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Prey Selection By Young Green Crabs (*Carcinus Maenas*), Rock Crabs (*Cancer Irroratus*) And American Lobsters (*Homarus Americanus*) In The Gulf Of Maine

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**PREY SELECTION BY YOUNG GREEN CRABS (*CARCINUS MAENAS*),
ROCK CRABS (*CANCER IRRORATUS*) AND AMERICAN LOBSTERS
(*HOMARUS AMERICANUS*) IN THE GULF OF MAINE**

BY

Joseph Sungail
B.S. University of West Alabama, 2006

THESIS

Submitted to the University of New England
in Partial Fulfillment of the
Requirements for the Degree of

Master of Science

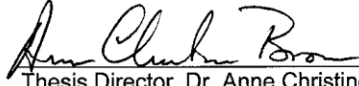
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Marine Sciences

August, 2010

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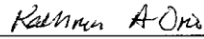
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DEDICATION

This thesis is dedicated to all my family and friends that believed in and supported me throughout my education.

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ABSTRACT

PREY SELECTION BY YOUNG GREEN CRABS (*CARCINUS MAENAS*), ROCK CRABS (*CANCER IRRORATUS*) AND AMERICAN LOBSTERS (*HOMARUS AMERICANUS*) IN THE GULF OF MAINE

by

Joseph Sungail

University of New England, August, 2010

The intertidal zone in the Gulf of Maine supports large populations of three species of decapods. Young green crabs (*Carcinus maenas*), rock crabs (*Cancer irroratus*) and American lobsters (*Homarus americanus*) co-exist in close proximity and forage on similar prey species. Competition for prey resources could have major implications for the populations of these predators. This experimental study focuses on determining the potential for interspecific competition between these decapods for prey resources. Young green crabs (25 - 35 mm carapace width), rock crabs (25 - 35 mm carapace width) and American lobsters (25 - 35 mm carapace length), were collected along with the prey species blue mussels (*Mytilus sp.*), rock barnacles (*Semibalanus balanoides*) and common southern kelp (*Saccharina latissima*) from the intertidal of the southern section of Saco Bay in the Gulf of Maine. Claw measurements were taken, prey size and prey species preference was tested and caloric value of prey was determined. Morphological measurements indicated that all three decapod species had different sized chela relative to body size. The three

predators preferred similar sized mussels and barnacles, and had similar handling times for both of these prey species. None of the three predator species consumed measurable amounts of kelp. Rock crabs and lobsters preferentially selected mussels over barnacles, while green crabs consumed equal amounts of both prey species. The preferred mussel size was smaller than the calculated optimum while the optimal barnacle size was eaten. These results suggest that while green crabs, rock crabs and lobsters have differing claw morphologies, they select similar prey and consume prey at the same rate. Therefore there is a possibility of intense interspecific competition among these predators.

1. INTRODUCTION

The rocky intertidal is a diverse and complex ecosystem (Lewis, 1964). The dynamics between predator and prey in this habitat have provided a wealth of insights into the ecological interactions of many species (see review by Underwood, 2000). Some of the more abundant and noticeable benthic predators in this habitat are decapod crustaceans (Ojeda and Dearborn, 1990). This group of predators has a huge potential to shape the ecology of this vast and important habitat (Menge, 1983; Tyrrell *et al.*, 2006).

There have been a wide range of studies concerning the ecology of American lobsters (*Homarus americanus*), rock crabs (*Cancer irroratus*) and green crabs (*Carcinus maenas*) (Reilly and Saila, 1978; Menge, 1983; Ojeda and Dearborn, 1991; Grosholz and Ruiz, 1996; Jones and Shulman, 2008). However, research regarding interspecific foraging interactions between young (animals that are either immature or just becoming reproductively active) of these species has been largely ignored. All three species have been shown to utilize areas of the Gulf of Maine as a nursery for their young (Berrill, 1982; Palma *et al.*, 1999), with some of them remaining in the nursery habitat for several years (Berrill, 1982; Cowan *et al.*, 2001). Larvae from both the American lobster and rock crab have been found to settle and mature on cobble substrate in close proximity to one another (Palma *et al.*, 1999). Sub-adult American lobsters and green crabs

were regularly observed within one to two meters of each other in Passamaquoddy Bay, Canada (Lynch and Rochette, 2009). Also, young of all three species have been collected from an area around Biddeford Pool, Maine on cobble substrate (Brown, unpub. data). With such highly active predators in close proximity the possibility for interspecific competitive interactions is high.

Diet studies have shown that American lobsters, rock crabs and green crabs in various areas utilize a wide range of food resources (Ojeda and Dearborn, 1991; Stehlik, 1993; Sainte-Marie and Chabot, 2002; Brown, unpub. data). When examining stomach contents of young lobsters, green crabs and rock crabs in the Gulf of Maine, three categories that made up the largest portion of each species' stomach volume were barnacles (*Balanus* sp.) (40%), mussels (*Mytilus* sp.) (30%) and brown algae (20%) (Brown, unpub. data). These three prey items have been observed being preyed upon and found in the stomachs of all predator species both in the Gulf of Maine and abroad (Rangeley and Thomas 1987; Ojeda and Dearborn, 1991; Stehlik, 1993; Sainte-Marie and Chabot, 2002; Baeta *et al.*, 2006; Tyrrell *et al.*, 2006). This shows that similar prey is being consumed regularly by the young of all three decapods species. However, it is still unknown if a preference for a particular size group or prey species exists for each decapod predator.

Consumption of the same prey species does not necessarily infer direct competition. The ability to utilize prey resources may vary among these three decapods causing either an increase or decrease in interspecific competition. There are morphological differences among adults of each species that may

account for resource partitioning between these decapods. Moody and Steneck's (1993) findings suggest a functional dichotomy exists among the adults of each of the three species. The lower dexterity of the American lobster compared to the crabs, coupled with differing claw morphologies creates contrasting foraging tactics when they are presented with mussels. Lobsters are restricted to crushing, while both crab species can crush, chip and pry open mussels. These differences allowed for the rock and green crabs to successfully attack larger mussels and have shorter handling times than the lobsters by utilizing complex attack methods. The two crab species also differ from one another in regards to their chelae. Rock crabs have slightly smaller claws relative to body size than green crabs (Vermeij, 1977), which could have an effect on prey choice.

There have been few studies examining the interspecific competition between the American lobster, rock crab and green crab of any life history stage. Rossong *et al.* (2006) showed that adult [53 - 76 mm carapace width(cw)] green crabs out-competed juvenile [28 – 57 mm carapace length(cl)] lobsters for food. It has also been found that when competing for a limited food resource adult (63 - 75 mm cw) green crabs were generally first to the food and were able to defend it from sub-adult (55 - 70 mm cl) American lobsters. However, when the American lobster was first to the food it successfully defended it (Williams *et al.*, 2006). An opposing result was seen by Lynch and Rochette (2009), who observed lobsters were not negatively impacted by green crabs of a similar body mass and even found evidence of lobsters utilizing green crabs as prey. Various pairings of decapods demonstrate differing degrees of behavioral influences. Adult rock crab

foraging is not affected by the presence of an adult Jonah crab (Salierno *et al.*, 2003); however, a barrier separated the rock crab and Jonah crab during the experiment. Thus, there is still a possibility that these two species could exhibit competitive interactions and an effect on each other's foraging behavior if they are not segregated. When allowed to interact, Jonah crabs consume less food when in the presence of American lobsters (Siddon and Witman, 2004). These observed interactions demonstrate the ability for decapods to influence foraging in heterospecifics.

The present evidence suggests that young American lobsters, young rock crabs and young green crabs inhabit the rocky intertidal, prey upon mussels, barnacles and algae, and are capable of affecting the foraging behavior of one another. Better understanding these interactions is important because of the commercial value of lobsters and the need to maintain the fishery (Anonymous, 2009). The effect of the invasive green crab on the two native decapods and their prey preferences also requires more investigation in order to determine their impact on the ecosystem. Young crabs (25 - 35 mm cw) and lobsters (25 - 35 cl) are very abundant in the mid to low intertidal in Saco Bay and all three species are able to be found within a meter of each other (personal observation). Even though the crabs and lobsters differ in age and mass at this size range, ecologically this is an important life stage for all three species. The lobsters are beginning to actively forage outside of their shelters (see review by Lawton and Lavalli, 1995) and the crabs are just becoming sexually mature (Reilly and Sails, 1978; Crothers, 1967). Survival of the young is important for the propagation of

each species. The loss of juveniles via interspecific competition could have a major impact on adult populations, especially American lobsters since they rely on lower post settlement mortality due to their lower fecundity compared to the rock crab (Palma *et al.*, 1998). This study will address whether there is overlap in prey preferences among these three decapod predators. This will be done by presenting each crab and lobster with mussels, barnacles, and kelp in a range of sizes to determine preference for prey size. Then all three prey items of the preferred size will be simultaneously presented to test for prey species preference. Finally claw morphology and caloric content of prey will be used to further compare prey utilization of young American lobster, rock crabs and green crabs.

2. METHODS

2.1. Specimen collection and maintenance

Predators

Young American lobsters (*Homarus americanus*), green crabs (*Carcinus maenas*) and rock crabs (*Cancer irroratus*) were collected on cobble substrate by hand in the intertidal zone around Biddeford Pool, Maine (43°26'32.42"N, 70°20'28.34"W), and via suction sampling (around Wood Island, Maine (43°27'17.68"N, 70°20'6.62"W) in approximately 6 meters of water). See Table 1 for size information of specimens collected. Only animals that were undamaged (all appendages fully regenerated) and hard shelled were used in this study. All specimens were housed in individual holding containers constructed out of 7.6 cm diameter PVC pipe for crabs and 10.2 cm diameter PVC pipe for lobsters, which were soaked in sea water for one day prior to use, in the flow through sea water system in the Marine Science Center (MSC) at the University of New England (UNE). The rate of water flow was approximately 83 ml/sec. The water temperature in the system ranged from 9.7⁰C to 26.8⁰C during the six and seven month testing periods, in 2007 and 2008 respectively, with an average temperature of 16.5⁰C. Salinity ranged from 28.7 ppt to 35 ppt with 29.6 ppt being the average. Due to these fluctuations in environmental conditions

statistics were utilized to determine their correlation with predator behavior. The three species were maintained in separate 72 cm X 180 cm sea water trays to prevent any possible interspecific chemical cues from affecting behavior. All crabs and lobsters were exposed to a lighting regime reflective of the local natural light:dark cycle (10 - 14 hours of light) by exposure to white light via a 60 watt clear light bulb during the day and a 25 watt red light bulb during the night. All three species were fed chopped fish until satiated the day after they were collected from the field to standardize last meal. Then food was withheld for five days, after which prey preference testing was performed.

Prey

Mussels (*Mytilus* sp.), rock barnacles (*Semibalanus balanoides*) and common southern kelp (*Saccharina latissima*) were collected by hand from the same areas as the predator species. Mussels were maintained in flowing sea water separate from the predators at UNE until they were used in experiments. Barnacles were collected from the field on the day of any experiment in which they were used. Each barnacle was carefully removed from the rock substrate by working a chisel carefully around the base of the animal. A small drop of LocTITE[®] super glue was then applied around the circumference of the base and the barnacle was placed onto an acrylic sheet. The glue was allowed to dry for one hour prior to being submerged in water. Kelp was also collected the same day it was utilized in an experiment. It was then cut into various pieces depending on the experiment (see below).

