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Temperature and Predator Effects on Green Crabs (*Carcinus maenas*) and Their Distribution in South Slough National Estuarine Research Reserve

by

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A thesis submitted in partial fulfillment of the
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Abstract

The invasive green crab (*Carcinus maenas*) has increased in abundance and distribution among Oregon's estuaries. Its global success in establishing in new environments and tolerance for abiotic stressors, such as temperature, raises concern for *C. maenas* to negatively influence native crab species, especially given global climate change. To improve in predicting invasion impacts, this work analyzed the results from a controlled tank experiment at Portland State University and the field data on a population of *C. maenas* in South Slough National Estuarine Research Reserve (SSNERR). The aquarium experiment documented predation pressure on *C. maenas* across a range of temperatures (9° to 30°C) and predatory crabs *Callinectes sapidus*, *Cancer productus,* and, as a control *C. maenas.* The behavioral responses of prey *C. maenas* were observed across temperature and predator combinations. There were five categories of behavioral responses measured in time duration. The west Atlantic *C. sapidus* preyed heavily on *C. maena*s, especially at warmer water temperatures; however, east Pacific *C. productus* preyed much less on *C. maenas* and only at the cold temperatures, suggesting different trajectories of biotic resistance across the coasts as waters warm. Crab behavior aligned with the predation findings. For example, *C. productus* were most active at 9°C and all died at 27°C and higher. In tanks with *C. productus, C. maenas* were most aggressive at warm temperatures. In contrast *C. maenas* spent more time feeding at 9°C when in tanks with *C. sapidus* and, surprisingly, also with *C. productus*. Crab trap data from SSNERR was plotted on a map to identify surrounding habitat and bottom substrate of areas with high catch per unit effort (CPUE) of *C. maenas* in the last six years. Mean CPUE of *C. maenas* was below five throughout the SSNERR region with sites closest to the mouth of the estuary having the highest CPUE rates. Little structure was surrounding trapping sites; however, there was seagrass at sites with the highest CPUE of *C. maenas*. The mean CPUE difference of native species prior to (2002-2016) and following (2016-2021) *C. maenas* abundance increase in 2016 was compared to the mean CPUE of *C. maenas* in the last six years. Results indicated no correlation between the CPUE of *C. maenas* influencing the difference of CPUE of native crab species. The tolerance and predation avoidance demonstrated from prey *C. maenas* in warmer temperatures indicate their ability to acclimate and/or adapt in stressful climate change conditions of higher water temperatures. This is of concern due to the increasing potential to negatively affect Oregon native crab species, such as *C. productus* over time.

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List of Abbreviations

AIC – Akaike information criterion

BC – Blue crab (*Callinectes sapidus*)

CI – Confidence Interval

CPUE – Catch Per Unit Effort

EFH – Essential Fish Habitat

GAM – Generalized Additive Model

GC – Green crab (*Carcinus maenas*)

OCMP – Oregon Coastal Management Program

ODFW – Oregon Department of Fish and Wildlife

OSU – Oregon State University

PCW – Proportional Carapace Width

PSU – Portland State University

RR – Red Rock crab (*Cancer productus*)

SD – Standard Deviation

SSNERR – South Slough National Estuarine Research Reserve

Introduction

Invasive species can alter the environments they occupy and are therefore a common component in environmental management programs. In some cases, invasive species cause negative and/or harmful disturbances to ecological communities within a short time span after introduction (Crooks and Solué, 1999). Invasive species' behaviors and responses in recipient regions are unpredictable as they can be highly adaptable and their survival abilities can vary from one population to another (Young and Elliot, 2020). A globally successful invasive species that has demonstrated this is the Green Crab, *Carcinus maenas,* which is native along the coasts of western Europe and northern Africa, including the coasts from Norway and Iceland to Morocco (Young and Elliott, 2020). *Carcinus maenas* was first discovered along the west coast of North America in 1989 (Cohen et al., 1995) and Oregon's coast as early as the late 1990's, with transportation indirectly assumed to be from ballast water of commercial vessels to California and then currents carrying them to higher latitude regions (Behrens Yamada et al., 2019).

At high densities, *C. maenas* have created strong ecological and economic impacts in several regions throughout the globe (Grosholz and Ruiz, 1996). For example, previous research from the northwest Atlantic has reported devastating effects on bivalve resources and aquatic grass habitat (Whitlow, 2009 & McDonald et al., 2001). *Carcinus maenas*' impact from uprooting eelgrasses have induced behavioral plasticity in bivalves to burrow deeper and grow longer siphons (Whitlow, 2009). Within the eastern Pacific, where *C. maenas* have more recently invaded, they have been documented to reside in habitats that function as a nursery for juvenile native invertebrates and outcompete Dungeness crabs, *Metacarcinus magister*, of similar or lesser size posing concern for future stocks of this harvested species (McDonald et al., 2001).

Carcinus maenas have yet to achieve high abundances along the Oregon coast; however, they are known to have established populations in several estuaries (Behrens Yamada et al., 2019). Increases in water temperatures and unexpectedly strong El Niño events have allowed *C. maenas* to spread from San Francisco waters, where they were initially observed, and northward along the eastern Pacific (Hunt and Behrens Yamada, 2001 & Behrens Yamada and Gillespie, 2008). These crabs achieved higher populations in California and British Columbia, Canada but their numbers have significantly increased in Oregon and Washington in recent years (de Rivera et al., 2007 and Behrens Yamada et al., 2019). This is supported by the increase in spatial range and capture rate of *C. maenas* within traps since their notable increase in Oregon in 2016 (Schooler et al., 2020). However, these capture rates may not accurately quantify *C. maenas* densities since females sometimes avoid traps due to aggressive males and to protect their broods for successful larvae release (de Rivera et al., 2007). Higher densities of *C. maenas* can lead to ecological changes that affect populations of native species, alter food webs, and even destroy foundational eelgrass beds of estuarine habitat (Howard et al., 2019).

Estuaries are susceptible ecosystems to be invaded by non-native species due to their fluctuating abiotic features such as temperature, nutrient exchange, and salinity (Jamieson et al., 1998). In fact, *C. maenas* are commonly seen within estuaries due to their tolerance to lower saline and higher temperature waters among shallow environments (McDonald et al., 2006 & Young and Elliott, 2020). *Carcinus maenas* were first recorded in Coos Bay, Oregon in 1996 which encompasses the South Slough National Estuarine Research Reserve (SSNERR), a federally and state managed reserve merged with human and natural communities (Trueblood et al., 2019). Coastal communities rely upon sustainable coastal resources for long-term economic development (Trueblood et al., 2019). However, with *C. maenas'* abundance increasing annually, such resources may be at risk (Grosholz and Ruiz 1996). Since *C. maenas* do not have a selective diet, they are not only well suited for survival if food sources become limited but can feed on a range of bivalves and crab species that the Reserve is responsible for managing (Miron et al., 2005). Additionally, the tolerance of *C. maenas* suggests that the species is fairly versatile on residing throughout the majority of the Reserve despite the fluctuating abiotic features that naturally pose challenges for survival or limitations for distribution (Behrens Yamada et al.,2019).

While *C. maenas* have been well studied, their distribution is difficult to predict as it differs among regions (Grosholz and Ruiz, 1996). Their habitat selection is not fully understood and knowing this information can aid in efficient removal efforts in SSNERR before their numbers become unmanageable. This data is important to understand because Oregon's estuaries are essential fish habitats (EFH), directly and indirectly supporting the growth and mature process for a range of wildlife including commercially important species such as rockfish (*Sebastes* spp.) and Pacific oysters (*Magallana gigas*) and even habitat building species such as native eelgrass (*Zostera marina*) (Gallagher and Heppell, 2010 & Muething et al., 2020). Furthermore, climate change events which have been occurring more frequently in recent years, can cause a decrease in biotic resistance from native species that would prevent further distribution of *C. maenas* (de Rivera et al., 2005). Knowing how stressed environmental conditions of climate change can alter interspecies behavior, and how habitat is correlated to *C. maenas* abundance can assist in understanding *C. maenas* distribution and managing them in Oregon (Hellmann et al., 2008).

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Chapter One: Temperature and Predator Effects on *Carcinus maenas*

Introduction

Species invasions are predicted to be more successful in temperate climates compared to tropical ones, partly due to the biotic interactions and diversity of the native species (Freestone et al., 2013). Communities with higher diversity fill more niche roles, creating biotic resistance, and limiting non-native or invasive species establishment (Beaury et al., 2020). While Ackerman et al. (2017) expected to see this pattern from seeded forest plots on Puerto Rican islands, as native species should have expended resources such as space and soil nutrients, their results reflected a positive correlation between invasive and native species richness. Several studies propose that extrinsic factors, including natural disturbance, spatial area of observation, and/or physical environmental stressors, influence biotic interactions of native species (Ackerman et al., 2017, Beaury et al., 2020, & Dethier and Hacker, 2005). These alterations in biotic interactions can present an opportunity for invasive species to succeed in establishment or spread (Dethier and Hacker, 2005). Such opportunities can be expedited with frequent climate change events that are altering environmental factors and posing additional stressors for native communities (Hellmann et al., 2008).

In particular, climate change poses drastic influences to the ocean environment through stratification, which can limit nutrient column exchange, cause acidification, shifting currents and circulations, and increasing water temperatures that directly and indirectly alter water quality (Henson et al., 2016 & Gattuso et al., 2018). Consequently, this impacts marine and aquatic communities and aids opportunities for non-native or invasive species to advance on their pathway of a successful invasion (Hellmann et al., 2008). For example, invasive species of a fouling community collected from Bodega Bay, California were observed to have death rates at higher temperatures than native species. The invasive species' tolerance for higher temperatures facilitated spread on experimental platforms as native species died and fell off platforms at lower temperatures (Sorte et al., 2010).

Increased temperatures are quite applicable recently as spontaneous warming events, such as large regions of increased sea surface temperature called 'warm blobs,' have been observed in the Pacific Ocean (Chen et al., 2021). The 'warm blob' of 2015 caused cascading effects to native communities by amplifying algae blooms to become toxic, inhibiting transport of phytoplankton, which are important primary producers, limiting food sources for multiple consumers throughout the food web, and creating stressful environmental conditions for an extended period of time (Cavole et al., 2016). If warming events like 'warm blobs' continue to occur more frequently, their effects can prevent the efficiency of biotic resistance and allow non-native and invasive species with higher tolerance thresholds to establish, increase populations and/or spread (Gattuso et al., 2018 & Hellmann et al., 2008). This is a growing concern in the Pacific Northwest as a particularly aggressive crab species, *C. maenas*, has been increasing in abundance and distribution with the aid of El Niño events providing transportation from regions of northern California where they are highly abundant (Behrens Yamada et al., 2017).

Studies have observed the ability of native crabs to biologically resist *C. maenas* including the Blue Crab (*Callinectes sapidus*), by restricting distribution, and Red Rock crabs, *Cancer productus*, by consuming more of the higher preferred oyster prey (de Rivera et al., 2005 & Hunt and Behrens Yamada, 2001 & Ens et al., 2021). In fact, in coastal waters of Australia, the high diversity of native crab species is assumed to provide the biotic resistance against *C. maenas* (Sinclair, 1997). However, performance and survivorship of native crabs can be compromised if their ecosystems experience extensive climate and/or temperature changes (Cavole et al., 2016). The combination of *C. maenas'* high tolerance to abiotic change and the reduced survivorship of native crab species, could enhance invasion success with further distribution of *C. maenas* (Soundarapandian et al., 2008). To predict this possible outcome, Dr. C. de Rivera and colleagues conducted a tank experiment with the goal of observing *C. maenas* behavioral responses when exposed to varying temperature changes, which provides insight into warming conditions from climate change. A second goal was to identify how temperature affects the degree of biotic resistance from different predator species of crab through predation. With less biotic resistance from native species and increased environmental stressors from climate events we expected to see invasive *C. maenas* surpass establishment and distribution challenges and be more responsive even in environments with stressors or disturbances.

The aim of the analyses was to understand the following: 1) how does mortality in *C. maenas* vary based upon temperature conditions, predator identity and the interaction of the two, 2) how does *C. maenas* behavior change or vary across temperature conditions, predator identity and the interaction of the two, and 3) how does predator behavior vary across temperatures with *C. maenas* prey present?

Due to the general trend of crabs predating on smaller sized confamilial crabs, we would expect to see higher mortality of *C. maenas* when they are relatively small compared to the predator, yet mortality will decline with increased temperatures due to the higher tolerance of *C. maenas* in warm temperatures (Miron et al., 2005). Since Behrens Yamada et al. (2019) found *C. maenas* to reside in warmer water temperatures, then we can expect to observe no effect on behavioral responses from *C. maenas* as tank temperatures increase, regardless of their role as predator or prey. However, we would expect predatory crab species *C. productus*, a native species that resides within a small range of temperature conditions, to be less responsive as temperatures drastically change, particularly at warmer temperatures (Freestone et al., 2013). This is thought to be applicable with *C. sapidus* but with colder temperatures as their range in the Atlantic is dominated at lower latitudes and limited at higher latitudes when compared with *C. maenas* presences (Rogers et al., 2018).

Methods

Organism Acclimation Procedure:

The analysis was conducted using data from a tank experiment conducted in 2007 and 2008 at the Bodega, California Marine Lab and in 2013 at Portland State University within the marine lab of the Science Research and Teaching Center. Crabs were kept in holding tanks and at their collection temperature with the use of flow-through tanks. Holding tanks held conspecific species that were fed fish and food pellets every other day. Crabs were slowly brought to each experimental temperature, spending at least two hours at each 1.5°C interval from their holding temperature.

Lab Procedure:

Crab behavior responses and predation were measured in 80 L aquaria across a gradient of eight temperatures, from 9° to 30°C, for prey-sized *C. maenas* and their predators. The *C. maenas* used as prey ranged from 50 to 74 mm in carapace width, averaging 60.9 mm, and size classes were distributed evenly across temperature treatments. There were three manipulations of crab composition for each trial: a) three to four prey *C. maenas* along with one predator *C. maenas* (mean = 78.9 mm, range =75-81 mm carapace width) as a control, b) three to four small *C. maenas* and one *C. sapidus* (mean = 158.3 mm, range =142-170 mm carapace width, including long outer spines), and c) three to four small *C. maenas* and one *C. productus* (mean = 132.0 mm, range = 120-146 mm carapace width). At first, four of the small *C. maenas* were used but, because of later shortages in supply of the crabs, the number of prey crabs was reduced to three. Experiments for all 9°, 15°, 21°, and 27° C treatments were conducted concurrently on 30-31 January and for 12°, 18°, 24°, and 30° C treatments on 19-20 February 2007 in the Bodega Marine Lab as well as August 2013 in the Portland State University marine lab. Four additional replicates were run, 27 February to 1 May, 2007 and again in 2013. For temperature-predator combinations: there were a total of five replicates for control tanks at 9°, 15°, 21°, and 27° C, for tanks with a *C. sapidus* predator at 15°, 18°, 21°, 24°, and 27° C, and for tanks with a *C. productus* predator at 9°, 15°, 18°, 21°, and 24° C. Temperature order was randomized for these replicates. The 30°C temperature treatments were not replicated for *C. productus* as all attempts resulted in death at 27 ° and 30° C temperatures. The aquaria had a 7.5 cm sandy-mud layer on the bottom and was filled with aerated, filtered seawater. Each aquarium was divided in two with a removable plexiglass. At the start of each experiment, three or four prey *C. maenas* were placed on one side of the divider and one predator-sized *C. sapidus, C. productus*, or *C. maenas* was placed on the other. After a 24-hour acclimation period, the divider was removed and a variety of sized bivalve prey (clams and mussels) were added, in excess, then observations started.

Behavioral responses and predation on prey *C. maenas* were quantified using several sampling methods. Two observers recorded behavior responses of the predator and a randomly selected prey, the focal crab, for 30 minutes. Behavior responses were quantified based upon five categories of 'Still', 'Active', 'Feeding/Foraging', 'Aggression', or 'Avoidance' and the length of time of the response in seconds. The behavior categories were identified as the following responses: 1) 'Still' included buried in mud, exposed but still, still but moving mandibles, 2) 'Active' included moving in place, walking, swimming, digging, 3) 'Feeding/Foraging' included probing sediment, handling or consuming food, 4) 'Aggression' included a forceful motion towards another crab with the attempt or success of coming in contact, and 5) ‘Avoidance’ included when a crab moved away from an aggressive crab.

Data from each set of two observers were averaged; when only one sample (e.g., the crab died or was eaten from a previous replicate or the data were later lost) was available, the value from the one half-hour observation period was used. In addition, tanks were scanned at least 16 consecutive times every half hour starting between 8:30 and 10:30 AM on the first day to record behavior and predation and an additional 5 scans, once every 2 hours, on the second day to check for predation of any crabs.

Analysis:

Data were analyzed using the R Studio (version 4.1.1), (see appendix for details). Results from the 2007 and 2008 Marine Lab as well as 2013 Portland State University were combined since there was no significant difference in the year factor when experiments were carried out, which provided a total sample size of 26 tanks. Prey killed (marked as 1) or not (marked as 0) was run through a binomial logistic regression model in response to the three predator species present, date (as a blocking factor), temperature, and proportional carapace width (PCW); PCW is the width of each prey crab divided by the width of its associated predator. This full model of three predictor variables resulted in high p-values of two of the predator species which prompted a reduced model to be run through a binomial logistic regression. The reduced model omitted predator as a predicting variable and assessed the relations of temperature and PCW to prey killed. The reduced model’s higher Akaike information criterion (AIC) value and lower McFadden indicates that it does not fit the data as well as the full model. Therefore, the logistic regression was run with the full model and followed up with an odds ratio to qualify the strength of the predicting variables to the mortality of prey *C. maenas.*

Behavioral responses from 2007 and 2013 were used to come to a total of 163 experimental units. Data were first analyzed by subsetting based on the role of predator or prey and graphed to quantify the frequency of the five behavior responses across the eight temperatures. Additionally, frequencies of behavioral responses were graphed based upon predator species present with the prey *C. maenas* or the crab species when focusing on predator crabs. Predator and focal prey data were further analyzed by summing the time individual crabs spent in each behavior response.

