed. To test if the active selection was significant the Wilcoxon non-parametric sign test was used comparing expected (eq. 2 – 4) and observed weights eaten.

All the statistical analysis was calculated using the statistical programs Mystat version 12 (Mystat 2007) and Microsoft Office Excel 2003 on the PC.

3. Results

3.1 Consumption

Test one

Eggs were the least consumed of the three prey types presented during test one. The correlation between the amount (g) of eggs eaten per crab and weight of the crabs was not significant (ρ = 0.525 and CI = - 0.039, 0.880) (Figure 3a). There was more sea urchins (average weight 93.72 g) consumed than eggs (average weight 17.96 g, W p = 0.002) and scallops (average weight 67.68 g, W p = 0.045). The correlation between sea urchins eaten per crab and weight of the crab was significantly positive (ρ = 0.675 and CI = 0.189, 0.891) (Figure 3a). There was more scallops consumed than eggs (W p = 0.005). The correlation between amount of scallops eaten and weight of the crab was not significant (ρ = 0.419 and CI = - 0.205, 0.843) (Figure 3a).

Test two

Eggs were the least consumed prey in test two. There was a drop in the amount (g) of eggs eaten in test two with an average weight of 9.78 g consumed, compared to test one with an average weight 17.96 g consumed (W p = 0.031) (Figure 3a and 3b). The correlation between the size of the crab and the amount of eggs they consumed was significantly negative (ρ = - 0.646 and CI = - 0.260, -0.866) (Figure 3). The weight and number of sea urchins eaten in test two (average weight 36.84 g) was significantly less than in test one (average weight 93.72 g, W. p = 0.001). Sea urchins were less consumed than scallops (average weight 82.95 g) in test two (W p = 0.008). The consumption of sea urchins was positively correlated with crab weight (ρ = 0.537 and CI = 0.103, 0.806) (Figure 3b). Scallops were the most consumed prey in test two

(W p = 0.004 when compared with eggs and W p = 0.008 when compared with sea urchins). There was no significant (W p = 0.183) increase in the average weight of scallops consumed in test two (89.95 g) compared to test one (67.68 g). The correlation between the size of the crab and the amount of scallops consumed was significantly positive (ρ = 0.627 and CI = 0.117, 0.884) (Figure 3b).

There were six crabs that ate sea urchins in test one but not in test two and two crabs did not consume sea urchins in either test. Three crabs stopped eating eggs in test two, one started eating eggs in test two and one ate only eggs in both tests (Figure 3). Three crabs did not eat scallops in either test.

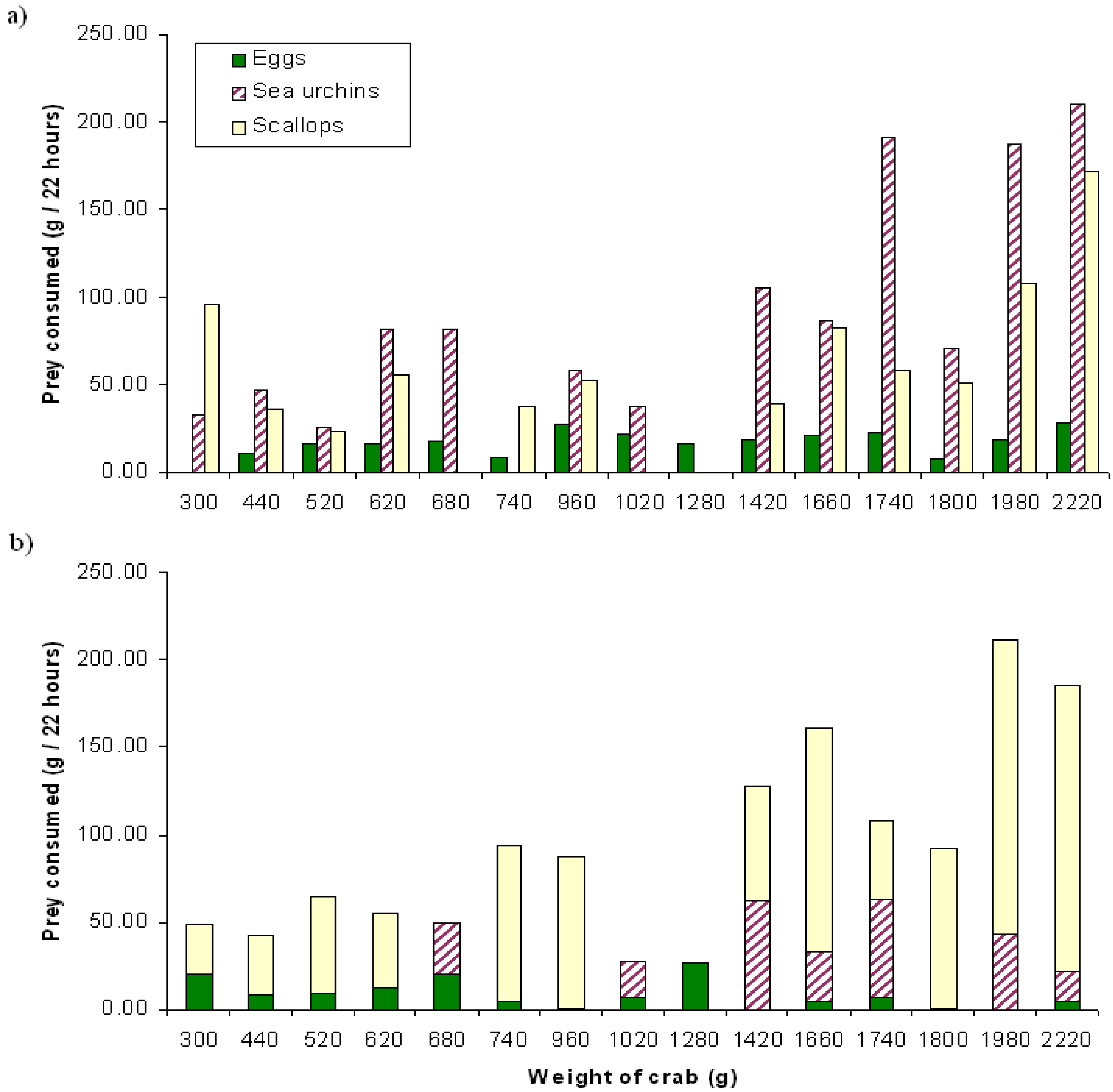

Figure 3. Consumption rate: gram prey eaten per individual over a 22 hour period. a) test one where each prey item was presented alone and b) test two where all prey items were presented together. *n* = 15

3.2 Selectivity

Eggs were significantly the most selected by the crabs in the smallest size group (α_i = 0.61) (Figure 4). There was no significant selection of eggs in the middle size group (α_i = 0.34) and the crabs had selectivity significantly lower than α_i = 0.33 for the largest size group (α_i = 0.08) (Figure 4). Scallops were significantly the most selected by the crabs in the largest size group (α_i = 0.77). In contrast, there was a no significant selection for scallops by the middle and smallest size groups (α_i = 0.52 and α_i = 0.34). Crabs selectivity for sea urchins had a lower than α_i = 0.33 selectivity for all the size groups (α_i = 0.05 for the smallest group,

α_i = 0.13 for the middle group and α_i = 0.15 for the largest group) (Figure 4).

