ABUNDANCE OF THE ASIAN SHORE CRAB *HEMIGRAPSUS SANGUINEUS* IN AND ADJACENT TO THE DELAWARE BAY: EVIDENCE OF INVASIVE CRASH AND RETURN OF NATIVE SPECIES

by

Corey Schab

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ABSTRACT

The Asian shore crab *Hemigrapsus sanguineus* has been introduced to multiple rocky habitats outside its native range and is considered an invasive species on the East Coast. The Delaware Bay region represents one of these locations and contains established populations of this intertidal, brachyuran species. Previous studies conducted in the University of Delaware Harbor, a location within this invaded region, indicated that *H. sanguineus* had displaced native mud crabs as the dominant species in this habitat. This trend had been observed at many locations in the North American range of the species. However, surveys conducted a decade later, during 2011 and 2012, have indicated a reverse in the previous trend and have shown significantly higher abundance and biomass of *Panopeus herbstii*, a native mud crab, compared to *H. sanguineus*. These results document the first evidence of a decline in the population of *H. sanguineus* along the East Coast of the USA.

Chapter 1

INTRODUCTION

1.1 General Ecology of the Asian Shore Crab, *Hemigrapsus sanguineus*

The introduction of non-native species to any ecosystem stimulates interactions that could harm the native community and cause extensive economic loss (Cox, 1999). In the marine environment, abundance of invasive species has been shown to correlate directly with increase in frequency of disease among native species, disturbance of fisheries, and reduction in biodiversity (Molnar et al, 2008; Cox, 1999). In the United States alone, invasive species caused a loss of US $97 billion from 1906-1991 (Cook et al., 2007). The European green crab, *Carcinus maenas*, was introduced to the eastern coast of the United States in the 1800's and to the West Coast in the 1990's (MacDonald et al. 2007). The species now causes a loss of US $60,000-$130,000 annually due to shellfishery destruction on the West Coast, calculated from ecological and economic models (Grosholz et al., 2011). Grosholz et al. (2011) predicted further losses of US $1.21 million annually if the range of *C. maenas* expands north to Washington and Alaska.

Other bio-invasions are less understood regarding their economic impact (Griffen, 2011; Soors et al., 2010). For example, *Hemigrapsus sanguineus*, the focus of this study, was initially found in southern New Jersey in 1988 (McDermott, 1991; Williams and McDermott, 1990), and although the species is well studied, economic impact remains unclear. *H. sanguineus* is a brachyuran crab belonging to the family

Varunidae and native to the northwest Pacific Ocean, ranging from Russia to Hong Kong (50°N-22°N) (McDermott, 1998). The initial introduction in New Jersey was most likely via ballast water discharged from ocean-going vessels entering the Delaware Bay and estuary (McDermott, 1998), which is home to one of the largest port complexes in the USA (Kim and Johnson, 1998). By 1995, the range of *H. sanguineus* had spread southward to Cape Charles, Virginia and northward to Cape Anne, Massachusetts (McDermott, 1998b). This invasion continued to spread rapidly northward for another five years, but has decelerated since (Bourdeau and O'Connor, 2003; Lohrer et al., 2000). The species now extends from Cape Hatteras to central Maine (Griffen, 2011). Many studies have focused on *H. sanguineus*; however, there are still uncertainties concerning its population dynamics, interaction with native species, and distribution within the intertidal zone (Lohrer et al., 2000; Epifanio, 2013).

Many factors can contribute to the initial proliferation of an invasive species. Factors such as spawning period and strategy, diet, and additional competitive adaptations accumulate to provide superiority over other species. *H. sanguineus* has been shown to exhibit these competitive advantages during interaction with native crabs. For example, *H. sanguineus* has an expanded spawning season when compared to native, East Coast species (McDermott, 1998), exhibits opportunistic omnivory (Brousseau et al, 2005), and demonstrates competitive success for food and space (Jensen et al., 2002).

