The Status of Green Crabs (*Carcinus maenas*) in the Damariscotta River: Population Dynamics and Competition Influenced Niche Partitioning

A Senior Thesis Presented to

The Faculty of the Department of Organismal Biology & Ecology

Colorado College

By

Anita Wray

Bachelor of Arts Degree in Organismal Biology and Ecology

May, 2019

Approved by:

Dr. Marc Snyder
Primary Thesis Advisor

Dr. Brian Linkhart
Secondary Thesis Advisor

Abstract

Invasive species have the potential to drastically shift the community composition of habitats through increased competitive interactions. In economically important ecosystems, this can cause populations to decline and economies to collapse. The European Green Crab (*Carcinus maenas*) is an omnivorous and prolific crab which has invaded much of both North American coasts, causing damage to some major bivalve fisheries. My study sought to identify the population trends of the green crab along a river estuary system in the Gulf of Maine. In addition, my study investigated the potential for interspecific competition between rock crabs (*Cancer irroratus*) and green crabs. Subtidal traps were placed biweekly along the shoreline of the Damariscotta River for the 2013, 2014, 2015, and 2018 summer seasons. Carapace width, total weight, sex, ovigerous status, and number of intact legs per individual were quantified for each individual of both species (N=1,208). A caged in-lab experiment was used to observe potential competition for food between rock crabs and green crabs of the same size. My study was unable to find a significant difference between 2015 and 2018 green crab catch rates, suggesting there was no population growth present. In addition, rock crabs were identified as the dominant species in my lab trials. This study suggests that competitive dominance in the native crab species could have the potential to shift the habitat of the invasive green crab to a higher position in the water column, which could limit any further population growth. As green crabs significantly contributed to the collapse of many bivalve fisheries (e.g. the soft-shelled clam), this result could help to inform more effective fisheries and aquaculture management.

Introduction

Interactions between species have the potential to alter species' distributions and influence major habitat shifts. Organisms' interactions can vary, but competitive interactions are the most well studied. Competitive interactions have the potential to play a large role in community composition, animal behavior and population dynamics (Latham, 1999). Understanding competitive interactions can help inform how a species will interact with its environment, and provide critical conservation or remediation information.

Of the many types of competition that exist between species, resource competition, when two similar species use and compete for a shared resource, is the most widespread. Resource competition likely alters the way in which competing species use limited resources, often resulting in a negative outcome for both species. Commonly, one species becomes dominant and is able to successfully defend the limited resource from the other species resulting in competitive exclusion (Ricklefs & Relyea, 2018). Competitive exclusion can result in local extinction, parapatry, and range limitation (Grether et al, 2017). Studies conducted on terrestrial ungulates suggest that interspecific competition from an introduced species significantly decreased the size of native populations, and in a few cases, has caused local extirpation (Latham, 1999). Competitive exclusion has also been documented as causing an inverse relationship between species populations, suggesting that one species is present at a high density where the other is not.

On the other hand, competitive interactions can to lead to sympatric coexistence which can be displayed as character divergence, niche partitioning or a stronger development of reproductive isolation. Studies suggest that aggressive interference can foster niche partitioning in mice, which would allow species coexistence on a regional scale (Grether et al., 2017). Competitive exclusion and sympatric coexistence can potentially influence the population dynamics of species by shifting each species distribution. Understanding these competitive interactions between species thus can be critical in understanding the larger ecological role of both species.

Understanding competitive interactions between species is becoming increasingly important, as global climate change continues to drive novel interspecific interactions through shifting habitat ranges (Kordas et al., 2011). More often seen in marine systems, such novel interspecific interactions are due to the introduction and increase of invasive species. Invasive species are often introduced into environments in which their fundamental niche is already occupied, and they either adapt or outcompete their potential competitors (Mooney & Cleland, 2001). If sympatric coexistence occurs between a native and invasive species, there is potential for large scale ecological impacts due to a shift in the native species' range caused by niche partitioning. On the other hand, if competitive exclusion occurs, these invasive species could change the structure and function of marine ecosystems, threaten economically important species, and require implementation of highly ineffective remediation efforts. Understanding the possible impacts of an invasive and native species' interactions can provide critical information on the long-term effects of climate induced marine invasions.

The impact of invasive species can be further exacerbated if the ecosystem is already facing stress. In marine ecosystems, climate warming and the rapid loss of species diversity has been marked as a leading cause for ecosystem stress (Larkin, 1996). The Gulf of Maine is one of the fastest warming marine ecosystems in the world, with a steady 0.026˚C/year increase in surface temperature over the past 30 years, and a 0.25˚C per year shift since 2004 (Pershing et al., 2015). This suggests that the Gulf of Maine is warming faster than 99% of the worlds ecosystems. The North American Atlantic rocky coastline is also one of the most species depauperate shallow marine ecosystems in the world, which puts an even larger emphasis on investigating invasive species entering this system (Steneck, 2002). The Gulf of Maine also has many extremely productive fisheries, totaling over 16,000 active harvesters and 7,000 in the lobster industry alone (Maine Department of Marine Resources, 2017). Many small communities along the coast rely on stable fishing populations in order to drive their economy. For the aforementioned reasons, particular attention has been payed to invasive species along the Gulf of Maine for their potentially larger impacts.

There have been over 33 documented marine invasions along the Gulf of Maine, belonging to 10 different plant and animal phyla (USGS, 2018). One of the more understudied invasions along the Gulf of Maine is the European Green Crab (*Carcinus maenas)*. The European Green Crab has been listed as one of the most detrimental invasive species in the world, due to "their serious impact on biological diversity and/or human activities" (Lowe et al., 2000). The European Green Crab has invaded the coasts of Australia, South Africa, and both Atlantic and Pacific coasts of North America (Welch, 1968 & Cohen et al., 1995). In many of these locations, there is documented loss of biodiversity and a direct impact on local fisheries due to this invasion (Sorte et al, 2016). The distribution of the green crab is thermally limited on the eastern coast of the United States and was first introduced in 1817 in Long Island Sound (Welch, 1968). As ocean temperatures have warmed, the green crab has been able to expand its invasive range and now has fully established populations from Delaware Bay to Newfoundland (Grosholtz & Ruiz, 1996). Historical records tracked the northward movement of green crabs and were able to identify a significant population in central Maine by the late 1930s (Welch, 1968). Welch (1968) was able to identify pulses and retreats in green crab populations along the coast of Maine which were consistent with warming patterns in the 1930s, 1950s, and 1970s, with severe cooling patterns in between. As temperatures have warmed, scientists have noted a significant increase in population density and geographic distribution of green crabs along the entire east coast (Macdonald et al*.,* 2018). The current status of the green crab population across many areas of the Gulf of Maine are unknown. Understanding the population dynamics of this species is critical to better understand its potential invasion and subsequent potential impacts.

European green crabs are omnivorous predators that have a generalist diet and consume organisms belonging to over 104 plant and animal families (Cohen et al., 1995). Some interspecific interactions with this invasive crab are well studied. Invasive green crabs have caused severe declines in bivalve, gastropod and eelgrass populations, including the drastic decline of the soft-shell clam population and subsequent market crash (Trussell et al., 2006, Baeta, 2006). In addition, green crabs have been documented to significantly harm commercially important bivalve populations which include blue mussel (*Mytitlis edulis)* and eastern oyster (*Crassostrea virginica*) through intense predation (Sorte et al., 2016). One of the most important regions for eastern oyster farming is the Damariscotta River. Uniquely this river has little freshwater output, cold temperatures, and strong nutrient rich tides, making it an extremely proliferate growing area for oyster farms. Over 73% of Maine's harvested oysters come out of the

Damariscotta River, making it an extremely important region to protect from predators such as the green crab (Maine DMR, 2016). Long-term monitoring studies have been in place to record the population density of green crabs along the Damariscotta River, but limited work has been done to interpret these data. In addition, no formal studies on the population dynamics have been completed, which are necessary to understand the rate of invasion. By formally analyzing the population trends, scientists will be able to further protect this ecologically and economically important region of Maine.