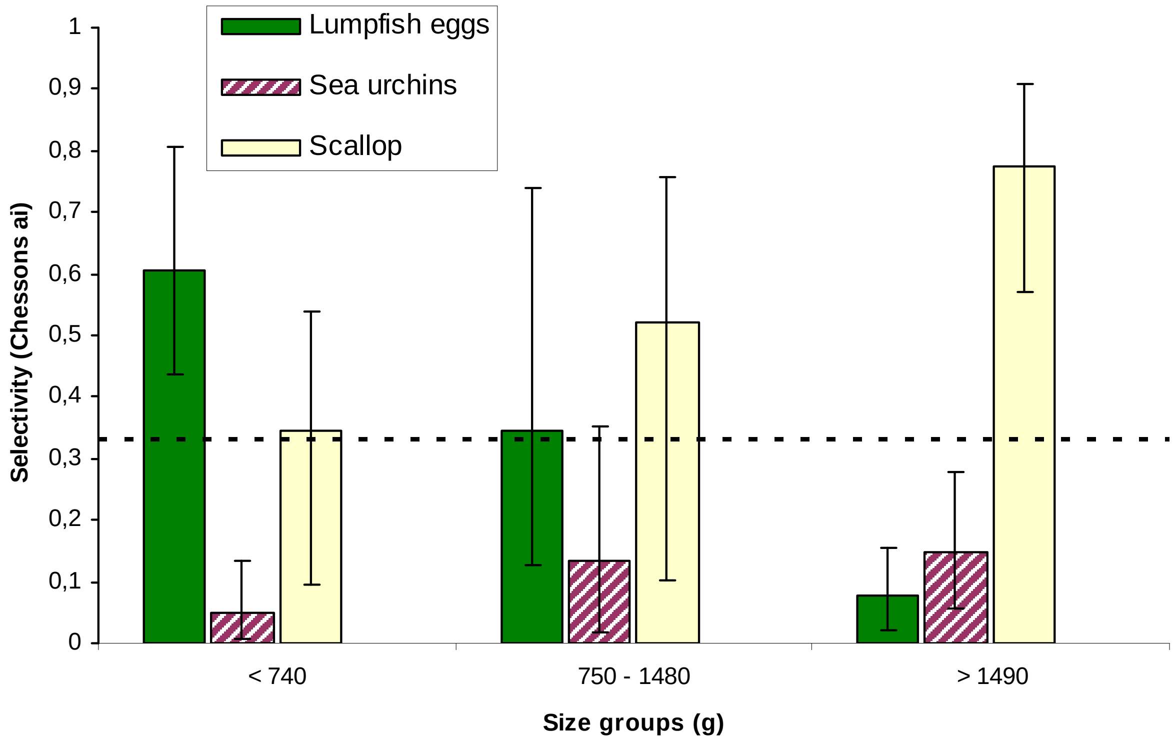

Figure 4. Prey selection in test two where all prey were presented together (measured by the selectivity index, α). The dashed line indicates no selection (α = 0.33). n = 5 crabs in each size group. The 95% confidence intervals are shown by vertical bars.

3.3 Active selection

There was no significant active selection for lumpfish eggs when all crabs were considered as one group (W p = 0.158). Ten crabs had a negative active selection, one had no active selection and four had a positive active selection (Figure 5a both graphs). The data set was divided in two sub-sets to estimate selection in small crabs (size 300 – 1020 g, n = 8) and large crabs (size 1280 – 2220 g, n = 7). There was no significant active selection in either crab size groups. The small crabs displayed a neutral active selection (4 crabs actively selected eggs and 4 did not) (W $p = 1$) while the large crabs displayed a significant negative active selection (W $p = 0.028$). There was a significant negative active selection for sea urchins across all the sizes (W $p = 0.002$). Twelve crabs had a negative active selection, two had no active selection and one had a positive active selection (Figure 5b both graphs). There was a significant positive active selection for scallops across all the crab sizes (W $p = 0.003$). One crab displayed negative active selection, three had no active selection and 11 had a positive active selection (Figure 5c both graphs).

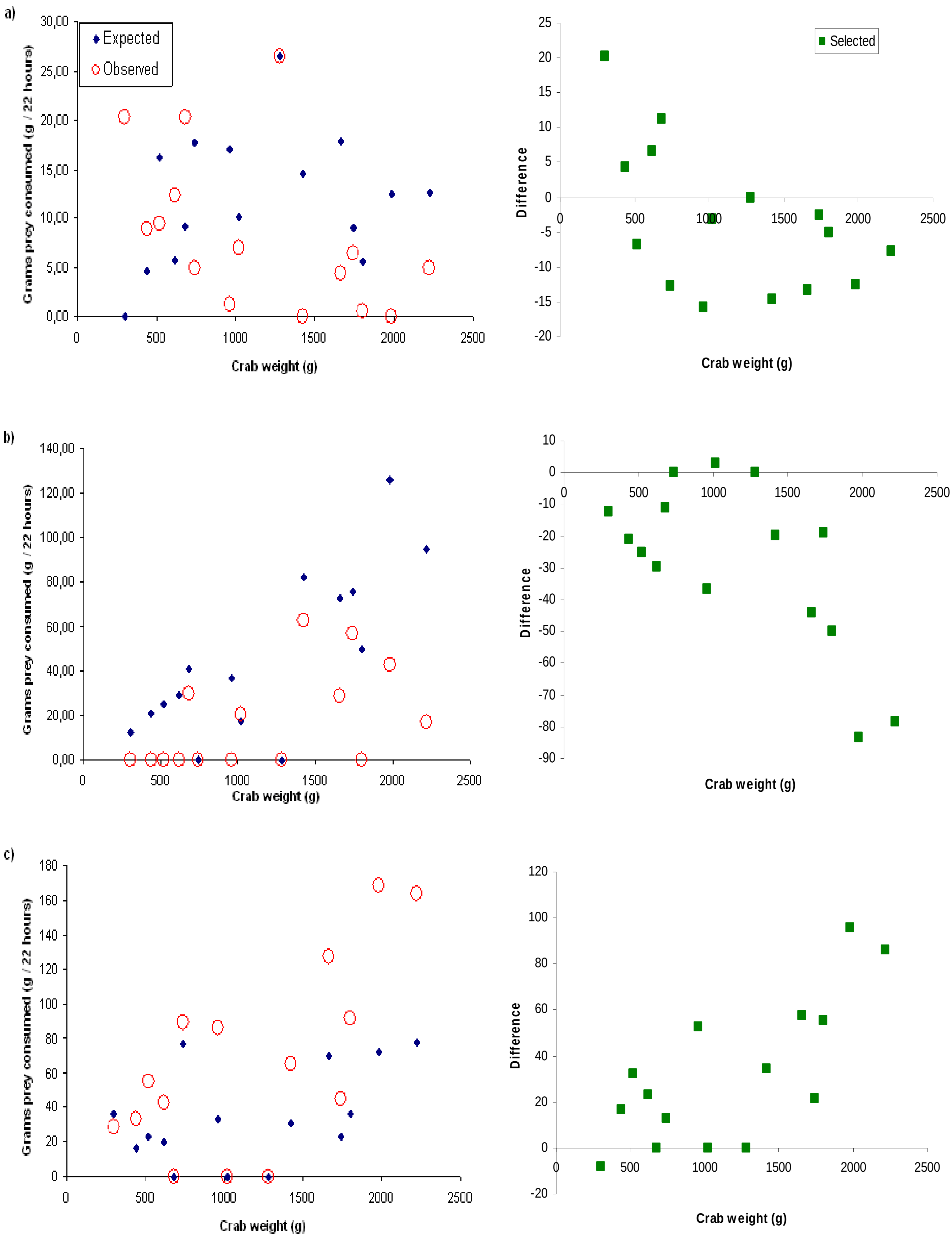

Figure 5. Comparison of expected and observed consumption of eggs (a), sea urchins (b) and scallops (c) in test two is presented in the graphs to the left. The differences between observed and expected are presented in the graphs to the right. The expected consumption is calculated from consumption data in test two.