Successful spawning is crucial for population sustainability, and many species maximize the size of annual cohorts by high levels of fecundity, favorable timing of larval release, or possessing longer spawning duration than competitors. *H.*

sanguineus displays an extended spawning period compared to co-occurring native crab species in the Delaware Bay region. McDermott (1998) determined that the species spawns from late April through September in the Mid-Atlantic region, while native mud crabs (e.g., *Panopeus herbstii*) spawn from June-August (Jones et al., 1995).

The reproductive behavior of *H. sanguineus* in its home range appears to be directly related to water temperature, as breeding season extended from June-August at 43°N (Takahashi et al., 1985), from April-August (Kurata, 1968) at 35°N, and from March-October (Fukui, 1988) in areas at 33°N, equivalent latitude to southern North Carolina (McDermott, 1998). These results demonstrate the tight correlation between spawning duration and water temperature. The native home range of *H. sanguineus* is located in a temperate climate, dominated by the Kuroshio Current, that shows similar seasonal variation to the temperate climate of the western Atlantic, dominated by the Gulf Stream current (Mann and Lazier, 2006). For this reason, it is important to consider the distribution of *H. sanguineus* in its native range and compare that with East Coast distributions. The data also present evidence that would support the possibility of further expansion of *H. sanguineus* in North America, as Hong Kong is about 22°N (analogous to Cuba) and the current southern-most range on the East Coast is 33°N. Presently, it is unclear why the species has not invaded regions south of Cape Hatteras because event-scale phenomena, such as hurricanes, would favor occasional transport of larvae southward beyond the cape (Byers and Pringle, 2006; Epifanio and Garvine, 2001).

Feeding strategies are also an important determinant of the success of non-indigenous species in newly invaded habitats. Laboratory experiments conducted by

Brousseau et al. (2005) showed evidence of opportunistic omnivory in the Asian shore crab. This study tested preferential diet of *H. sanguineus*, comparing crab densities versus type of diet—macroalgae or animal. Specifically, the diet preference of *H. sanguineus* expanded with an increase in population density. This result has led to further concern toward native prey populations (in particular the blue mussel, *Mytilus edulis*, the seaweeds, *Enteromorpha* spp., *Chondrus cripsus*, and the barnacle, *Semibalanus balanoides*) if *H. sanguineus* populations continue to expand.

In another dietary investigation, Lohrer et al. (2002) conducted a two-year study on the impact of *H. sanguineus* on mussel populations in Long Island Sound and found that densities of juvenile *M. edulis* (<10 mm) decreased by a factor of five as a consequence of *H. sanguineus* predation (Lohrer et al. 2002). Additional laboratory experiments by Lohrer et al. (2002) showed that individual *H. sanguineus* consumed 100-150 juvenile blue mussels d^{-1}. These results demonstrate the high predation pressure that these crabs can exert on native *M. edulis*, perhaps leading to direct ecosystem implications and subsequent economic costs. The blue crab, *Callinectes sapidus*, another important fishery species and native to the western Atlantic, relies on *M. edulis* as a prey source, and this could result in further economic losses due to the impact on *C. sapidus* populations (MacDonald et al., 2007).

Competition for food is another determinant of success of newly invasive species. Studies by MacDonald et al. (2007) compared agonistic behavior among *H. sanguineus*, *C. maenas*, and *C. sapidus*. Competition for food, agonistic interactions, and predator defense were tested, and results indicated that juvenile *C. sapidus* were outcompeted in all categories. In conspecific trials for food, all crabs were measured and equal carapace width was controlled. One individual of each species was then placed in the same experimental chamber with a mussel in the center for food. Results showed that *C. sapidus* only pursued food 57% of the time when either *C. maenas* or *H. sanguineus* were present (MacDonald et al., 2007). The latter two discovered food 100% of the time with *C. sapidus* presence.

For agonistic trials, a "win" was recorded if a crab was able to take food from another crab, defend food from being taken, or deter an approaching crab in trials where food was not involved. When comparing *C. sapidus* with *H. sanguineus*, the MacDonald et al. (2007) study showed that percentage of fights lost was significantly greater for *C. sapidus* compared to *H. sanguineus* or *C. maenas*. *H. sanguineus* showed high instigation percentage and high win percentage during conflicts.