2.2. Claw Morphology

From April 16th to November 15th of 2008 46 green crabs, 70 rock crabs and 51 lobsters between 19.23 and 63.65 cw or cl (for crabs and lobsters respectively) were collected. To ascertain any differences in claw volume, mechanical advantage and prey handling aptitude among the decapod predators the carapace width (crabs), carapace length (lobsters), chela width, chela height, chela length, maximum claw gape, the distance between the dactylus pivot point and the insertion of the closer apodeme (L1) and the distance between the dactylus pivot point and the tip of the dactylus (L2) (Figure 1) were measured for 46 green crabs, 70 rock crabs and 51 American lobsters for both chelae to the nearest 0.01 mm using digital calipers. All claw measurements were divided by the carapace width or length of the individual in order to compare claw size relative to body size between species. Principal component analysis (PCA) was performed on all chela dimensions, gape and (L1/L2) in relation to carapace length or width of the dominant (crusher) claw of the green crab and lobster and the right claw of the rock crab. PCA was performed using NTSYSpc (version 2.10d). MANOVA with Tukey HSD post hoc tests were performed via R (v 2.8.1) on the resulting principal component coordinates to determine differences among the morphology of the species.

2.3. Testing apparatus

All prey preference trials were performed in one of two identical acrylic testing apparatuses (Figure 2). Both were placed side by side in flowing sea water. Holes were drilled at both ends of the apparatus to allow water to flow from the prey area to the acclimation chambers where the predators were confined for fifteen minutes. The sides of the apparatuses were constructed using black acrylic in order to prevent the animals from seeing into the adjacent testing apparatus. The only wall that was transparent was the one closest to the prey, which allowed for unhindered observation of predation events. Perforated transparent acrylic doors were used to confine the predator in the acclimation chambers during acclimation. The doors were then removed via transparent fishing line so that the animal did not see the observer.

2.4. Prey size selection

From June 23rd to November 18th of 2007 36 American lobsters, 39 green crabs and 34 rock crabs between 25 mm and 35 mm cl or cw were collected. Each predator was used three times, once for each of the prey species. The order that the prey was presented to each subject was randomly determined. Between each test the predator was fed chopped fish for one day and not fed for five days. During feeding trials the prey was placed into the testing apparatus in the center of the prey presentation area while the crab or lobster was placed into

one of the four acclimation chambers, randomly selected. There was a fifteen minute acclimation time before the chamber's door was raised releasing the predator. The predator's actions were then video recorded using a Panasonic PV-L559 VHSC Palmcorder for one hour or until it finished feeding. For mussel size preference trials, fourteen mussels (*Mytilus* sp.) ranging from 5 mm to 40 mm in length were allowed to attach to a 9 cm X 10 cm acrylic plate for twenty-four hours prior to being presented to a single crab or lobster. Ten barnacles (*Semibalanus balanoides*) ranging from 4 mm to 16 mm in basal diameter were glued to a 9 cm X 10 cm acrylic plate and then were offered to the predator during barnacle size preference trials. Kelp (*Saccharina latissima*) was cut longitudinally and laterally into ~1.5 cm X 7 cm pieces. The kelp was also finely chopped and left mostly intact with pieces approximately 20 cm long. All four kelp cuts [2 longitudinal, 2 lateral, chopped (made from the equivalent of 2 longitudinal or lateral cuts) and 1 intact] were placed in the prey presentation area simultaneously for kelp preference trials. All trials were performed during the night under red light, due to the predators being nocturnal feeders, and viewed remotely via camcorder. If a crab or lobster molted within a week of any trial the data from that trial was discarded to avoid behavioral changes associated with molting from influencing prey choice. The size of prey consumed (mussel length, barnacle basal diameter or size of kelp piece) and the handling time (the time from first contact with the prey item until it is consumed and the remains discarded) was recorded for each trial. For each prey species the size of the first prey item consumed by each predator species was compared using Systat (v12)

to run an analysis of covariance (ANCOVA) to determine any differences in prey size selection among the American lobster, green crab and rock crab and if salinity, temperature or predator size (cw or cl) affected the size preference. Systat (v12) was also used to perform nonlinear regressions on the relationship between handling time and mussel shell length for each of the three decapods. ANCOVAs were performed using Systat (v12) to compare the relationship among \log_{10} transformed handling time, mussel length, barnacle basal diameter, salinity, temperature and predator size (cw or cl) among the three predators.

2.5. Prey species selection

A subset of the specimens collected from April 16th to November 15th of 2008 used for claw morphology comparisons were used in the prey species trials. This subset consisted of 22 American lobsters, 40 green crabs and 39 rock crabs between 25 and 35 mm cl or cw. Each of these predators was tested once by simultaneously presenting the preferred size of mussels, rock barnacles and pieces of kelp. Five mussels (*Mytilus* sp.) ranging from 10 - 15 mm in length, five barnacles ranging from 8 - 12 mm in basal diameter and two pieces of longitudinally cut kelp approximately 7 cm X 2 cm were offered in the prey presentation area in each trial. Kelp was still used in these trails even though none was consumed during the prey size selection trails in order to reaffirm the predator's indifference towards this prey item. Barnacles were glued to a 9 cm X 10 cm acrylic sheet and the two pieces of kelp were secured to a separate 9 cm

X 10 cm acrylic sheet with a small drop of glue at one end of each strip. Mussels were allowed to naturally attach to a 9 cm X 10 cm acrylic sheet for twenty-four hours. A small drop of glue was also placed on each mussel in case glue affected prey choice. All three acrylic sheets that contained the prey items were placed side by side in the testing apparatus for the trials. Predators were acclimated for thirty minutes in a randomly chosen acclimation chamber and then were allowed one hour to feed. All trials took place during the night under red light and were recorded using a camcorder. If a crab or lobster molted within a week of any trial the data from that trial was discarded. A Friedman's test with Wilcoxon post hoc test was performed using SPSS 11.0 (v 11.0.2) to determine if any prey species was consumed more than the others by each decapod species.

2.6. Profitability

Thirty six *Mytilus* sp. ranging from 10 mm to 30 mm in length and 300 *Semibalanus balanoides* ranging from 8 mm to 14 mm basal diameter were collected from May through September 2009 in the same locations as previous predator and prey collections. Mussel length, width and wet weight were measured. The flesh was then scraped from the shell and weighed. Then the flesh was placed into a Fisher Scientific Isotemp[®] oven (model 615G) for twenty-four hours at 60⁰C. The dry flesh was then weighed and a relationship between mussel length and dry tissue weight was calculated using Microsoft Excel[®].

Barnacle basal diameters and wet weight were measured for the first 100 randomly selected barnacles. This tissue was used for one of the calorimetric measurements, which was obtained by scraping the tissue out of the shell. The tissue for the other two calorimetric measurements was separated from the shell by dissolving the shell in 31% hydrochloric acid (HCl) and then rinsing the tissue in distilled water. Previous studies have shown that mussel tissue was not significantly altered by the HCl (Thayer *et al.*, 1973). Therefore, it is assumed that any tissue degradation that occurred in the presence of the HCl is minimal as all three calorie readings were close in value. After the tissue was separated from the shell it was weighed and then dried at 60⁰C for twenty-four hours and then reweighed. A relationship between basal diameter and dry flesh weight was then calculated using Microsoft Excel[®].

One gram of dried flesh of either mussel or barnacle was then compressed into a pellet and placed into a Parr 1341 oxygen bomb calorimeter that had been standardized using benzoic acid with a Parr 1760 thermometer. The caloric values were then calculated by multiplying the temperature rise with the energy equivalent of the calorimeter then subtracting the heat released by burning the ignition wire and the production of nitric acid and sulfur. Then the remainder was then divided by the mass of the sample in order to obtain cal/g (Parr Instrument Co., 1993). A fixed acid correction of 10 calories and a sulfur correction of 0% were used in all calculations. Error caused by these fixed values should be within tens of calories (Parr Instrument Co., 1993).

RESULTS

3.1. Claw morphology

The average for each claw morphology/body size ratio is given in Table 2. Principal component analysis (PCA) showed that all three decapod species have distinctive claw size to carapace width/length ratios (Figure 3). There is significant difference along principal component (PC)1 ($p = 2 \times 10^{-16}$) among all species, however there is no difference between them along PC2 ($p = 0.4$). Combined both principal components explain 97.61% (PC1 = 83.98%, PC2 = 13.63%) of the variance with heavy positive loadings of all claw measurements except for mechanical advantage (L1/L2), which has a negative loading on PC1 (Table 3). Rock crabs had the smallest claws relative to body size followed by green crabs and finally lobsters had the largest relative claws. The opposite trend is seen in relation to L1/L2 ratios with lobsters having the lowest ratio and rock crabs having the highest.

3.2. Prey size selection

Mussels

A total of 27 green crabs, 26 rock crabs and 30 lobsters were presented a range of mussel sizes. There was no significant difference between the lengths of mussels presented to each decapods species ($p = 0.1$). Salinity ($p = 0.1$), temperature ($p = 0.9$) and predator size ($p = 0.6$) did not have a significant effect on the size of mussels selected. Thirteen green crabs consumed mussels ranging from 7.40 mm to 16.15 mm in length. Thirteen rock crabs consumed mussels ranging from 5.70 mm to 18.50 mm. Six lobsters consumed mussels ranging from 7.65 mm to 22.10 mm in length. The average lengths (\pm SD) of the first *Mytilus* sp. consumed by each crab or lobster were 11.53 mm (\pm 5.21), 11.40 mm (\pm 4.13) and 13.73 mm (\pm 5.57) for green crab, rock crab and lobster respectively. There were no significant differences among these means (Figure 4, $p = 0.3$).

Salinity ($p = 0.5$), temperature ($p = 0.1$) and predator size ($p = 0.4$) did not have a significant effect of the handling time of mussels. Handling times for mussels increased exponentially with mussel length (Figure 5, Table 4). There was also no difference in handling times for mussels of various sizes between the three predator species ($p = 0.9$). Since there was no difference between species, data was pooled from all predators to show that there was a significant increase in handling time with mussel size ($p = 2 \times 10^{-7}$).

Barnacles

A total of 29 green crabs, 25 rock crabs and 30 lobsters were presented a range of barnacle sizes. There was no significant difference between the basal diameter of barnacles presented to each decapods species ($p = 0.5$). Salinity ($p = 0.2$), temperature ($p = 0.06$) and predator size ($p = 0.2$) did not have a significant effect on the size of barnacles selected. The average basal diameter of the first *Semibalanus balanoides* consumed by each crab or lobster were 11.06 mm (± 2.53) (ranging from 6.3 mm to 15.25 mm), 10.11 mm (± 2.87) (ranging from 6.30 mm to 15.25 mm) and 7.75 mm (± 3.18) (ranging from 5.5 mm to 10.00 mm) for green crab ($n = 22$), rock crab ($n = 19$), and lobster ($n = 2$) respectively. There were no significant differences among these means (Figure 6, $p = 0.2$).

Salinity ($p = 0.2$), temperature ($p = 0.8$) and predator size ($p = 0.3$) did not have a significant effect of the handling time of barnacles. No difference was detected for barnacle handling times between the decapod species ($p = 0.5$, Figure 7, Table 5). All species data was combined and showed a significant relationship between handling time and barnacle basal diameter ($p = 0.03$).