Limited work has been done identifying predators of the European green crab in their invasive range. In their intertidal habitat, green crabs have been observed and identified as prey for two gull species, but only the herring gull (*Larus marinus*) occurs in New England (Rome & Ellis, 2004). No studies have been able to identify if they have any subtidal predators. Due to ecosystem shifts in the Gulf of Maine caused by overfishing, there are limited large predatory finfish populations that would serve as effective predators including cod (*Gadus morhua*) and wolfish (*Anarhichas lupus*) (Steneck et al., 2012).

Although no predators have been identified for the green crab in the Gulf of Maine, many researchers have hypothesized that competitive interactions between native crustacean species are present in this ecosystem (Grosholz & Ruiz, 1996). The rock crab (*Cancer irroratus*) is a native crab in the Gulf of Maine, which has similar documented habitat and dietary overlap with the green crab (Grosholz & Ruiz, 1996). Interactions between the rock crab and green crab have the potential to be competitive, but limited studies have investigated this relationship. Scientists have hypothesized that sympatric coexistence could occur, due to population maintenance of these two species over the past few decades (R. Steneck, *personal communication*). As the green crab is becoming more established along the Maine coast, it is imperative that we understand the interactions between the two species, specifically if sympatric coexistence does in fact occur. Previous laboratory experiments have identified that green crabs were competitively dominant over both the Dungeness crab (*Cancer magister*) and the blue crab (*Callinectes sapidus*) for food resources in the western United States (McDonald et al., 2000). In addition, many studies have identified green crabs as competitively dominant over the extremely valuable American Lobster (*Homarus americanus*) in the Gulf of Maine, but no other crustacean species have been studied in this ecosystem (Harr and Rochette, 2012). The green crab is a quick and aggressive crab that can outcompete many other crustacean species for food and habitat (Ropes, 1968). This has led to competitive exclusion in many cases, which has been documented to decrease the population density of subordinate species (McDonald et al., 2000). Understanding the interspecific interactions between rock crabs and green crabs will help to inform researchers, fishermen and stakeholders on the status of the green crab invasion, which could lead to the implementation of remediation efforts along the Gulf of Maine. In order to widely understand the impact of the green crab invasion, it is imperative that researchers understand the potential population size and subsequent interactions in this ecosystem. This project investigated two major components in the green crabs' populations: population dynamics and the potential for interspecific competition.

The first goal of this project was to investigate: **What is the status of the population of green crabs and rock crabs in the Damariscotta River?** Due to the extreme warming event along the Gulf of Maine, I hypothesized that populations of green crabs showed a steady increase over the past five years. Because green crabs and rock crabs occupy similar niches along the Damariscotta River, I expected to find an inverse relationship between rock crab and green crab population densities. I tested these hypotheses by placing weekly subtidal and biweekly intertidal traps throughout the 2018 summer season.

My second goal investigated: **Is resource-based competition between green crabs and rock crabs leading to niche partitioning between the two species?** Many studies have suggested that competitive dominance is directly correlated with the size of each individual (Warner, 1970). However, Harr and Rochette (2012) suggested that smaller green crabs can decrease larger American Lobster survival rates, contradicting typical competition scenarios. Therefore, I hypothesized that this competitive dominance would persist for green crab and rock crab populations. This would have the potential to drive rock crabs into a deeper habitat niche and could potentially allow green crab populations to grow due to increased habitat availability. I tested these hypotheses by performing in-lab interspecific competition trials which investigated resource and direct competition.

Methods

Study Site

All data were collected from May 30th to August 10th, 2018. Field studies were conducted in the Damariscotta River in Lincoln County, Maine. This 19-mile long river has been used for fishing for over 2,500 years. Field surveys were conducted within ~0.4km of the Darling Marine Center pier in Walpole, Maine. The tidal range in my study site varied from 2.5 to 4 m, with a strong tidal current of 0.8 kph. This river ecosystem experiences large fall phytoplankton blooms, which tied with a high current and insignificant salinity gradient makes for a very productive ecosystem for primary consumers (Bullard et al., 2003). Commercially, the Damariscotta River is the most productive area in the state of Maine for oyster production as well as being home to the first mussel farm in the state.

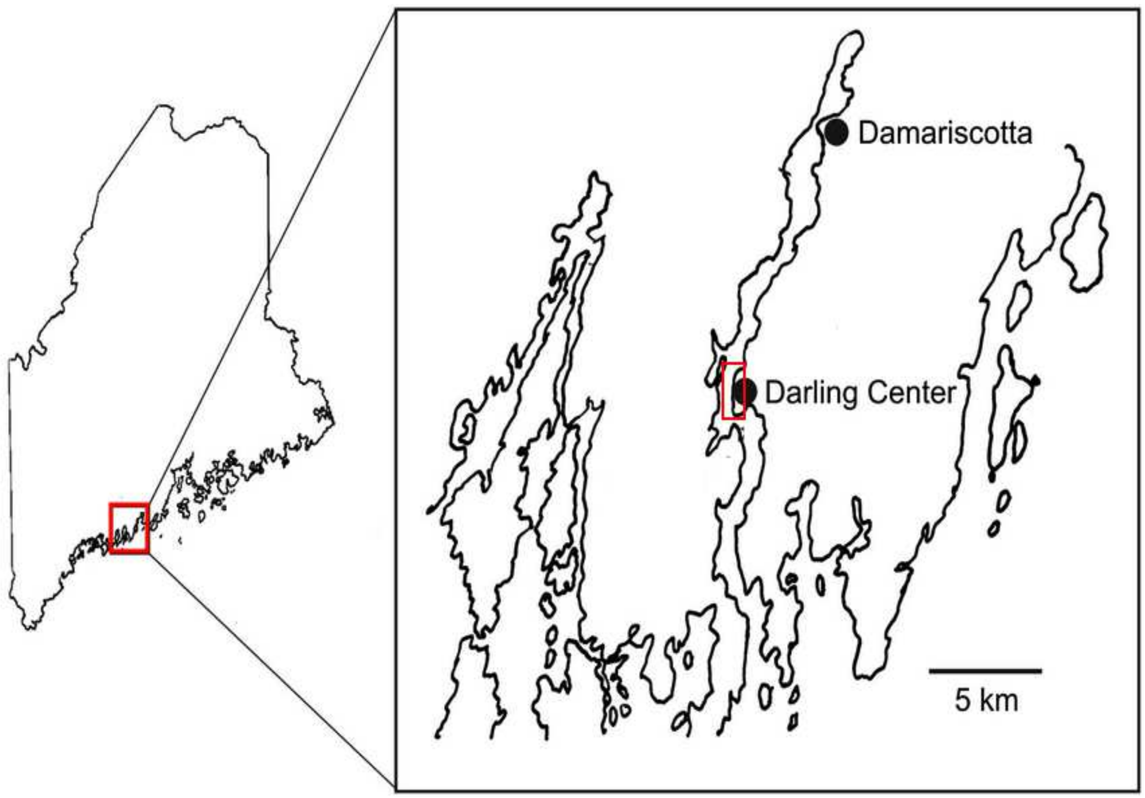

Figure 1: Map of Study Sites in Coastal Maine. Map shows where in the Damariscotta River the intertidal and subtidal traps were placed. In addition, all crabs taken for the competition trials were captured in this area. Figure is adapted from Bullard et al. (2003).