Finally, predation defense was characterized by carapace thickness and breaking strength (MacDonald et al., 2007). Results indicated that both parameters were significantly greater for *H. sanguineus* than *C. sapidus*. Cumulatively, these data confirm the potential threat of *H. sanguineus* toward native species, particularly juvenile *C. sapidus*, resulting from its competitive advantages.

Competition for space is yet another important factor when considering probability of invasive success. Jensen et al. (2002) showed direct support for this factor in their study on space competition between *H. sanguineus* and *C. maenas*. *C. maenas* was the most abundant intertidal species in Long Island Sound before the introduction of *H. sanguineus*. Jensen et al. (2002) showed that, when co-occurring in the same confined area, *C. maenas* was found under shelter only 6.6% of the time. This value had dropped from 42% when *C. maenas* occupied space alone. These data show the replacement of one invasive species by another.

Steinberg et al. (2011) conducted a study that further investigated space competition by *H. sanguineus*. Shelter experiments included two species of *Hemigrapsus* native to the Northeast Pacific (*H. oregonensis and H. nudus*) and *H. sanguineus*. Individuals from each of these species were paired with each other, and all possible combinations of species were tested. Results indicated that co-occurring species heavily impacted juvenile *H. sanguineus* and that both *H. oregonensis* and *H. nudus* out-competed *H. sanguineus* juveniles for shelter usage (Steinberg et al., 2011). However, despite the juvenile crab trials, *H. sanguineus* adults, males in particular, displayed a high affinity for shelter and were not affected by the presence of the other species. These results begin to explain why *H. sanguineus* has not become established on the West Coast of the United States. The two West Coast crab species tested appear to have advantages over *H. sanguineus* juveniles in this category of competition.

Factors that control the vertical distribution of *H. sanguineus* in the intertidal have been studied in both the native and introduced range of the species. In its native range, the species occurs mainly in the upper half of the intertidal zone, a distribution originally determined in its newly invaded habitat on the East Coast as well (Fukui and Wada, 1983; Takada and Kikuchi, 1991; McDermott, 1992, 1998b). More recent studies, however, have shown its distribution to include the lower intertidal and even subtidal habitat (Gilman and Grace, 2009; McDermott, 1998b; Takahashi et al., 1985). In fact, the distribution of *H. sanguineus* in the intertidal appears to be controlled by the amount of available shelter, rather than vertical position *per se* (Lohrer et al., 2000a,b). The extensive ability of *H. sanguineus* to utilize the whole intertidal zone leads to further stress on native species, whether plant or animal. As mentioned above, the broad diet of this crab supports the idea of a greater impact with expanding vertical range.

Overall, it is evident that introduced species, such as *H. sanguineus*, are capable of producing large populations in suitable habitats. Their life histories and competitive characteristics enable them to out-compete certain natives, giving them a better chance of survival. These types of invasions typically follow four stages: 1) arrival, 2) settlement, 3) expansion and 4) persistence (Schmidt et al., 2007; Mollison, 1986; Reise et al., 2006). However, invasive populations sometimes decline after the persistence stage, as evidenced by extensive work on the Chinese mitten crab, *Eriocheir sinensis*, which proliferated during the first ten years of its arrival in Germany, but then began to decline a decade later (Panning, 1939; Attrill et al., 1996; Dittel and Epifanio, 2009). This boom-and-bust phenomenon also occurred in other areas of Europe and most recently in San Francisco Bay on the West Coast of the USA. In contrast, other *E. sinensis* populations have displayed delayed population increases. For example, Ingle (1986) provided evidence of *E. sinensis* introduction into the United Kingdom in 1935; however, it was not until the early 1990's that populations started to expand.

1.2 Historical Distribution in Delaware Bay

An unpublished study by Park et al. (2005) documented the status of *Hemigrapsus sanguineus* in the University of Delaware (UD) Harbor near the mouth of the Delaware Bay in 2001 and tested the relationship between megalopal supply and adult crab abundance. Park et al. determined that abundance of *H. sanguineus* in 2001 was significantly greater than the abundance of native species, including the mud crab *Panopeus herbstii.* Similar results were reported from nearby locations by Brown (2005) who monitored crab abundance at Slaughter Beach in southern Delaware Bay and in Indian River Bay, a lagoonal estuary about 25 km farther south along the Delaware coast. Moreover, results of the Park et al. study revealed that the abundance of adult *H. sanguineus* was not coherent with megalopal data, which showed much higher settlement of native mud crab megalopae at the study location.