The data were not normally distributed and there was a non-linear relationship between the predictor and response variables. Therefore, the data were run through generalized additive models (GAM). GAM allowed flexibility in interpreting the patterns of the data by separating the predictor variables into sections, using smoothing functions, and provided a visual display to identify the response function between the variables. The p-value outputs from GAM provide a measurable significance of the nonlinear relationship between the summed time of each of the five behavior responses and temperature based upon crab species. This is not to be interpreted as a best-fit-line but a general predictive pattern among the variables. Prey data was subset based upon behavior and then plotted to represent the three species of predators that were present in tanks with the focal crabs while predator data was subset based upon behaviors and plotted based upon which of three species of predators expressed the behavior response. Time spent with 'Avoidance' was omitted from predator species due to too few occurrences (n=16) of the behavior.

Results

A total of twenty-six crabs were deceased by the end of the experiment. Twenty-two of those deaths were prey-sized *C. maenas* and four of those were focal crabs seen to be predated upon by *C. sapidus* in aquaria of 30°C. Twenty of the *C. maenas* were predated by *C. sapidus* in all tank temperatures with the exception of 9°C. One prey *C. maenas* was predated upon by a larger *C. maenas* predator after it had recently molted at a temperature of 27°C and another was predated upon by a *C. productus* at a temperature of 9°C. The remaining four deceased crabs were *C. productus,* with their deaths likely caused by stress from tank temperatures of 21°C or greater.

The full and reduced logistic regression models were compared with the use of AIC and McFadden pseudo-R squared values. The full model analysis had an estimated quality AIC of 97.5 and a McFadden pseudo-R squared maximized likelihood value of 0.4. The reduced model resulted in an AIC of 118.7 and McFadden pseudo-R squared value of 0.2. An ANOVA was run between the two models indicating the models were significantly different with a p-value of less than 0.00001 (0.000003). Several factors affected whether *C. maenas* would be eaten. Prey *C. maenas* were more likely to be eaten when *C. sapidus* were the predators (Logistic regression p= 0.03; Figure 1.1), temperatures were warmer (Logistic regression p= 0.03) and the predator size was larger compared to the prey size (Logistic regression p=0.004; Table 1.1, Figure 1.2). In contrast, no significant relationship was detected in the mortality of prey *C. maenas* with *C. productus* predator (Logistic regression p=0.9) or *C. maenas* predator present (Logistic regression p=0.4) with only one predation event with each species (Table 1.1). The odds ratio was carried out with the full model to compare predicting variable of *C. maenas* as predator to the other predicting variables. If *C. sapidus* predators are present, the likelihood that *C. maenas* are eaten increased by over 100% (3402%) relative to a *C. maenas* predator, and if *C. productus* are present, predation would increase prey killed by 15% (refer to Table 1.1 for values and confidence intervals (CI)When it came to the non-predator variables, a temperature increase by one degree would increase the likelihood of predation by 11% and a PCW increase by a unit would decrease the likelihood of predation by 99% Table 1.1).

The most frequent behavioral response from prey crabs was 'Still', regardless of predator present, with 698 occurrences (Figure 1.3). The least occurring response was 'Avoidance', regardless of predator, with 121 occurrences (Figure 1.3). **'**Active' behavioral response resulted in 530 occurrences, 'Feeding/Foraging' with 340 occurrences, and 'Aggression' with 206 occurrences (Figure 1.3). When the five behavioral response occurrences from prey were compared to the temperature gradient, 'Still' was the most frequent occurrence for all temperatures except 12° and 18°C which had 'Feeding/Foraging' as the most frequent behavioral response (Figure 1.4). 'Avoidance' was the least frequent behavioral response for temperatures 12°, 18°, 21°, 24°, and 30°C (Figure 1.4). ‘Aggression’ was the least frequent behavioral response for temperatures 9°, 15°, and 27° from prey (Figure 1.4).

The most frequent behavioral response from all predator species was ‘Still’ with 780 occurrences total (Figure 1.5). The least occurring response was ‘Avoidance’ regardless of predator, with 33 occurrences (Figure 1.5). ‘Active’ resulted in a total of 614 occurrences, ‘Feeding/Foraging’ with 263 occurrences, and ‘Aggression’ with 263 occurrences (Figure 1.5). When the five behavioral response occurrences from predators were compared to the temperature gradient, ‘Still’ was the most frequent occurrence across all temperatures (Figure 1.6). ‘Avoidance’ was the least frequent behavioral response for all temperatures except 30°C which did not have any occurrence of ‘Avoidance’ or ‘Active’ responses from the predators (Figure 1.6).

Generalized additive models processed for prey data indicated that all relationships between temperature and any of the three predators was significant with the time prey *C. maenas* spent for any of the five behavior responses (p-values were <2e-16 for all combinations) (Table 1.2). The time spent ‘Still’ increased as temperatures increased for all three predators present, however there was some variation at lower temperatures with predators *C. maenas* and *C. productus* (Figure 1.7a and b). Time spent being ‘Active’ increased with *C. sapidus* and *C. productus* present but decreased with *C. maenas* predators (Figure 1.8). ‘Feeding/Foraging’ slightly decreased with warmer temperatures for all predators present, however time first increased at lower temperatures with *C. sapidus* predators (Figure 1.9). Time spent ‘Aggression’ decreased with *C. maenas* and *C. sapidus* predators but peaked in time at 20°C with *C. maenas* predators (Figure 1.10a and b). The inverse was seen when *C. productus* predators were present with an increase in time spent 'Aggression' as temperatures increased (Figure 1.10c). 'Avoidance' decreased with *C. maenas* and *C. sapidus* predators present but with peak time occurring at 20°C with *C. maenas* predators (Figure 1.11a and b). There was some variation in time when *C. productus* predators were present as time decreased from temperatures 9°-20°C but slightly increased at higher temperatures (Figure 1.11c).

Generalized additive models processed for predator data indicated that most relationships between temperature and time spent for any of the five behavior responses were significant (p = <2e-16) with the exception of time spent in 'Aggression' by *C. productus* predators (p = 0.503) (Table 1.3). Time spent 'Still' varied for *C. maenas* and *C. sapidus* predators while *C. productus* time 'Still' increased for temperatures 21°C and higher (Figure 1.12). Time spent 'Active' varied for all predators. Time 'Active' peaked for *C. maenas* at 18°C, *C. sapidus* peaked between temperatures 9° and 30°C, and *C. productus* peaked at 9°C (Figure 1.13.) Similar variable patterns were seen for two predators with time spent 'Feeding/Foraging,' with a peak at 18°C for *C. maenas*, and at 21°C for *C. sapidus* (Figure 1.14a and b). Time spent 'Feeding/Foraging' for predator *C. productus* increased from temperatures 18°C and higher (Figure 1.14c). As for time spent in 'Aggression', *C. sapidus* peaked at low and high temperatures while *C. maenas* peaked at high temperatures (Figure 1.15).

Discussion

These results provide information on the biotic resistance capabilities against *C. maenas* if temperatures were to be increased by climate change. The outputs of logistic regression support a nonlinear relationship among the predicting variables, predator species present and PCW, to the response variable, mortality of prey *C. maenas,* across temperatures. Prey *C. maenas* were less likely to be killed if PCW was low. The lack of size discrepancy could allow prey to be a more effective competitor, however, there was high uncertainty for the PCW as a predicting variable. It is possible that claw size (chela height or width) could have been an influence on mortality as Sneddon et al. (2000) observed that *C. maenas* with larger claws were stronger competitors in fights between crabs of the same carapace size.

The single predation event from a *C. maenas* predator was possibly by chance as the prey had recently molted was an opportunity to a more accessible meal than the provided bivalves, which could explain the high range of uncertainty of this predicting variable. Prey mortality was largely driven by *C. sapidus* presence within warmer temperatures. Despite the large range of uncertainty from *C. sapidus* as a predicting variable, prior studies observed an increase in *C. maenas* mortality and their distribution was limited in the Chesapeake Bay region due to biotic resistance from high abundances of *C. sapidus* (de Rivera et al., 2005). The same may be possible for Oregon's coastal waters as *C. productus*, of large size, were observed to predate on tethered *C. maenas* and consumption is a main factor for biotic resistance (Kimbro et al., 2013 & Jensen et al., 2007). In this experiment, *C. productus* predated at low temperatures which has been observed in previous of *C. productus* and *C. maenas* interactions in temperatures 11-14°C (Hunt and Behrens Yamada, 2004). However, *C. productus* morality at higher temperatures suggests they are not a reliable biotic resistor under stressful environmental conditions, such as warmer waters (Hellmann et al. 2008).

Biotic resistance can be limited by stressful abiotic factors as observed with invasive marsh grass, *Spartina anglica*, outcompeting native species for space due to elevated levels of water salinity (Dethier and Hacker, 2005). The Pacific Northwest has been experiencing extreme heat fluxes which can pose cascading environmental stressors, especially within marine and aquatic environments (Gattuso et al.,2018). Since *C. maenas* introduction in Oregon, there have been two warm blobs, 2004-2005 and 2013-2015, and heat dome events in summer 2021 which caused what is termed a "marine heatwave" (Chen et al., 2021 & Vaughan, 2021). Such events can cause drastic disturbances to the environment, such as change in water quality and movement, and species interactions which then aid invasive species, like *C. maenas,* to overcome thresholds of biotic resistance (Hellmann et al., 2008 & Dethier and Hacker, 2005).

These analyses of competition and predator pressure on *C. maenas* behavior response provided assumptions on *C. maenas* abilities during heatwave-like conditions. The two behaviors most applicable to competition and predation between crab species would be 'Feeding/Foraging' and 'Aggression' (Tran et al., 2014)**.** As temperatures increased, 'Feeding/Foraging' times were shorter regardless of the predator species present, suggesting less energy could be exerted for consumption within intense temperatures (Figure 1.9). There was a similar pattern for ‘Aggression’ when *C. maenas* predators were present, indicating intraspecific combat may be minimal at elevated temperatures (Figure 1.10a). The opposite was observed when *C. productus* predators were present with the longest time occurring at high temperatures and peak times occurred around 20 °C with *C. sapidus* predators (Figure 1.10b). Therefore, *C. maenas* appear to be resistant, with the use of aggression, to biotic interactions of native species when temperature conditions are similar to a heatwave event.

When assessing the time of the same two behavior responses observed from predator species, *C. maenas* were ‘Feeding/Foraging’ for shorter times at high temperatures while *C. sapidus* and *C. productus* were ‘Feeding/Foraging’ for longer times at the same temperatures (Figure 1.14). This indicates that the native species were able to consume food even under stressful temperature conditions. For ‘Aggression’, *C. sapidus* showed the most varied times, suggesting that the species can apply such behavior within a range of temperature conditions (Figure 1.15b). *C. maenas* showed little variation with the longest time at the highest temperatures and *C. productus* indicated minimal variation in time spent ‘Aggression’ (Figure1.15a and b). The lack of varied time for ‘Aggression’ suggests that *C. productus* may not be able to adjust to extreme temperature change and apply sufficient biotic resistance. However, predator sized *C. maenas* demonstrated similar results suggesting that at smaller sizes, *C. maenas* have the better ability to adapt to temperature changes when ‘Aggression’ behavior is needed.

These preliminary trends may lead to stronger correlations and predictions with continued experimentation on *C. maenas* behavior with a larger sample size. For purposes of predicting influences towards native species in regions of the eastern Pacific, where *C. maenas* have more recently invaded, future studies should observe the interactions between *C. maenas* with *C. productus* more closely (Behrens Yamada et al., 2019). Such interactions should be carried out with manipulated environments that mimic climate change environmental conditions, such as a gradient of salinity and/or pH levels expected under ocean acidification. Additionally, there may be other environmental factors that could influence *C. maenas* response and, knowing that their lack of dexterity prevents them residing securely in areas with wave action, their habitat preference should be explored (McDonald et al., 2006).

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Appendix A: Chapter One Results

Table 1.1 Odds Ratio Output to Logistic Regression *Logistic regression model coefficients of the full model with prey mortality as the response variable to predictor variables predator species (C. maenas, C. sapidus, C. productus), temperature and proportional carapace width, including date as a blocking factor.*

Predictor Variable	**Estimated Coefficient**	**Odds Ratio**	**95% CI**	**P-value**
C. maenas as predator	22.0	3.4e9	4.7e-14 & 3.7e36	0.4
C. sapidus as predator	3.6	33.5	2.8 & 1.4e03	0.03
C. productus as predator	0.1	1.2	0.03 & 49.9	0.9
Temperature	0.1	1.1	1.01 & 1.2	0.03
Proportional Carapace Width	-9.2	9.8e-05	7.1e-08 & 2.3e-02	0.004

Table 1.2 GAM Analysis of Prey Behavior *Generalized additive model outputs of prey C. maenas summed time for each of the five behavior responses (Still, Active, Feeding/Foraging, Aggression, Avoidance) across a temperature gradient when present with one of three predator species (C. maenas, C. sapidus, C. productus)*

Predator Present	Chi square	Reference df	p - value
Prey Behavior Response: Still		Deviance explained = 16.8%	Sample Size (n) = 116
C. maenas	5766	3.638	< 2e-16
C. sapidus	1199	3.997	< 2e-16
C. productus	1810	3.983	< 2e-16
Prey Behavior Response: Active		Deviance explained = 13.3%	Sample Size (n) = 71
C. maenas	948.3	1.998	< 2e-16
C. sapidus	446.6	1.999	< 2e-16
C. productus	707.3	1.999	< 2e-16
Prey Behavior Response: Feeding		Deviance explained = 29.6%	Sample Size (n) = 48
C. maenas	3779	2.000	< 2e-16
C. sapidus	1533	1.997	< 2e-16
C. productus	1765	2.000	< 2e-16
Prey Behavior Response: Aggression		Deviance explained = 18.4%	Sample Size (n) = 44
C. maenas	329.5	2.000	< 2e-16
C. sapidus	329.5	2.000	< 2e-16
C. productus	329.5	2.000	< 2e-16
Prey Behavior Response: Avoidance		Deviance explained = 25.8%	Sample Size (n) = 34
C. maenas	124.4	2.000	< 2e-16
C. sapidus	329.5	2.000	< 2e-16
C. productus	324.5	2.000	< 2e-16

Table 1.3 GAM Analysis of Predator Behavior *Generalized additive model outputs of three predators (C. maenas, C. sapidus, C. productus) summed time for each of four behavior responses (Still, Active, Feeding/Foraging, Aggression) across a temperature gradient*

Predator Species	Chi square	Reference df	p - value
Predator Behavior Response: Still		Deviance explained = 16.4%	Sample Size (n) = 116
C. maenas	5754	4.000	< 2e-16
C. sapidus	3472	4.000	< 2e-16
C. productus	1358	3.998	< 2e-16
Predator Behavior Response: Active		Deviance explained = 14.7%	Sample Size (n) = 63
C. maenas	417.2	2.000	< 2e-16
C. sapidus	2754.9	2.000	< 2e-16
C. productus	1595.8	2.000	< 2e-16
Predator Behavior Response: Feeding		Deviance explained = 11.2%	Sample Size (n) = 43
C. maenas	1033.3	2.000	< 2e-16
C. sapidus	1119.7	2.000	< 2e-16
C. productus	102.3	1.995	< 2e-16
Predator Behavior Response: Aggression		Deviance explained = 18.8%	Sample Size (n) = 50
C. maenas	59.780	2.000	< 2e-16
C. sapidus	1463.87	2.000	< 2e-16
C. productus	0.515	1.138	0.503