Kelp

No animals consumed measurable amounts of *Saccharina latissima* during any trial. Some would investigate the various cuts of kelp by manipulating it with their chela and maxillipeds.

3.3. Prey species selection

A total of 28 green crabs, 30 rock crabs and 20 lobsters were presented the preferred sizes of all three prey species at once with 13, 20 and 10 of each respective predator consuming a food item. No crabs or lobsters consumed a measurable amount of kelp. When taken as a whole, all three decapod species consumed more mussels than barnacles (Table 6). However, this was only significant for rock crabs ($p = 0.005$) and lobsters ($p = 0.004$). Green crabs showed no preference between mussels and barnacles ($p = 0.1$). The only other non significant difference between food choice was found in lobsters between kelp and barnacles (Table 7).

3.4. Profitability

The caloric content of dry mussel ($n = 5$) and barnacle ($n = 3$) flesh was determined to be 4028 cal/g (± 27.46) and 4554 cal/g (± 21.59) respectively. Profitability for various mussel and barnacle sizes was calculated by dividing the calculated mass of flesh by its calculated handling time (Figure 8, 9). Mussel flesh was calculated using formula (1) and barnacle flesh was calculated with formula (2). Handling time was calculated using the "All" formula in Table 4 and Table 5 for mussels and barnacles respectively.

$$\text{Log}_{10} \text{ dry weight (g)} = -5.75 + 3.17 \log_{10} \text{ length (mm)} \quad (n = 35, r^2 = 0.95) \quad \text{(1)}$$

$$\text{Log}_{10} \text{ dry weight (g)} = -4.79 + 2.61 \log_{10} \text{ length (mm)} \quad (n = 100, r^2 = 0.73) \quad \text{(2)}$$

4. DISCUSSION

4.1. Claw morphology

The chela measurements from this study show that green crabs, rock crabs and lobsters all have distinctive relative claw sizes. Claw size and shape have been used to estimate prey preference (Smallegange and Van der Meer, 2003) and interspecies differences in prey preference (Vermeij, 1977; Moody and Steneck, 1993; Seed and Hughes, 1995). Both mechanical advantage ($L1/L2$) and claw height have been heavily used when estimating claw strength (Seed and Hughes, 1995). Looking at both is important because height gives an estimate of muscle size while the $L1/L2$ ratio shows how efficiently the force produced by the muscle is transferred to the prey. The mechanical advantage can also give insights into the diet of the crab, since high mechanical advantage generally causes a claw to close slower. Thus crabs with low mechanical advantage should have quicker claws for catching highly mobile prey, while low mechanical advantage allows for slower claws that produce more force used for crushing slow moving heavily armored prey. The values found in this study for relative claw heights and widths are slightly smaller than reported in previous studies (Vermeij, 1977; Elner and Campbell, 1981). Vermeij (1977) measured preserved specimens, that were on average larger than the current study, of

green crabs (28.9 – 78.0 mm cw) and rock crabs (44.0 – 134.0 mm cw) from various museums around the world and found that the average claw height /carapace width ratio for male crabs was 0.269 for the green crab and 0.229 for the rock crab. The current study found a ratio of 0.23 (± 0.016) and 0.19 (± 0.0063) for male green crabs and rock crabs respectively. Although these values are slightly lower, the difference between the two crab species is approximately the same (0.04 compared to 0.038). Vermeij (1977) also looked at claw width/carapace width, finding male green crabs to have a ratio of 0.176 and rock crabs to have a 0.122 ratio. The values are once again higher than the ones currently observed [0.15 (± 0.01) for male green crabs and 0.11(± 0.0049) for male rock crabs]. The between species differences in Vermeij (1977) compared to the current results were not as close for this claw ratio (0.054 for the Vermeij study and 0.032 for the current study. Thus, claw height and claw width ratios found in both studies show green crabs have relatively larger chela compared to rock crabs. Elner and Campbell (1981) determined the mechanical advantage (L1/L2) of lobster crusher claws to be 0.33 (± 0.014) and 0.16 (± 0.007) for male and female lobster respectively. The current study determined the average mechanical advantage for both sexes to be 0.20 (± 0.028). Elner and Campbell (1981) used lobsters between 50 and 170 mm cl, which are larger than the current studies specimens and they are sexually mature. The reason the current studies value falls between the prior calculations could be due to the change in claw size that is associated with age and maturity (Conan *et al.*, 2001). As males age their claws become larger relative to their carapace length at a greater rate

than females (Elner and Campbell, 1981). The current studies animals are young enough not to be seriously affected by this change in claw size ratio. This would cause the ratio to be lower than the adult male ratio found by Elner and Campbell (1981).

The spread of the claw morphology data points in Figure 3 shows that both crab species have relatively low intraspecific variability compared to lobsters. It is possible that this spread is partially caused by the changing claw to body size ratios that are associated with maturation in the lobster, since males have a larger ratio than females as they mature (Conan *et al.*, 2001). It could also be due to the plasticity of the claw, which can become larger and stronger when feeding on hard shelled prey (Smith and Palmer, 1994). Thus, lobsters could be foraging on a wider variety of prey than the crabs in the field, which could possibly reduce interspecific competition. Claw shape is also affected by lobsters settling on complex substrate such as shell causing a greater claw asymmetry compared to those settling on a substrate such as sand (Goldstein and Tlusty, 2003). All crabs and lobsters for the current study were collected from cobble substrate; however, they are of a sufficient size to have traveled away from their initial settling substrate. A combination of these factors and perhaps some unknown ones could explain the higher intraspecific variability among lobsters.

The differences in morphology between these decapod species would initially support the notion that these three species would prefer different prey, either in size and or species. However, external morphology does not completely represent the prey acquisition capabilities of a decapod. There are confounding

factors such as longer sarcomere length in the claw muscles and larger apodeme plate can increase the force a claw can apply (Seed and Hughes, 1995). Taylor (2001) shows that direct comparisons of claw strength based on claw morphology between genera of crabs should be done with caution since the relationship between strength and claw size varies with species. Along with brute strength, the dexterity of a crab or lobster can allow for diverse attack methods, giving them an advantage over other species when foraging on certain prey items. The differing claw morphologies would indicate that these predators would select and handle prey differently. However, this is not the case.

4.2. Prey size selection

Mussels

Although the claw morphology data would lead one to believe that these three decapod species would differ in their aptitude to consume mussels, all three predator species had similar handling time for mussels of similar size across the size range (5.05 – 22.1 mm). This could be explained by the various attack tactics these species utilize. While lobsters have bigger claws than the crabs, they are limited to only crushing their prey while the crabs can utilize more complex attack methods such as edge chipping, boring and prying (Elner, 1978; Moody and Steneck, 1993). This difference could explain the lower (yet not statistically significant) handling times of the lobster (Figure 5). This limitation to only crushing would also theoretically cause the handling time for larger mussels

to escalate more dramatically for the lobster than for the crabs. There is evidence of this with the one large mussel consumed by the lobsters having a very high handling time, causing the trend line to be steeper for the lobster. If more data were available for the lobsters the difference between them and crabs may become significant. While there is some observation of behavior and theoretical evidence to support the idea that lobsters may have a different handling time profile than the two crab species, the green crab and rock crabs are very similar. This is expected due to similar mussel opening tactics and claw ratio differences that are within a few hundredths of each other.

With similar handling times it is not surprising that the preferred mussel size for each species is the same. There is evidence that these species' preferences overlap. With the crabs being very close (a difference of only 0.13 mm) in average mussel size consumed and the lobster having a slightly higher average (~2.2 mm greater than the crabs). The selection of these sizes might also be affected by the size of mussel most commonly encountered in the field since it has been shown that crabs can be trained to preferentially select a size class of mussels (Smallegange *et al.*, 2008). As with handling time the small sample size of lobsters possibly prevents the detection of a preference for a different size class than the crabs. The preferred mussel size of green crabs in the size range of interest falls within the preferred range found in other studies. (Mascaro and Seed, 2001; Enderlein *et al.*, 2003). The profitability curves generated from the current study show that the optimum mussel size to be around 20 mm (Figure 7). The average size consumed by the crabs was lower

than this (11 mm). The selection of smaller than optimal mussels is thought to be a way to minimize claw damage and therefore allow the crab to forage optimally over a large time scale and allow the crab to have a greater overall fitness (Smallegange and Van Der Meer, 2003; Aronhime and Brown, 2009).

Barnacles

Similar to mussels, no significant differences for the size of rock barnacles consumed were found among the three predator species. The crabs selected sizes closer to one another (a difference of 0.95 mm) than the lobster (~2.3 mm different from the crabs). Like the predation on mussels there was a significant effect of prey size on handling time. However, the relationship is weak with a r^2 value of 0.111 which shows that barnacle size was not a major factor in the consumption of the prey. It is doubtful that the artificial attachment method is completely responsible for this weak correlation between basal diameter and handling time. The reattachment of barnacles was done by dispensing a small amount of glue around the base, thus, larger barnacles should be more secure. Also, qualitatively barnacles were more difficult to remove from the artificial substrate that they had been glued to than their natural substrate using a chisel, showing that the barnacles were firmly attached to the acrylic sheet. It is possible that there is a critical size at which barnacles are equally difficult to attack. This may be due to the smaller barnacles being harder to grip than larger ones until the barnacle reaches a certain size at which point the crab can apply all the force it needs to overcome the barnacle's defenses. This difficulty with gripping prey was very apparent in the lobster. Lobsters generally had to turn on their sides in

order to properly grasp a barnacle in a way that they could crush it. This awkward attack method resulted in very few successful predation events. An increase in base diameter might also increase the probability that there is a weakness in the protective plates or the attachment to the substrate that the decapods could exploit. This thought is given some weight when considering the attack methods of the crabs. Most crabs started out their attack by working their chela along the base of the barnacle where it was attached to the substrate. This natural behavior could be the crabs' way of attacking the barnacle at its weakest point in order to pry it from the substrate. Gubbay (1983) found that the larger a barnacle is the more force is required to crush them or pull them from the substrate and the force required to remove the barnacle is less than the crushing force. Green crabs were observed in the collection area attacking the base of barnacles in the same manner observed during the lab feeding trials. In the lab nearly all of the barnacles consumed by green crabs were pulled off the substrate (18 out of 22), while rock crabs pulled off slightly less than half of the total consumed (8 out of 19). The other barnacles were hollowed out by the crab forcing its claws into the aperture of the barnacle and pulling out the tissue. The rock crabs relatively smaller claws may allow it easier access via the aperture, which could account for the increased usage of this attack method compared to the green crab.

Kelp

No specimen consumed measurable amounts of the common southern kelp. Several specimens did investigate the kelp by manipulating it with their chelae and maxillipeds but would not consume it. Various personal observations both in

the field and lab indicate that both green crabs and rock crabs do eat kelp. However, in all these observations the kelp was either in the process of decomposition or it had various organisms growing on it. In all the experimental trials healthy, fresh pieces of kelp that were free of all fouling organisms were used. Thus, *Saccharina latissima* seems not to be desirable to green crabs, rock crabs and lobster in its fresh state. This may be due to predator deterring chemicals that the kelp produces or the kelp may not be profitable for the crab or lobster to eat and is only ingested secondarily as encrusting organisms are consumed. Previous diet studies have commonly found algae in the stomachs of these decapods, however, the algae was only a minor part of the overall stomach content (Ojeda and Dearborn, 1991; Stehlik, 1993; Sainte-Marie and Chabot, 2002; Baeta *et al.*, 2006). Further testing is required to better understand this predator prey interaction.