The purpose of my thesis work in 2011 and 2012 was to assess changes in *H. sanguineus* and *P. herbstii* populations in the UD Harbor and an adjacent station along the Lewes-Rehoboth Canal (Canal Station). Specifically, weekly and bi-weekly, replicated samples were done at three intertidal elevations to determine abundance, standing crop (i.e., biomass), and carapace width. The details of this study are shown in *Chapter 2* below. During 2012, I conducted an additional investigation to explore the population status of these two species in habitats north and south of the initial study stations. *Chapter 3* describes this detailed, geographic exploration, which quantified the abundance, biomass, and carapace width of crabs at three elevations within the intertidal zone. Finally, *Chapter 4* illustrates an explicit comparison of my 2011 and 2012 data from UD Harbor with the Park et al. (2005) study. The methodologies of these two studies are nearly identical; therefore, comparison is relevant and can document any changes in the respective populations. Exact locations of the five study stations are illustrated in Figure 1.1.

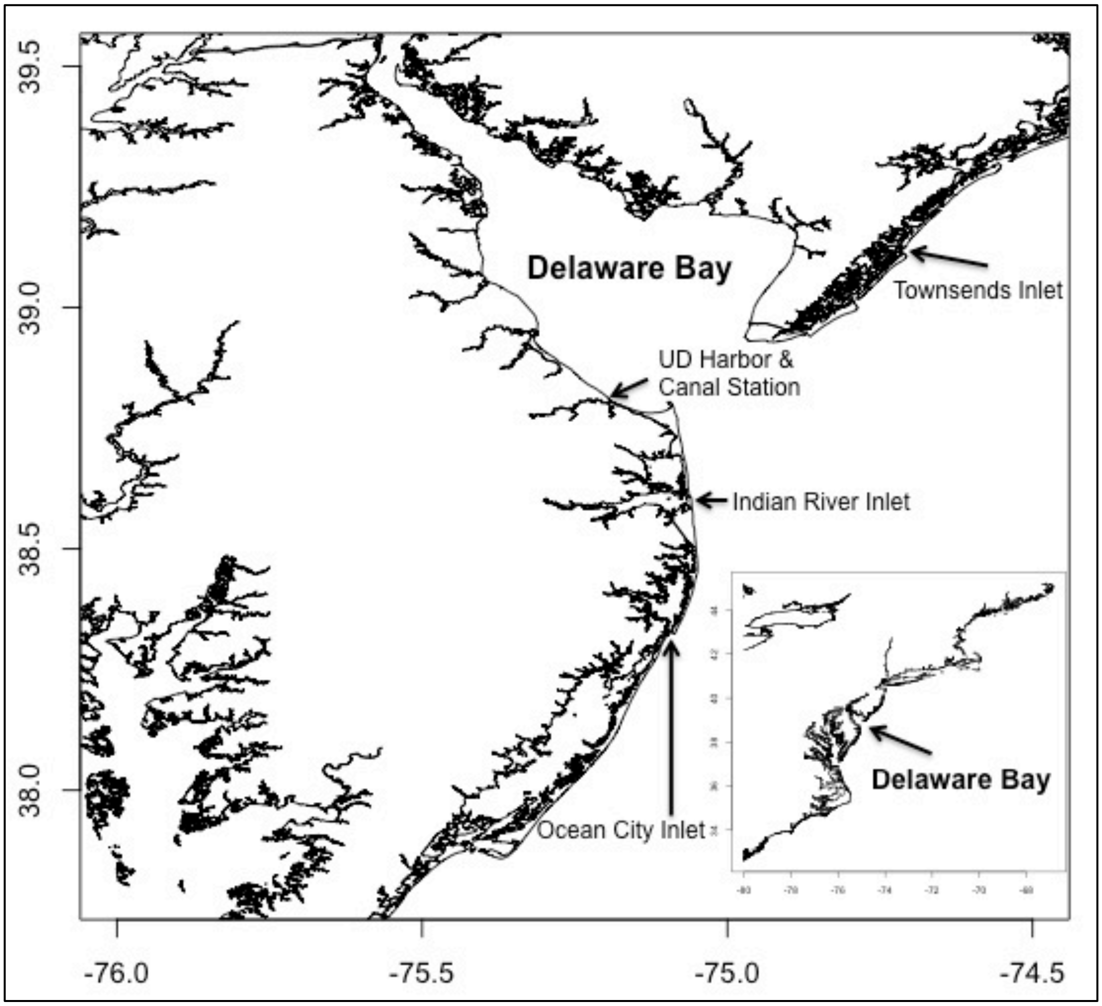

Figure 1.1: Map of Study Stations for 2011 and 2012 Investigations. Arrows on large map show the location of study sites near Delaware Bay. Inset shows location of Delaware Bay on east coast of USA. Longitude is shown on the X-axis. Latitude is shown on the Y-axis.

1.3 Hypothesis and Research Questions

In this thesis I test the hypothesis that there has been a reversal in abundance and standing crop of *H. sanguineus* and *P. herbstii* at the original study site in UD

Harbor and at comparable locations within 50 km north or south. The following research questions provide basis for the studies described in the remaining chapters:

1. Do abundance and standing crop differ between the two species at the UD Harbor and Canal stations?
2. If so, are these differences consistent over the two-year observation period?
3. Are the differences in abundance and standing crop between the two species consistent at different elevations in the intertidal zone?
4. Do these differences exist at comparable habitats north and south of the UD Harbor?
5. Regarding abundance and standing crop, does the present status of *H. sanguineus* and *P. herbstii* in UD Harbor differ from the observations made in 2001?