Subtidal Crab Survey

My subtidal and intertidal protocol follows similar procedure found in Welch (1968), Hunter and Naylor (1993), and MacDonald (2018). All subtidal traps were placed directly adjacent to the Darling Marine Center pier, approximately 10 meters apart. Six modified shrimp traps were placed 1-2 meters below mean low water (MLW). Traps were baited with herring and collected 23-26 hours after placement. After collection, traps were hinged open and dropped in the same location to ensure consistency. Carapace width, species, sex, molting status, number of claws, and ovigerous status were recorded for each crab identified. Traps were collected weekly from June 20th-August 10th. Due to variation in trapping dates in historical data, dates were collected as days after May 1st.

Intertidal Crab Survey

All intertidal surveys were taken directly above the subtidal traps, approximately 1-3m above MLW and directly adjacent to the Darling Marine Center pier. One m^2 quadrats were randomly placed along the substrate. Quadrats were excluded if they did not contain greater than 50% flippable rock or rockweed (*Ascophyllum nodosum*). Carapace width, species, sex, molting status, number of claws, and ovigerous status were recorded for each crab identified. Ten replicates per trial were placed and repeated biweekly from June 27-July 20th.

Competition Study

This protocol was adapted from Belair & Miron (2006). Approximately 40 green crabs and 30 rock crabs were collected from the subtidal survey traps. Male green crabs and female rock crabs with a carapace width of 75-80mm were included in the trials. The sex difference was used to model the most likely scenario in the field, as most of my trapping surveys suggested a female dominated rock crab and male dominated green crab environment. Individuals were housed in ~10cm^2 wire cages with no more than 3 individuals of the same species and food starved for two days prior to trials. Cages were kept in a tank in the flowing seawater laboratory of the Darling Marine Center with a consistent water flow originating from the site of capture. No fighting was observed during the holding period for either species. After the food starvation period, one crab of each species was selected to participate in a trial. Only crabs with a fully intact carapace (including 2 functional claws) were included in the trials. Each crab was placed in a 6-quart storage box with clear sides and a mesh top (Sterilite model #16428960) for 5 minutes for adequate habitation prior to trial. One crab of each species was then placed together in one storage box with a 1in x 1in piece of frozen herring bait. Data were recorded on feeding and fighting behaviors of both species for 30 minutes. In this study, I defined any fighting as any interaction between the two species in which they had raised chelae or were in physical contact with one another. A crab was documented as winning a contest when a fighting behavior was observed, followed by a successful obtainment of the herring bait. Twenty-six trials were taken over the course of 3 weeks. All individuals were returned to the Damariscotta River following their trial.

Statistical Analyses

I attempted to perform a factorial ANOVA (analysis of variance) on my catch rate data, but was unable to due to the inconsistent data collection period in previous seasons. I performed a one-way ANOVA on both season and year separately to investigate if the population has grown significantly in the previous five years. I also performed a two-tailed t-test on the carapace width for each species to identify if the two species of crab significantly differed in size. For my intertidal survey, I performed two-tailed t-tests on all quantitative data that I collected to identify any significant differences in the population and density of crabs utilizing this zone. For my competition survey, I used a simple linear regression to examine if there is a relationship between time each species spent on food. Finally, I performed a one-tailed t-test to investigate whether green crabs won significantly more competitive trials. All analyses were calculated using a 0.05 statistical threshold. All statistical analyses and graphs used the statistical program R.

Results

Intertidal Survey

In the intertidal zone, we primarily identified green crabs in the juvenile stages in areas covered by over 75% rockweed. No rock crabs were found in the intertidal zone during the 2018 season. My intertidal survey had significantly lower green crab density (individuals/m^2) than the 2016 survey (Table 1, two-tailed t-test, df = 24, t = 2.0, $p = 0.02$). The average carapace width in the intertidal survey (22.25 mm ± 1.36) was significantly less than the subtidal survey, which corresponds with previous studies that suggest that the intertidal zone is a nursery ground for juvenile green crabs (Hunter & Naylor, 1993). I did find evidence (intact crabs or post-molt carapaces) of 5 adult green crabs either during molting or immediately post-molting, which is consistent with previous studies which suggest that the intertidal zone also provides shelter for adults during molt. Claw and leg condition varied among sites, but most individuals possessed two claws and all eight legs.

Subtidal Survey

I did not observe any significant difference in Catch per unit effort (CPUE, as defined in Figure 1) from 2015 to 2018 (Figure 2 & 3). My results did suggest that there is a reciprocal correlation between green crab and rock crab abundance (Figure 4). As the summer progressed, green crab abundance in the traps increased significantly. During my study, I caught 24 green crabs and 17 rock crabs per trap per day on average. Trap hauls were predominantly male (87.5% male) at the beginning of the summer, but became slightly female dominated (56% female) over the four month season. This is consistent with previous studies which suggest that ovigerous females are not attracted to food bait and thus will not enter traps until later in the season (Hunter & Naylor, 1993). Of the 1208 crabs caught in the subtidal traps, only 5 were ovigerous females. The average carapace width of rock crabs was significantly larger than that of green crabs (One sample two-tailed t-test, df = 1194, t = 14.13, $p > 0.05$, Figure 5).

Competition Study

Fighting was observed in 25/26 trials with an average fighting time of 197.8 ±35.66 seconds (SE) or approximately 15% of the time. The native rock crab won a significant proportion of the fights (72.15% ± .065, one-tailed t-test, df = 25, t = 3.65, $p >$ .001). I observed no significant difference between the amount of time each species spent on the food (two-tailed t-test, df = 25, t = 1.66, p = .10). The food was fully consumed in only 2 trials. Simultaneous feeding was only observed in one trial and lasted approximately 17 seconds. In trials where the green crab fed for over 500 seconds, the rock crab was not observed eating for more than 350 seconds (Figure 6). Conversely, in any trial in which the rock crab fed for more than 350 seconds, the green crab fed for less than 250 seconds. Green crabs did not feed in four trials, and rock crabs did not feed in three trials.