4.3. Prey species selection

The rock crab and lobster both preferred mussels over barnacles and kelp, while green crabs preferred either mussels or barnacles over kelp. Stomach content has also shown that bivalve mollusks make up a larger portion of gut content in lobsters (Ojeda and Dearborn, 1991; Sainte-Marie and Chabot, 2002) and rock crabs (Ojeda and Dearborn, 1991; Stehlik, 1993). The lobster preference for mussels is expected due to their observed difficulty handling barnacles. Green crabs were less selective than the other species. This more

generalist approach to prey selection could contribute to the green crabs successful spread to most temperate coastal regions of the world (Grosholz and Ruiz, 1996). Rangeley and Thomas (1987) found that green crabs between 21 mm and 29 mm in cw prefer rock barnacles over dogwhelks and periwinkles and observed green crabs actively preying on barnacles at night. In the current study it is interesting that barnacles were not preferred over mussel by the crabs, since from the evidence they seem to be more profitable. When comparing barnacle basal diameter to mussel length the barnacle has more calories and their handling times are very close as well (Figures 5, 7). It is possible that given the poor correlation between barnacle size and handling time that barnacles present a more variable meal to the crabs. This variability in the handling times could dissuade the crabs from relying on barnacles as a food source when mussels are available.

4.4. Conclusion

The results of this study provide strong evidence that young green crabs, rock crabs and American lobsters compete for food resources. All three are readily found in close proximity to one another in several locations (Berrill, 1982; Palma *et al.*, 1999; Lynch and Rochette, 2009) at densities around 1 per m² with lobsters and green crabs approaching 6 per m² in some areas (Palma *et al.*, 1999; Griffen *et al.*, 2008; The Lobster Conservancy, 2009). They prefer similarly sized prey and prey species and are equally able to exploit these prey resources.

This overlapping of resource utilization has major implications for all three of the species. The rock crab and green crab are just becoming sexually mature (Reilly and Sails, 1978; Crothers, 1967) at the size examined in this study and the lobsters still have years before maturing and are just starting to venture out of their shelters to actively forage (see review by Lawton and Lavalli, 1995). If these species are significantly impacting each other's nutrient uptake, then a potential bottle neck could form at this size range causing a decrease in the adult populations. This in turn could have an impact on the highly valuable lobster fishery. Direct competition studies between young of green crabs, rock crabs and lobsters should be carried out to further investigate the impact these species have on each other and the possibility of prey switching when in one another's presence (Siddon and Witman, 2004).

REFERENCES

- Anonymous, 2009. DMR lobster research, monitoring, and assessment program. <<http://www.maine.gov/dmr/rm/lobster/research.htm>> Accessed 2010 June 6.
- Aronhime, B.R., Brown, K.M., 2009. The roles of profit and claw strength in determining mussel size by crabs. *J. Exp. Mar. Biol. Ecol.* 379, 28-33.
- Baeta, A., Cabral, H.N., Marques, J.C., Pardal, M.A., 2006. Feeding ecology of the green crab, *Carcinus Maenas* (L., 1758) in a temperate estuary, Portugal. *Crustaceana* 79 (10), 1181-1193.
- Berrill, M., 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *J. Crust. Biol.* 2 (1), 31-39.
- Conan, G.Y., Comeau, M., Moriyasu, M., 2001. Are morphometrical approaches appropriate to establish size at maturity for male American lobster, *Homarus americanus*? *J. Crust. Biol.* 21 (4), 937-947.
- Cowan, D.F., Solow, A.R., Beet, A., 2001. Patterns in abundance and growth of the juvenile lobster, *Homarus americanus*. *Mar. Freshwater Res.* 52, 1095-102.
- Crothers, J.H., 1967. The biology of the shore crab *Carcinus maenas* (L.) 1. The background – anatomy, growth and life history. *Field Studies* 2 (4), 407-434.
- Elnor, R.W., 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia* 36, 333-344.
- Elnor, R.W., Campbell, A., 1981. Force, function and mechanical advantage in the chelae of the American lobster *Homarus americanus* (Decapod: Crustacea). *J. Zool. Lond.* 193, 269-286.
- Enderlein, P., Moorthi, S., Rohrscheidt, H., Wahl, M., 2003. Optimal foraging versus shared doom effects: interactive influence of mussel size and epibiosis on predator preference. *J. Exp. Mar. Biol. Ecol.* 292, 231-242.
- Goldstein, J.S., Tlusty, M.F., 2003. Substrate determinants and developmental rate of claw asymmetry in American lobsters, *Homarus americanus*. *J. Crustacean Biol.* 23 (4), 890-896.
- Griffon, B.D., Guy, T., Buck, J.C., 2008. Inhibition between invasives; a newly introduced predator moderates the impacts of previously established invasive predator. *J. Anim. Ecol.* 77, 32-40.
- Gubbay, S., 1983. Compressive and adhesive strengths of a variety of British barnacles. *J. Mar. Biol. Ass. U.K.* 63, 541-555.

- Grosholz, E.D., Ruiz, G.M., 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. *Biol. Conserv.* 78, 59-66.
- Jones, P.L., Shulman, M.J., 2008. Subtidal-intertidal trophic links: American lobsters [*Homarus americanus*(Milne-Edwards)] forage in the intertidal zone on nocturnal high tides. *J. Exp. Mar. Biol. Ecol.* 361, 98-103.
- Lawton, P., Lavalli, K.L., 1995. Postlarval, juvenile, adolescent, and adult ecology. In, *The Biology of the lobster Homarus americanus*, edited by J.R. Factor, Academic Press, London, pp. 47-88.
- Lewis, J.R., 1964. *The ecology of rocky shores*. English University Press, London, UK.
- Lynch, B.R., Rochette, R., 2009. Spatial overlap and interaction between sub-adult American lobsters, *Homarus americanus*, and the invasive European green crab *Carcinus maenas*. *J. Exp. Mar. Biol. Ecol.* 369, 127-135.
- Mascaro, M., Seed, R., 2001. Foraging behavior of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* L. *Marine Biology* 139 (6), 1135-1145.
- Menge, B.A., 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* 58, 141-155.
- Moody, K.E., Steneck, R.S., 1993. Mechanisms of predation among large decapod crustaceans of the Gulf of Maine Coast: functional vs. phylogenetic patterns. *J. Exp. Mar. Biol. Ecol.* 168, 111-124.
- Ojeda, F.P., Dearborn, J.H., 1990. Diversity, abundance and spatial distribution of fishes and crustaceans in the rocky subtidal zone of the Gulf of Maine. *Fish. Bull. NOAA* 88, 403-410.
- Ojeda, F.P., Dearborn, J.H., 1991. Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. *J. Exp. Mar. Biol. Ecol.* 149, 13-44.
- Palma, A.T., Steneck R.S., Wilson C.J., 1999. Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. *J. Exp. Mar. Biol. Ecol.* 241, 107-136.
- Palma, A.T., Wahle, R.A., Steneck, R.S., 1998. Different early post-settlement strategies between American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* in the Gulf of Maine. *Mar. Ecol. Prog. Ser.* 162, 215-225.
- Parr Instrument Co., 1993. 1672 thermometer operating instruction manual. Parr Manual No. 283MM. Moline, Ill. Pp. 6-1.
- Rangeley, R.W., Thomas, M.L.H., 1987. Predatory behavior of juvenile shore crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 108, 191-197.
- Reilly, P.N., Saila, S.B., 1978. Biology and ecology of the rock crab, *Cancer irroratus* Say, 1817, in the southern New England waters (Decapoda, Brachyura). *Crustaceana* 34 (2), 121-140.
- Rosson, M.A., Williams, P.J., Comeau, M., Mitchell, S.C., Apaloo, J., 2006. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). *J. Exp. Mar. Biol. Ecol.* 329, 281-288.

- Sainte-Marie, B., Chabot, D., 2002. Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands. *Fishery Bulletin* 100, 106-116.
- Salierno, J.D., Rebach, S., Christman, M.C., 2003. The effects of the interspecific competition and prey odor on foraging behavior in the rock crab, *Cancer irroratus* (Say). *J. Exp. Mar. Biol. Ecol.* 187, 249-260.
- Seed, R., Hughes, R.N., 1995. Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *J. Exp. Mar. Biol. Ecol.* 193, 177-195.
- Siddon, C.E., Witman, J.D., 2004. Behavioral indirect interactions: Multiple predator effects and prey switching in the rocky subtidal. *Ecology* 85 (11), 2938-2945.
- Smallegange, I.M., Hidding, B., Eppenga, J.M.A., Van der Meer, J., 2008. Optimal foraging and risk of claw damage: how flexible are shore crabs in their prey size selectivity? *J. Exp. Mar. Biol. Ecol.* 367, 157-163.
- Smallegange, I. M., Van Der Meer, J., 2003. Why do shore crabs not prefer the most profitable mussels? *Journal of Animal Ecology* 71, 599-607.
- Smith, L.D., Palmer, A.R., 1994. Effects of manipulated diet on size and performance of brachyuran crab claws. *Science* 264 (5159), 710-712.
- Stehlik, L.L., 1993. Diets of the brachyuran crabs *Cancer irroratus*, *C. borealis*, and *Ovalipes ocellatus* in the New York Bight. *J. Crust. Biol.* 13 (4), 723-735.
- Taylor, G.M., 2001. The evolution of armament strength: evidence for a constraint on the biting performance of claws of durophagous deapods. *Evolution* 55 (3), 550-560.
- Thayer, G.W., Schaaf, W.E., Angelovic, J.W., 1973. Caloric measurements of some estuarine organisms. *Fish. Bull.* 71, 289-296.
- The Lobster Conservancy, 2009. Juvenile lobster monitoring program. Quarterly newsletter published by The lobster Conservancy, Friendship, Maine. 4p.
- Tyrrell, M.C., Guarino, P.A., Harris, L.G., 2006. Predatory impacts of two introduced crab species: inferences from microcosms. *Northeastern Naturalist* 13 (3), 375-390.
- Underwood, A.J., 2000. Experimental ecology of rocky intertidal habitats: what are we learning? *J. Exp. Mar. Biol. Ecol.* 250, 51-76.
- Vermeij, G. J., 1977. Patterns in crab claw size: the geography of crushing. *Systemic Zoology* 26 (2), 138-151.
- Williams, P.J., Floyd, T.A., Rossong, M.A., 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and the sub-adult American lobster, *Homarus americanus* (Milne Edwards). *J. Exp. Mar. Biol. Ecol.* 329, 66-74.

Table 1. Crab and lobster size [carapace width (cw) for crabs, carapace length (cl) for lobsters and weights for all] range, average and standard deviation for all specimens used in the three parts of this study. Weights were not recorded for the crabs and lobsters used in the prey size selection experiment. The crabs and lobsters used for prey species selection were a subset of the claw morphology animals.