Chapter 2

INVESTIGATION OF THE DISTRIBUTION OF *HEMIGRAPSUS SANGUINEUS* AND *PANOPEUS HERBSTII* AT TWO ADJACENT STATIONS CONNECTED TO THE DELAWARE BAY

2.1 Introduction

Hemigrapsus sanguineus was first discovered on the East Coast of the USA at Townsends Inlet, New Jersey, in 1988 (Williams and McDermott, 1990: McDermott, 1991). There have been many studies examining the established populations of this species since this discovery, and most have shown the numerical dominance of *H. sanguineus* and the consequential displacement of native species (Williams and McDermott, 1990; McDermott 1991; Ahl and Moss, 1999; Lohrer, et al., 2000). Initially, studies of populations on the east coast of North America provided evidence of distributions in the upper half of the intertidal (McDermott, 1992, 1998b), as seen in the native Asian range of the species (Fukui and Wada, 1983; Takada and Kikuchi, 1991). However, other studies have shown a distribution mainly in the lower and middle intertidal, as seen in southern New England (Ledesma and O'Connor, 2001). More recent work has determined that the vertical range of *H. sanguineus* can encompass the whole intertidal and even extend into subtidal habitat, as seen in Long Island Sound locations (Gilman and Grace, 2009). Despite differing results regarding vertical zonation, it has been determined that the amount of shelter is the key factor in attracting the species, regardless of vertical location in the intertidal (Ledesma and O'Connor, 2001; Lohrer et al., 2000).

In rocky habitat around the Delaware Bay region, *H. sanguineus* interacts directly with *Panopeus herbstii*, a native mud crab, throughout the intertidal zone. Although there is no natural rocky habitat in this region, man-made structures such as riprap, jetties, groins, and breakwaters offer extensive areas of shelter, and studies by Park et al. (2005) and Brown (2005) have investigated established populations of *H. sanguineus* in these habitats. The University of Delaware (UD) Harbor and an adjacent station along the Lewes-Rehoboth Canal (Canal Station) provide rocky habitat for *H. sanguineus* and *P. herbstii* and were chosen for a survey of abundance and biomass during the summer and fall seasons of 2011 and 2012.