3.4 Handling time and video analysis

Average handling time

When feeding on eggs the crabs had an average handling time of 18 minutes (Standard deviation (SD) = 13 minutes) (Figure 6). The average handling time for sea urchins was 94 minutes (SD = 92 minutes) (Figure 6). For scallops, the average handling time was 104 minutes (SD = 68 minutes) (Figure 6). The handling time for eggs was significantly lower than the other two prey items, while sea urchins and scallops were not significantly different from each other.

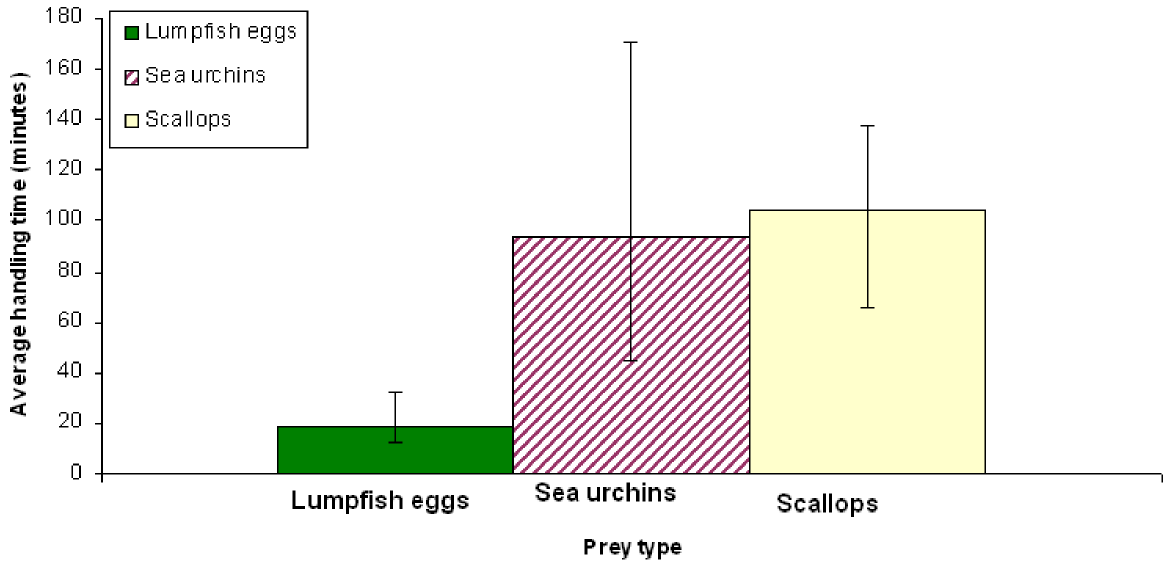

Figure 6. The average handling times for eggs (n=12), sea urchins (n=5) and scallops (n=9). The bars show the 95% confidence interval.

Individual handling time

The average handling time varied amongst prey type as well as between crabs (Figure 7 and Table A4). There was no significant correlation between size of the crab and handling time for eggs (ρ = - 0.526 and CI = - 0.763, 0.365). There were not many sea urchin handling sequences filmed, (n = 5) and Spearman rank correlation coefficient indicated no significant correlation between crab weight and handling time (ρ = - 0.410 and CI = -1, 0.875) (Figure 7). The correlation between size of the crab and handling time for scallops was not significant (ρ = - 0.538 and CI = - 0.996, 0.240) (Figure 7).

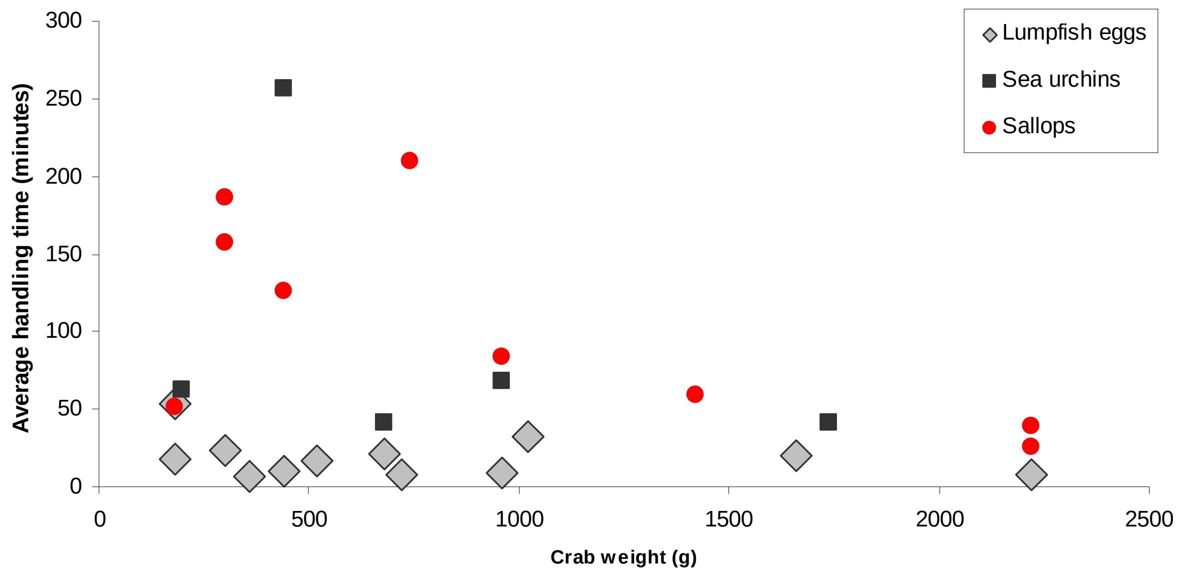

Figure 7. The average handling time (minutes) the individual crabs used when handling the prey items lumpfish eggs, sea urchins and scallops.

Video and visual observation

The video recordings showed that the crabs had very individual behavior in the experiment tank as well as during handling and consumption of prey. The crabs were often stressed at the start of the experiment after due to handling. They would walk along the tank wall in circles and try to climb the wall. After some time, ranging from 30 minutes – 3 hours, the crabs would slow down their movements, start to grab prey on the tank bottom and forage. Some crabs showed possible resting behavior lasting 20 – 30 minutes. Resting periods were characterized by the crab lowering its carapace to the tank bottom and straightening its legs.