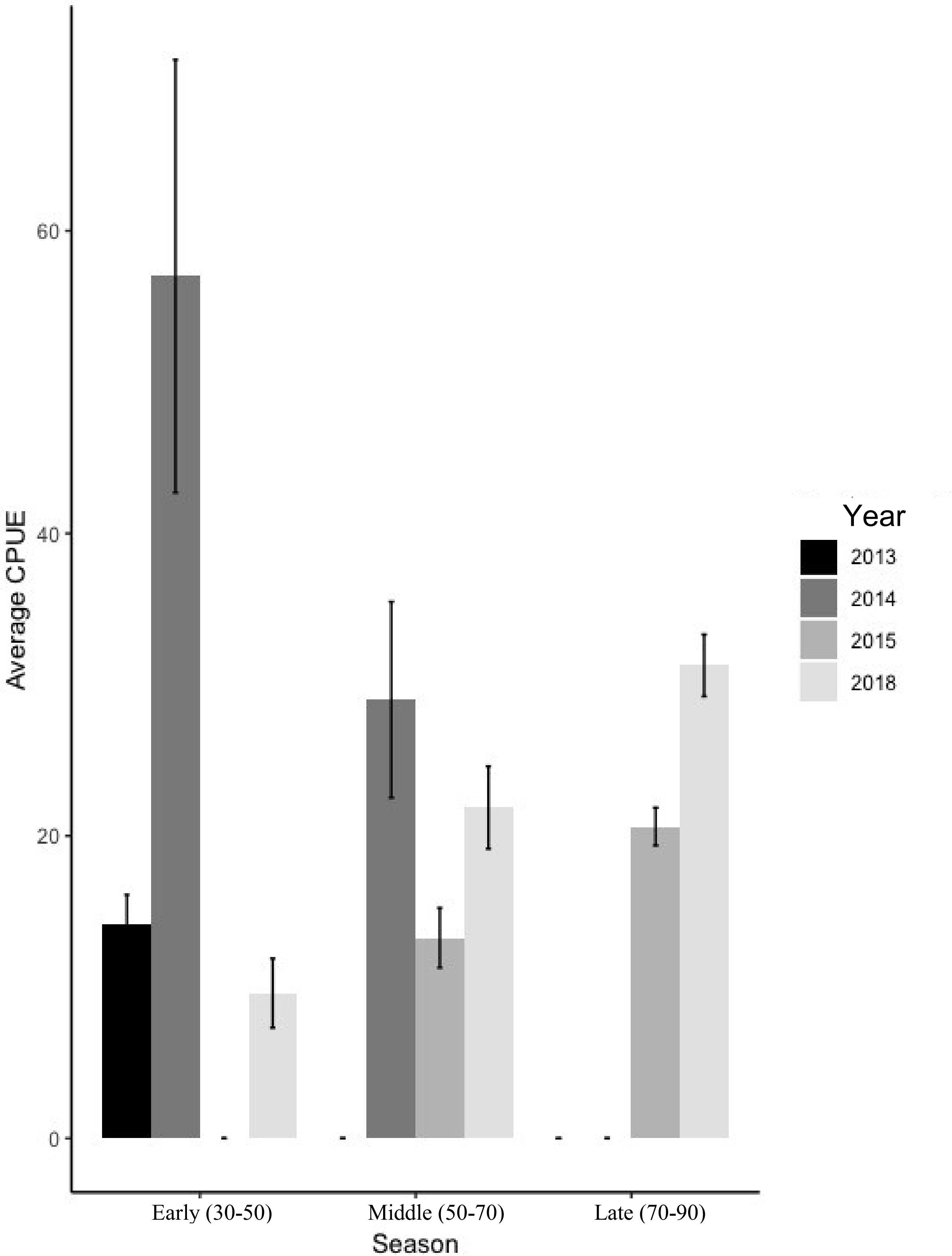

Figure 2: Average CPUE of *Carcinus maenas* from 2013-2018. CPUE was defined as catch per trap per day. Seasons were 30-50, 50-70 and 70-90 days past 5/1. No significant trend was identified per year, but there was a significant difference between each season (F= 7.76, df=2, $p< 0.0001$).

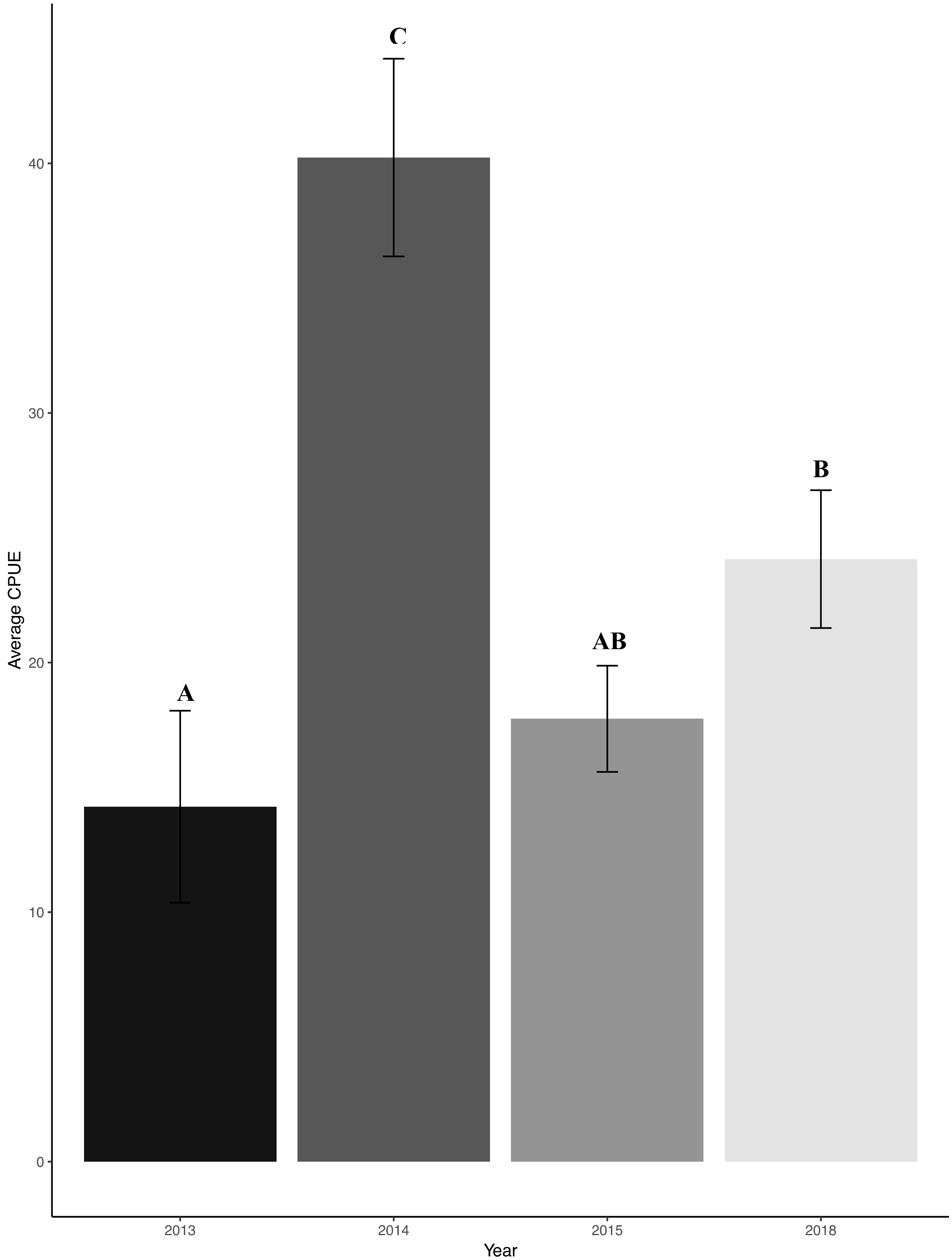

Figure 3: CPUE per year for *Carcinus maenas*. A one-way ANOVA showed that there was a significant difference between years ($F=9.95$, $df=3$, $p<0.001$). Results from multiple paired t-tests are above each bar. Results showed no significant difference between 2015 and 2018, and 2015 and 2013.

Table 1: Intertidal Trap Surveys. Two-sample t-tests were performed to compare average number of crabs and average carapace width between the two years (*P= 0.02, 0.04*).