This chapter presents results of the 2011 and 2012 investigations with the purpose of assessing the present status of *H. sanguineus* and *P. herbstii* populations at the UD Harbor and Canal stations. My investigation of the vertical distribution of these species within the intertidal included comparisons of abundance, biomass, and carapace width in the upper, middle, and lower intertidal zones. The respective comparisons between the two species were done separately in each of the three zones. Vertical benthic sampling was done to observe the distribution of the two species throughout the intertidal at both sites, while additional horizontal sampling in the mid-intertidal provided high-frequency observations of temporal changes in the population at the Harbor Station.

2.2 Methodology

<u>Horizontal Benthic Sampling</u>

Populations of *Hemigrapsus sanguineus* and *Panopeus herbstii* at the UD Harbor Station (38°47'15.41"N, 75° 9'39.97"W) were examined through replicated horizontal sampling conducted in the mid-intertidal zone. Collections occurred from mid-June through October during the 2011 sampling season and from mid-June through September in 2012. It was determined that observations during the month of October in 2011 did not provide new information concerning temporal or spatial variation in the crab populations, eliminating the need to sample during October of 2012.

Initially, 20 sites were designated and marked along a 25-m transect parallel to the shoreline in the mid-intertidal zone, shown in Figure 2.1 below. This sampling

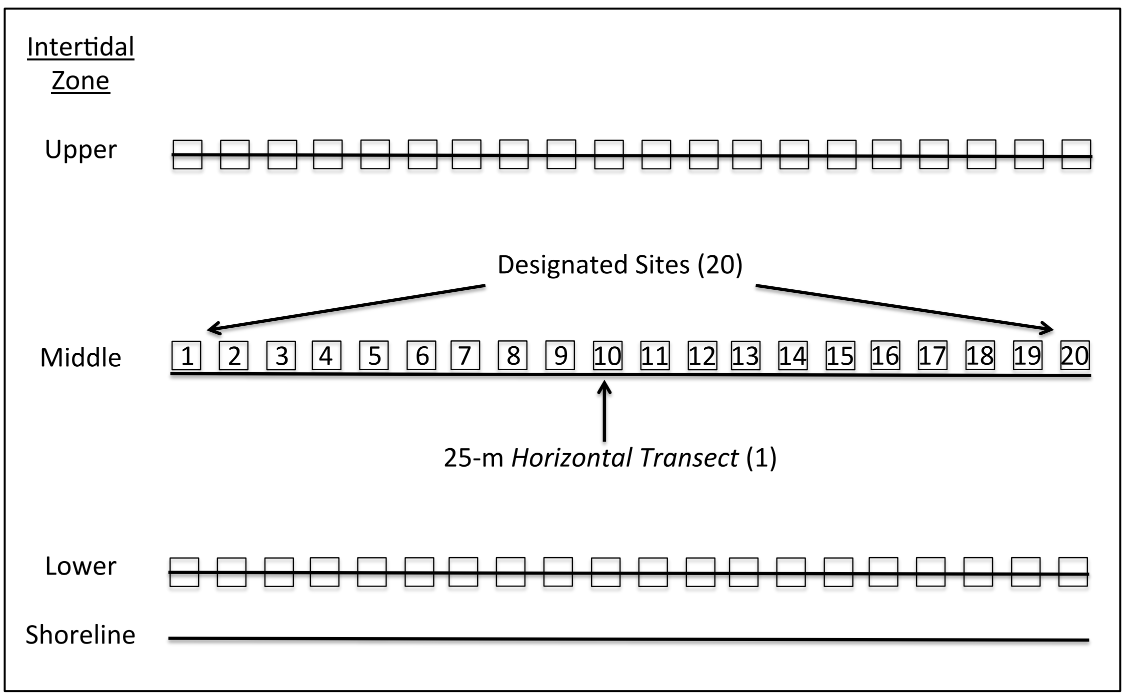

Figure 2.1: Horizontal Benthic Sampling Design. Numbered boxes show the arrangement of sampling locations in the middle intertidal zone. Open boxes show corresponding locations in the upper and lower intertidal zones. Mean low-water shoreline is shown as a horizontal line at the bottom of the figure. Sampling was restricted to the middle intertidal zone.