In nearly all cases, eggs were eaten when the crabs walked over or near them (Tables A1 and A2). Once the eggs were found, the crabs started pulling at the egg lump, pulling off individual eggs and pieces of egg lump which they passed to their mouthparts. Some crabs spent only 1 – 5 minutes eating before moving on, while others would spend up to 102 minutes lying over the egg lump, pulling at it and eating the eggs. A lot of the eggs and egg lumps were spread (spilled) over the tank bottom during the pulling and eating.

Crabs of all sizes appeared to have difficulty picking up and removing sea urchins from the tank bottom. Large sea urchins were the least preyed upon; small and medium sized sea urchins were most preyed upon (Table A5). Some crabs crushed the sea urchin with the large crushing chela (claw), pulling out the meat with the smaller chela so that only crushed bits of sea urchin were left. Other crabs would pick up the sea urchin, bring it to their mouthparts and consume the whole animal, leaving only small remains of the prey on the tank bottom. The smallest crabs spent time searching for sea urchins of a suitable size. They ate medium sized sea urchins and when they encountered a large specimen they were not able to crush it due to their small chela size (Table A5). In these instances they often ate some of the spikes on the sea urchin, where there also may have been consumption of suction feet.

Some mall crabs used longer time to find a scallop they would consume. They would grab some scallops and try to open them, then discard them and try other prey. Some of the crabs lost their grip on scallops due to the scallops swimming behavior. Once scallops were caught, the crab would crush the shell along edge or on the umbo. The shell was then further crushed or ripped apart using both chelae, holding the scallop with the crushing chela the fleshy parts were removed using the small chela. Some crabs crushed scallops and ate nothing or only a very small portion before discarding the rest. This behavior was observed in both tests. In test one, three crabs had this behavior, while in test two six crabs showed this behavior (Tables A1 and A2). Crabs often came back to opened scallops several times during the observation period eventually eating all the soft parts.

When the prey items remaining in the experiment tanks after the tests were analyzed, a number of crab behaviors during foraging could be noted. A number of crabs had ripped the whole egg lump from the rock and spread eggs and pieces of egg lump on the tank bottom. There were seven crabs that had displayed this behavior in test one. In test two, two crabs had displayed this behavior. When examining the sea urchins it appeared that crabs had pulled off spikes and suction feet, this was noted as round areas on the sea urchins with no spikes. Two crabs had this behavior in test one, and two crabs had this behavior in test two. There were also a number of sea urchins and scallops that were cracked but not consumed, these were termed discarded. This was characterized by holes in the body or shell. In test one, only one crab discarded sea urchins and three crabs discarded scallops. In test two, one crab discarded sea urchins while eight crabs discarded scallops.

3.5 Egg spillage and prey size selection

Egg spillage

There was a lot of "spillage" where eggs and pieces of egg lump were pulled from the main egg lump and spread on the tank bottom. An average of 85.46 g out of 153.9 g eggs were spilled per crab in test one and 46.99 g out of 154 g eggs were spilled per crab in test two (Tables A1 and A2). There was no significant correlation between size of the crab and amount of eggs they spilled in either test (ρ = 0.282 and CI = - 0.248, 0.731 for test one and

ρ = 0.344 and CI = - 0.145, 0.741 for test two).

Prey size selection

In test one, the average sea urchin size consumed was 40.04 mm, while in test two the average the average sea urchin size consumed was 39.27 mm. There was no significant change in average sea urchin size consumed in the two tests and no significant correlation between weight of the crab and the average size consumed (ρ = - 0.076 and CI = - 0.507, 0.470 for test one and ρ = 0.4486 and CI = - 0.818, 1 for test two). In test one, the average scallop size consumed was 63.54 mm while in test two it was 66.29 mm (Table A5). There was no significant change in the average scallop size consumed in the two tests and there was no significant correlation between the size of the crab and the average prey size they consumed (ρ = - 0.209 and CI = - 0.588, 0.360 for test one and ρ = 0.179 and CI = - 0.395, 0.601 for test two).

4. Discussion

4.1 Prey selection

Most other diet studies performed on the red king crab show that they have a diverse diet, but that often one or more prey item species are dominant (Jewett et al. 1982, Sundet et al. 2000; Jørgensen 2005, Jørgensen and Primicerio 2007, Britayev et al. 2010). This was also the case in this experiment where eggs were the most selected prey item by two of the size groups and scallops by three of the size groups. Scallops were the most actively selected prey by all size groups. Prey selection may be explained by a property of the prey item itself such as size, energy content and ability to escape, or their availability and thereby their encounter rate in the environment. Selection may also be based on the crabs individual characteristics and capabilities such as their size, handling techniques and feeling of gut fullness.

Lumpfish eggs

That all the crabs consumed eggs at some point during the experiment indicates that all crabs were capable of consuming them (Figure 3). The results from the active selection analysis for the entire test group, however, showed no significant active selection for eggs (Figure 5a).

A possible explanation for the significant selection observed in the small and medium size groups in test two is that eggs were easier to get a hold of and consume and had no means of protection which the other prey items had. Therefore, they may have been consumed by passive selection. This type of selection may also have been the case for the large crabs, which, although they did not display any significant positive selection or active selection, consumed eggs in both tests.

The higher average consumption of eggs in test one compared to test two may have been due to the crabs hunger after being starved for 26 or 48 hours and the fact that there were no other prey choices. In test two, the correlation between consumption of eggs and size of the crab was negative which could indicate that as the size of the crabs increased the crabs started to select other prey types over eggs.

Lumpfish eggs have an energy content (4.99 KJ/g wet weight) that is higher than that found in the other prey items presented (1.62 KJ/g wet weight in sea urchins and 2.63 KJ/g wet weight in scallops) (Lønning 1988, Brey 2001). The crabs may therefore not need to consume a large amount of eggs to satisfy their energy need. The eggs could also be giving the crabs a stronger feeling of gut fullness than the other prey, since a majority of the consumed parts of the other prey consisted of soft parts. The outer membrane on the lump fish eggs was often still intact and not digested when feces from crabs that had consumed eggs were found on the tank bottom.

Four of the smallest crabs (although not a statistically significant number) appeared to display a positive active selection for the eggs (Figure 5). Stomach content analysis has shown that small crabs often consumed a higher number of prey items that are small and easy to handle such as polychaets, sea stars, small bivalves, small sea urchins and fish remains (Jørgensen and Primicerio 2007, Pavlova 2009, Britayev et al. 2010). This may be a reason behind the apparent active selection found in the smallest crabs.

The placement of the eggs in the tank may have an effect on the amount of eggs consumed. The eggs were only present in one corner of the tank. This may have caused the encounter rate between the crab and the eggs during random movements in the tank to be lower than for the other prey items. Had the encounter rate been higher more eggs may have been consumed.