Year	Average # Of Crabs (crab/m^2)	Average Carapace Width (mm)	Maximum Size Observed (mm)
2016	10.0 ± 1	7.24	48
2018	4.2 ± 0.58	22.25mm ± 1.36	66

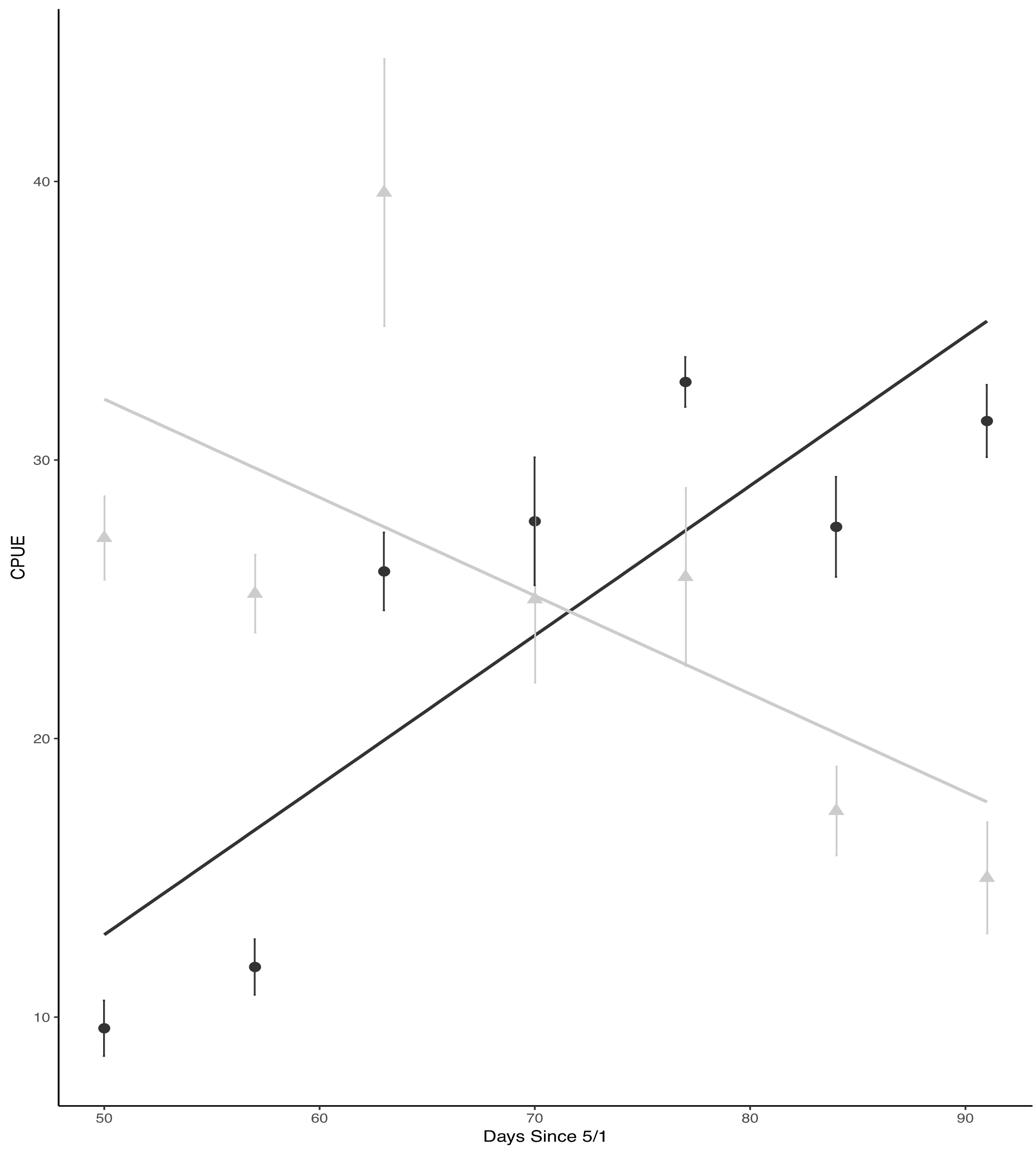

Figure 4: Average CPUE for *Carcinus maenas* and *Cancer irroratus*. The black points show green crab catch per unit effort (CPUE) as the summer season progressed. Grey points show rock crab CPUE. Rock crab abundance showed a weak negative slope (r^2=0.43) whereas green crab abundance showed a stronger positive slope (r^2=0.72).

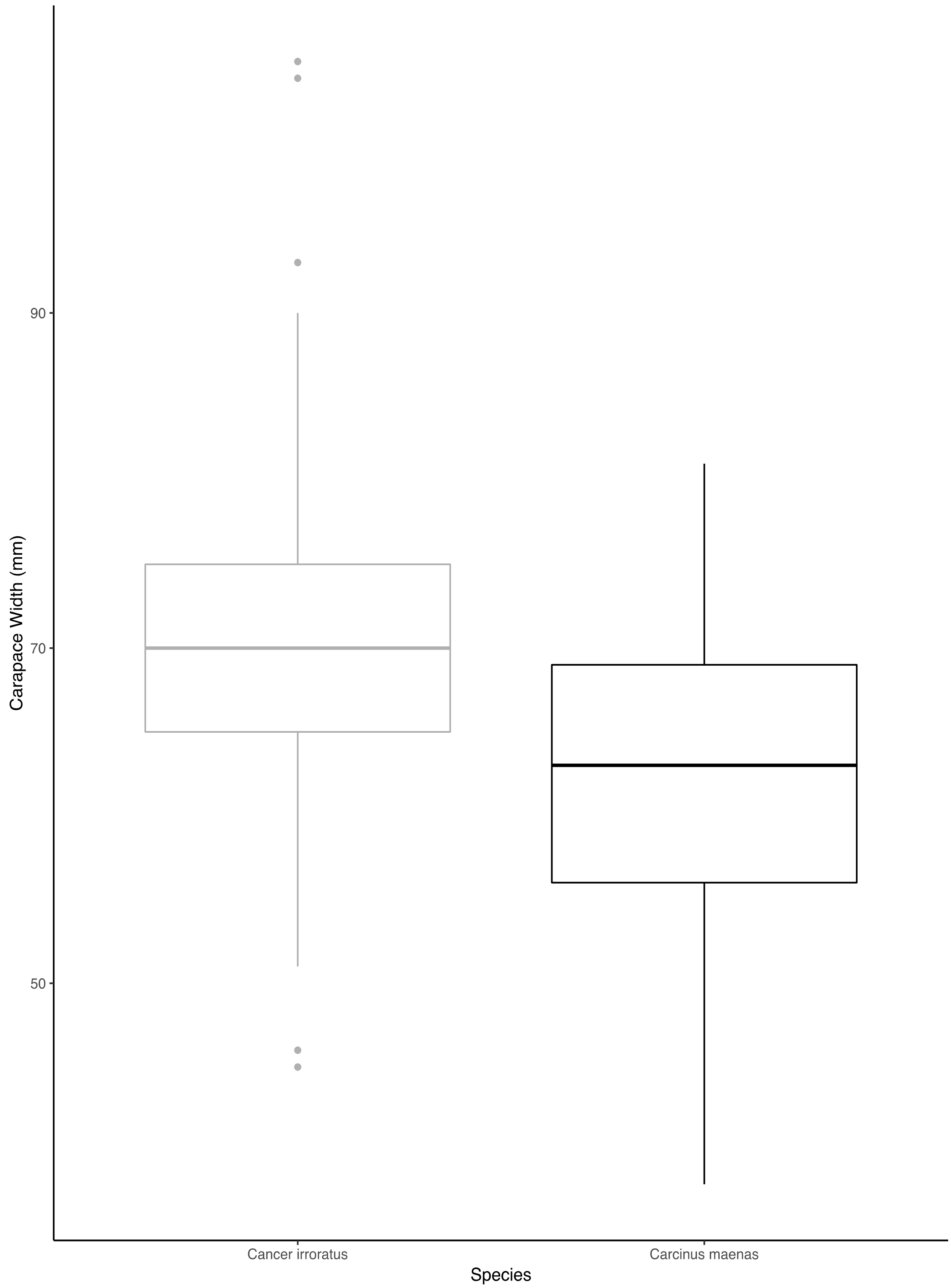

Figure 5: Distribution of Carapace Width of *Carcinus maenas* and *Cancer irroratus* in subtidal traps. The grey box represents the native rock crab, and the black box is the invasive green crab. *Cancer irroratus* were, on average, larger than *Carcinus maenas* (two-sample t-test, $p < 0.001$).