Crabs and lobsters used for claw morphology							
Predator species	Cw or cl range (mm)	Average cw or cl (mm)	Cw or cl SD	Weight range (g)	Average weight (g)	Weight SD	n
Green crab	26.40 - 61.58	32.94	6.58	4.24 - 46.2	8.99	7.27	46
Rock crab	19.23 - 63.65	33.55	8.33	1.16 - 38.26	7.3	6.24	70
American lobster	20.29 - 53.17	34.96	7.9	6.07 - 121.39	39.39	29.19	51
Crabs and lobsters used for prey size selection							
Predator species	Cw or cl range (mm)	Average cw or cl (mm)	Cw or cl SD	Weight range (g)	Average weight (g)	Weight SD	n
Green crab	25.45 - 34.85	29.51	2.55	NA	NA	NA	39
Rock crab	25.20 - 34.65	29.85	2.89	NA	NA	NA	34
American lobster	25.10 - 34.55	29.95	2.61	NA	NA	NA	36
Crabs and lobsters used for prey species selection							
Predator species	Cw or cl range (mm)	Average cw or cl (mm)	Cw or cl SD	Weight range (g)	Average weight (g)	Weight SD	n
Green crab	26.40 - 35.00	30.91	2.57	4.24 - 9.64	6.83	1.58	40
Rock crab	25.82 - 34.9	30.62	2.84	3.20 - 7.95	4.79	1.26	39
American lobster	25.56 - 34.68	30.29	2.83	13.02 - 35.54	22.18	7.14	22

Table 2. Average claw morphology/ body size ratios (\pm SD) for 46 *Carcinus maenas*, 70 *Cancer irroratus* and 51 *Homarus americanus*. Carapace width (cw) was used for crabs and carapace length (cl) was used for lobsters.

Predator species	Average chela height/cw (or cl) ratio	Average chela width/cw (or cl) ratio	Average chela length/cw (or cl) ratio	Average chela gape/cw (or cl) ratio	Average (L1/L2)/cw (or cl) ratio
Green crab	0.22 (\pm 0.19)	0.14 (\pm 0.012)	0.49 (\pm 0.04)	0.16 (\pm 0.033)	0.0084 (\pm 0.0020)
Rock crab	0.19 (\pm 0.0094)	0.11 (\pm 0.0085)	0.40 (\pm 0.02)	0.15 (\pm 0.025)	0.0086 (\pm 0.0025)
American lobster	0.49 (\pm 0.048)	0.28 (\pm 0.034)	1.22 (\pm 0.12)	0.37 (\pm 0.067)	0.0059 (\pm 0.0018)

Table 3. Loading scores for the first two principal components displayed in Figure 3.

Chela dimension	Principal component 1	Principal component 2
Chela height	0.987	0.117
Gape	0.952	0.145
Chela width	0.982	0.150
Chela length	0.986	0.120
l1/l2 ratio	-0.617	0.787

Table 4. Regression equations and r-squared values of handling time against *Mytilus* sp. length for all predators.

Predator	Equation	r ²
Green crab	$y = 110.154e^{(0.166*x)}$	0.618
Rock crab	$y = 121.821e^{(0.147*x)}$	0.601
American lobster	$y = 32.789e^{(0.197*x)}$	0.956
All	$y = 139.648e^{(0.134*x)}$	0.640

Table 5. Regression equations and r-squared values of handling time against *Semibalanus balanoides* basal diameter for all predators.

Predator	Equation	r ²
Green crab	$y = 68.040e^{(0.161*x)}$	0.367
Rock crab	$y = 272.421e^{(0.066*x)}$	0.034
American lobster	NA	NA
All	$y = 144.523e^{(0.109*x)}$	0.111

Table 6. Total number of prey species consumed by each of the predator species.

Predator species	Amount of Mussels consumed	Amount of Barnacles consumed	Amount of Kelp consumed	Total
Green crab	20	9	0	29
Rock crab	32	11	0	43
American lobster	18	1	0	19
Total	70	21	0	91

Table 7. Results from the post hoc Wilcoxon signed ranks test comparing prey species preference for all predators. A Bonferroni correction of 0.0170 is in effect due to multiple comparisons.

Decapod species	P value from Wilcoxon Signed Ranks Test		
	Kelp - mussel	Barnacle – mussel	Kelp – Barnacle
Green crab	0.005	0.120	0.024
Rock crab	0.000	0.005	0.016
American lobster	0.004	0.004	0.317

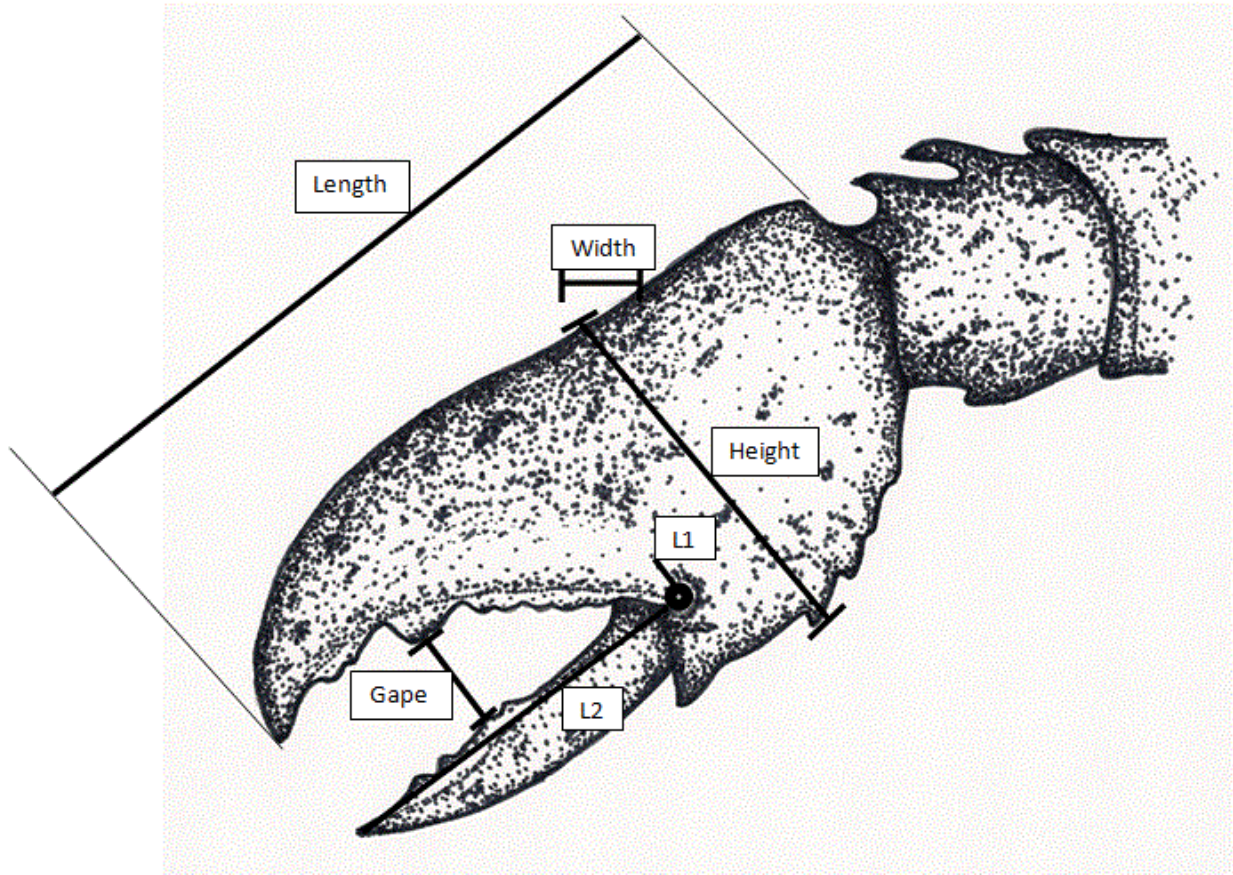


Figure 1. Morphological measurements taken from each chela for all three decapod species. L1 is the length between the pivot point to the insertion of the apodeme on the dactyl, and L2 is the distance from the pivot point to the dactyl tip. Gape was measured at the midpoint of the dactyl when the claw was open to its maximum extent. Height and width of the claw was measured at the midpoint of the manus. Length is the distance from the beginning of the propodus to the tip.

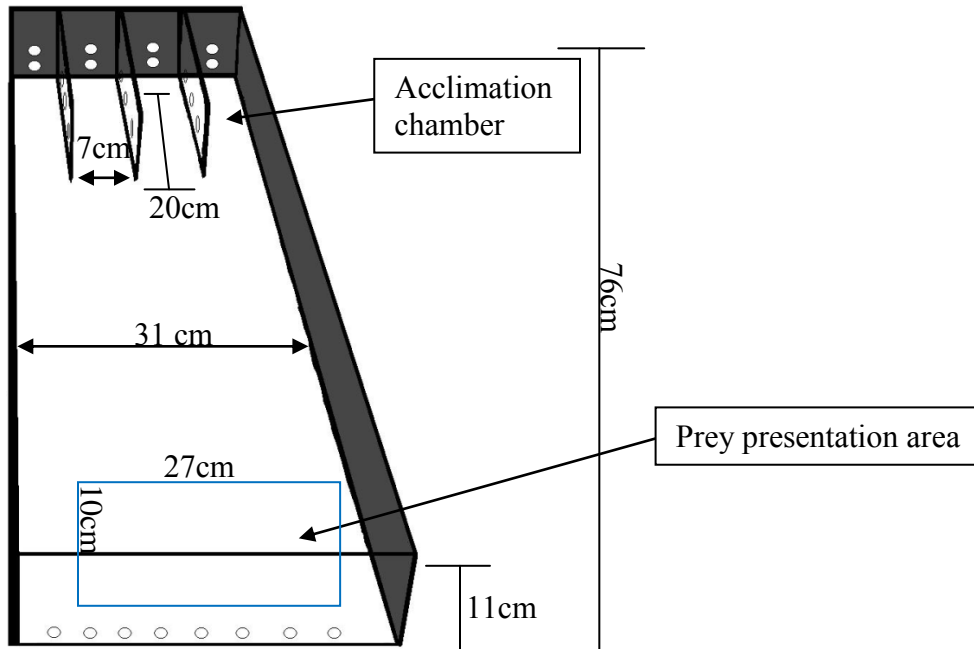


Figure 2. One of two identical testing apparatuses in which all of the prey selection trials were conducted.