The crabs used in this experiment may have never or only briefly encountered lumpfish eggs in the environment before and therefore may not have recognized them as valuable prey. In the environment, lumpfish eggs are patchily distributed and are only available during short periods of about 6 - 10 weeks once a year (Davenport 1985). The other two prey items are available in a larger number. In the Porsangerfjord where the crabs were caught, sea urchins have a population density of about 30 – 50 per m^2 in shallow water (Strand et al. 2007). A scallop bed located in the inner parts of the fjord has an estimated size of about 5 × 3 nautical miles and contains about 400 – 1200 g scallops per m^2 (Jørgensen 2005). They are also present year round, making the chances of earlier encounter higher. Having a choice of different prey items in test two, the crabs may have been choosing to eat prey they are familiar with.

Sea urchins

There was a negative selectivity as well as a negative active selection for sea urchins (Figures 4 and 5b). However, sea urchins were consumed by thirteen out of fifteen crabs when presented alone, which would indicate that most of the crabs were able to handle and consume sea urchins (Figure 3a).

Sea urchins contain the least amount of energy (1.62 KJ/g wet weight, including shell parts) out of the prey items used in this experiment (Brey 2001). The crabs in test one may therefore have consumed sea urchins in a larger amount than they normally would when other prey is available to cover their energy needs. In test two, six crabs stopped consuming sea urchins while the remainder consumed them in a lower amount compared with test one; the crabs could therefore be selecting the other prey items available. The lower frequency of sea urchins in the diet when other prey is available has also been observed in a feces and stomach content analysis performed by Pavlova (2009). In that study, sea urchin frequency in the diet was lower than mollusc, bivalve, polychaet and crustacean frequencies.

The average sea urchins sizes consumed (40.04 mm in test one and 39.27 mm in test two) are characterized as medium sized individuals. The crabs may therefore be displaying a size selection. Pavlova (2009) found through stomach content samples and feces analysis that juvenile and adult male crabs for the most part selected small and medium sized sea urchins in the field. In laboratory experiments, Jørgensen (2008) found that adult male king crab preferred prey larger than 30 mm and that for round prey such as sea urchins the upper size limit was 50 – 60 mm diameter/height. In this experiment, the average sea urchin size presented was 40 mm but a number of the sea urchins were as large 60 – 70 mm. Presenting a larger amount of small juvenile sea urchins may have resulted in a higher consumption.

Wong and Barbeau (2005) believe predators may evaluate prey based on some stimuli the predators receive such as the prey's strength and size compared to the other prey available in the environment. In test two in this experiment, the crabs may have evaluated the sea urchins as too large and too hard to open compared to the other two prey items available and therefore discarded most of them. This could have been a reason for the four crabs that had only ripped spikes off the sea urchins before discarding them and the smaller crabs that were seen testing the sea urchins before discarding and moving on to the next prey item (Tables A1 and A2).

Scallops

Scallops were the most consumed prey in test two (Figure 3b), the most selected prey by the middle and large size groups (Figure 4) and the most actively selected prey (Figure 5) by all crabs and size groups in this experiment. Three crabs, however, did not consume any scallops in either test. These individuals may not have been able to or chose not to handle and consume them. Active selection was evident because a majority of the crabs consumed more scallops than expected when given a choice of multiple prey types in test two. The high consumption and selection of scallops is also supported by other reports based on both stomach content analysis and laboratory experiments, where mollusks such as scallops have proved to be one of the dominant prey items selected and consumed (Jewett and Feder 1982, Jørgensen 2005, Jørgensen and Primicerio 2007, Britayev et al. 2010).

There may have been both passive and active selection behind the scallop consumption. Scallops were more evenly spread on the tank bottom than the other prey and therefore may have had a higher encounter rate. Crabs did not have to search long before they encountered scallops. Scallops can move by a form of swimming, but in a majority of the attacks by crabs scallops were not quick enough in their reaction and were therefore often caught and consumed. Scallops contained an intermediate amount of energy (2.63 KJ/g wet weight, including shell parts), higher than that found in sea urchins and lower than that found in eggs (Brey 2001). The crabs could have been actively selecting scallops over sea urchins when they had the choice available. A number of reports on feeding habits and stomach content analysis on king crab show that slow moving prey such as benthic molluscs and echinoderms are some of the most important prey species (Britayev et al. 2010).

Crabs may have found handling the scallops easier than sea urchins even though there was no significant difference in average handling times of the two prey types (Figure 6). Small crabs as well as large crabs were able to crack open scallops of different sizes. Therefore chela size may not have been a limiting mechanism for handling scallops as it seemed to be for sea urchins. In laboratory experiments, Jørgensen (2008) found that there was no upper prey size limit for handling flat bodied organisms such as scallops; adult and immature crabs were able to open scallops in a range of sizes. Small crabs have been found to have a claw strength that is much stronger than the resistance in a shell of 75 mm shell height (Jørgensen and Primicerio 2007). The largest scallop to have been observed crushed by an adult male crab was about 90 mm shell length (Jørgensen and Primicerio *op. cit.*). The crabs may therefore have actively selected scallops over sea urchins.

It has been hypothesized that crabs eat more scallops and barnacles after molting in spring time to replace the calcium carbonate and energy lost during the process (Falk-Petersen et al. 2011, Jørgensen and Nilssen 2011). It is therefore important to note that all the crabs used in this experiment had a clean carapace and were caught in May which is after the molting period. How much of the shell parts the crabs consumed in this experiment is unknown. A majority of the shell and shell fragments were left on the tank bottom after foraging but the crabs may have ingested small portions of the shell.

Factors in prey consumption and selection

The amount of food consumed and diet composition of the red king crab has been found to be season and area specific as well as being based on the most abundant prey species available (Jewett et al. 1982). The results found in this experiment may therefore be due to both the origin of the crabs as well as a combination of passive and active selection. Presenting a generalist predator like the king crab with only one prey item may not give them the correct selection of nutrients. The crabs may therefore have been able to select a more correct combination of prey in test two. The temperature in the experiment tanks could be an important factor in the amount of prey consumed and the diet observed; juvenile crabs have been found to increase their consumption with increasing temperature (Zhou et al. 1998).

Some crabs may not have encountered the prey items before the start of the experiment, and therefore may not forage on this new prey. This could be the case for the two crabs that did not consume sea urchins and the three crabs that did not consume scallops in either test one or test two (Figure 3a and 3b, Tables A1 and A2). Predators presented with a new prey organism need a learning period during which they handle the prey and develop a possible preference. During this learning process they learn better handling techniques and develop shorter handling times.

If a crab individual is not capable of learning how to handle a specific prey item, it could give an "observed preference" for only prey it knows how to eat (Singer 2000). However, Jackson and Underwood (2007) meant that using the same test individuals in both tests (no choice available vs. choice available) could give the individuals enough time to learn how to handle the new prey item and develop shorter handling times during test one. Therefore the observed selection could be due to a change in behavior based on their learning in test one. This may be a reason behind the six crabs that consumed a higher number of scallops in test two compared to test one (Figure 3 and Tables A1 & A2).

4.2 Treatment design limitations

It is important to point out that results gained from laboratory experiments may not be applicable to the real environment, because the environment is much more complex. However, they give an important indication of the interaction between predator and prey and can aid in the understanding of the results gained from field investigations as well as the predator's possible effect on their environment (Brousseau and Baglivo 2005).

This experiment tested a small number of crabs; using more crabs would have given stronger statistical significance to the results. Also, using a larger range of crab sizes may have given a stronger crab size to prey selection correlation, where a stronger indication of active selection for eggs may have become evident.