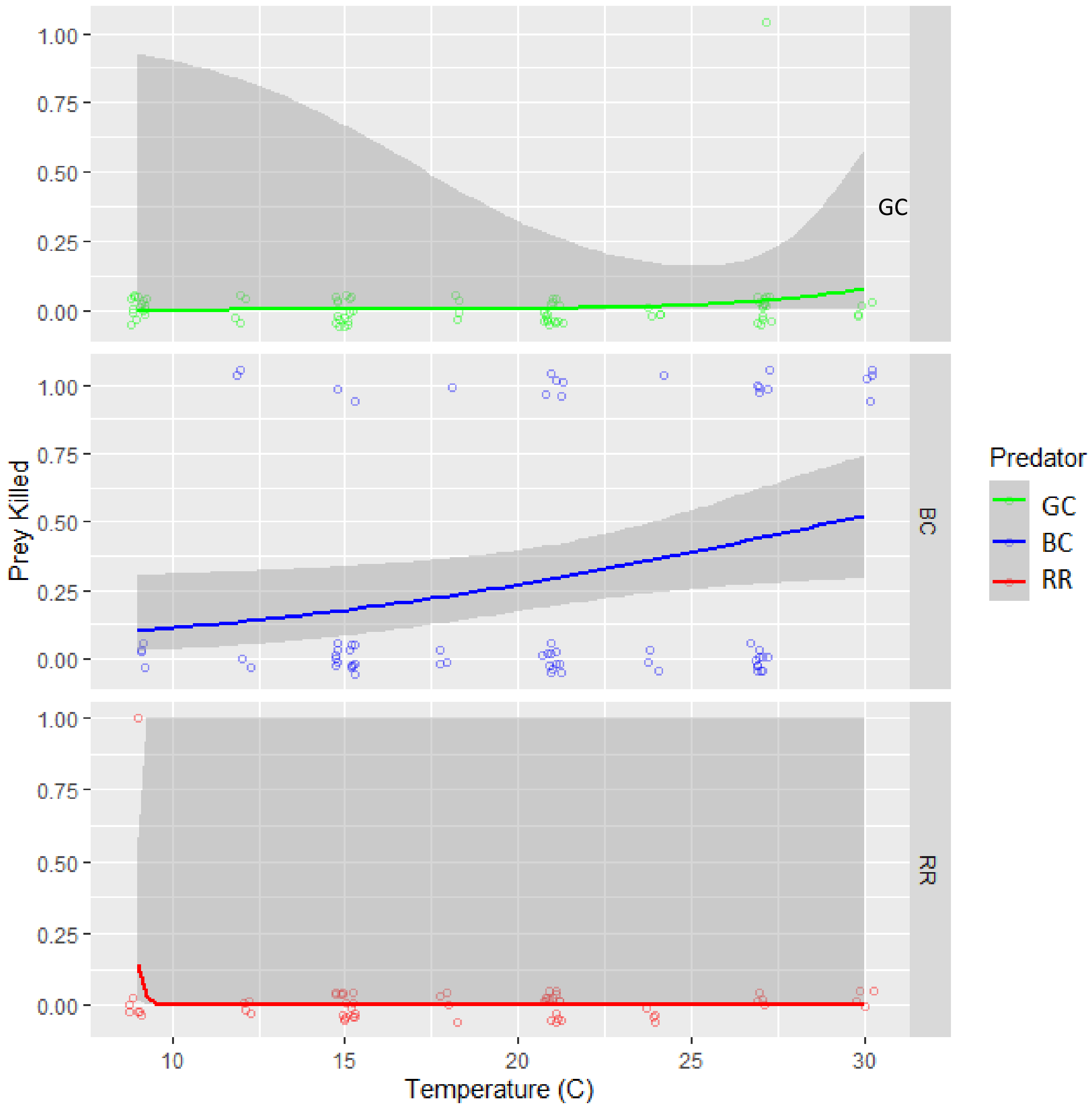

Figure 1.1 Logistic Regression of Temperature with Predation *Binomial logistic regression of prey killed in response to the eight temperatures from 9˚to 30˚Celsius when present with predators green crab (C. maenas, GC) indicated in green, with blue crab (C. sapidus, BC) indicated in blue, or with red rock crab (C. productus, RR) indicated in red.*

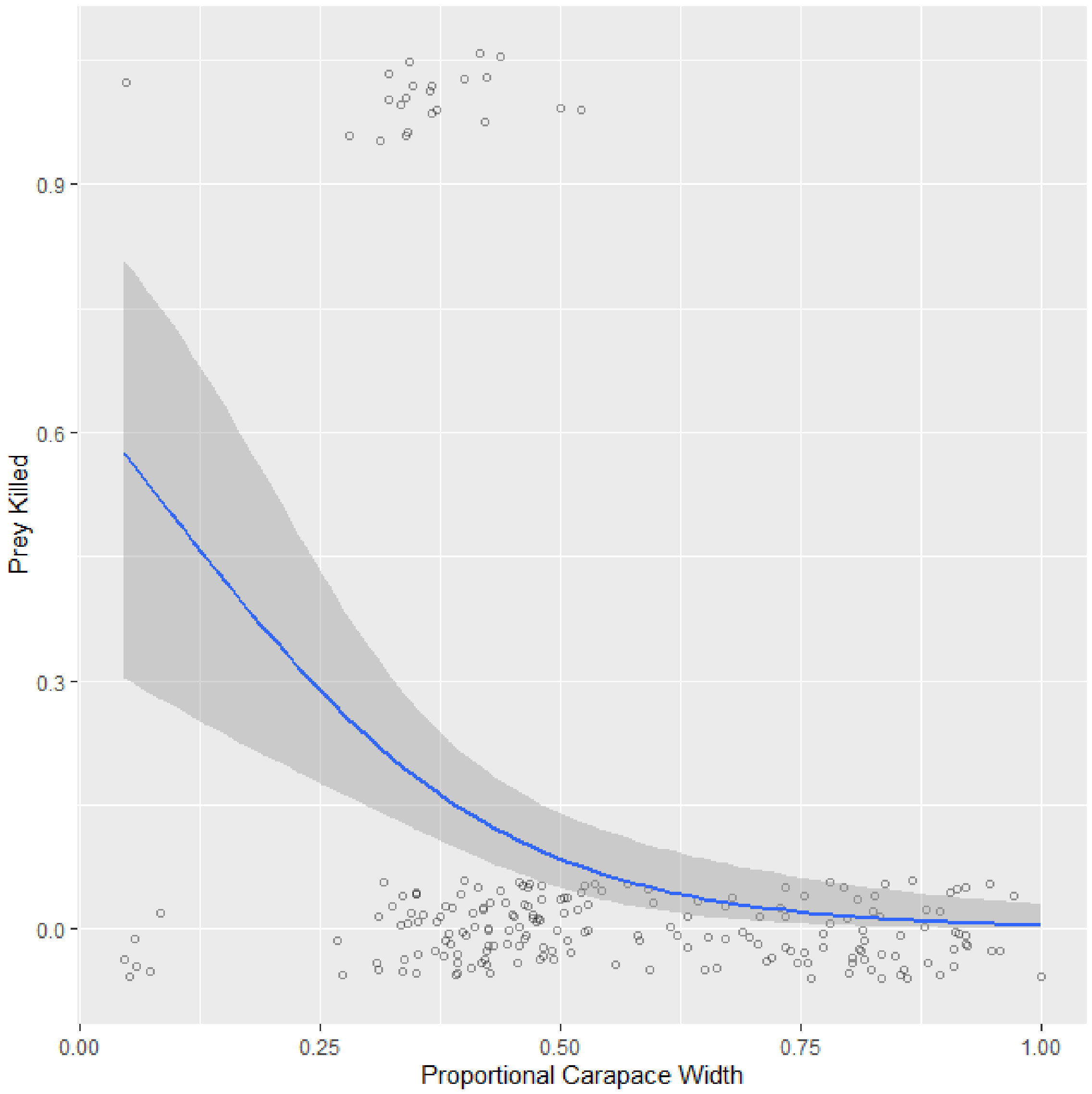

Figure 1.2 Logistical Regression of Body Size *Binomial logistic regression of prey killed in response to the prey crabs' proportional carapace width (PCW, prey carapace width divided by predator carapace width) to the predator present within the aquaria.*

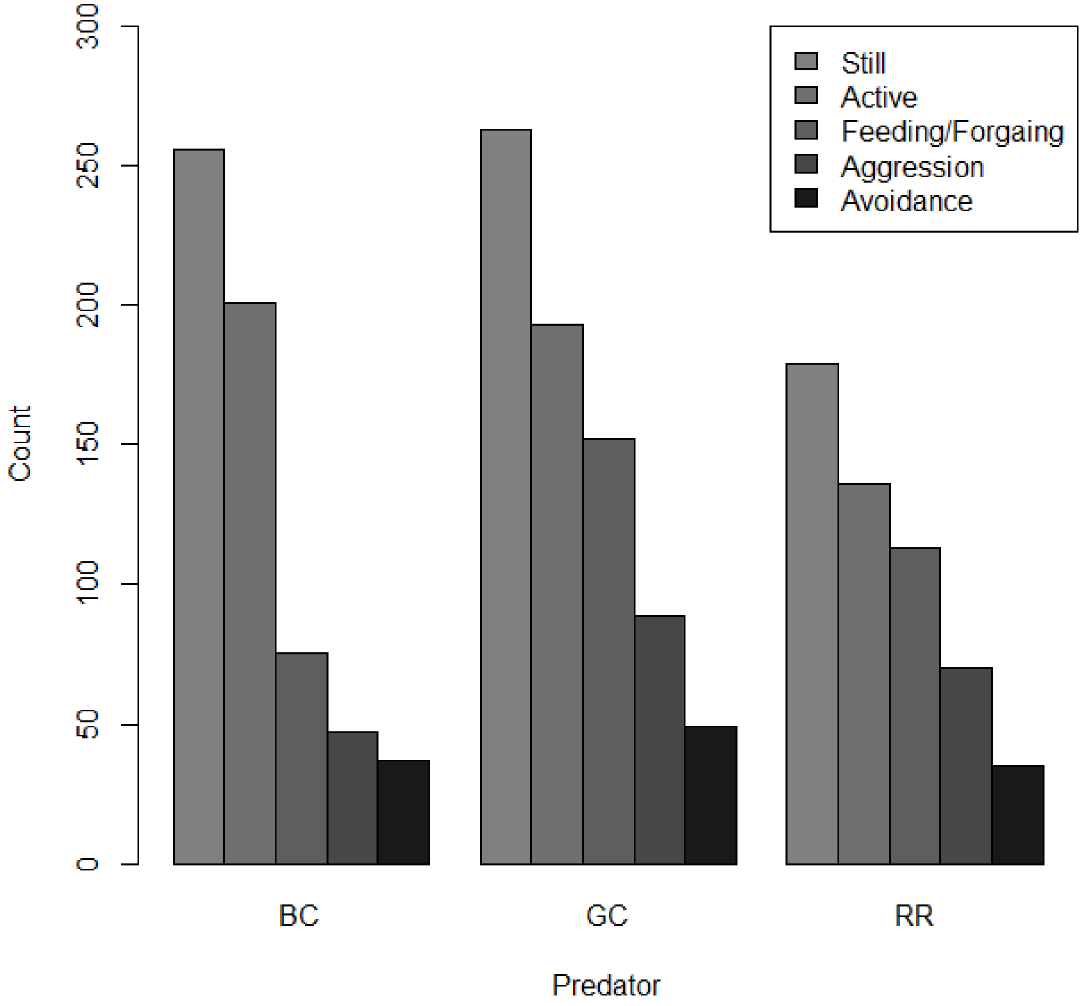

Figure 1.3 Behavior Count From Prey Across Predators *The frequency of prey behavioral response state categories of still, active, feeding/foraging, aggression, and avoidance from focal prey C. maenas in tanks when one of the three potential predators: blue crabs (C. sapidus, BC), green crabs (C. maenas, GC), and red rock crabs (C. productus, RR) were present. A grey color scale is used from lightest to darkest in order of still, active, feeding/foraging, aggression, then avoidance.*

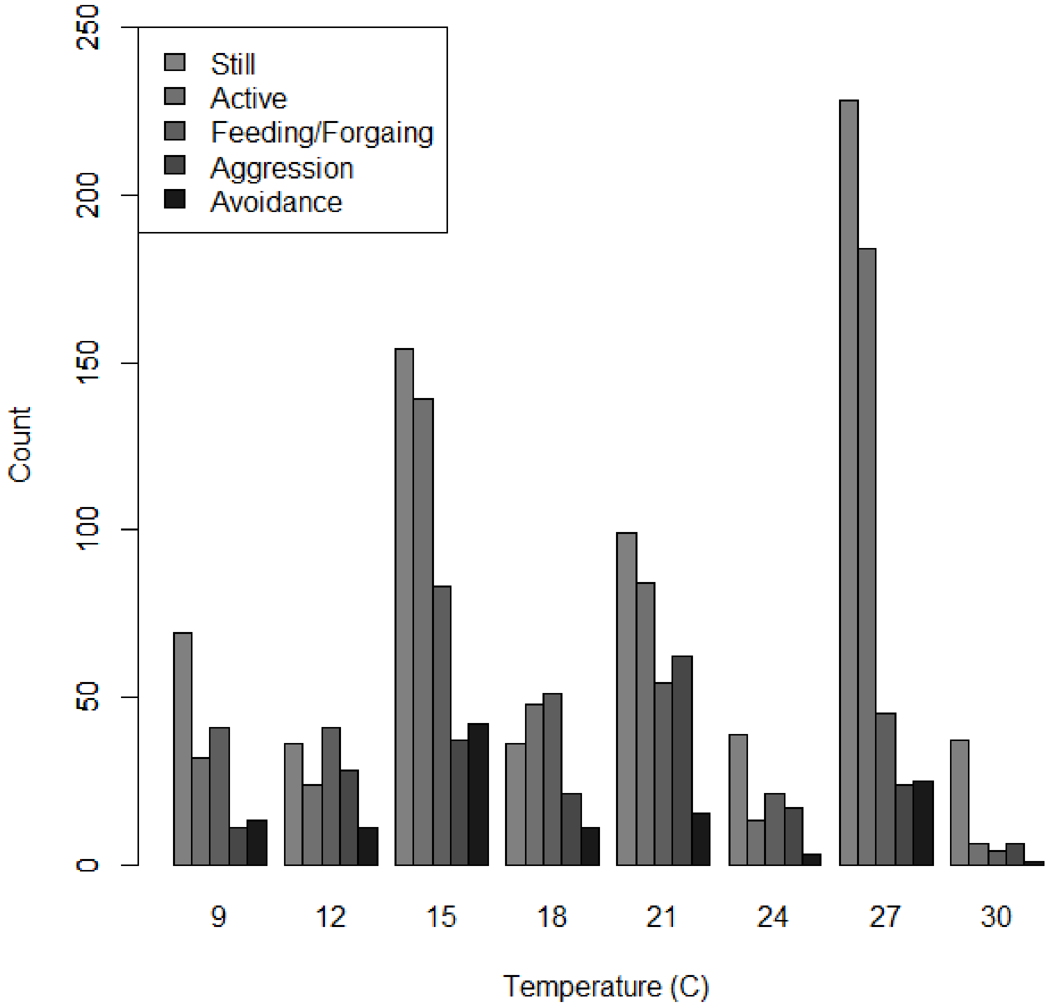

Figure 1.4 Behavior Count From Prey Across Temperatures *The frequency of prey behavioral response state categories of still, active, feeding/foraging, aggression, and avoidance from focal prey C. maenas in tanks based on the eight temperatures from 9˚ to 30˚ Celsius. A grey color scale is used from lightest to darkest in order of still, active, feeding/foraging, aggression, then avoidance.*

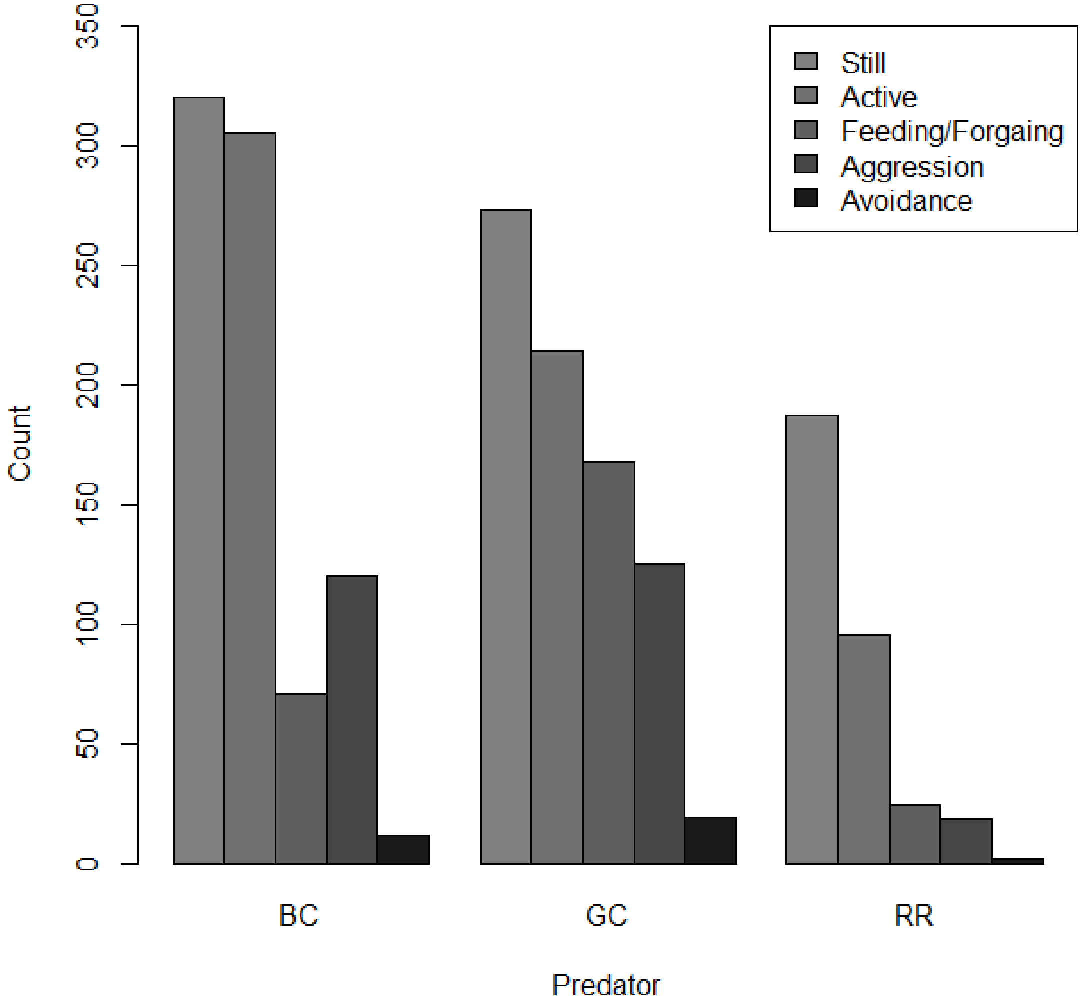

Figure 1.5 Behavior Count From Predators *The frequency amount across five behavioral state categories from the three potential predators: blue crabs (C. sapidus, BC), green crabs (C. maenas, GC), and red rock crabs (C. productus, RR) when present with prey C. maenas. A grey color scale from lightest to darkest is in order of still, active, feeding/foraging, aggression, then avoidance.*