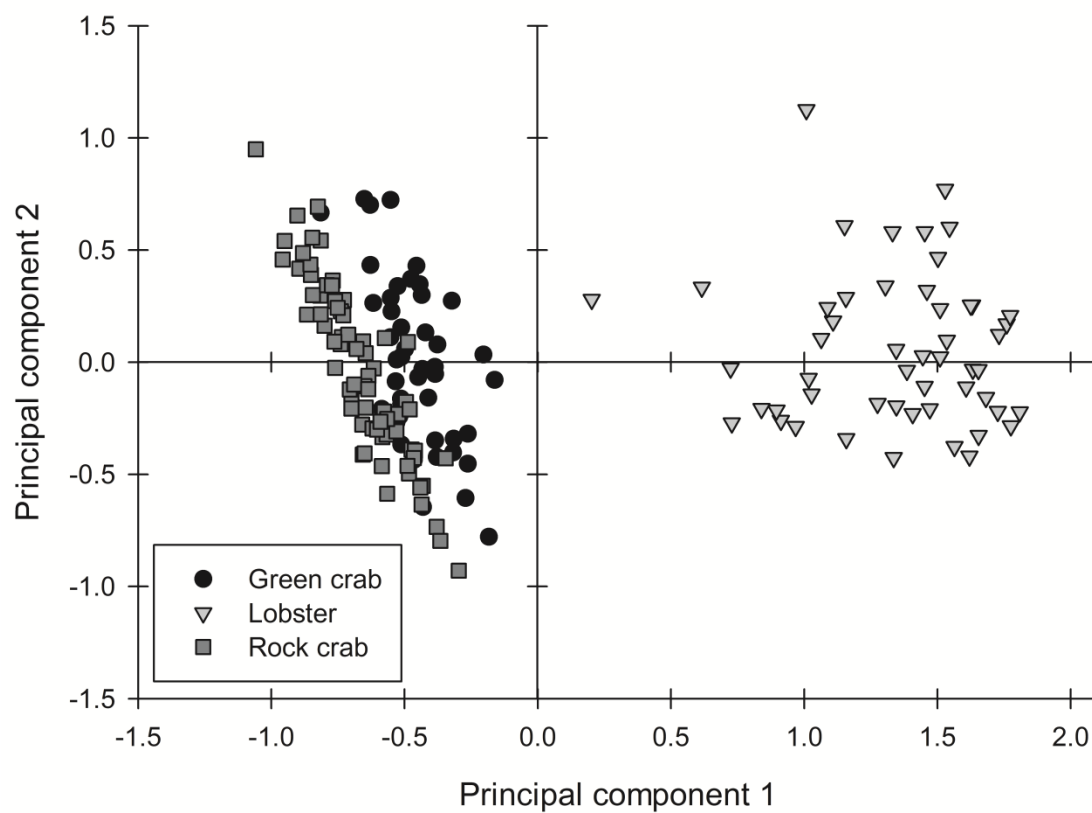


Figure 3. Results for principal component analysis on chela dimensions in relation to carapace width/length. See Table 1 for factor loading.

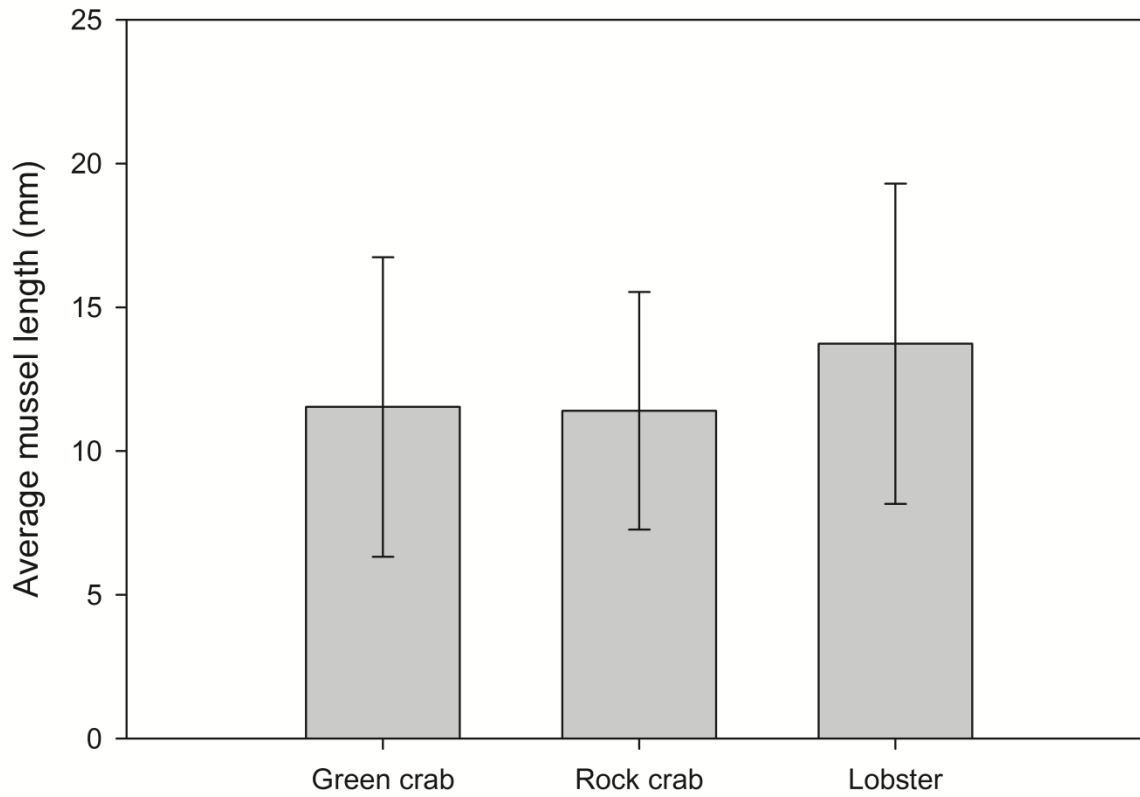


Figure 4. The average length of the first mussel consumed by each predator species. Error bars represent ± 1 standard deviation. There is no significant difference among the predators ($p = 0.3$).

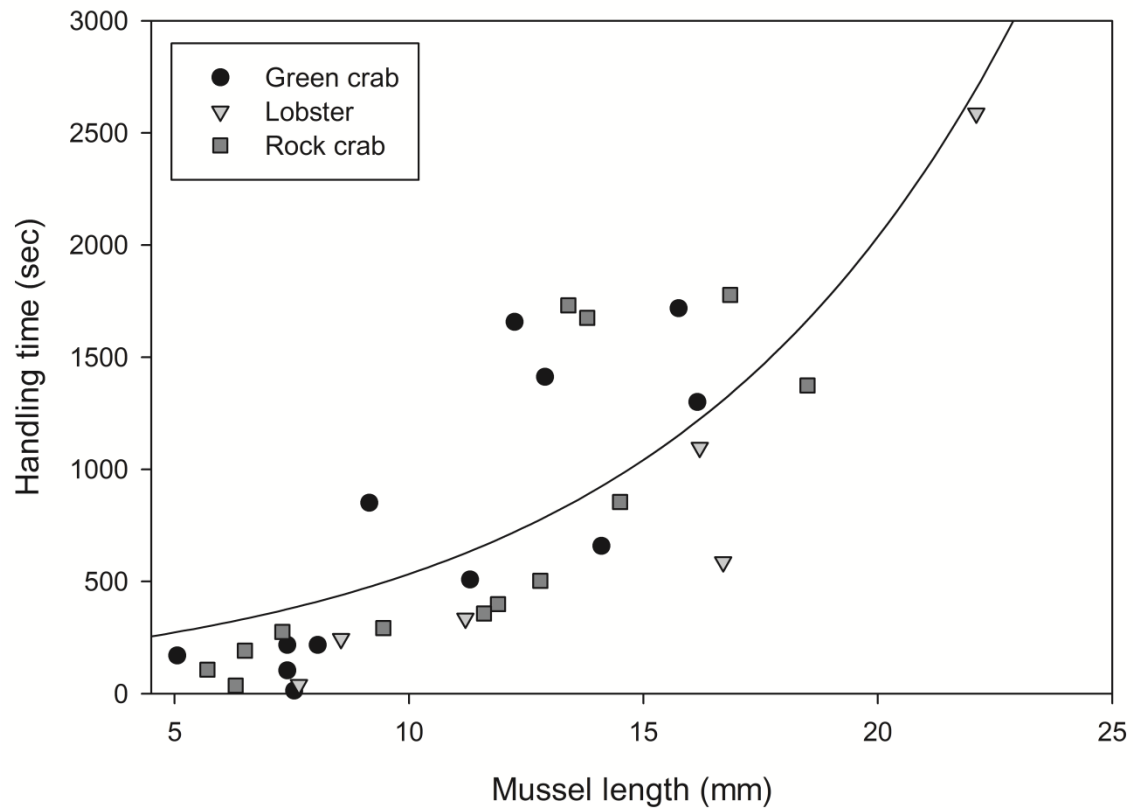


Figure 5. Handling times of various lengths of *Mytilus* sp. for all three decapod species derived from handling times of first mussel consumed by all crabs and lobster ($p = 2 \times 10^{-7}$, $r^2 = 0.640$).

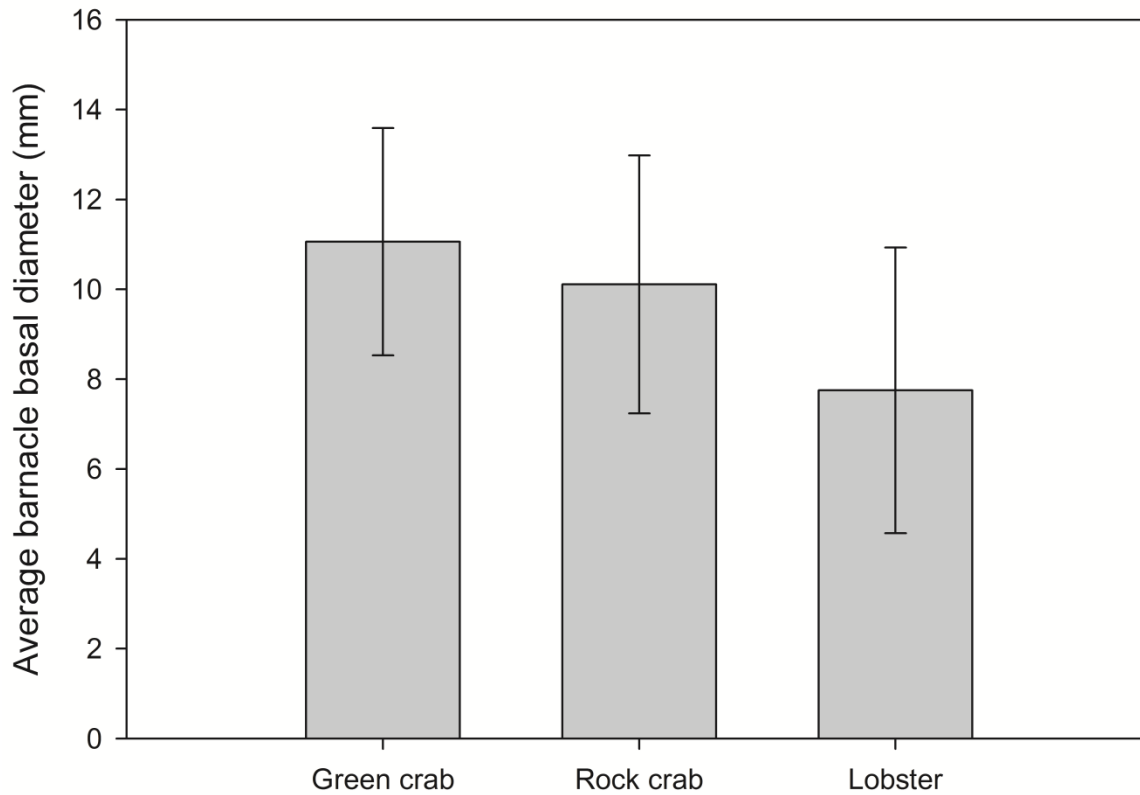


Figure 6. The average basal diameter of the first barnacle consumed by each predator species. Error bars represent ± 1 standard deviation. There was no significant difference among the predators ($p = 0.2$).