During the daily feeding of capelin to the crabs in the storage tanks (with 16 and 17 individuals), there appeared to be a strong aggressive and competitive foraging on the fish. Testing crabs alone and together with one or more crabs may reveal a density dependent result on egg predation and spillage. In a laboratory experiment performed by Lis Jørgensen, king crabs were presented with scallops and other prey at densities of 0.5, 1.5 and 3 crabs per m^2. The amount of scallops eaten per capita did not change with crab density but the amount of scallops caught, crushed/ruined and not eaten correlated with density of medium sized crabs (approximately 1450 – 1680 g) (Jørgensen 2005). This was a little higher than the average weight of the crabs used in this experiment (1159 g).

If the duration of the tests had been longer, giving the crabs more time to handle and consume the different prey items, there may have been a different amount of scallops and sea urchins consumed. However, a possible switching to an initially less selected prey item may then have occurred making selection and active selection more difficult to detect.

The presence of a defending lumpfish male in the experiment may have made it more difficult for large crabs to consume eggs. The lumpfish male may also have been able to fend off the smaller crabs. Defending male lumpfish are known to chase, bite and pick up predators. The best way to test this would be to do a field experiment.

An attempt was made to determine the amount of energy gained from the different prey items. However, the attempted calculations and analysis gave uncertain results. To remedy this, the energy content in the different prey items could have been found and calculated more accurately by measuring, weighing and marking the individual sea urchins and scallops presented. These remains could have been further dried to get the dry weight. This would give a more accurate overview over the energy content of the prey items. Had the crabs consumed the entire prey item it would have been possible to calculate the energy gained; the presence of sea urchin and shell fragments indicates the crabs did not consume the entire prey. In addition, literature data on energy content per gram wet weight (KJ/g wet weight) for the different prey items may not be accurate and applicable to the prey items presented in this experiment.

The videos analyses could have been performed more thoroughly. The average searching time for the prey items, the number of times the crab individuals encounter a prey item and the number of times a prey item was discarded could have been recorded. Finding encounter rates would give a better understanding of the selection and active selection observed, but such detailed analysis was beyond the scope of this project.

4.3 Possible environmental impacts

The introduction of the red king crab is considered to have possible negative effects on the benthic environment they invade in northern Norway: by consuming an array of organisms ranging from plants to animals and by reducing a number of slow moving species such as bivalve, echinoderm and polychaet populations in local inhabited areas. In invaded localities in the Varangerfjord, there has been a decline in benthic species diversity, most species have declined while some species appear to have disappeared (Oug et al. 2010). It is thought that the benthic community in areas with the highest densities of crabs will suffer the most. In the fjords and along the coast of Norway the crab population is more concentrated than in the Russian part of the Barents Sea, because the bottom topography is characterized by a steep incline to deeper waters (300 m) (Jørgensen and Nilssen 2011). The crab population may therefore become more concentrated and stay year round in these deep fjords and along the coast making the predation pressure stronger. Most of the crabs used in this experiment were able to handle and consume the prey items presented and could therefore (depending on the concentration) potentially have an effect on these prey species in the natural environment.

Lumpfish eggs

The results found in this experiment would indicate that the red king crab could potentially have a negative effect on lumpfish eggs. All the crabs in this experiment consumed and spilled eggs in test one and test two. In the sea, small juvenile crabs with a CW up to about 50 – 60 mm stay in shallow waters before maturing and going into deeper waters. They reach this size after about 5 years (Falk-Petersen et al. 2011). This would mean a 5 year overlap in time and space between these juvenile crabs and guarding lumpfish males with egg clutches. It is uncertain how much predation by a small crab would affect lumpfish eggs because there is, of yet, no knowledge on how well a guarding lumpfish male would be able to fend off a crab of this size. Adult crabs, which also consumed eggs, come into shallow waters during spring to spawn and could therefore also overlap with the lumpfish egg in both time and space, but for a more limited time period. Spawning female crabs have also been observed in protected areas with sea weed and in kelp beds where lumpfish choose to spawn (Jørgensen and Nilssen 2011).

All the crabs in this experiment spilled a large number of eggs and pieces of egg lump (Table A1 and A2). In the environment these eggs are likely to drift away from the lumpfish male with the water currents. The eggs will not receive proper care, are unlikely to hatch and are likely to be preyed upon by other predators. The red king crab can therefore have a much larger effect on the lumpfish eggs than previously expected. In test one, they ate and spilled twice the amount of eggs as they did in test two. It is therefore likely that egg lumps in areas with no associated fauna are more vulnerable than those in areas with much alternative prey.

The king crab fishery in eastern Finnmark (east of 26° East) is now based on harvesting only large crabs (130 mm CL and larger). As a consequence of this, it is thought that the population structure in this area may change over time to contain a large number of small individuals (Sundet 2010, Fossum 2011). Although smaller crabs consume less prey than large adult crabs per capita they have been found to destroy a larger amount of biomass than they consume because of their lower efficiency in handling prey (Pavlova 2007). In a field experiment performed in the Kola Bay by Pavlova (2008) there was a marked decline in benthos biomass in areas with a large number of juvenile crabs (5 crabs/100 m^2). This constant presence of smaller crabs and their low efficiency in handling prey such as lumpfish eggs, the presence of adult crabs in the spring coupled with the fishery on lumpfish females with roe each spring could contribute to a decline in the lumpfish population in years of low recruitment.

Sea urchins

It is thought that sea urchins that graze down seaweed and kelp forests can leave lumpfish eggs more open and easily available to predation (Anon. 2007). Such heavy grazing has been the case in the Porsangerfjord, where the crabs used in this experiment were caught. A number of important fish populations such as cod (*Gadus morhua*) and wolfish appeared to decline heavily after the deforestation (Sunnset 2008). Scientists researching this fjord are investigating if the king crabs consumption of sea urchins could help alleviate this reduction in seaweed and deforestation of the kelp forests (Sunnset *op. cit.*). The crab could therefore have contrasting effects on lumpfish eggs. Predation on sea urchins could help the eggs be less vulnerable to predation by other species through aiding in seaweed recovery, but at the same time the crabs could consume the eggs themselves. According to calculations done by Gudimov et al. (2003), adult male crabs are capable of consuming approximately 10 – 20% of the sea urchin population each year. This may not be a sufficiently high consumption to have a marked effect on the sea urchin population grazing on kelp. However, this effect would be dependent on both the density of crabs and how much effect small and medium sized crabs could have on sea urchin populations. This is not proven yet, but they could potentially have a negative effect as the crabs are found year round in areas with sea urchins.

As is the case in field observations (Gudimov et al. 2003, Pavlova 2009), both small and large crabs in this experiment consumed small to medium sized sea urchins. It has also been shown that female king crab have a significantly higher amount of sea urchins in their diet compared to males, therefore they may have a bigger effect on sea urchin population (Pavlova 2009). This could contribute to a decline in the number of sea urchins in coastal areas over time and may also change the size composition of sea urchins in local heavily predated areas. Small and medium sized sea urchins have been observed in crevices and under rocks in the Barents Sea (Falk-Petersen et al 2011). It has been hypothesized that this is a new anti predator behavior developed in the last couple of years (Falk-Petersen *op. cit*.).