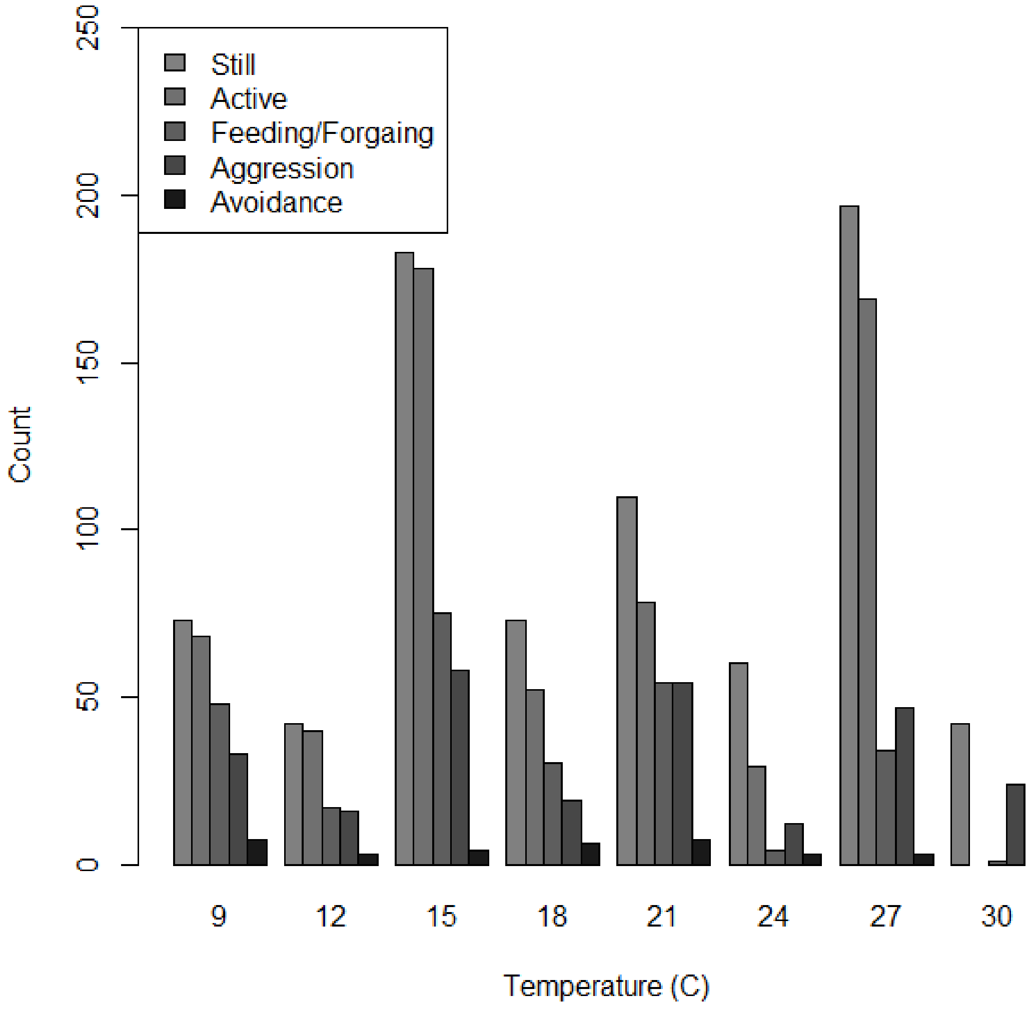

Figure 1.6 Behavior Count From Predators Across Temperatures *The frequency of predator behavioral response state categories of still, active, feeding/foraging, aggression, and avoidance in tanks based on the eight temperatures from 9˚to 30˚Celsius. A grey color scale is used from lightest to darkest in order of still, active, feeding/foraging, aggression, then avoidance.*

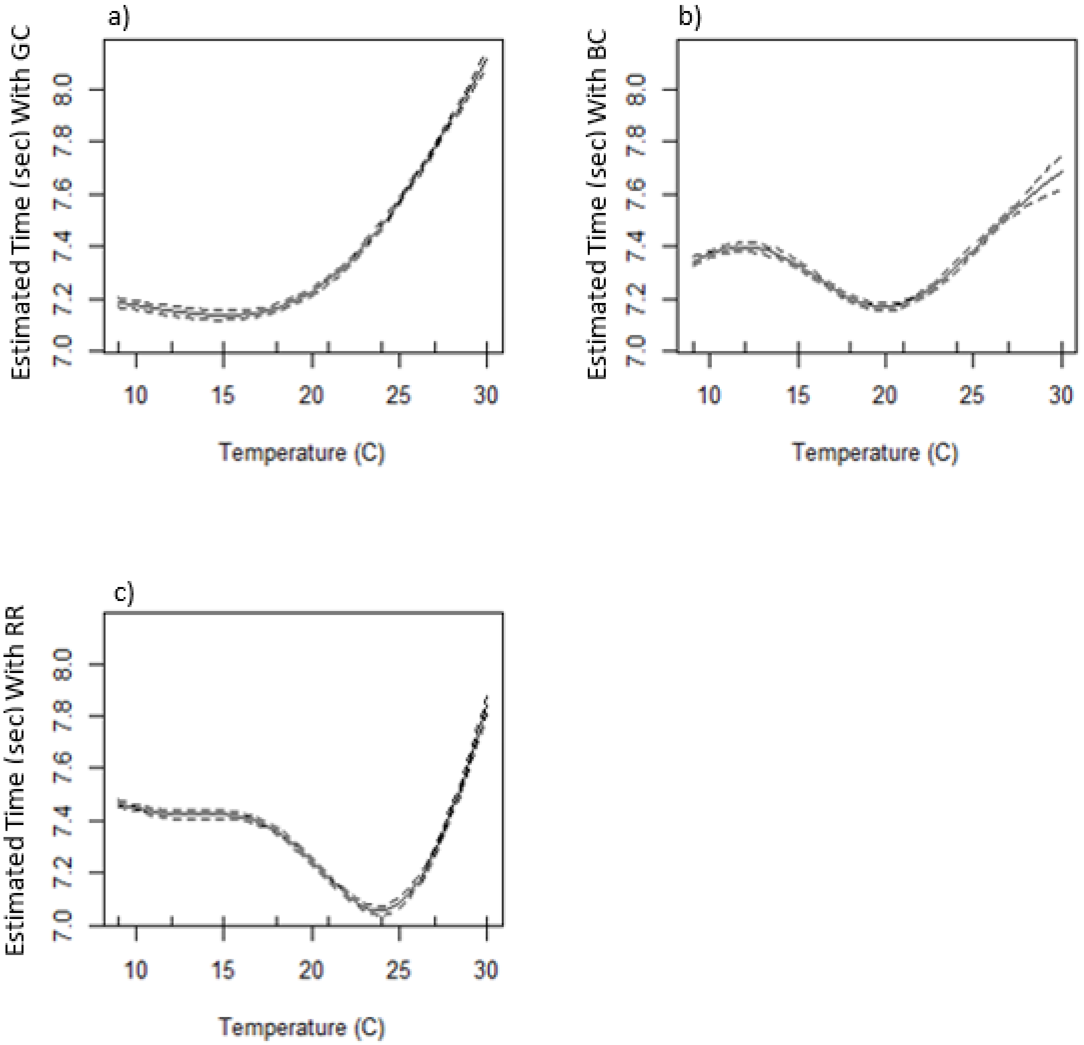

Figure 1.7 GAM of Prey 'Still' *Generalized additive model of the 'Still' behavior response from focal 'prey' green crab across temperatures based on predator species present of a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) as the predator.*

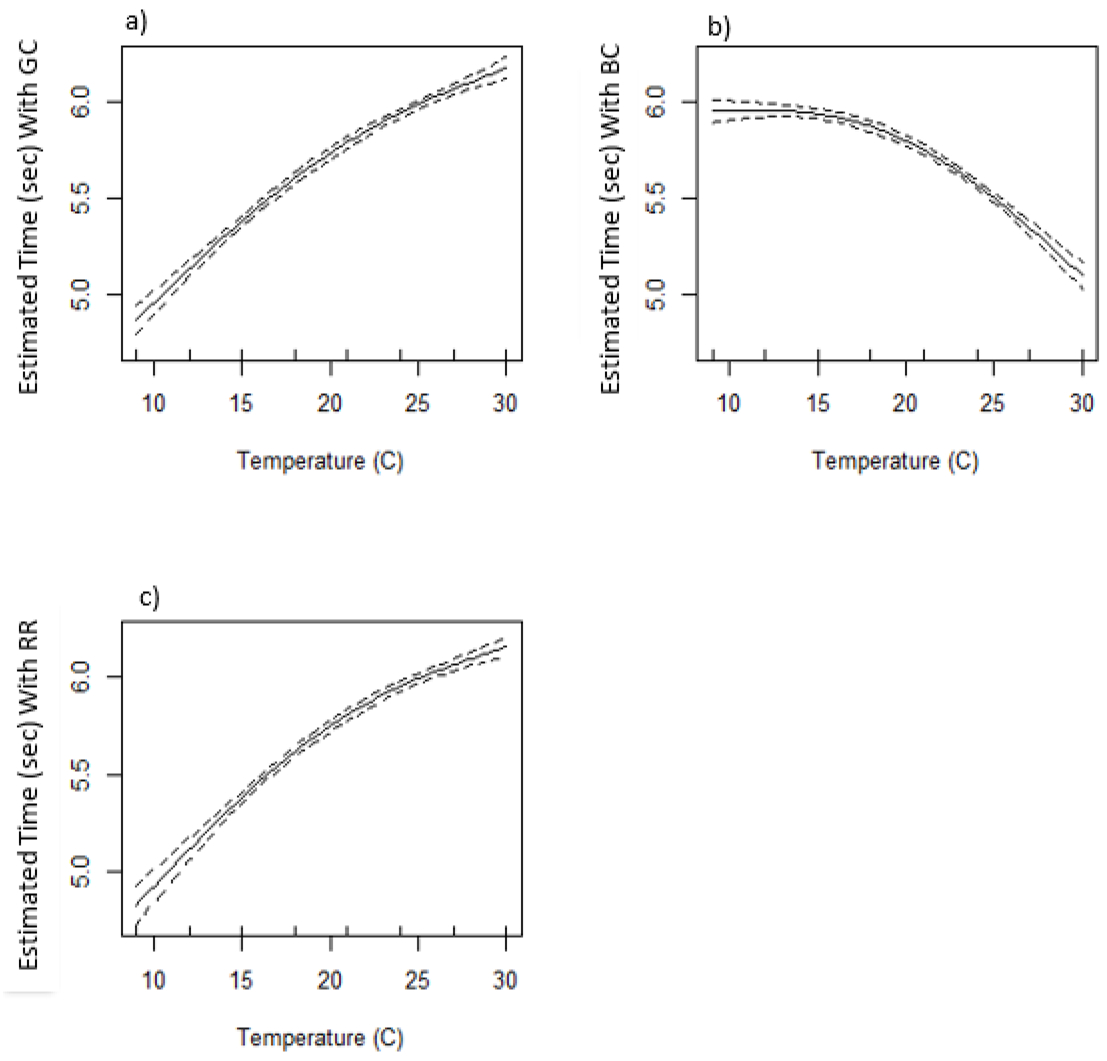

Figure 1.8 GAM of Prey 'Active' *Generalized additive model of the 'Active' behavior response from focal 'prey' green crab across temperatures based on predator species present of a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) as the predator.*

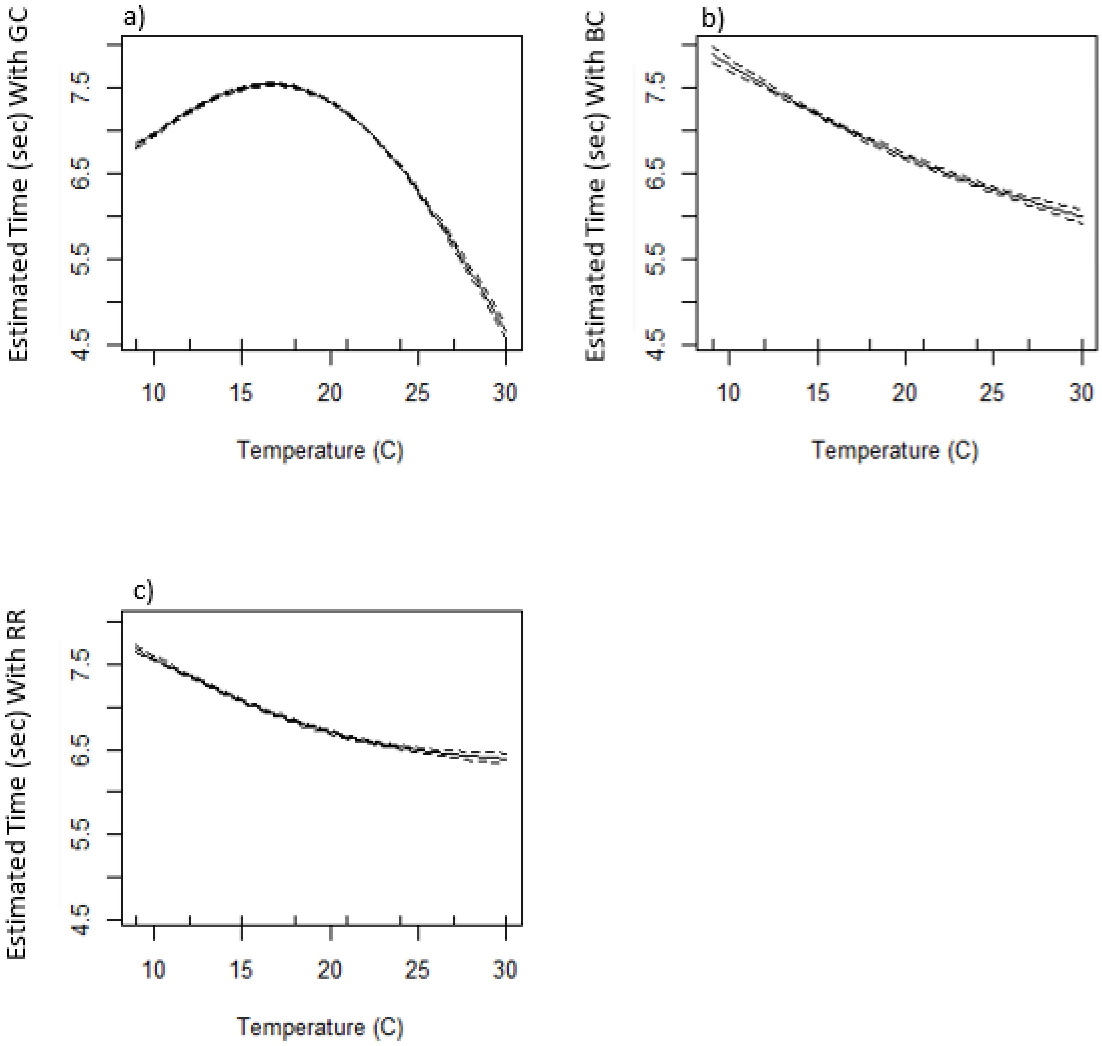

Figure 1.9 GAM of Prey 'Feeding/Foraging' *Generalized additive model of the 'Feeding/Foraging' behavior response from focal 'prey' green crab across temperatures based on predator species present of a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) as the predator.*

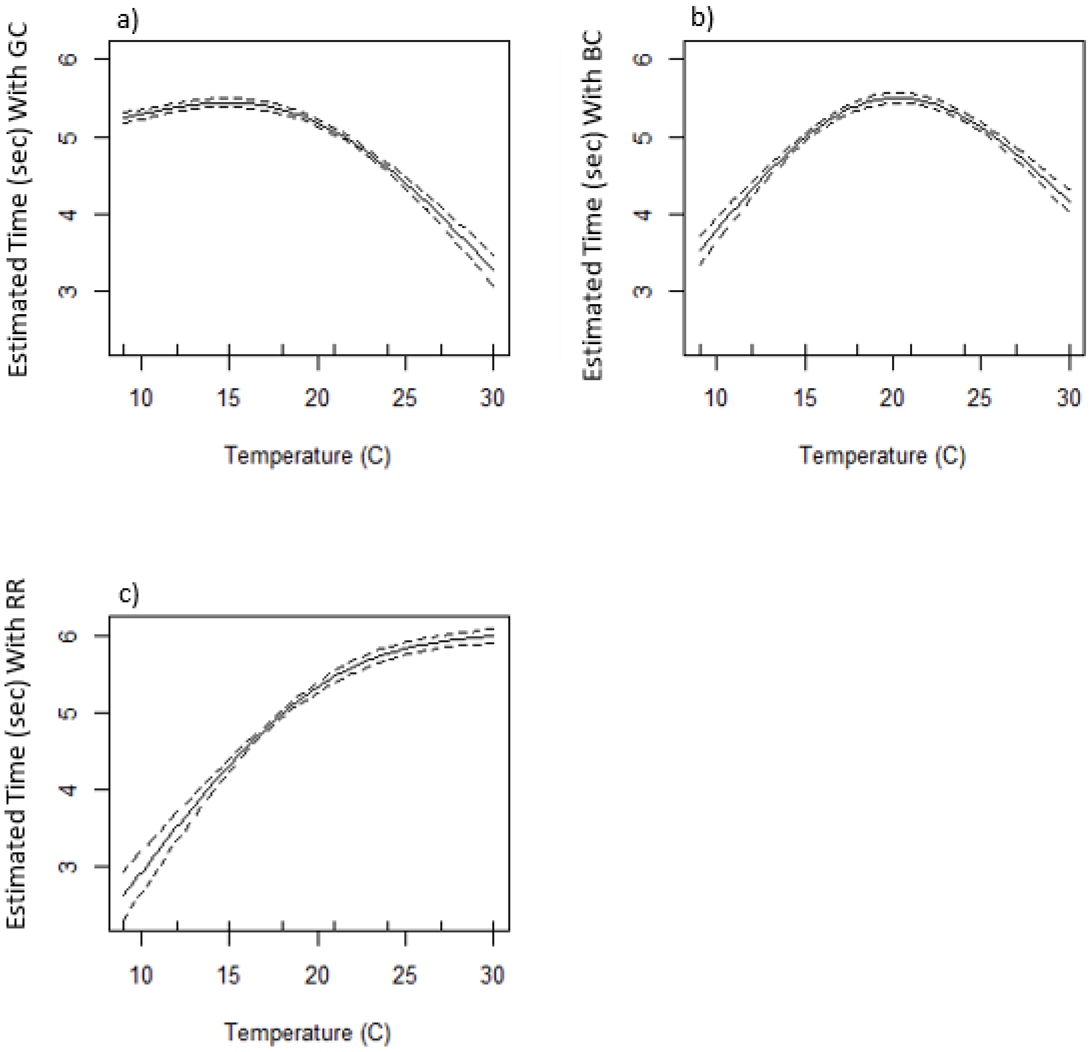

Figure 1.10 GAM of Prey 'Aggression' *Generalized additive model of the 'Aggression' behavior response from focal 'prey' green crab across temperatures based on predator species present of a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) as the predator.*