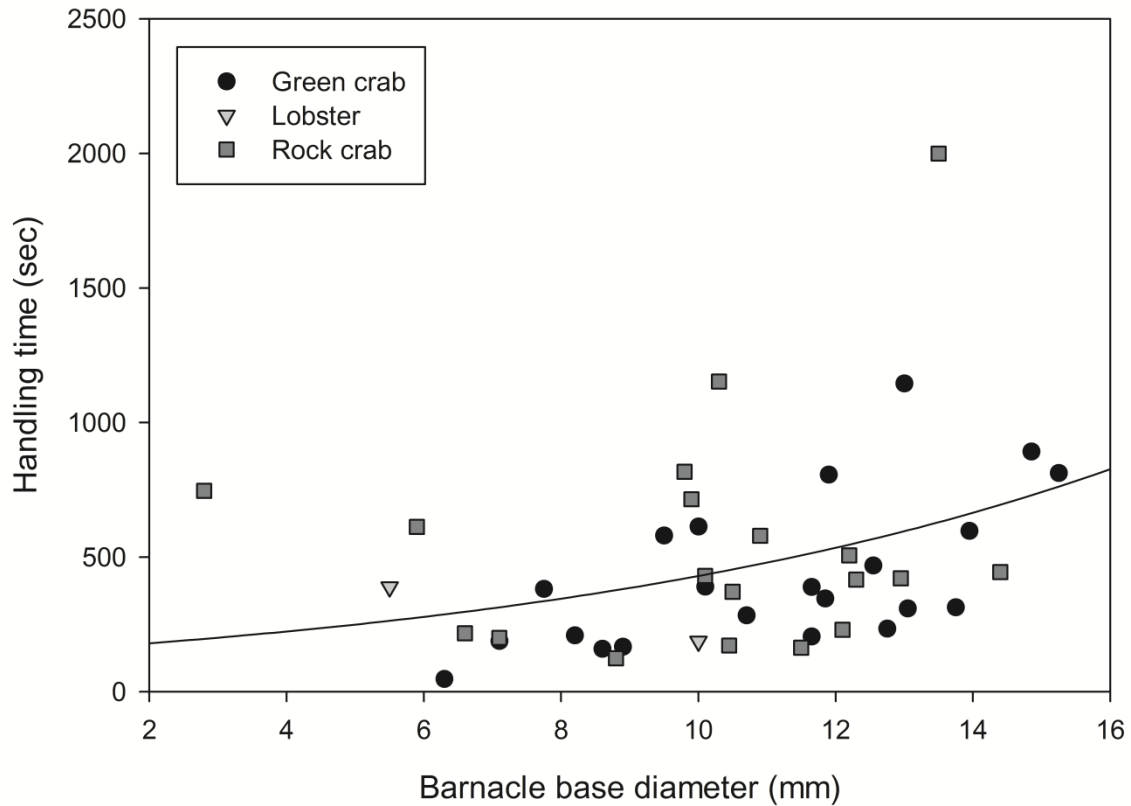


Figure 7. Handling times of *Semibalanus balanoides* of various basal diameters for each of the three decapod species derived from handling times of first barnacle consumed by all crabs and lobster. No difference was detected between handling times for the three predator species ($p = 0.5$). Barnacle base diameter had no significant effect on handling time ($p = 0.03$, $r^2 = 0.111$).

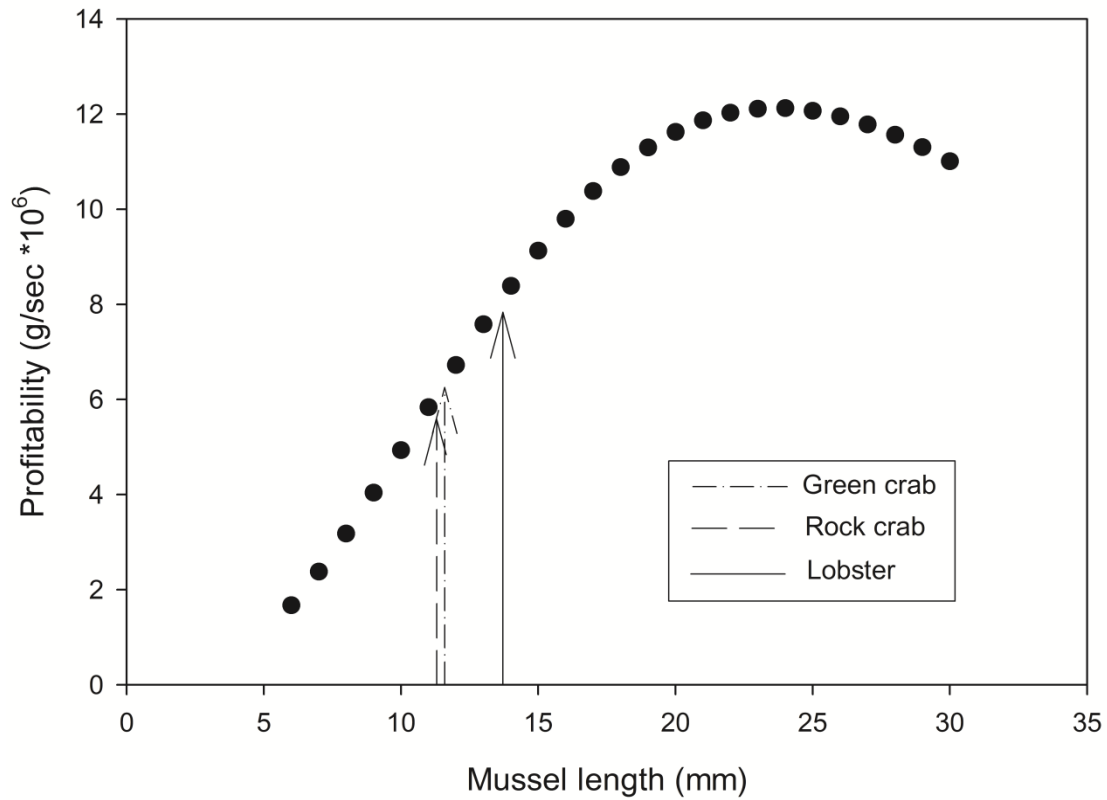


Figure 8. Profitability of mussels for all three predator species calculated by dividing dry mussel mass by handling time. The arrows represent the average length of mussels consumed by each predator species.

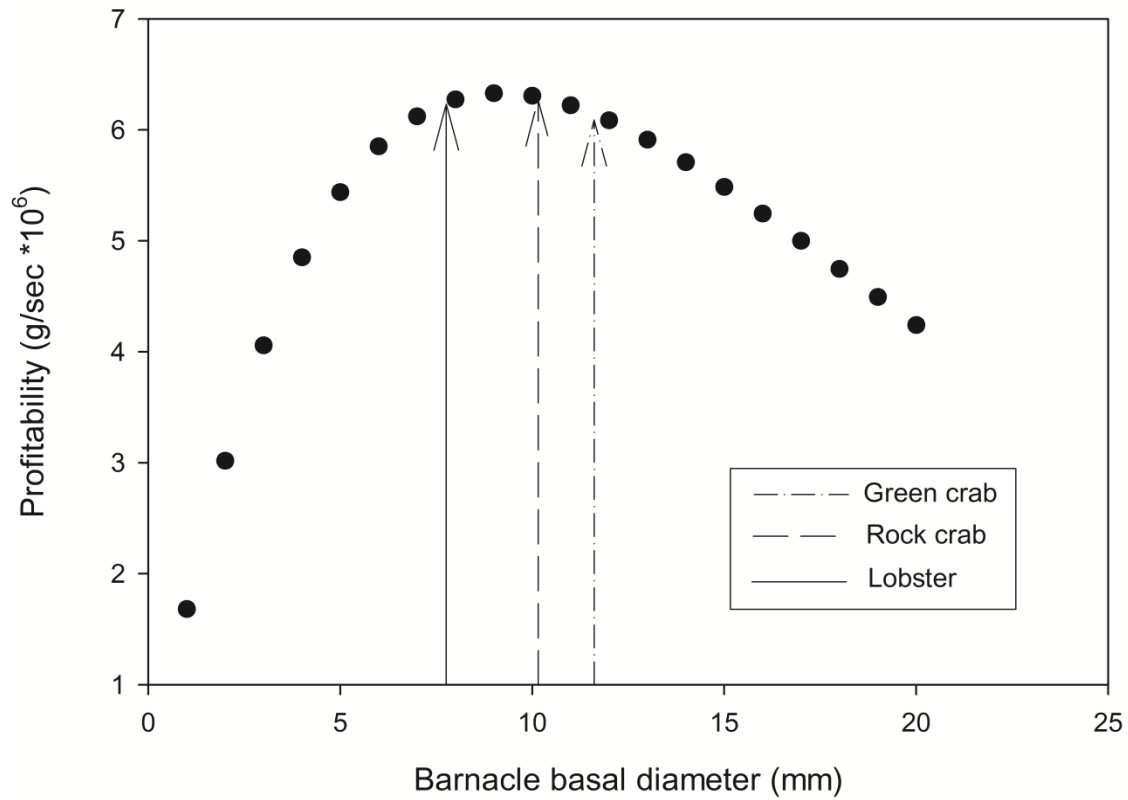


Figure 9. Profitability of barnacles for all three predator species calculated by dividing dry barnacle flesh mass by handling time. The arrows represent the average basal diameter of barnacles consumed by each predator species.

APPENDIX A



JOHN ELIAS BALDACCI
GOVERNOR

STATE OF MAINE
DEPARTMENT OF
MARINE RESOURCES
MARINE RESOURCES LABORATORY
P.O. BOX 8, 194 MCKOWN POINT RD
W. BOOTHBAY HARBOR, MAINE 04575-0008

GEORGE D. LAPOINTE
COMMISSIONER

June 5, 2007

SPECIAL LICENSE NUMBER 2007-70-03

Acting under the authority vested in the Commissioner of Marine Resources by virtue of 12 M.R.S.A. §6074(8)(D), I hereby issue subject to renewal a Special License to **DR. ANNE CHRISTINE BROWN**, Associate Professor of Life Sciences, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005-9599. This Special License exempts said ANNE CHRISTINE BROWN, Ph.D. from those portions of 12 M.R.S.A. §6431 relating to the taking and possession of undersized lobsters and crabs, in the course of her research on the influence of physiological and nutritional factors on the distribution of juvenile lobsters and crabs; and from those portions of Marine Resources laws and regulations, for education purposes in her marine biology and invertebrate zoology curriculum, for the collection of common marine organisms including collection of mussels from closed areas §6621 and §6747. This Special License is issued subject to the following conditions:

- 1. Who:** Dr. Anne Christine Brown and additional persons authorized under this special license for collection purposes under Project A: Joseph Sungail – UNE graduate student and associated personnel from the University of Maine's Darling Marine Center, plus personnel and students from the UNE, Biddeford in Dr. Brown's classes. Under Project B: Personnel and students from the University of New England, Biddeford in Dr. Brown's classes.
 - 2. What: Project A:** Up to 150 juvenile (undersized) lobsters and up to 150 juvenile crabs, of each species listed, may be hand collected or by SCUBA suction sampling and maintained. Crab species include: green crabs, *Carcinus maenas*, Asian shore crabs, *Hemigrapsus sanguinensis*, rock crabs, *Cancer irroratus* and Jonah crabs, *Cancer borealis*. Lobsters and crabs not sacrificed and in good health during experimentation shall be released in an appropriate manner except as noted under the conditions below.
Project B: Common marine organisms primarily invertebrates such as urchins, clams, mussels, whelks, scallops, etc and finfish species may be collected by hand, by small seine in shallow waters and by SCUBA suction sampling. Quantities of regulated organisms must be limited to the minimum necessary for Dr. Brown's marine curriculum.
 - 3. Where:** Southern Maine coastline, typically Fortunes Rock Beach, Biddeford Pool
 - 4. Conditions:**
 - Marine Patrol Division I, west of Port Clyde, tel. (207) 633-9595 or Marine Patrol Division II, east of Port Clyde, tel. (207) 667-3373, or the local Marine Patrol Officer, **shall be contacted** at least 24 hours **prior** to the start up of collecting activities and make arrangements as to the necessary frequency to contact them to provide the Special License (SL) number, location(s), dates of all activities, and name(s) of persons participating in the field work.
 - All research work with the Asian shore crab shall be conducted using crabs collected within Maine (Southern Maine region and Biddeford Pool) and research located only in a quarantine/isolation system at the UNE MRSC. The crabs shall be destroyed by autoclave at the end of the studies; containment water disposed of through a municipal treatment system or the MRSC chlorination de-chlorination system process before release; and all containment apparatus adequately disinfected. Under no circumstances are the animals, or untreated discharge water to be released into Maine waters.
 - **No marine organism authorized under this SL shall be used for human consumption.**
 - **No lobsters** are authorized to be collected by SCUBA diving/diver with the exception that they may be taken by suction sampling method described for Projects A and B.
 - Prior to any renewal a **report** on the research/status of **Project A** shall be provided to the Department at the end of the year and a **report** of the specimens collected under **Project B**. Reporting for Project A must also include the date, depth, location of suction sampling, volume of material, numbers (and sizes) of crabs and lobsters, in addition to other animals, and any algal material collected.
 - Additional conditions may be added at the discretion of the Commissioner.
 - Any infraction of these conditions or any violation of any Marine Resources laws shall be grounds for the immediate revocation of this Special License.
- This Special License **expires on December 31, 2007** and has one renewal.


GEORGE D. LAPOINTE
Commissioner
PRINTED ON RECYCLED PAPER

cc: Marine Patrol Division I; Carl Wilson
PHONE: (207) 633-9500

<http://www.Maine.gov/dmr>

FAX: (207) 633-9579

APPENDIX B



JOHN ELIAS BALDACCI
GOVERNOR

STATE OF MAINE
DEPARTMENT OF
MARINE RESOURCES
MARINE RESOURCES LABORATORY
P.O. BOX 8, 194 MCKOWN POINT RD
W. BOOTHBAY HARBOR, MAINE 04575-0008

GEORGE D. LAPOINTE
COMMISSIONER

April 4, 2008
SPECIAL LICENSE NUMBER 2008-35-04

Acting under the authority vested in the Commissioner of Marine Resources by virtue of 12 M.R.S.A. §6074(8)(D), I hereby issue subject to renewal a Special License to **DR. ANNE CHRISTINE BROWN**, Associate Professor of Life Sciences, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005-9599. This Special License exempts said ANNE CHRISTINE BROWN, Ph.D. from those portions of 12 M.R.S.A. §6431 relating to the taking and possession of undersized lobsters and crabs, in the course of her research on the influence of physiological and nutritional factors on the distribution of juvenile lobsters and crabs; and from those portions of Marine Resources laws and regulations, for education purposes in her marine biology and invertebrate zoology curriculum, for the collection of common marine organisms including collection of mussels from closed areas §6621 and §6747. This Special License is issued subject to the following conditions:

- 1. Who:** Dr. Anne Christine Brown and additional persons authorized under this special license for collection purposes under Project A: Joseph Sungail – UNE graduate student and associated personnel from the University of Maine's Darling Marine Center, plus personnel and students from the UNE, Biddeford in Dr. Brown's classes. Under Project B: Personnel and students from the University of New England, Biddeford in Dr. Brown's classes.
- 2. What: Project A:** Up to 150 juvenile (undersized) lobsters and up to 150 juvenile crabs, of each species listed, may be hand collected or by SCUBA suction sampling and maintained. Crab species include: green crabs, *Carcinus maenas*, Asian shore crabs, *Hemigrapsus sanguinensis*, rock crabs, *Cancer irroratus* and Jonah crabs, *Cancer borealis*. Lobsters and crabs not sacrificed and in good health during experimentation shall be released in an appropriate manner except as noted under the conditions below.
Project B: Common marine organisms primarily invertebrates such as urchins, clams, mussels, whelks, scallops, etc and finfish species may be collected by hand, by small seine in shallow waters and by SCUBA suction sampling; and the 23' R/V LLYR (ME 125J). Quantities of regulated organisms must be limited to the minimum necessary for Dr. Brown's marine curriculum.
- 3. Where:** Southern Maine coastline, typically Fortunes Rock Beach, Biddeford Pool
- 4. Conditions:**
 - Marine Patrol Division I, west of Port Clyde, tel. (207) 633-9595 or Marine Patrol Division II, east of Port Clyde, tel. (207) 667-3373, or the local Marine Patrol Officer, **shall be contacted** at least 24 hours prior to the start up of collecting activities and make arrangements as to the necessary frequency to contact them to provide the Special License (SL) number, location(s), dates of all activities, and name(s) of persons participating in the field work.
 - All research work with the Asian shore crab shall be conducted using crabs collected within Maine (Southern Maine region and Biddeford Pool) and research located only in a quarantine/isolation system at the UNE MRSC. The crabs shall be destroyed by autoclave at the end of the studies; containment water disposed of through a municipal treatment system or the MRSC chlorination de-chlorination system process before release; and all containment apparatus adequately disinfected. Under no circumstances are the animals, or untreated discharge water to be released into Maine waters.
 - **No marine organism authorized under this SL shall be used for human consumption.**
 - **No lobsters** are authorized to be collected by SCUBA diving/diver with the exception that they may be taken by suction sampling method described for Projects A and B.
 - Prior to any renewal a **report** on the research/status of **Project A** shall be provided to the Department at the end of the year and a **report** of the specimens collected under **Project B**. Reporting for Project A must also include the date, depth, location of suction sampling, volume of material, numbers (and sizes) of crabs and lobsters, in addition to other animals, and any algal material collected.
 - Additional conditions may be added at the discretion of the Commissioner.
 - Any infraction of these conditions or any violation of any Marine Resources laws shall be grounds for the immediate revocation of this Special License.

This Special License **expires on December 31, 2008** and has exceeded the number of renewals allowed pursuant to 12 MRSA §6074(6). A new application must be made to continue these exemptions next year.


GEORGE D. LAPOINTE
Commissioner

cc: ONE Marine Patrol Division I; Carl Wilson

<http://www.Maine.gov/dmr>

FAX: (207) 633-9579

APPENDIX C



JOHN ELIAS BALDACCI
GOVERNOR

STATE OF MAINE
DEPARTMENT OF
MARINE RESOURCES
MARINE RESOURCES LABORATORY
P.O. BOX 8, 194 MCKOWN POINT RD
W. BOOTHBAY HARBOR, MAINE 04575-0008

GEORGE D. LAPOINTE
COMMISSIONER

April 14, 2009

SPECIAL LICENSE NUMBER 2009-60-00

Acting under the authority vested in the Commissioner of Marine Resources by virtue of 12 M.R.S.A. §6074(8)(D), I hereby issue subject to renewal a Special License to **DR. ANNE CHRISTINE BROWN**, Associate Professor of Life Sciences, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005-9599. This Special License exempts said ANNE CHRISTINE BROWN, Ph.D. from those portions of 12 M.R.S.A. §6431 relating to the taking and possession of undersized lobsters and crabs, in the course of her research on the influence of physiological and nutritional factors on the distribution of juvenile lobsters and crabs; and from those portions of Marine Resources laws and regulations, for education purposes in her marine biology and invertebrate zoology curriculum, for the collection of common marine organisms including collection of mussels from closed areas §6621 and §6747. This Special License is issued subject to the following conditions:

1. **Who:** Dr. Anne Christine Brown and additional persons authorized under this special license for collection purposes under Project A:

Joseph Sungail – UNE graduate student and associated personnel from the University of Maine's Darling Marine Center, plus personnel and students from the UNE, Biddeford in Dr. Brown's classes. Under Project B: Personnel and students from the University of New England, Biddeford in Dr. Brown's classes.

2. **What, How: Project A:** Up to 150 juvenile (undersized) lobsters and up to 150 juvenile crabs, of each species listed, may be hand collected or by SCUBA suction sampling and maintained. Crab species include: green crabs, *Carcinus maenas*, Asian shore crabs, *Hemigrapsus sanguinensis*, rock crabs, *Cancer irroratus* and Jonah crabs, *Cancer borealis*. Lobsters and crabs not sacrificed and in good health during experimentation shall be released in an appropriate manner except as noted under the conditions below.

Project B: Common marine organisms primarily invertebrates such as urchins, clams, mussels, whelks, scallops, etc and finfish species may be collected by hand, by small seine in shallow waters and by SCUBA suction sampling.

Quantities of regulated organisms must be limited to the minimum necessary for Dr. Brown's marine curriculum.


Vessel: 23' RV LLYR (ME 125J), CFVS inspection expires 03-05-10.

3. **Where:** Southern Maine coastline, typically Fortunes Rock Beach, Biddeford Pool

4. Conditions:

- Marine Patrol Division I, west of Port Clyde, tel. (207) 633-9595 or Marine Patrol Division II, east of Port Clyde, tel. (207) 667-3373, or the local Marine Patrol Officer, shall be contacted at least 24 hours prior to the start up of collecting activities and make arrangements as to the necessary frequency to contact them to provide the Special License (SL) number, location(s), dates of all activities, and name(s) of persons participating in the field work.
- All research work with the Asian shore crab shall be conducted using crabs collected within Maine (Southern Maine region and Biddeford Pool) and research located only in a quarantine/isolation system at the UNE MRSC. The crabs shall be destroyed by autoclave at the end of the studies; containment water disposed of through a municipal treatment system or the MRSC chlorination de-chlorination system process before release; and all containment apparatus adequately disinfected. Under no circumstances are the animals, or untreated discharge water to be released into Maine waters.
- **No marine organism authorized under this SL shall be used for human consumption.**
- **No lobsters** are authorized to be collected by SCUBA diving/diver with the exception that they may be taken by suction sampling method described for Projects A and B.
- Prior to any renewal a report on the research/status of Project A shall be provided to the Department at the end of the year and a report of the specimens collected under Project B. Reporting for Project A must also include the date, depth, location of suction sampling, volume of material, numbers (and sizes) of crabs and lobsters, in addition to other animals, and any algal material collected.
- This SL is contingent upon vessels holding a current USCG commercial fishing safety inspection.
- Additional conditions may be added at the discretion of the Commissioner.
- Any infraction of these conditions or any violation of any Marine Resources laws shall be grounds for the immediate revocation of this Special License.

This Special License expires on December 31, 2009 and has four renewals.


GEORGE D. LAPOINTE
Commissioner

cc: Marine Patrol Division I; Carl Wilson

2009 MARINE PATROL CONTACT INFO
Marine Patrol Division I Office (west of Port Clyde)
Lieutenant Jon Cornish  **Tel: (207) 633-9595**

PHONE: (207) 633-9500

<http://www.Maine.gov/dmr>

FAX: (207) 633-9579