line was termed the *horizontal transect.* All sites along the transect contained at least 70% rock cover and were spaced at least 1 m apart. Prior to each sampling date, a random number generator was used to select 6 of the 20 sites for collection of specimens, and each randomly chosen site was considered a replicate. Sampling occurred weekly, within one hour of low tide, and consisted of placing a 0.25-m^2 quadrat on the substratum at each of the randomly chosen sites, turning over all rocks and stones within the quadrat area, and quickly collecting all crabs. Salinity and water temperature were measured in open water immediately adjacent to the sampling sites coincident with each weekly collection (YSI Model 30/10 FT). This overall sampling technique was similar to that used in earlier investigations of *H. sanguineus* populations in southern New England (Ledesma and O'Connor, 1991; Ahl and Moss, 1999; Lohrer et al., 2000, Lohrer et al., 2002).

After collection, all crabs were transported to the laboratory where they were identified to species, and carapace width was measured using calipers. Crab biomass was calculated using equations from Park et al. (2005). In that study, the researchers derived a relationship between carapace width (C) and dry weight to determine biomass (B) for both species via regression analysis. The relationships were:

$$B = 0.04\, e^{0.17C} \text{ for } \textit{H. sanguineus} \qquad (1)$$

and

$$B = 0.04\, e^{0.16C} \text{ for } \textit{P. herbstii} \qquad (2)$$

In order to minimize effects of sampling, all rocks were replaced carefully after each collection event, and all crabs were released in the area where they were originally collected after measurements were taken in the laboratory.

Vertical Benthic Sampling

Vertical benthic sampling was performed at the UD Harbor Station and at an adjacent location along the Lewes-Rehoboth Canal (38°47'18.34"N, 75° 9'39.30"W) (Canal Station). Sampling protocol was similar to that described above, but was conducted bi-weekly, from mid-July through October at each station during 2011, and from mid-June through September during 2012. Quadrat area and rock cover remained the same, as did the technique for capturing crabs. However, the sampling design consisted of five vertical transects, placed perpendicular to the shoreline, located at 3-m intervals along a line that extended for 12 m parallel to the shoreline. Each transect extended from the low to the high intertidal zone. Figure 2.2 illustrates the layout of this sampling design.

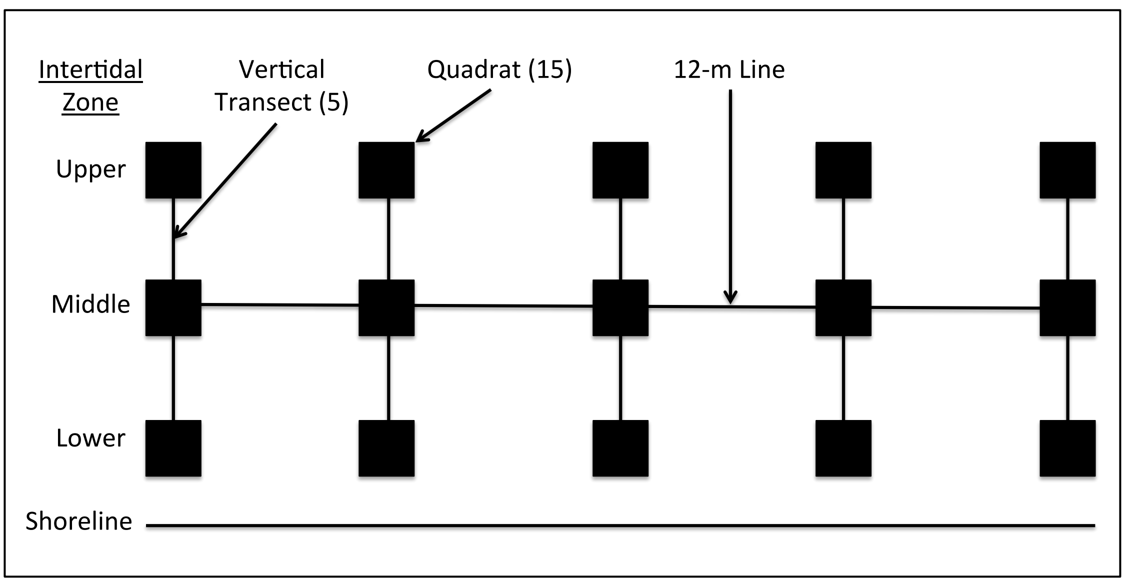

Figure 2.2: Vertical Benthic Sampling Design. Filled boxes show the location of sampling sites in upper, middle, and lower intertidal zones. Mean low-water shoreline is shown as a horizontal line at the bottom of the figure.