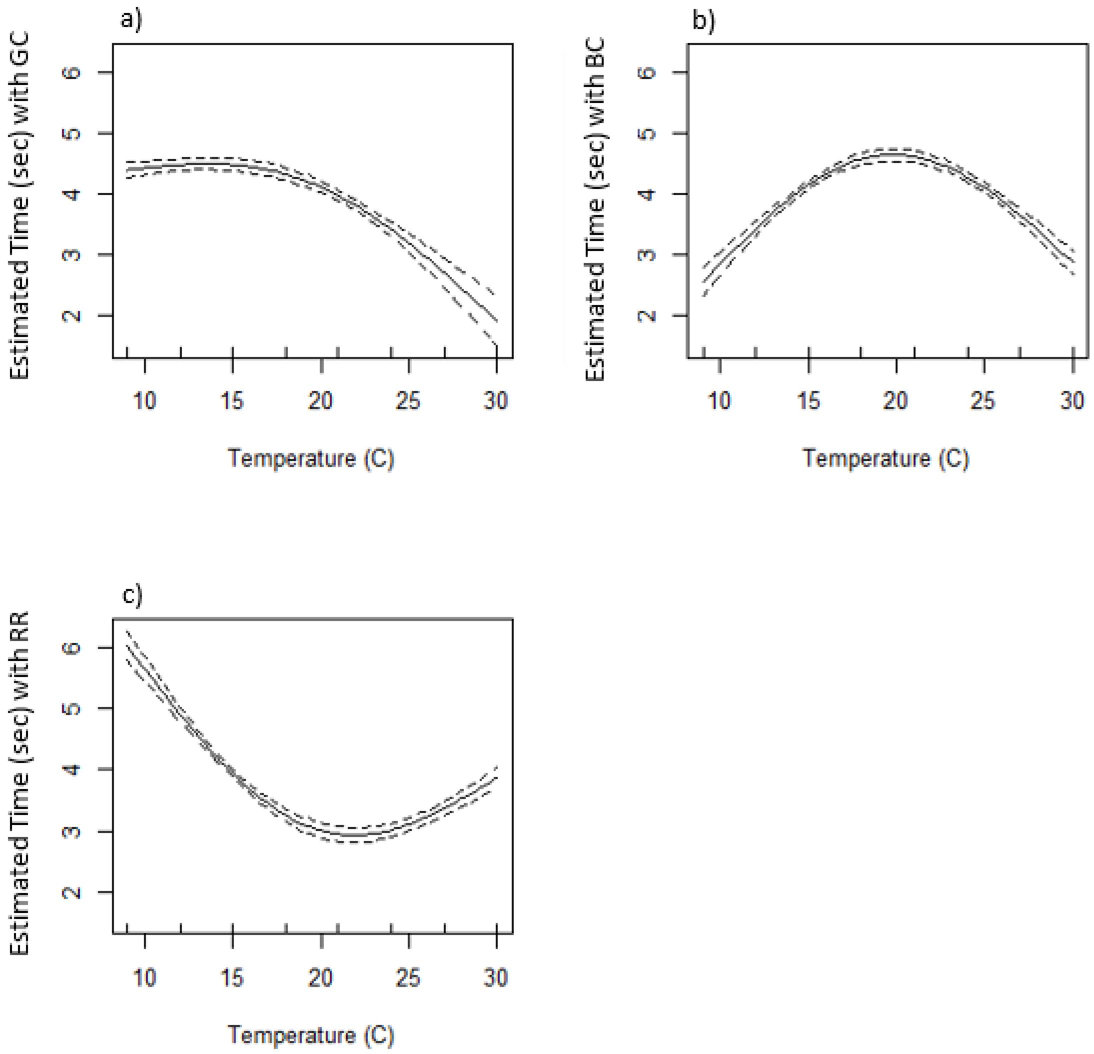

Figure 1.11 GAM of Prey 'Avoidance' *Generalized additive model of the 'Avoidance' behavior response from focal 'prey' green crab across temperatures based on predator species present of a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) as the predator.*

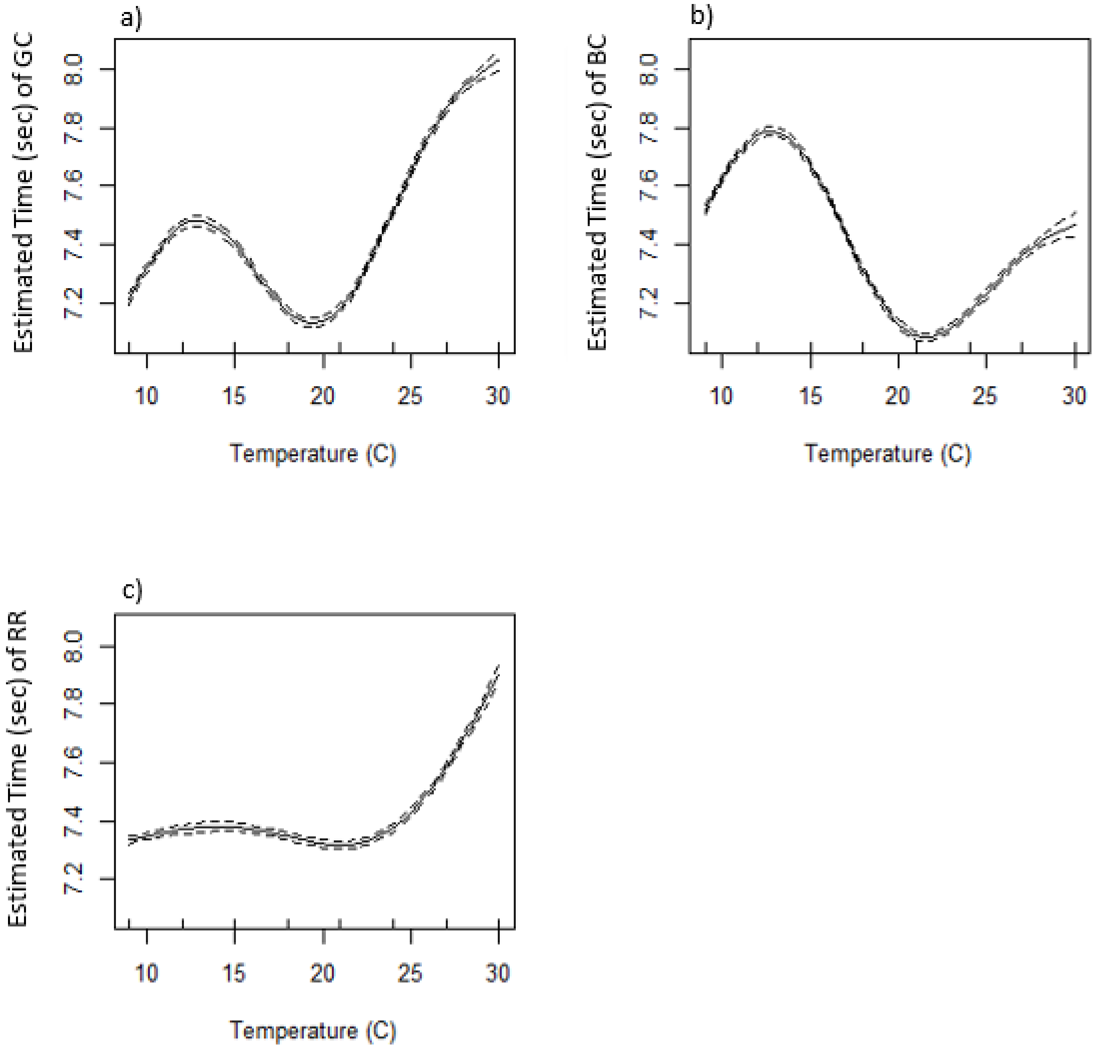

Figure 1.12 GAM of Predator 'Still' *Generalized additive model of the 'Still' behavior response from the three predator species a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) cross temperatures.*

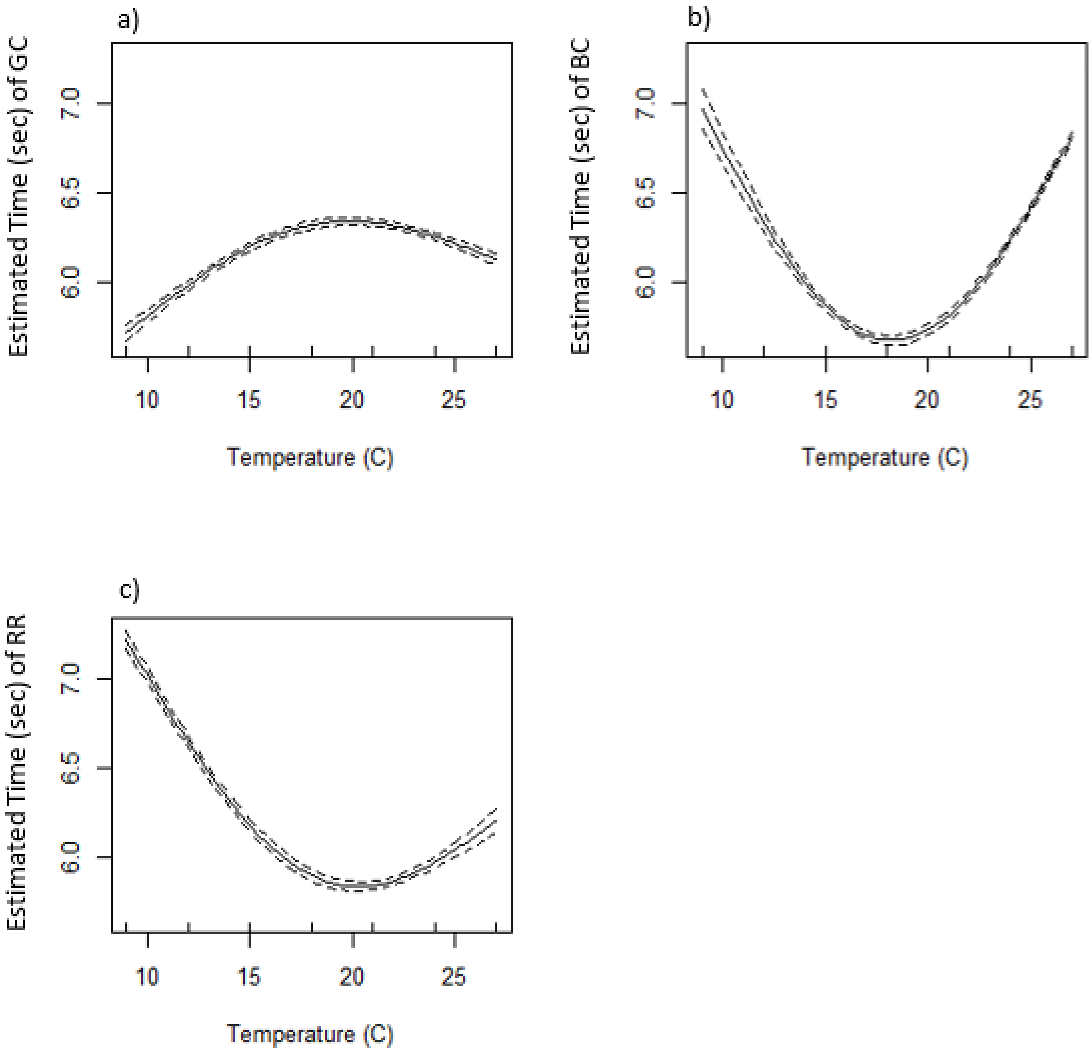

Figure 1.13 GAM of Predator 'Active' *Generalized additive model of the 'Active' behavior response from the three predator species a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) across temperatures.*

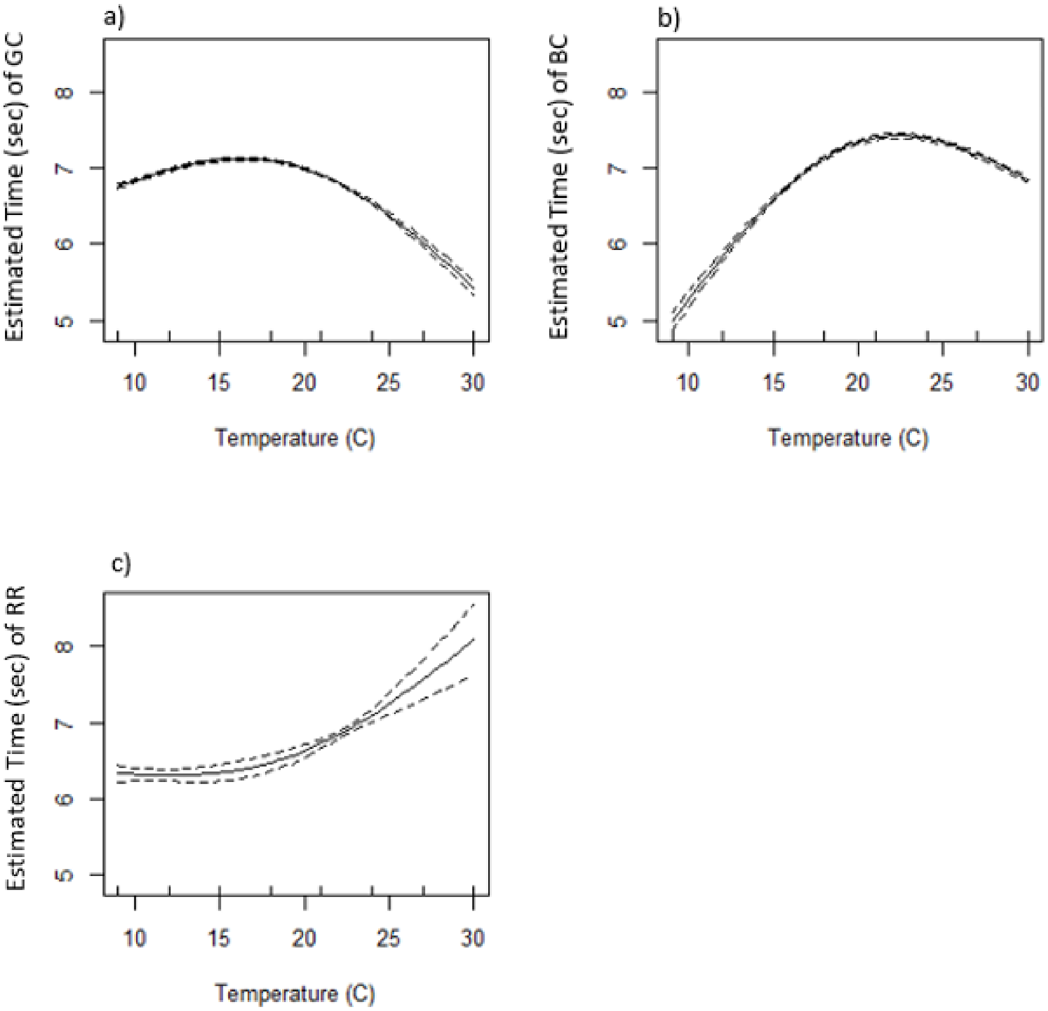

Figure 1.14 GAM of Predator 'Feeding/Foraging' *Generalized additive model of the 'Feeding/Foraging' behavior response from the three predator species a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) across temperatures.*