Scallops

In this experiment, there was a positive correlation between the amount of scallops consumed and the size of the crab (Figure 3). Large crabs may therefore have the biggest effect on scallop beds. They have larger chela and can open scallops in a range of sizes and results on handling times suggested that they are also able to open the scallops faster than the smaller crabs. However, large crabs are only present in shallow areas with scallop beds in spring and summer and therefore may have a large effect for only short periods each year (Jørgensen 2005). Small crabs are capable of handling larger scallops but often prefer small and medium sized scallops (Jørgensen and Nilssen 2011). Since they stay in shallow water for five years it would cause a steady predation on these scallop sizes. Over time, this could lead to lower scallop recruitment since they do not reach reproductive age until they are 3 – 6 years old (Jørgensen 2005). In this experiment, a lot of the crabs opened and discarded scallops without consuming them (11 incidences of discarding, Tables A1 and A2). This means that the king crab can have a larger effect on scallop beds than believed through stomach analysis. It has been shown through time series studies that scallop and echinoderm populations are declining in areas with king crab, both in the Bering Sea and in the Barents Sea (Varangerfjord, Motovsky Bay and Dal'nezelenetskaja Bay) (Falk-Petersen et al. 2011).

4.4 Main conclusions

The crabs did demonstrate different selection and active selection for the different prey items presented, significantly selecting eggs and scallops and actively selecting scallops. There was no significant active selection for lumpfish eggs when the king crab was given a choice of alternative prey items, although all the crabs were capable of handling and consuming eggs. The experiment showed that a larger amount of eggs were spilled than consumed meaning that the king crab can have a larger effect than expected through consumption alone. There was a significantly higher consumption of eggs and sea urchins when there was no choice of prey compared to when there was a choice available, the crabs consumption of scallops had the opposite pattern.

There appeared to be an increase in the amount of prey consumed with increasing crab size. The largest crabs appeared to have a more diverse diet than the smallest by including most prey items when given a choice. Energy content in the three prey items differed and may have been an underlying factor in the observed selection of the two most energy rich prey items: eggs and scallops. Handling time did not appear to be of importance in the consumption and selection of prey. For sea urchins, their shape and size may have been a limiting factor in the predation on them, this, however, was not apparent for the other two prey items.

In the environment, the red king crab could potentially have a negative effect on lumpfish eggs due to both their consumption and spillage. Juvenile and adult crabs also overlap with the spawning fish in both time and space, making the chances of predation high. There is, however, no data on how well a defending lumpfish male would be able to fend off a small sized king crab, therefore more knowledge is needed here. There appeared to be a selection for medium sized sea urchins in this experiment, as has been found in other diet research (Gudimov et al. 2003, Pavlova 2009), which could over time have an effect on local populations' size composition. Scallops were consumed by all the size groups used in this experiment, there was also a high occurrence of scallops being discarded after opening; this could lead to a steady predation by small sized crabs throughout the year and a seasonal predation by the adult crab population (Jørgensen 2005, Jørgensen and Primicerio 2007). Over time this could reduce local scallop populations, depending on the abundance of king crabs.

4.5 Further research

Most of the diet research performed in the Barents Sea has been done on adult male crabs. It would be beneficial to get a better understanding of both juvenile and female crab diets and their effect on the environment. Only 4 out of 23 papers based on king crab diet have been focused on juveniles (< 60mm CL) (Falk-Petersen et al. 2011). Juvenile crabs spend up to five years in shallow water and are thought to represent 80% of the total king crab population (Falk-Petersen op. cit.). The exact amounts of benthic biomass small crabs are able to consume and destroy also needs more consideration. Zhou et al. (1998) found in a laboratory experiment that adult female crabs had a significantly higher feeding rate than male crabs. They have also been found to choose a different array of prey items and size groups and have a different diet in some parts of the year (Jewett and Feder 1982, Sundet et al. 2000, Gudimov et al. 2003, Pavlova 2009).

More laboratory and field experiments where the prey items available have been better quantified could yield a more accurate result on the crabs selection, diet composition, consumption rate and prey damage. Stomach content analysis which most king crab diet research is based on can often be misleading. The crabs digestion is fast and before moving on to the stomach the food is passed through the gastric mill where food gets further masticated (Pavlova et al. 2007). Some prey items such as the soft parts in sea urchins and scallops and fish remains are often too digested to be quantified (Pavlova *op. cit.*). The crabs often damage prey without consuming them; this would not be quantifiable through stomach content analysis alone.

It is important to increase the knowledge surrounding the king crabs effect on the environment, which is still largely unknown and under a lot of debate. An increased research and understanding of the composition of the benthic ecosystems in areas threatened by invasion and those already invaded would give an increased understanding of how much effect the king crab has. There is a limited understanding concerning the composition of benthic fauna along the coast of Finnmark (Anon. 2007). To increase this understanding, institutions surveying the benthic environment along the coast of northern Norway should coordinate their results (Øseth 2008). Long term monitoring of a locality threatened by invasion would be beneficial to get an understanding of how an ecosystem changes before and after the invasion.

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6. Appendix

Table A1. Information and results for test one. With the crab length across the carapace from eye socket to the back portion of carapace (CL), crab width across the carapace (CW), the order in which prey was presented to them: sea urchins (U), eggs (E) and scallops (S); the tank and order they were tested in them, how many grams egg were eaten and spilled, how many grams sea urchins and scallops were eaten, the number of sea urchins and scallops were eaten.

Individual (nr)	Crab size (g)	Crab length (CL) mm	Crab width (CW) mm	Prey order	Tank order	Eggs (g)	Egg spillage (g)	Sea urchin (g)	Nr. of sea urchins eaten	Scallop (g)	Nr. of scallops eaten	Other behaviour noted
1	1420	121	136	SU - E - S	B - A - C	18.70	11.50	105.60	2	39.70	2	All eggs ripped from rock
3	300	84	94	E - SU - S	A - B - C	-	23.50	32.50	1	95.70	2	
6	1800	132	148	E - S - SU	C - B - A	7.80	19.60	70.30	3	50.90	3	All eggs ripped from rock
13	520	89	95	E - SU - S	C - B - A	16.40	6.30	25.60	1	23.50	1	2 sea urchins had spikes pulled off
14	1980	134	151	S - SU - E	A - C - B	18.70	63.70	188.40	7	108.00	5	All eggs ripped from rock
16	740	96	105	SU - E - S	A - B - C	8.60	59.00	-	-	37.30	2	All eggs ripped from rock
17	620	95	101	S - E - SU	B - A - C	16.00	37.90	82.00	1	55.30	1	1 discarded sea urchin
18	440	80	89	S - SU - E	B - C - A	10.30	67.10	47.10	3	36.10	3	3 discarded scallops
19	680	100	116	SU - S - E	A - C - B	18.30	135.00	82.10	3	-	-	
21	2220	133	154	SU - S - E	B - C - A	28.10	133.60	210.90	8	171.70	10	3 discarded scallops + all eggs ripped from rock
23	1660	122	141	E - SU - S	C - A - B	21.10	89.30	86.50	5	82.90	5	Only sand left from sea urchins
24	1280	115	131	E - SU - S	B - A - C	15.90	130.00	-	-	-	-	All eggs ripped from rock
26	1740	123	142	S - E - SU	A - B - C	23.00	144.20	192.00	6	58.70	2	1 discarded scallop + all eggs ripped from rock
27	1020	103	120	S - E - SU	A - C - B	21.70	137.10	37.20	2	-	-	Only sand left from sea urchins
30	960	107	115	SU - S - E	C - B - A	26.80	130.40	58.20	2	52.40	2	1 sea urchin had spikes pulled off
Total	17380	1634	1838			251.40	1188.20	1218.40	44.00	812.20	38.00	
Average	1158.67	108.93	122.53			17.96	79.21	93.72	3.38	67.68	3.17	
Standard deviation	615.26	18.18	22.53			6.15	52.10	63.50	2.36	41.41	2.52	