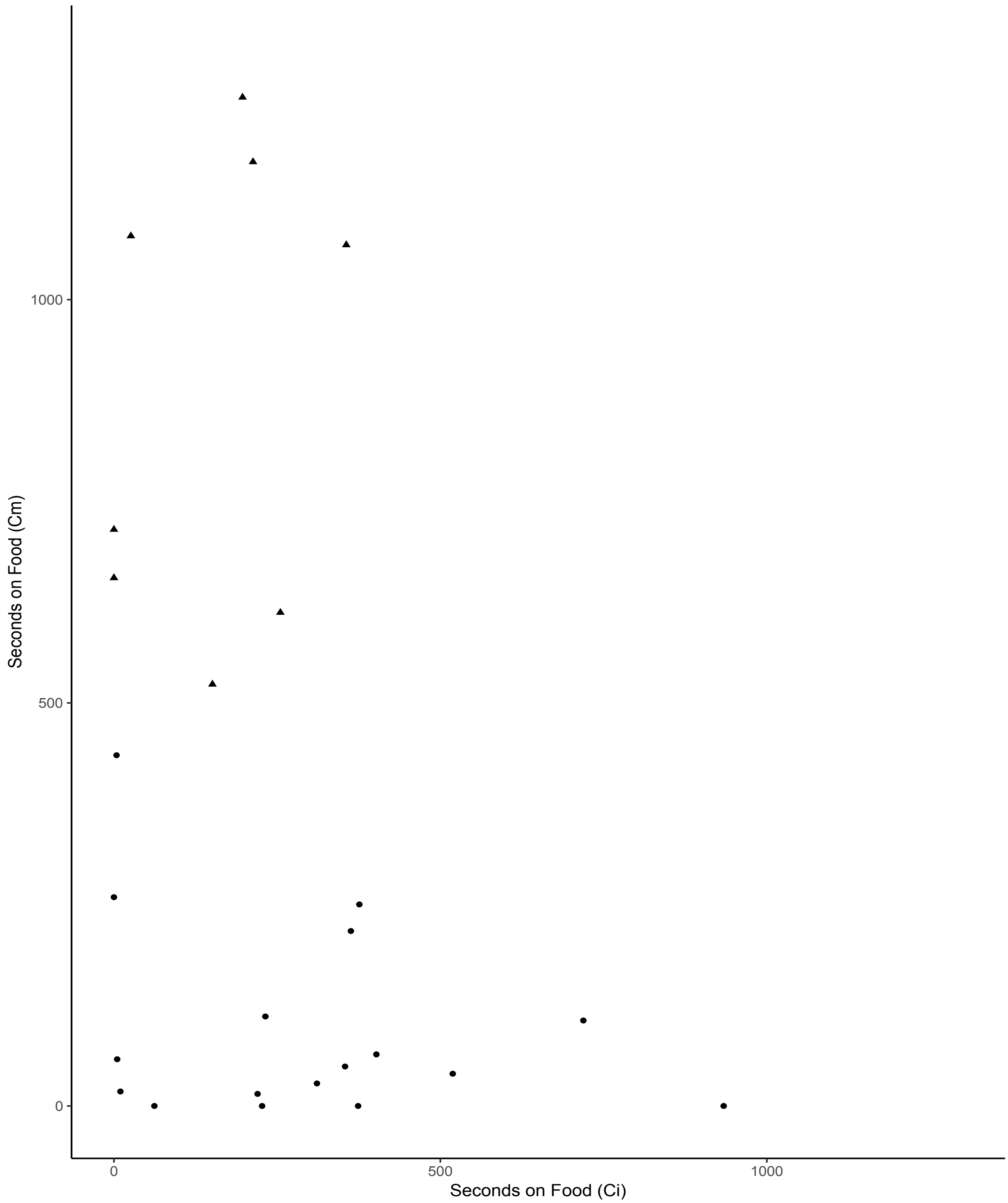

Figure 6: Time each species spent on food in 30-minute trial. Regression lines were non-significant. Triangles indicate trials in which the invasive green crab spent over 500 seconds on the food. Circles indicate trials in which the green crab spent less than 500 seconds on the food.

Discussion

Population Survey

My study identified no significant change between 2016 and 2018 in subtidal green crab abundance. Conversely, my study identified a decrease in intertidal density from 2016 to 2018. 2014 subtidal catches were significantly higher than in 2018 (Figure 2). This suggests that the population levels had begun to stabilize within this ecosystem, and the shifts in CPUE are most likely due to annual fluctuations. This result is inconsistent with my hypothesis that abundances would increase significantly. Previous studies have reported a direct correlation between temperature and green crab abundance in the Gulf of Maine, stating that temperature is the sole limiting factor regarding this species growth rate (Welch, 1968). Although the Gulf of Maine continues to warm at an alarming rate, the population of green crabs have begun to stabilize suggesting that temperature is not the only limiting factor for this populations' growth. Although temperature likely plays a large role in green crab population dynamics, other factors such as resource based competition and disease could also stabilize this population.

It is important to note that the significant decrease in recruits this season could be due to the colder than average winter temperatures in early 2018. Specifically, in the Damariscotta River, much of the surface water froze, which is atypical for most 21st century winters (Maine DMR, 2018). The northeast coast of Maine remains as part of the upper latitudinal limit for green crabs. Although it has been documented that green crabs are capable of surviving in water temperatures below 0˚C, temperature does have a documented impact on recruitment numbers. Studies have shown that due to the colder winter temperatures, green crabs extrude their eggs earlier, settle earlier and reach sexual maturity at a smaller size (Yamada & Kosro, 2010). This suggests that green crab populations along the coast of Maine grow more slowly than populations in their southern invasive range (Yamada & Kosro, 2010). Quinn (2018) was able to correlate the abundance of green crabs with 7 environmental factors including winter and spring temperature, suggesting that winter temperature has a significant impact on interannual population density of green crabs (Quinn, 2018). This research suggests that the population size for the 2018 season is lower than the seasonal average. By continuing this study for the next few years, researchers will be able to definitively determine if the population of green crabs has stabilized along the Damariscotta River.