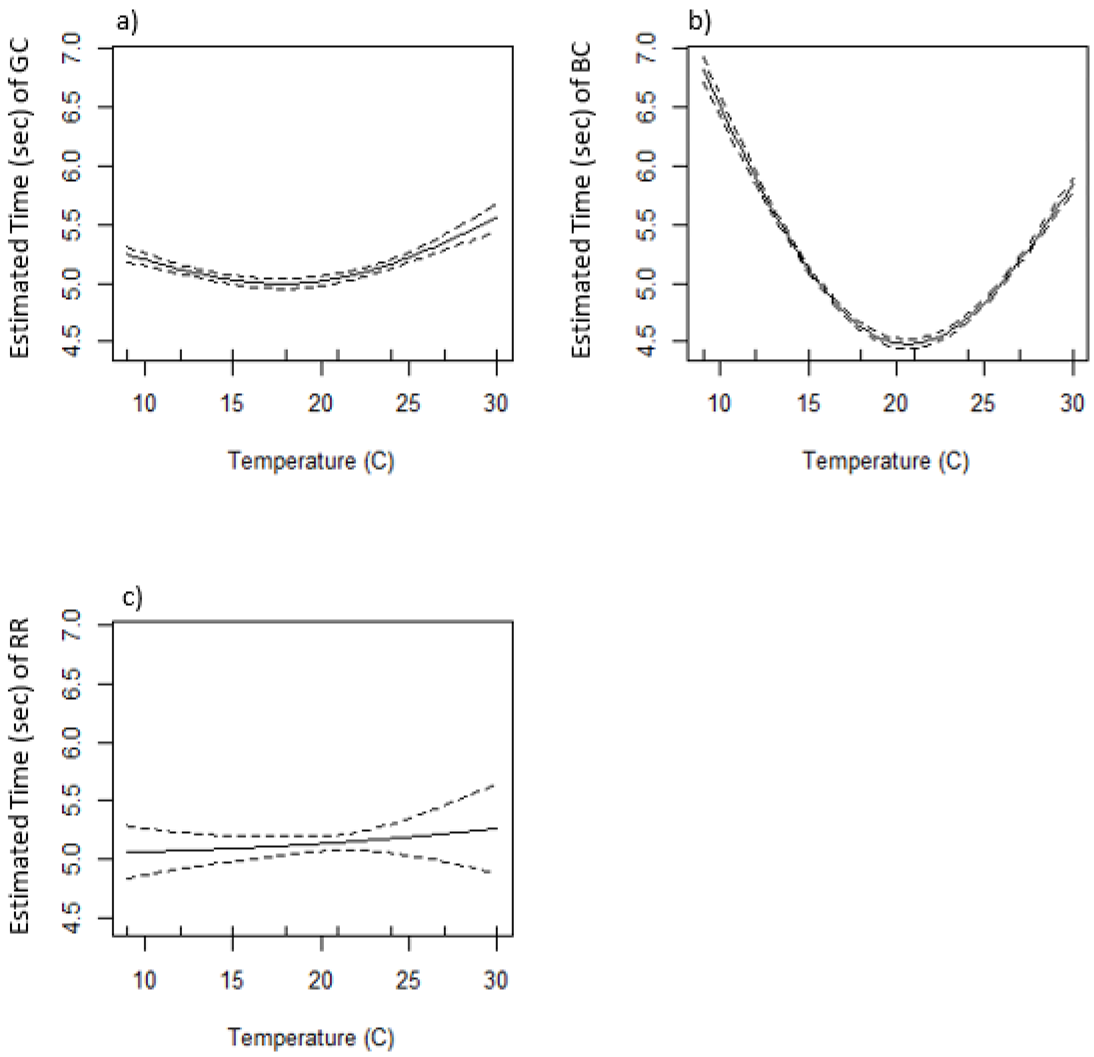

Figure 1.15 GAM of Predator 'Aggression' *Generalized additive model of the 'Aggression' behavior response from the three predator species a) C. maenas (GC), b) C. sapidus (BC), or c) C. productus (RR) across temperatures.*

Chapter Two: *Carcinus maenas* Distribution in South Slough

Introduction

Habitat preference among organisms is selected based on several factors including food availability, refuge accessibility, and even gender and age of individuals (Shepherd and Lank, 2004). Management research utilizes this process to help establish areas of protection for endangered or threatened species, as seen with cetacean species in high density in the northern Alboran Sea, as or even for detecting targeted species, as seen with Atlantic sturgeon commonly found within gravel or sand habitats (Cañadas et al., 2004 & Stein et al., 2011). Furthermore, habitat preference can aid in predicting regions vulnerable to non-native species introductions or where an invasive species can establish and spread (Carlton, 1996 & Petren and Case, 1998).

Invasive species, those species not originally present in the native assemblage and that pose negative ecological, economic, or health impacts, can create major management challenges (Blackburn et al., 2011 & Hellman et al., 2008). There are numerous management methods to reduce the influence of invasive species, including direct removal, restoration of the impacted environment, selective genetic manipulation of the invasive species, biological control with the use of another species to target the invasive species, public awareness, and even applying no action (Giakoumi et al., 2019). In some cases, multiple methods could be effective. For example, the combination of prescribed burning, mowing, and biological control by a beetle that predates on seeds, applied together most effectively controlled invasive Scotch broom (*Cytisus scoparius*; Herrera-Reddy et al. 2012).

There are important factors to consider when selecting a management method, such as the type of environment the invasive species is in, especially within marine ecosystems due to connectivity through water (Giakoumi et al., 2019). This high potential for connectivity likely contributes to the global distribution of *C. maenas,* the green crab, which is established on nearly every continent. Their larvae were able to be easily transported via commercial vessels in the ballast water (Behrens Yamada and Gillespie, 2008). The deposit of *C. maenas* in different marinas allowed localized populations to establish and even adapt where populations among higher latitudes, on average, are larger carapace width size than populations at lower latitudes on coastal North American (Kelley et al., 2011). Despite the impacts of *C. maenas* being well observed in regions they have invaded for longer periods of time, further investigations should be carried out in recently invaded regions to predict the ecological impacts *C. maenas* can have on native species (Young and Elliot, 2020).

Native crab species have been observed to predate on *C. maenas* in adult stages; however, there is a concern for species whose earlier life stages, of significantly smaller size, reside in habitats with *C. maenas* (de Rivera et al., 2005 & Hunt and Behrens Yamada, 2001). With *C. maenas* predating on smaller size prey, there can be direct implications on future stocks of native crabs as well as indirect impacts towards other consumers, such as migrating avian species, who rely on such stocks for food and nourishment (Grosholz and Ruiz, 1996)**.** While there are extensive studies of *C. maenas* and interspecies interactions in a lab setting, regional studies can sometimes interpret the influence from a local population and identify patterns more accurately.

The distribution of *C. maenas* throughout Oregon estuaries may be influenced by the resources required for survival, such as habitat refuge as seen with other crab species (Dionne et al., 2003). Estuaries are highly dynamic providing a range of habitats paired with fluctuating environmental conditions and reduced wave action, creating an ideal environment for the invasive *C. maenas* (Jamieson et al., 1998). *Carcinus maenas* were first observed in South Slough National Estuarine Research Reserve (SSNERR) in 1996 and their abundance and distribution has increased in recent years (Behrens Yamada and Gillespie, 2008). Cultured and natural stocks of marine and aquatic species within the reserve can be at risk with the rise of *C. maenas* as they have a diverse feeding diet (Miron et al., 2005).

The abundance of *C. maenas* has increased throughout South Slough but varies from site to site with a pattern yet to be determined (Schooler et al., 2020). Determining a pattern can then be used to decide where removal efforts may be most important and effective in limiting *C. maenas* abundances in order to sustain the SSNERR ecosystem (Kimbro et al., 2013). An effective approach to determine a pattern is to assess the habitat preference of *C. maenas* with the use of their abundance from crab trapping efforts. Through exploratory analysis, we can determine the following within SSNERR: 1) what type of habitat surrounds crab traps with *C. maenas* with high catching rates, 2) has the catch per unit effort (CPUE) of *C. maenas* increased over time, especially in recent years, 3) does the presence of *C. maenas* correlate with the abundance of native crab species found, 4) what type of habitat should future trapping efforts be focused on to target *C. maenas*?

Based upon prior research of *C. maenas,* if there are high CPUE rates of *C. maenas* then they are likely to occur at sites in SSNERR with habitat of hard structure such as rock, natural debris, and bivalve beds while lower CPUE rates would be located at sites with less structure (McDonald et al., 2006). We would expect to see higher CPUE in years following the El Niño events, which would be beyond 2016, since El Niños allow northern transport of *C. maenas* from California (Behrens Yamada and Gillespie 2008). The aggressive behavior of *C. maenas* allow them to be stronger competitors and continue to increase in catch per unit effort (CPUE) rate, as they have from the recent five years in SSNERR, beyond 5.50 CPUE (Schooler et al., 2020). In turn, we can expect to see low CPUE of native crabs, like *Hemigrapsus oregonensis,* due to long term impacts of predation pressure (de Rivera et al., 2011).

Methods

Data Sources:

To determine if habitat could be used as a distribution indicator for *C. maenas*, maps were created using GIS modeling (ArcGIS Pro) that included information about crab abundances and habitat types. Habitat type codes used for geospatial information and analysis of South Slough used data collected (2014) by the Oregon Coastal

Management Program (OCMP) in partnership with SSNERR and Oregon Department of Fish and Wildlife's (ODFW) Shellfish and Estuarine Assessment of Coastal Oregon (SEACOR) project (Lanier et al., 2018). Habitat identification and descriptions were updated in 2018 following the Coastal and Marine Ecological Classification Standard (CMECS) (FGDC, 2012).

Crab species information was derived from data collected over the past 20 years (2002-2021) under the management of SSNERR and Dr. S. Behrens Yamada of Oregon State University (OSU), following the methods of Behrens Yamada and Davidson (2002). These data included the identity of five common crab species, their catch per unit effort (CPUE, number of crabs per number of traps each having a 24-hour deployment) from 11 set crab trap locations throughout SSNERR. These species were the green (*Carcinus maenas*), yellow shore (*Hemigrapsus oregonensis*), purple shore (*Hemigrapsus nudus*), Dungeness (*Metacarcinus magister*), and red rock (*Cancer productus*) crabs that were retrieved from Fukui and minnow traps.

Analysis:

We used R Studio (version 4.1.1) to determine relationships between the abundance of the five species of crab within SSNERR. The crab species data were subset to include trap deployments and recoveries during the summer season for the months of June through August. This timeline was selected due to frequency of trap deployment and recovery as well as being the time span common for mating of *C. maenas* (Young and Elliott, 2020). Since *H. nudus* was present in only two traps throughout the 20-year timeline; it was omitted from analyses. The annual CPUE during summer months of the four remaining crab species were analyzed to determine if there was an increase over time. Two years were not included because data were not collected in 2015 and because only one trap was deployed in 2010, which would not represent the CPUE in South Slough adequately. We used 2016 as the cutoff for trapping data from the past six years (2016-2021) to summarize the mean CPUE of the four crab species at the eleven sites in the SSNERR. Sites that had a mean CPUE of zero for *C. maenas*, *M. magister*, and *C. productus* were omitted, resulting in nine remaining sites. A multiple regression was used to determine the relationship between the average CPUE of crabs in the last six years with the trapping locations' distance to the mouth of South Slough estuary. Since the data did not fit assumptions of normality and liner response, we used polynomial relationships to examine the distributions of the crab species.

To determine if the increase of *C. maenas* posed an influence on native crab species, linear regressions were used to examine the effect of the natural log of the mean CPUE of *C. maenas* of the past six years on the natural log of the difference in the mean CPUE of each native crab species for 2016 to 2021 (after substantial *C. maenas* populations increase) minus the mean CPUE of each native crab species 2002 to 2015 (before *C. maenas* increase).

When assessing habitat preference of *C. maenas*, habitat identification codes derived from OCMP were divided into two axes of habitat type and bottom substrate. Subgroups of bottom substrate were generalized to their group type (i.e., silt or clay was classified as mud) for basic identification with the use of the CMECS catalog. Habitat type was categorized into eight identities and bottom substrate into nine identities throughout the SSNERR. (These identities are described in Appendix B, Table 2.1 and Table 2.2). The habitat identities were layered with the use of ArcGIS Pro (version 2.6.0) and appropriately symbolized with color and patterns based on classification. Buffers of 50 meters were set around the eleven trapping locations to describe the surrounding habitat type and bottom substrate as well as determine how frequently they occurred around the eleven crab traps. The average CPUE of *C. maenas* from the past six years (2016-2021) per trapping site was plotted using gradually sized symbols, demonstrating areas that had a higher CPUE rate with a larger sized symbol.

Results

Prior to 2017, the native *M. magister* maintained the highest mean CPUE annually compared to the other crab species with the exception of 2003, even though its CPUE strongly fluctuated among years (Figure 2.1). Most extreme, the one trap that had been set in 2010 had a high abundance of *M. magister,* 271 individuals, but only one *C. maenas. Carcinus maenas* mean CPUE steadily increased after 2015 and the highest CPUE to date occurred in 2021. Nonetheless, the mean CPUE of *C. maenas* in the past six years from the summer months and across all trapped sites in South Slough sites did not exceed a rate of 5.0. *H. oregonensis* numbers were high 2016-2018, but then drastically decreased in years 2019 and later. *Cancer productus* was rare in the South

Slough traps, continuously yielding a low to zero mean CPUE throughout the 20-year timeline (Figure 2.1).

The *C. maenas* catch typically displayed moderate variability (Figure 2.2). The trapping site with the highest mean CPUE, years 2016-2021, of *C. maenas* was Joe Ney Slough (mean = 4.7 ±5.4 standard deviation (SD)) which was the site third closest to the mouth of the estuary. No other South Slough sites exceeded a CPUE rate of 2.0 (Figure 2.2). Sites, Metcalf Marsh (mean = 1.6 ±2.0 SD) and Charleston Boat Basin (mean= 1.5 ±1.5 SD) had the next highest CPUE rates, which were sites closest to the mouth of the estuary.

However, a multiple regression analysis of the CPUE of *C. maenas* in response to the estimated distance to the mouth of the estuary was not normally distributed, suggesting a non-linear correlation. Therefore, we fit polynomial lines to examine crab species distribution patterns along the distance gradient to examine where crab species overlapped. The CPUE of *C. maenas* overlapped with *Cancer productus'* low CPUE around 2,000 meters up the estuary (Figure 2.3) Peak CPUE of *C. maenas* overlapped with *M. magister* around 2500 meters into the estuary but *M. magister* had its CPUE peak at 6000 meters where there were low CPUE rates of *C. maenas* (Figure 2.3). *Hemigrapsus orogenesis* overlapped during *C. maenas* CPUE peak as well but had its peak further into the estuary around 8,000 meters in (Figure 2.3).

The increase in mean CPUE rate of *C. maenas* during the recent six years appeared to have little influence on native species as all regressions of *C. maenas* versus the change in CPUE rate of native crab species yielded low R^2 values (*H. oregonensis* = 0.03, *M. magister* < 0.01, *C. productus* = 0.3) (Table 2.3, Figure 2.5, Figure 2.6, Figure 2.7).

There were seven habitat types surrounding the crab trapping sites. In order of most to least frequent, these habitats included algae and seagrass (19), wetland (13), aquatic bed (12), marsh (8), seagrass (7), woodland (2), and biota (1) (Table 2.4). Additionally, there were six areas surrounding trapping sites that had no habitat identification provided. The five bottom substrates, in order of most frequent to least, were unconsolidated (27), sand and mud mixture (25), mud (7), no bottom substrate (4), sand (2), and artificial structure (2)(Table 2.5).

Discussion

Despite the increase in *C. maenas* abundance and distribution in recent years, the species density may be too low in South Slough to have a negative impact on native crab species (Behrens Yamada et al., 2019). The low mean CPUE throughout SSNERR may be the reason there was no correlation since the 2016 increase in CPUE of *C. maenas* compared with the change in CPUE of native crabs. The annual high CPUE rate of *M. magister* was consistent with previous research finding they make up a significant portion of biomass in estuaries in the Pacific Northwest (Holsman et al., 2006). While adult *M. magister* are targeted and trapped in coastal and open ocean environments, they utilized estuaries as nurseries for larval dispersion and juveniles reside there up to two years before migrating to deeper waters (Armstrong et al., 2003). *M. magister* distribution in South Slough was found to peak just beyond halfway upstream to the furthest trapping site. However, this population may be of too small size to apply predation or competition towards *C. maenas* the two species' higher CPUE rates overlap. If *M. magister* were applying such biotic resistance, then *C. maenas* CPUE rates would be lower at overlapping distances in South Slough.

Though typically having low CPUE, *Hemigrapsus oregonensis* were caught in high numbers in 2016-2018. This temporary increase in CPUE rate may be due to only minnow traps being set at several sites during that timeline. The average size of *H. oregonensis* is 25 mm for populations among the Pacific Northwest, which means the mesh size of the Fukui traps is not effective in trapping them (Jenson and Egnotovich, 2015). Possibly, *H. oregonensis* either avoided the Fukui traps with large predators or escaped predation by entering the minnow traps, thus possibly skewing the accuracy of their CPUE rate. Therefore, as trapping surveys continue, there should be a standard procedure of using two styles of traps, Fukui and minnow, at sites throughout SSNERR. This peak in *H. orogenesis* may also be from the frequency of traps being deployed further upstream where higher CPUE rates of them are seen, possibly avoiding areas of *M. magister* and *C. maenas* overlapping.

The low CPUE rate of *C. productus* throughout the 20-year timeline is not fully understood. The rate could be the result of the type of traps that were deployed further into the estuary but there has not been any literature to suggest this. *Cancer productus* distribution may be limited to the mouth of the estuary, as we observed their highest

CPUE to be at the Charleston Boat Basin and (Figure 2.2). As osmoconformers, *C. productus* may not be able to survive in areas that highly fluctuate in salinity (Carroll and Winn, 1989). The higher CPUE rates of *C. productus* and *C. maenas* at the one site, Charleston Boat Basin, further supports Hunt and Behrens Yamada's (2004) observation in Yaquina Bay of little overlap of *C. productus* and *C. maenas* distribution. It is not fully understood if this is driven by environmental conditions, habitat preference, or competition, however it does indicate that there is little interaction between the species. Therefore, biotic resistance from *C. productus* towards *C. maenas* may not be a likely interaction in South Slough, which makes removing *C. maenas* a more urgent concern.

The only trend in habitat preference *C.* maenas was among seagrass which was only found surrounding sites Joe Ney Slough and Indian Point South as it recruited the highest mean CPUE rate of *C. maenas.* The majority of the habitat surrounding the traps in SSNERR lacked structure with the exception of seagrass bottom substrate. With their morphology being less dexterous compared to most other crab species, *C. maenas* prefer habitat of structure, such as rock, bivalve beds and eelgrass, to better grasp their surroundings to prevent becoming dislodged from wave action or use as refuge (McDonald et al., 2006). However, populations of *C. maenas* in Australia were found in wave actions areas, further demonstrating their adapting capabilities (Thresher et al., 2003). Within South Slough, *C. maenas* have inhabited a wide range of habitats including standard sediment, as was reflected within numerous areas of unconsolidated habitat.

This may have been a response to indirect factors, such as the die-off of eelgrass which was presumed to be the result of a wasting disease (Geierman et al., 2020). Food source could be the driver as well since bivalve species, the prey of preference for several crab species, can use less energy to burrow into sediment, rather than hard structure, to escape predator threats (Sassa et al., 2011).