Table A2. Information and results for test two. With the crab length across the carapace from eye socket to the back portion of carapace (CL), crab width across the carapace (CW), which tank they were tested in, how many grams egg were eaten, how many grams eggs were spilled, how many grams sea urchins and scallops were eaten, the number of sea urchins and scallops consumed. Total amount of prey the crabs ate and other behavior.

Individual (nr)	Crab size (g)	Crab length (CL) mm	Crab width (CW) mm	Tank	Eggs (g)	Egg spillage (g)	Sea urchin (g)	Nr. of sea urchin eaten	Scallop (g)	Nr. of scallops eaten	Total amount of food eaten (g/22hours)	Other behaviour noted
1	1420	121	136	B	-	-	62.50	3	65.30	2	127.80	1 discarded scallop
3	300	84	94	C	20.30	70.70	-	-	28.60	2	48.90	1 discarded scallop
6	1800	132	148	C	0.50	18.10	-	-	91.40	5	91.90	1 discarded scallop
13	520	89	95	B	9.40	-	-	-	55.30	2	64.70	
14	1980	134	151	A	-	94.20	42.80	2	168.20	9	211	1 discarded scallop
16	740	96	105	A	4.90	8.40	-	-	89.16	2	94.06	2 discarded scallops + all eggs ripped from rock
17	620	95	101	A	12.30	-	-	-	42.90	3	55.20	
18	440	80	89	B	8.90	6.40	-	-	33.00	1	41.90	2 sea urchins with spikes pulled off
19	680	100	116	C	20.30	29.80	29.90	1	-	-	50.20	1 sea urchin had spikes pulled off
21	2220	133	154	C	4.90	47.80	16.80	1	163.40	8	185.10	1 discarded sea urchin + 1 scallop
23	1660	122	141	A	4.40	133.90	28.70	1	127.50	7	160.60	
24	1280	115	131	A	26.50	129.70	-	-	-	-	26.50	All eggs ripped from rock
26	1740	123	142	B	6.50	8	56.60	2	44.70	2	107.80	Only sand left from sea urchins
27	1020	103	120	B	7.00	26.40	20.60	1	-	-	27.60	1 discarded scallop
30	960	107	115	C	1.20	26.50	-	-	85.90	5	87.10	1 discarded scallop
Total	17380	1634	1838		127.1	599.90	257.9	11.00	995.36	48.00	1380.36	
Average	1158.67	108.93	122.53		9.78	49.99	36.84	1.57	82.95	4.00	92.02	
Standard deviation	615.26	18.18	22.53		41.94	46.43	17.63	0.79	48.09	2.73	2.73	

Table A3. Latin square design used during test one. Which design and which tank the crab started in was chosen at random.

Crab nr	Tank A	Tank B	Tank C
21	Eggs - day 3	Sea urchins - day 1	Scallops - day 2
26	Scallops - Day 1	Eggs - day 2	Sea urchins - day 3
23	Sea urchin - day 2	Scallops - day 3	Eggs - day 1
6	Sea urchins - day 3	Scallops - day 2	Eggs - day 1
1	Eggs - day 2	Sea urchins - day 1	Scallops - day 3
14	Scallops - day 1	Eggs - day 3	Sea urchins - day 2
16	Sea urchin - day 1	Eggs - day 2	Scallops - day 3
18	Eggs - day 3	Scallops - day 1	Sea urchins - day 2
3	Eggs - day 1	Sea urchins - day 2	Scallops - day 3
27	Scallops - day 1	Sea urchins - day 3	Eggs - day 2
30	Eggs - day 3	Scallops - day 2	Sea urchins - day 1
24	Sea urchins - day 2	Eggs - day 1	Scallops - day 3
17	Egg - day 2	Scallops - day 1	Sea urchins - day 3
19	Sea urchins - day 1	Eggs - day 3	Scallops - day 2
13	Scallops - Day 3	Sea urchins - day 2	Eggs - day 1

Table A4. Average handling time in minutes used by the individual crabs viewed based on (n) observations.

Crab nr.	Crab weight (g)	Test nr.	Avg. handling time egg, min. (n)	Avg. handling time sea urchins, min. (n)	Avg. handling time scallops, min. (n)
1	1420	One	-	-	59 (2)
3	300	One	-	-	186 (2)
3	300	Two	23 (7)	-	157 (2)
4	360	One	7 (4)	-	-
6	1800	One	53 (4)	-	-
6	1800	Two	18 (2)	-	52 (5)
7	720	One	7 (21)	-	-
13	520	One	17 (21)	-	-
14	1980	One	-	62 (7)	-
16	740	One	-	-	210 (2)
18	440	One	-	257 (3)	-
18	440	Two	10 (10)	-	126 (1)
19	680	Two	21 (10)	41 (1)	-
21	2220	One	-	-	39 (10)
21	2220	Two	8 (4)	-	25 (8)
23	1660	One	20 (10)	-	-
26	1740	One	-	41 (6)	-
27	1020	Two	32 (9)	-	-
30	960	One	-	35 (2)	
30	960	Two	9 (1)	-	84.20 (5)
Total	16560		224	468	939
Average	1104		19	94	104
N (n)	15		12 (103)	5 (19)	9 (35)
Standard deviation	642.55		13	92	68

Table A5. The average size (mm) of the prey items sea urchins and scallops the crabs consumed in test one and test two.

Individual (nr)	Crab size (g)	Average sea urchin size in test 1 (mm)	Average scallop size in test 1 (mm)	Average sea urchin size in test 2 (mm)	Average scallop size in test 2 (mm)
1	1420	45.0	57.5	-	71.8
3	300	33.0	67.0	-	62.0
6	1800	38.7	56.7	-	65.0
13	520	44.0	62.0	-	63.5
14	1980	43.7	60.0	43.6	62.2
16	740	-	74.0	-	71.0
17	620	47.0	-	-	62.7
18	440	44.0	67.3	-	73.0
19	680	-	-	29.0	-
21	2220	40.5	60.9	38.0	66.8
23	1660	32.4	58.5	48.0	65.9
24	1280	-	-	-	-
26	1740	39.7	66.0	43.0	73.0
27	1020	28.5	-	34.0	-
30	960	44.0	69.0	-	58.6
Total	17380.00	480.50	698.90	235.6	795.50
Average	1158.67	40.04	63.54	39.27	66.29
Standard deviation	615.26	5.85	5.49	6.98	4.86