Competition Trials

My preliminary results suggest that the native rock crab has the potential to be competitively dominant, which could help explain the population stabilization of green crabs over the past 5 years. There were no observations in my trials in which both crabs fed simultaneously on the food for a significant period of time, which suggests that when resources are limited competition is present between these two species. In addition, the rock crab won a significant proportion of the fights. My study was also able to identify a positive correlation between time the rock crab spent on food and time spent fighting. This correlation suggests that as rock crabs spend more time fighting, they are likely to win more fights and thus have more access to food resources. These findings are inconsistent with my hypothesis that green crabs were likely the dominant species. Many studies have also found that in two competitive crustacean species, larger individuals are competitively dominant over smaller individuals, especially when fighting for food resources (Shoener, 1983, Richards & Cobb, 1986). My results suggest that the average rock crab is slightly larger than the average green crab. (Figure 5). Although my study was limited to individuals of the same size, the rock crab is likely dominant for both similar size and size dominant scenarios. The rock crab population is significantly larger on average, which would increase the likelihood of competitive dominance in scenarios.

Werner and Hall (1977) reported that competition in two similar species of sunfish (Centrarchidae) caused a habitat shift in the competitively subordinate species. When exposed to the same habitat, the competitively dominant species occupied the more favorable niche, where the smaller subordinate species migrated to a less preferred niche. Since the green crab is able to occupy both the intertidal and subtidal zone, I propose that the rock crab has effectively limited the depth distribution of the green crab thus enabling only a small habitat in which the green crab can survive without predators or resource competition. This conclusion is similar to that found in (Werner & Hall, 1977) but has yet to be proposed for crustaceans in the Gulf of Maine. The resulting sympatric coexistence is further justified by my population survey suggesting that both rock crab and green crab populations are stable within this ecosystem. In this scenario, the competitively dominant rock crab would occupy the deeper and more favorable space while the green crabs would be forced further into the rocky intertidal zone. In the intertidal zone, the green crab has less opportunity to obtain food resources and is exposed to a larger predation risk due to gulls (Rome & Ellis, 2004). During my release of the captured crabs, I observed gulls waiting near the drop off location that would subsequently feed on crabs immediately after release suggesting that there is a high level of predation occurring in my site, as well as along the Damariscotta River. Further investigation would be necessary to determine the intensity of predation by the herring gull, and whether it is a driving factor affecting population size.

Typically, the rock crab is a subtidal species and is rarely seen in the intertidal ecosystem. The results from this study suggest that green crabs have been able to become an established species in the Damariscotta River because they have successfully filled the warmer shallower habitats that are too stressful for the native crabs. This is consistent with the findings of Belair and Miron (2007), who suggested that populations of green and rock crabs were observed avoiding each other both passively (temporally) and actively (spatially). Sympatric coexistence likely caused the interspecific avoidance as a method to avoid competition (Belair & Miron, 2007).

In my traps, I observed a decline in rock crab abundance and an increase in green crab abundance as the summer progressed suggesting that either species of crab will actively avoid a trap in which there is already an abundance of the other species present. These observations are consistent interspecific avoidance, as seen in Belair and Miron (2007). Interspecific avoidance is commonly seen in species with competitive interactions. Niche overlap is likely between these two species, and has been documented in camera traps placed at various depths (A. Wray, *personal observation*). The exclusion of green crabs driven by the native rock crab could be a factor in the limited population growth of the green crab. Population limitation due to interspecific avoidance has been documented previously in marine environments. Studies suggests that a population of a non-native clam in the northeastern Pacific has stabilized due to niche partitioning with a native clam species (Byers, 2002). The native species was able to relegate invasive populations to spaces not normally inhabited by the native individuals. Consistent with my study, these new spaces experienced high levels of predation, and suboptimal growing conditions which limited population growth (Byers, 2002).

Impact on Community Composition

Few studies have investigated the ecological impact of marine invasions using both an experimental and observational approach. In addition, many studies have failed to investigate the multi-level ecosystem impacts of invasive species in marine environments. The invasion of green crabs in California has significantly reduced the abundance of 20 invertebrate species, suggesting strong top down control over many prey species (Grosholz et al., 2000). An increase in abundance of green crabs over the subsequent years also has the potential to decrease shorebird abundance by reducing the abundance of prey in the intertidal zone. Studies such as these along the Gulf of Maine are critical in understanding the long-term effects of the green crab invasion. The invasion of green crabs along the eastern coast of North America is one of the longest documented invasions of green crabs (Welch, 1968). By studying this system specifically, researchers can better predict the long-term impact of green crab invasions in other ocean systems. As many researchers across the Gulf of Maine have historical records of intertidal composition including biomass and dominance, collaborative studies could yield potentially important information (R. Steneck, *personal communication*).

Studies have shown that ecosystems exist in one stable state which have the ability to flip into another stable state when exposed to various ecosystem pressures. As studied by Steneck et al. (2013), various fishing pressures and continuous decades of overfishing have caused the Gulf of Maine subtidal ecosystem to lock into a stable state dominated by large coralline algae and crustaceans. This flip and lock resulted in a loss of the previously observed ecosystem which was dominated by kelp and predatory finfish. This concept of ecosystem flip and locks have been studied in other systems such as the Australian temperate reef communities. This flip and lock was likely caused by ocean warming as a result of climate change (Wernberg et al. 2016). Both temperature shifts and the introduction of invasive species have the potential to cause ecosystem flips. Ecosystem 'flips' can not only shift species distribution, but completely alter community composition (Steneck et al., 2013). Future work examining the potential for a green crab-induced ecological flip in the intertidal rocky coastline could be instrumental in understanding the effects of a now fully established green crab population.

Potential for Fishery Establishment

Competitive interactions between species can be directly reliant on the length of time that both species have been able to interact (Matheson and Gagnon, 2012). Most competition studies involving invasive species only study these interactions in the first few years of invasion. As species behaviors tend to develop over time, this leads to a misunderstanding of the long-term interactions that are present between species (Matheson & Gagnon, 2012). Matheson & Gagnon (2012) conducted a similar competition study as my study, but suggested that the competitive interactions seen in their experiment might not be fully developed, due to a shorter invasion timeline of green crabs in their study site (Matheson & Gagnon, 2012). Their study was conducted in Newfoundland, where populations of green crab had been established for 15 - 17 years. Unlike in Newfoundland, the competitive relationships between rock crabs and green crabs in the Gulf of Maine have been present for over 100 years. This suggests that observations in my study are representative of two well-developed populations.

Since my study is able to predict the long-term interactions between these species, the implications can be much more far reaching. For example, this study can help to inform proper management of both the Maine crustacean and bivalve fisheries (Sorte et al., 2016). My study suggests that methods in which mussel, soft shell clam and/or oyster traps are secured at least 6 meters below MLW would likely decrease predation by green crabs, and result in lower mortality rates and higher CPUE. This will not only reduce predation on the bivalves, but can reduce food availability for the green crab thus increasing overall intraspecific competition.

My study also suggests that remediation efforts can now be put into place to remove the green crab from ecosystems along the Gulf of Maine. Parks Canada Conservation and Restoration was able to successfully trap and remove green crabs in order to restore eelgrass beds in a semi-closed ecosystem in Nova Scotia (Gabriel Beaulieu, *personal communication*). Although this method has proven to be successful, I believe this will not be the best management solution for fisheries in Maine. In isolated systems, especially within economically important regions such as the Damariscotta River, this method could potentially save species from local extinction due to green crab predation.