Future studies of *C. maenas* distribution should include a range of habitat, specifically including structured areas of artificial fixtures (i.e., boat ramps and bridges), rock, and accumulated bivalve/biotic remnants. The original eleven sites should continue to be monitored as their long-term data can aid in assessing lag time of *C. maenas* and their timeline thresholds of invasion and distribution since their introduction (Rossong et al., 2012). Furthermore, *C. maenas* responses to lack of habitat may alter their feeding behavior, as seen in the western Atlantic where adult *C. maenas* targeted juvenile native crab species *Dyspanopeus spp.* over juvenile *C. maenas* as prey (Gehrels et al., 2016).

The tolerance abilities and steadily increasing abundance of *C. maenas* indicates a management plan should be considered for SSNERR. In other estuaries throughout North America, the most effective method of management for *C. maenas* has been reducing numbers through trapping efforts. In California, traps were deployed in different regions within Bodega Harbor, which indicated that trapping efforts should focus in the lower intertidal to maximize removal efforts (de Rivera et al., 2007). In Newfoundland, Canada researchers found that the trapping efforts were more successful when baited with squid or cod, despite *C. maenas* being generalist predators (Favaro et al., 2020). The use of Fukui traps is effective but selective for adult *C. maenas* which can allow a boom of juvenile *C. maenas,* due to lack of predator pressures from the cannibalistic adult *C. maenas,* causing future stocks of *C. maenas* to increase (Grosholz et al., 2021). Therefore, different types of traps, such as minnow traps, should be set at the same sites as Fukui traps in order to best catch juveniles. In addition, seining or habitat traps could be used (de Rivera et al., 2007). Another method of management to prioritize in marine environments is public outreach and education (Giakoumi et al., 2019).

While active entrapment can be effective, accidental collection and proper disposal of *C. maenas* from people recreationally fishing or observing can aid in reducing *C. maenas* numbers. Public education efforts can include proper identification of distinctive features (i.e., the five marginal points on each side of the carapace) of *C. maenas* can be posted at estuaries frequented by the public and provide recommendations on what to do with *C. maenas* when found. *Carcinus maenas* have inspired new recipes, much of which focus on a broth but are edible as softshell crab (“Green Crab Recipes” n.d.). Furthermore, their carcasses can be used as a natural fertilizer due to the calcium in the shell, or even as bait for fishing purposes, as is used on the east coast (Nekvapil et al., 2021).

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Appendix B: Chapter Two Results

Table 2.1 Habitat Descriptions *Identifying descriptions of the habitat types found in South Slough*

Habitat Type	**Description**
Algae	Area dominated by non-vascular algae species
Algae & Seagrass	Co-occurring elements of algae and seagrass within the habitat
Aquatic Bed	Marine or estuarine water column with low percentage (less than 30%) of other habitat identities
Biota	Holds various life histories and taxonomic characteristics of the dominant life forms
Marsh	A co-occurrence of aquatic bed with herbaceous and/or halophytic vegetation
Seagrass	Area dominated by seagrass or eelgrass species
Wetland	Consists of shrub-dominated woody vegetation less than 6 meters in height or perennial plants
Woodland	Holds most woody vegetation greater than 6 meters in height and can include tidal forests

Table 2.2 Bottom Substrate Descriptions *Identifying descriptions of the bottom substrates found in South Slough*

Bottom Substrate	**Description**
Artificial Structure	Composition of natural, mineral material that were incidentally or intentionally placed by humans
Biogenic	Landforms and physical features created by living organisms which includes classes of algae, coral, ooze, organics, shell, and worms
Gravel	Sediment with rock fragment particles larger than 2mm in size
Mud	Sediment with rock fragment particles less than 0.0625mm in size
Mud & Sand	Co-occurring elements of mud and sand present within the substrate
Rock	Igneous, metamorphic or sedimentary rock with particle size greater than 4.0 meters in any dimension and covering greater than 50% of the substrate surface
Sand	Sediment with rock fragment particles between 0.0625 and 2 mm in size

Table 2.3 Linear Regression Results *The R^2values and equations to the natural log linear regressions of the last six-year mean CPUE of C. maenas to the change in mean CPUE of native crab species of years 2016-2021 from 2002-2015.*

Crab Species Combination	**R^2 value**	**Fitted Equation**
C. maenas and *H. oregonesis*	0.025	$y = 0.43 + 0.076x$
C. maenas and *M. magister*	0.0061	$y = 1.5-0.083x$
C. maenas and *C. productus*	0.28	$y = -1.1-1.6x$

Table 2.4 Count of Habitat *The count of the various habitat types within a 50-meter radius of the trap locations in South Slough National Estuarine Research Reserve*

Habitat Type	**Frequency**
Algae & Seagrass	19
Aquatic Bed	12
Biota	1
Marsh	8
Seagrass	7
Wetland	13
Woodland	2
No Identification	6

Table 2.5 Count of Bottom Substrate *The count of the various bottom substrates within a 50-meter radius of the trap locations in South Slough National Estuarine Research Reserve (this is not out of number of traps)*

Bottom Substrate	**Frequency**
Artificial Structure	2
Mud	7
Mud & Sand	25
Sand	3
Unconsolidated	27
No Bottom Substrate	4

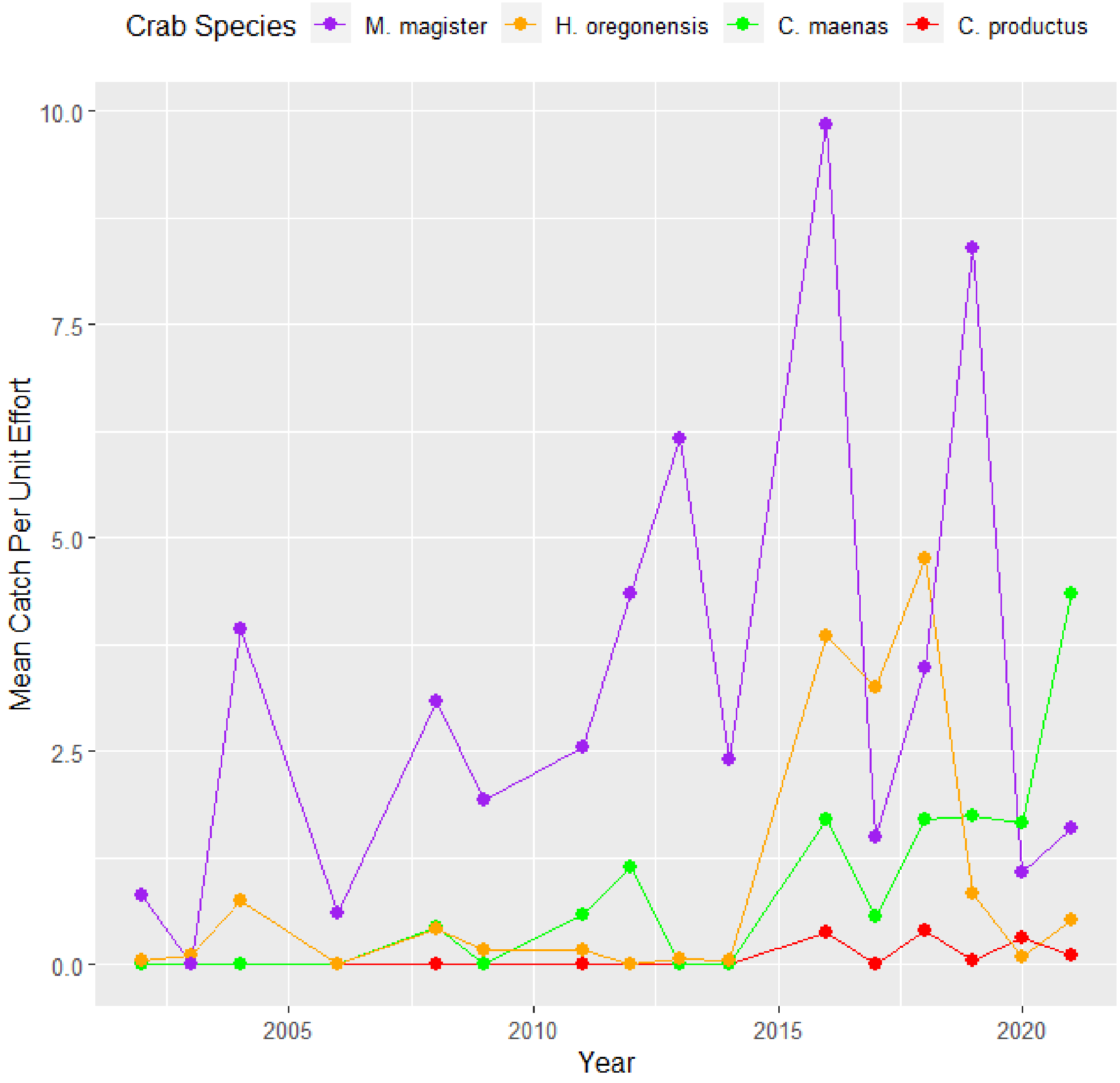

Figure 2.1 CPUE Over Time *Line graph of the yearly CPUE of the crab species M. magister (purple), H. oregonensis (orange), C. maenas (green), and C. productus (red) collected with the use of minnow and Fukui traps between June through August from 2002 to 2021 averaged across the eleven sites in South Slough, Oregon.*

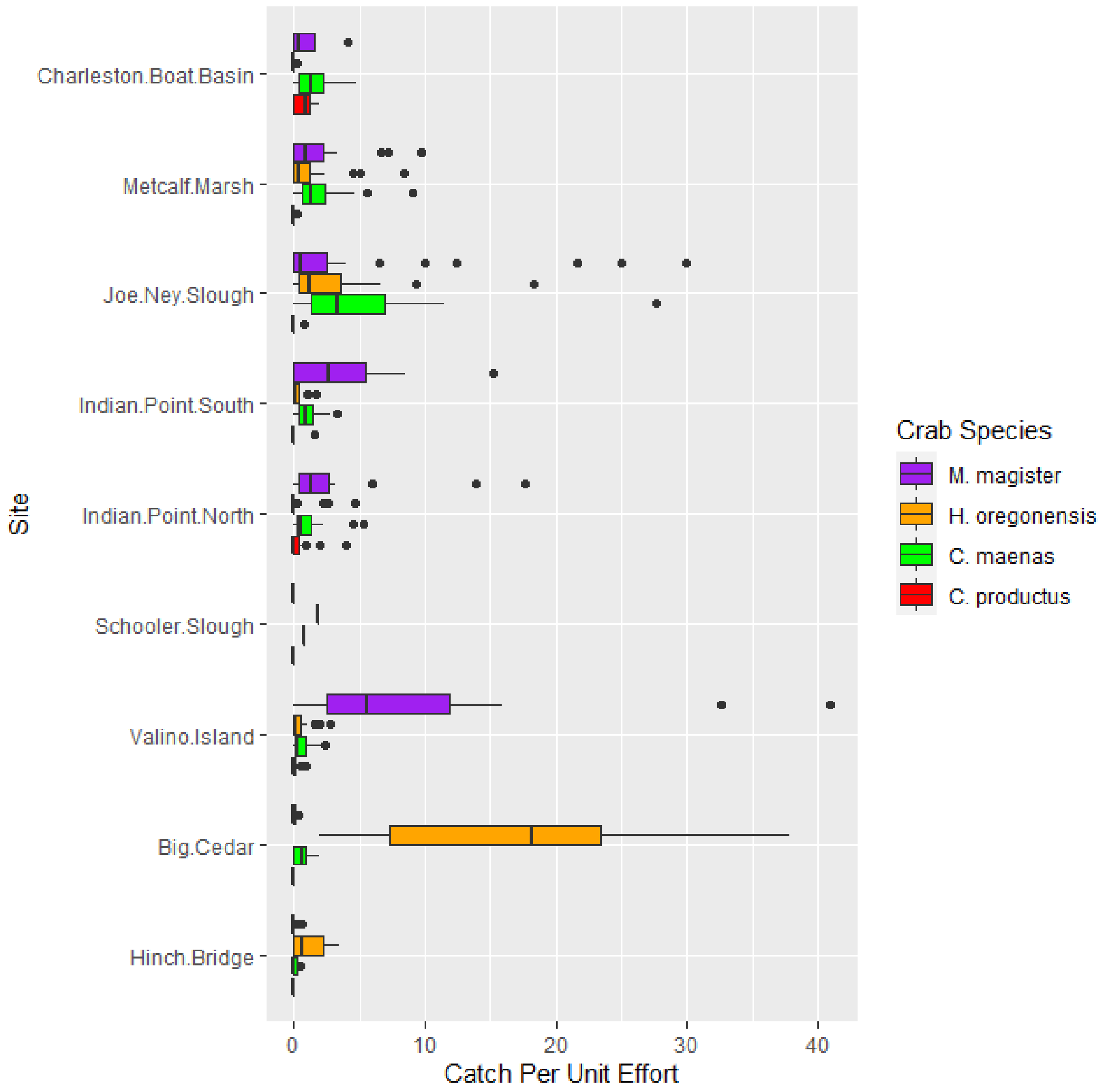

Figure 2.2 CPUE at Sites in South Slough *Box and whisker plot of catch per unit effort (CPUE) of crab species M. magister (purple), H. oregonensis (orange), C. maenas (green), and C. productus (red) from minnow and Fukui box traps at nine sites, listed north to south, in South Slough from 2016 to 2021. Two sites were omitted because they had a CPUE of zero for C. productus, C. maenas, and M. magister.*

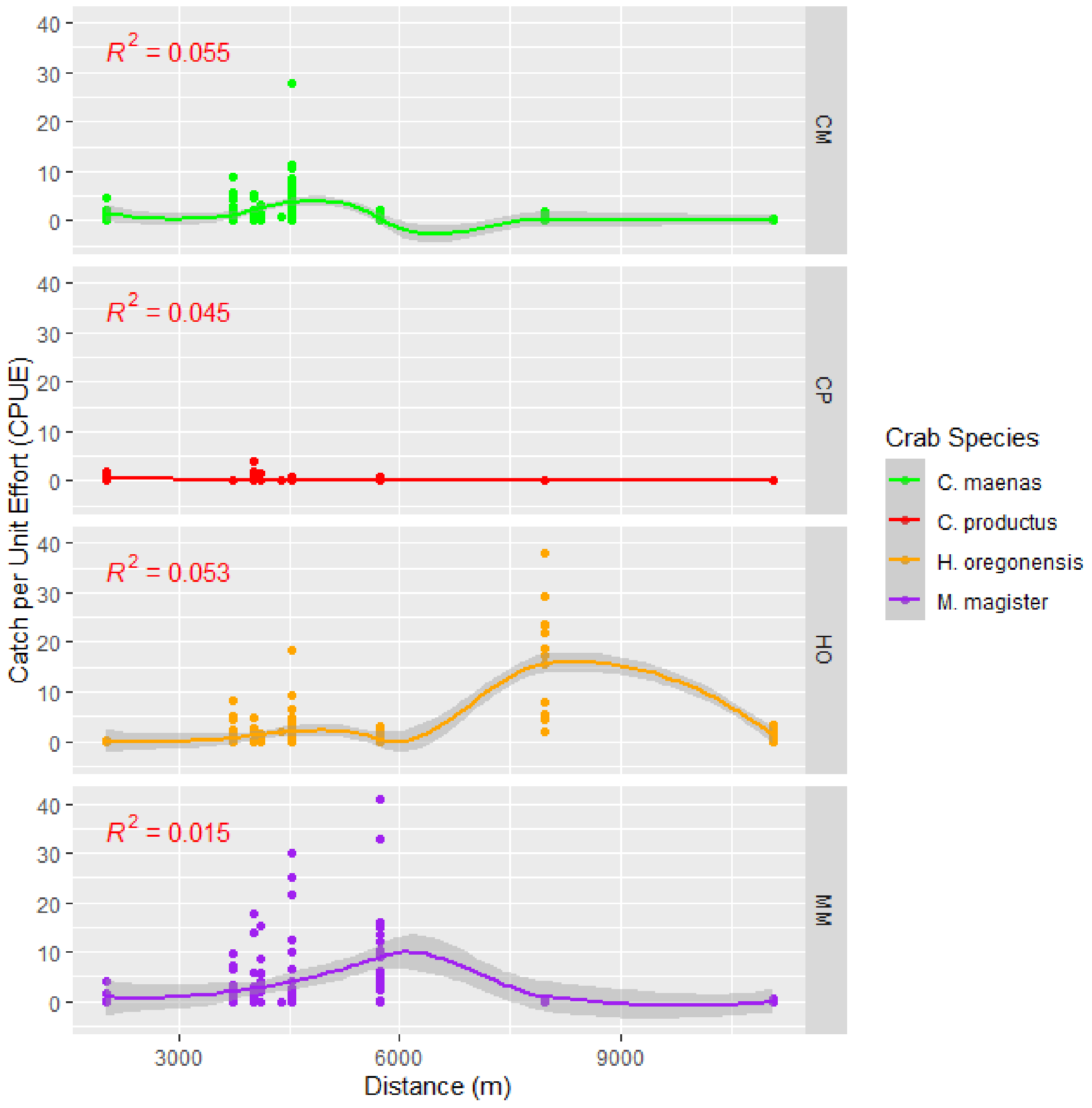

Figure 2.3 CPUE Across Distance *Regression of the CPUE of C. maenas in the past six years (2016-2021) across the estimated distances of trapping locations in South Slough with fitted polynomial lines.*