Researchers, culinary chefs, and fishery managers have begun to work on an effective method to introduce green crabs into the culinary market in the United States. Venetian chefs have been able to successfully market a similar species (*Carcinus esturarii*) as an edible soft-shelled crab much like the blue crab along the southeastern coast of the United States (Marissa Macmahon, *personal communication*). Establishing and growing a market for soft-shelled green crab across the United States could prove to be the most successful method for minimizing the intensity of the invasion (Porier et al., 2018). Plans to control green crabs should consider the potential consequences that such control might also have for native species such as the American lobster and rock crab. An abundance of trapping materials, including traps for lobster, shrimp and crab in the Gulf of Maine have been directly correlated with the entanglement of marine mammals in fishing gear (Firestone et al, 2008). This is extremely important as the Gulf of Maine is the summer feeding ground for the critically endangered North Atlantic Right Whale (*Eubalena glacialis*) (Firestone et al, 2008). In order to mitigate this risk, I suggest that future work on green crabs should attempt to identify if ‘hot spots’ for this species exist. This can help to inform proper and safe management for the future of this species.

Acknowledgements

Dr. Robert Steneck from the University of Maine was instrumental throughout my thesis project, both hosting me as a research intern and as a thesis advisor. Katie Raffier and Emma Ober helped tremendously in the field, hauling many traps over the course of the summer. Timothy Miller assisted me with laboratory setup in the wet lab. Professors Marc Snyder and Brian Linkhart helped with the many drafts of this paper. In addition, I would like to thank the Darling Marine Center, the NSF and the Colorado College OBE department for providing me with funding for this project. Finally, I would like to thank all of my fellow DMC interns for spending many hours setting up traps and testing different methodologies with me.

References

Baeta, A., et al (2006). Feeding Ecology of the Green Crab, *Carcinus maenas* (L., 1758) in a Temperate Estuary, Portugal. *Crustaceana* 79 (10): 1181-1193.

Bélair, M. Miron, G. (2009). Predation behaviour of Cancer irroratus and Carcinus maenas during conspecific and heterospecific challenges. *Aquat. Biol* 6: 41-49

Bullard S.G., Davis C.V., Shumway S.E. (2013). Seasonal patterns of ascidian settlement at an aquaculture facility in the Damariscotta River, Maine. *J Shellfish Res* 32:255–264

Byers, J.E. (2002). Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia* 130:146–156

Cohen, A., Carlton J., Fountain M. (1995). Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Marine Biology* 122 (2): 225-237.

Firestone J., Lyons S.B., Wang C., Corbett J.J. (2008). Statistical modeling of North Atlantic right whale migration along the mid-Atlantic region of the eastern seaboard of the United States. *Biological Conservation* 141:221-232.

Grether G.F., Peiman K.S., Tobias J.A., Robinson B.W. (2017). Causes and consequences of behavioral interference between species. *Trends Ecol Evol* 32:760–772.

Grosholz E.D., Ruiz G.M., Dean C.A., Shirley K.A., Maron, J.L., Conners, P.G., (2000). The Impacts of a Nonindigenous Marine Predator in a California Bay. *Ecology* 81(5): 1206–1224

Grosholz ED, Ruiz GM (1996). Predicting the Impact of Introduced Marine Species: Lessons From the Multiple Invasions of the European Green Crab *Carcinus maenas. Biological Conservation* 78: 59-66

Harr M., Rochette R. (2012). The effect of geographic origin on interactions between adult invasive green crabs *Carcinus maenas* and juvenile American lobsters *Homarus americanus* in Atlantic Canada. *Journal of Experimental Marine Biology and Ecology* 422-423: 88-100.

Hunter E, Naylor E (1993). Intertidal migration by the shore crab *Carcinus maenas*. *Mar Ecol Prog Ser* 101: 131-138

Kordas, R., Harley C., O'Connor M. (2011). Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology* 400: 218-226

Larkin, P. A. (1996). Concepts and issues in marine ecosystem management. *Review of Fisheries Biology and Fisheries.* 6: 139-164.

Latham, J. (1999). Interspecific interactions of ungulates in European forests: an overview. *Forest Ecology and Management* 120:13–21.

Lowe S. et al (2000). 100 of the World's Worst Invasive Species. A Selection from the Global Invasive Species Database. *Aliens:* 1-12

MacDonald, A., Hamilton D. (2018). Distribution and Habitat Use of the Invasive *Carcinus maenas* and the Native *Cancer irroratus* in Intertidal Zones in the Upper Bay of Fundy, Canada. *Northeastern Naturalist* 25(1): 161-18

Maine Department of Marine Resources (2016). Commercial Fisheries Landings by Zone.

Maine Department of Marine Resources (2018). Boothbay Harbor Temperature Log

Matheson K., Gagnon P. (2012). Temperature mediates non-competitive foraging in indigenous rock (Cancer irroratus Say) and recently introduced green (Carcinus maenas L.) crabs from Newfoundland and Labrador. *J Exp Mar Biol Ecol* 414-415: 6-18

McDonald P.S., Jensen G.C., Armstrong D.A. (2000). The competitive and predatory impacts of the nonindigenous crab (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *J Exp Mar Biol Ecol* 258:39–54

Mooney H. A., Cleland E. E. (2001). The evolutionary impact of invasive species. *PNAS* 98(10):5446-5451

Pershing, A., Alexander A., et al. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350(6262): 809-812.

Poirier, L.A., Tang S., Mohan J., et al (2018). A novel bycatch reduction device (BRD) and its use in a directed fishery for non-indigenous green crabs (*C. maenas*) in Atlantic Canada. *Fisheries Research* 204: 165-171

Quinn, B.K. (2018). Dramatic decline and limited recovery of a green crab (Carcinus maenas) population in the Minas Basin, Canada after the summer of 2013. *Peer J*, 17(6).

Richards, R.A. and Cobb, J.S., (1986). Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(11): 2250-2255.

Ricklefs, R.E. and Relyea R., (2018). Ecology: The Economics of Nature. Freeman, W.H. & Company.

Rome, M., Ellis J. (2004). Foraging Ecology and Interactions between Herring Gulls and Great Black-backed Gulls in New England. *Waterbirds* 27(2): 200-210.

Ropes, J.W. (1968). The Feeding Habits of the Green Crab, *Carcinus maenas* (L.) *Fishery Bulletin* 67(2): 183-203.

Schoener T.W. (1983). Field experiments on interspecific competition. *Am Nat* 122:240-285

Sorte, C., et al (2016). Long-term declines in an intertidal foundation species parallel shifts in community composition. *Global Change Biology* 23(1): 341-352.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner (2002). Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future. *Environmental Conservation* 29:436–459.

Steneck, R.S., Lealand, A., McNaught, D.C., Vavrinec, J. (2013). Ecosystem Flips, Locks and Feedbacks: The Lasting Effects of Fisheries on Maine's Kelp Forest Ecosystem. *Bulletin of Marine Science* 89.

Trussell, G.C., Ewanchuk, P.J. & Matassa, C.M. (2006). The fear of being eaten reduces energy transfer in a simple food chain. *Ecology* 87: 2979–2984

U.S. Geological Survey. (2018). Nonindigenous Aquatic Species Database. Gainesville, Florida.

Welch, W. (1968). Changes in Abundance of the Green Crab, *Carcinus maenas* (L.), in Relation to Recent Temperature Changes. Maine Resource Documents 3.

Warner, G.F. (1970). Behavior of Two Species of Grapsid Crab during Intraspecific Encounters. *Behaviour* 36: 9-19

Wernberg, T. et al. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science* 353:169–172

Werner E., Hall D. (1977). Competition and Habitat Shift in Two Sunfished (Centrarchidae). *Ecology* 58: 869-876

Yamada S.B., Kosro P.M. (2010). Linking ocean conditions to year class strength of the European green crab, *Carcinus maenas*. *Biol. Invas,* 12:1791–1804