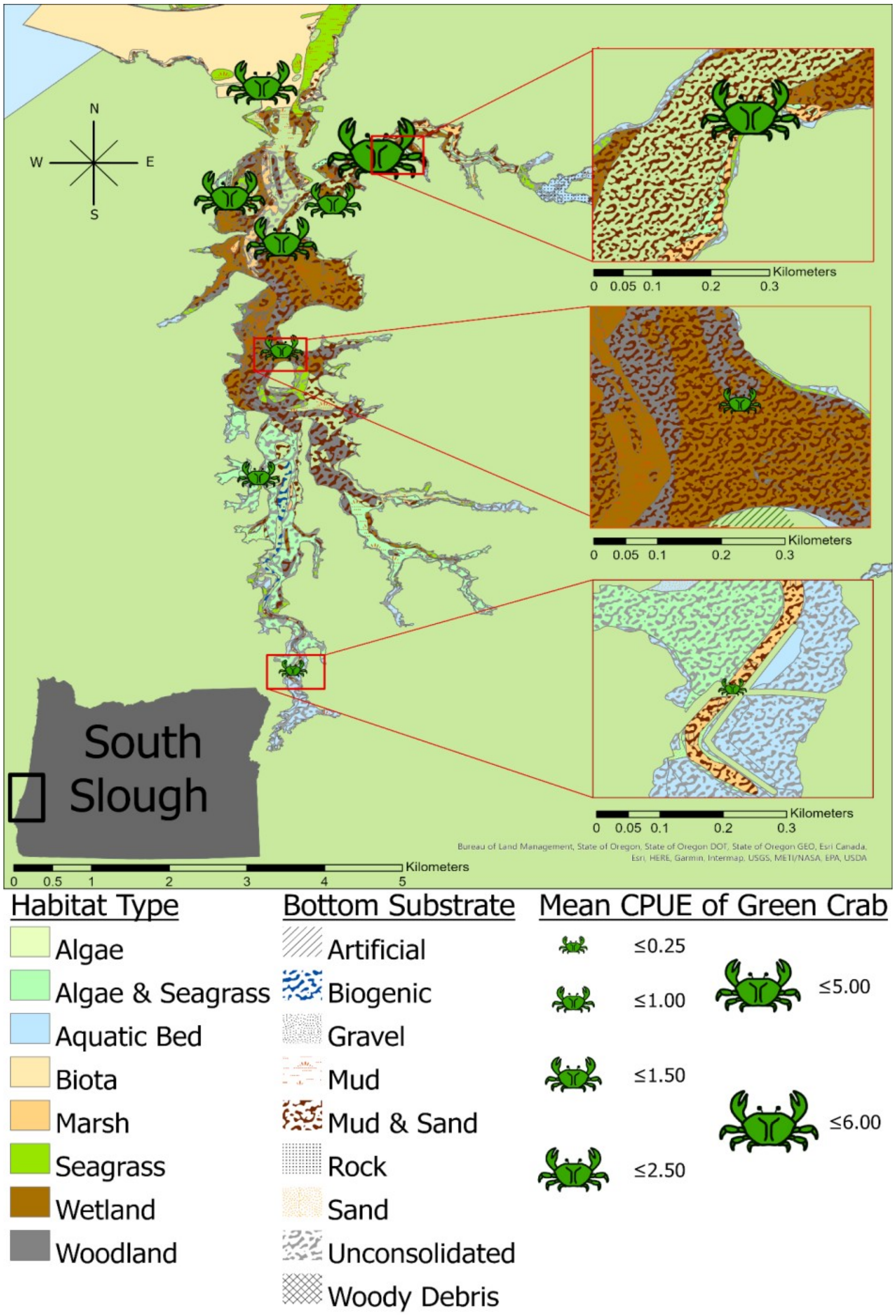

Figure 2.4 South Slough's Habitat and Crab CPUE *Map of the South Slough region of Coos Bay illustrating the habitat based upon the two axes of habitat type, and bottom substrate with graduated symbols of green crabs to indicate the mean catch per unit effort (CPUE) of the C. maenas at trapping sites. The three insets each show a region with a different green crab catch, from highest catch on the top to lowest at the bottom, and illustrate how much habitat type can change in a small area.*

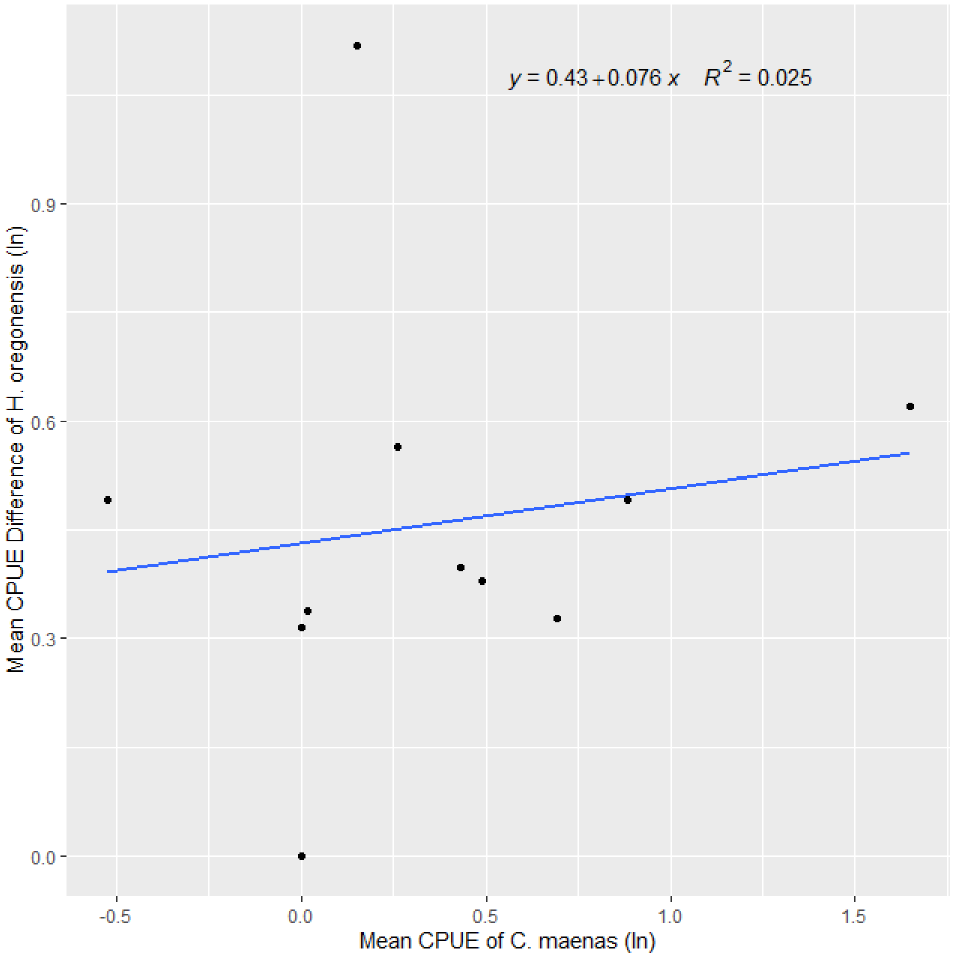

Figure 2.5 Correlation in CPUE Between Green and Yellow Shore Crabs *The natural log mean CPUE of C. maenas at different sites in South Slough, Oregon, averaged across years from 2016-2021 in relation to the mean natural log CPUE difference of H. oregonensis from years (2002-2015) prior to the years (2016-2021) following the significant increase of C. maenas.*

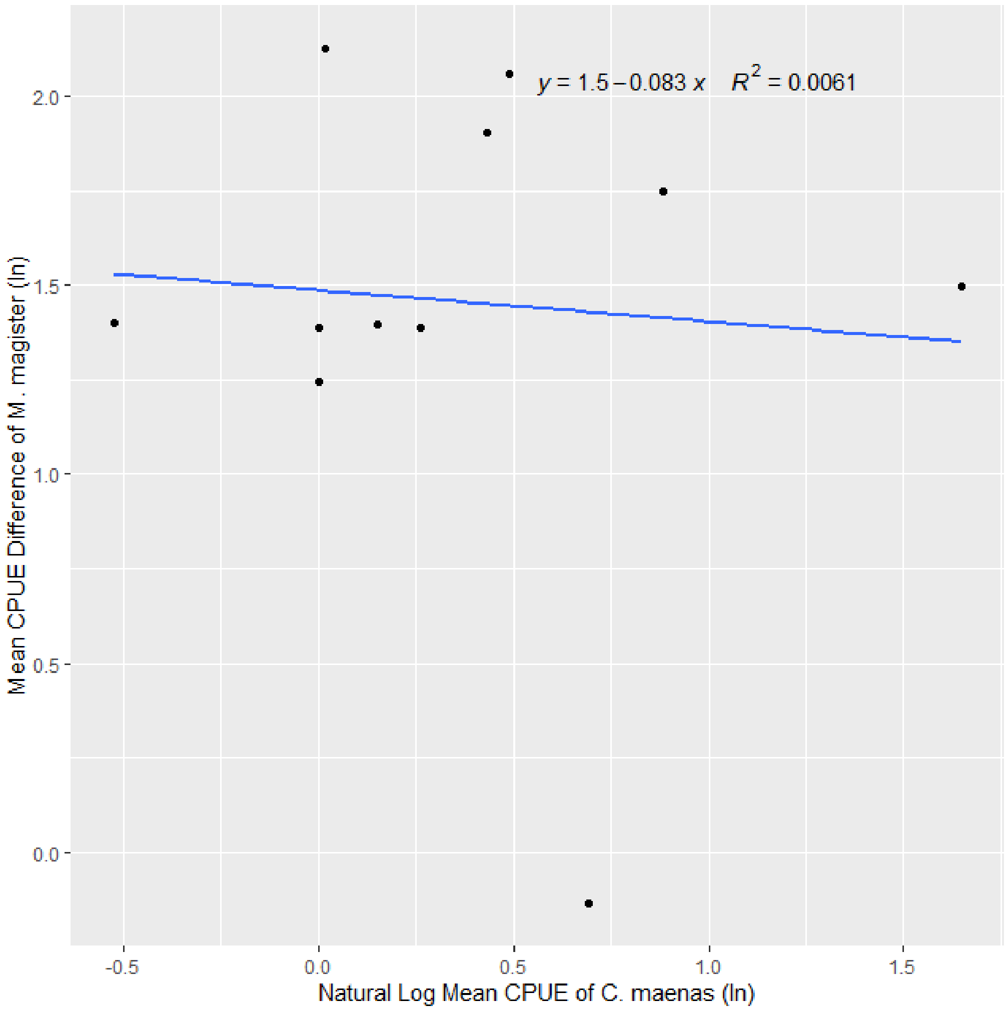

Figure 2.6 Correlation in CPUE Between Green and Dungeness Crabs *The natural log mean CPUE of C. maenas at different sites in South Slough, Oregon, averaged across years from 2016-2021 in relation to the mean natural log CPUE difference of M. magister from years (2002-2015) prior to the years (2016-2021) following the significant increase of C. maenas.*

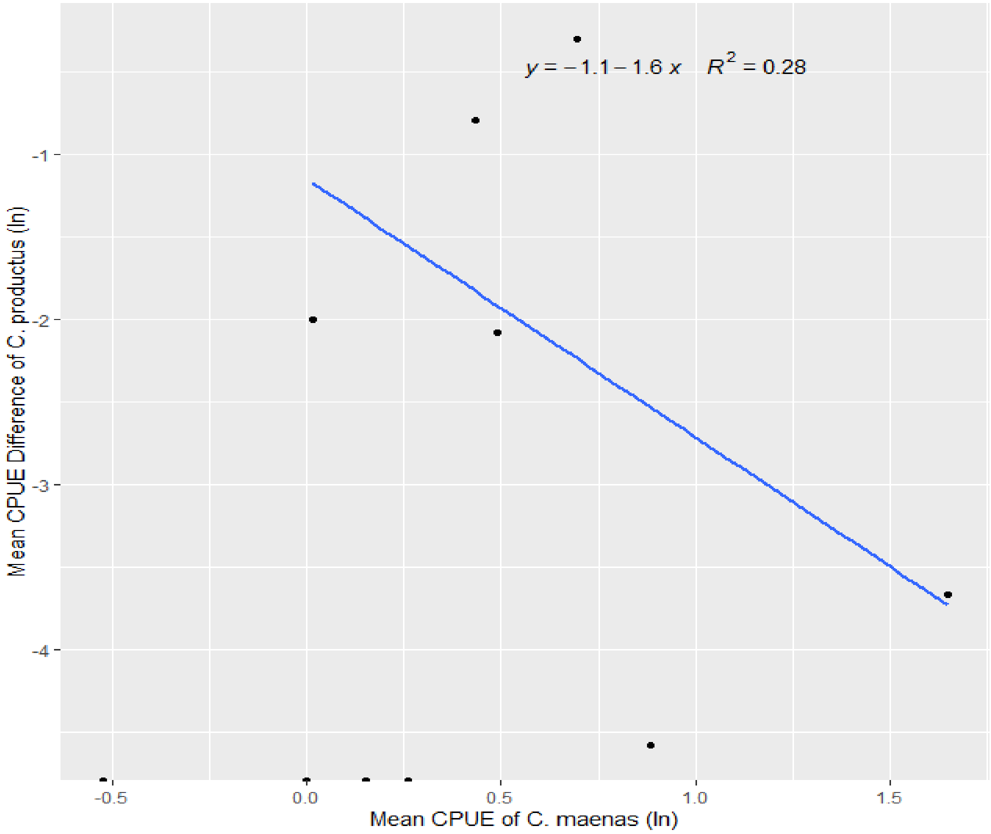

Figure 2.7 Correlation in CPUE Between Green and Red Rock Crabs *The natural log mean CPUE of C. maenas at different sites in South Slough, Oregon, averaged across years from 2016-2021 in relation to the mean natural log CPUE difference of C. productus from years (2002-2015) prior to the years (2016-2021) following the significant increase of C. maenas.*

Overall Conclusions

Despite *C. maenas* abundances having yet to reach a point of significant influence to native species abundance in South Slough, *C. maenas* should continue to be monitored (Behrens Yamada et al., 2019). The warm blobs in the Pacific Northwest caused numerous die-offs of native species including fish and invertebrates (Cavole et al., 2016). Such conditions of environmental stress with reduced biotic resistance are optimal for *C. maenas* to outcompete native species and advance their distribution among estuaries. Therefore, thorough understanding *C. maenas* habitat preference, their responses to stressors of climate change, and whether biotic resistance from native predators can be overcome, we can design effective management methods to contain *C. maenas* numbers.

From these results, we understand that temperature alone does not appear to have an effect on *C. maenas* mortality however predator identity does. The majority of the mortality occurred in aquaria with *C. sapidus*, a species known to cause biotic resistance against *C. maenas* in the Atlantic (de Rivera et al., 2005). The single mortality events occurred by the predators *C. maenas* and *C. productus* were determined as coincidences due to prey being in vulnerable conditions. Mortality of *C. maenas* was more likely to occur with a higher size discrepancy between predator *C. sapidus* and prey *C. maenas;* lower PCW resulted in higher the probability of mortality among prey *C. maenas*. While management methods of biological control have been tested with the use of parasites in crabs, it would not be advised to use this approach as it would be difficult for the process to be selective for only *C. maenas* and could pose mortality of native species (Goddard et al.,2005).

All behavioral responses from prey *C. maenas* were determined to be significantly influenced by temperature and predator species present. The most relevant behaviors of *C. maenas* to predict their abilities to overcome biotic resistance were 'Feeding/Foraging' and 'Aggression'. Time spent 'Feeding/Foraging' decreased regardless of predator species present which suggest it was not a primary response within warmer temperatures. Time spent 'Aggression' decreased when *C. maenas* or *C. sapidus* predators were present, again suggesting this was not a primary response within warmer temperatures. However, when *C. productus* were present, time spent 'Aggression' increased while *C. productus* 'Aggression' behavior response did not change across temperatures. This could indicate that *C. maenas* will be able to overcome biotic resistance from *C. productus* as they will not apply any predation pressure when environmental conditions are stressed with increased temperatures. *Cancer productus* may be able to apply biotic resistance through competition as they exhibited an increase in 'Feeding/Foraging' within increased temperatures but the interaction between Pacific native *C. productus* and invasive *C. maenas* should be further investigated.

Knowing *C. maenas* behavior response to temperature change can aid in predicting their distribution among Oregon estuaries. However, identifying their habitat preference will provide information on effective management efforts. *Carcinus maenas* were collected at nine of the eleven sites in South Slough within the past six years, demonstrating their ability to reside within a range of salinity conditions. Despite their ability to overcome environmental stressors, such as salinity and temperature change, mean CPUE rates were fairly low at trapping locations. The three sites that had the highest CPUE rate of *C. maenas* were located closest to the mouth of the estuary and two of those sites had the only form of structure sufficient for gripping, which was seagrass. Despite the low mean CPUE rates, *C. maenas* have been increasing in abundance each year since 2017. Again, *C.* maenas have yet to reach abundance to reflect a correlation to the native species CPUE rate for *M. magister*, *H. oregonensis,* and *C. productus.* However, management actions should be applied as early as possible to contain *C. maenas* growing abundance and distribution.

In the case of SSNERR, trapping efforts should continue and target preferred habitats, such as seagrasses. Trapping devices should include Fukui and minnow traps as they are capable of capturing *C. maenas* of juvenile and adult life stages. These traps should continue to be deployed in the eleven sites of South Slough but additional traps should be set within structure environments. Structure can include artificial fixtures as there has been a die-off of eelgrasses within SSNERR and *C. maenas* might alter their habitat preference due to the lack of the natural resources of seagrass. Whether or not this is applicable to other estuaries in Oregon is undetermined. Therefore, habitat preference of *C. maenas* populations from other estuaries, such as Netarts, Tillamook, and Yaquina Bay, should be studied for comparison.

Additional management efforts should include the public, as community science can aid in documenting *C. maenas* distribution, especially in regions that are not thoroughly researched. Detailed identification of *C. maenas* should be provided at outreach events or on message boards, as their polychromatic shells may allow them to be confused with native crab species, especially as juveniles. The public can contribute information through a user-friendly platform, such as iNaturalist, for experts to review for accuracy as well as providing the public with feasible solutions for this nuisance species.

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