Crabs were collected in the low, middle, and high intertidal zones along each transect. Collections within each of the respective zones were considered replicates. Overall, there were 5 replicated samples taken from each of the three intertidal zones during every sampling event. Distance between tidal heights was consistent among the replicates, however it differed between stations due to differences in the slope of the intertidal zone. Carapace width, biomass, water temperature, and salinity were recorded using the same methodology described above.

Statistical Analysis

The status of *Hemigrapsus sanguineus* and *Panopeus herbstii* populations was determined by testing differences in abundance (density), biomass, and carapace width between the two species for both stations. Separate analyses were conducted for each station. Non-parametric, two-sample Mann-Whitney-Wilcoxon tests were applied because data did not meet the assumptions for parametric analysis of variance, even after log, square root, or arc-sin transformation (Shapiro-Wilk normality test). For horizontal benthic sampling, average values of abundance (density), biomass, and carapace width were calculated for each species during each week of sampling. Averages were calculated from the six randomly chosen samples taken each week. Each weekly average value was considered a replicate, and the mean value of these replicates was used in subsequent Mann-Whitney-Wilcoxon analysis to compare differences between *H. sanguineus* and *P. herbstii*. Separate analyses were conducted for each parameter. Statistical analysis for vertical benthic sampling was similar, but mean values were calculated separately for each tidal height, yielding discrete comparisons between species at the lower, middle, and upper intertidal zones. Alpha-level was set at 0.05 for significance testing, and the tests were two-tailed. In addition, means and standard deviations were calculated for both sampling methods and at the upper, middle, and lower intertidal zones for vertical benthic sampling. All tests were performed using R (Version 2.14.1), a computational statistical software program.

2.3 Results

Horizontal Benthic Sampling

Collections at the UD Harbor Station during the 2011 and 2012 sampling seasons revealed the occurrence of both *Hemigrapsus sanguineus* and *Panopeus herbstii* in the mid-intertidal zone. During 2011, there were 33 total *H. sanguineus* caught and 233 total *P. herbstii* (Table 2.1). Mean density of *P. herbstii* was significantly greater than *H. sanguineus* ($p < 0.01$). Likewise, *P. herbstii* mean biomass was significantly greater than *H. sanguineus* ($p < 0.01$). Mean carapace width for *H. sanguineus* was significantly greater than *P. herbstii* ($p < 0.01$).

Table 2.1: Horizontal Benthic Sampling in UD Harbor in 2011. The top two values are totals and the remaining values are means of 20 weeks of sampling from June through October. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

Parameter	***H. sanguineus***	***P. herbstii***
Total Crabs Caught	33	233
Density*	1.1 (2.3)	7.8 (6.8)
Biomass*	2.7 (6.9)	6.4 (8.8)
Carapace Width*	22.3 (5.0)	16.8 (3.6)

There was evidence of declining *P. herbstii* abundance in the mid-intertidal as the season progressed, while *H. sanguineus* remained at low abundance throughout the sampling period (Fig. 2.3). Week 19 showed an unusually high abundance of *H. sanguineus*, but the following week revealed abundances similar to previous values. This may reflect ephemeral movement of crabs within the habitat (Brousseau et al., 2002). Mean biomass showed virtually the same pattern as mean density and supports the overall differences in mean biomass shown in Table 2.1 (Fig. 2.4). There was no apparent trend in carapace width for either species during the period July-October, 2011 (Fig. 2.5); however, the plot supports the overall larger size of *H. sanguineus* at the UD Harbor Station seen in Table 2.1.

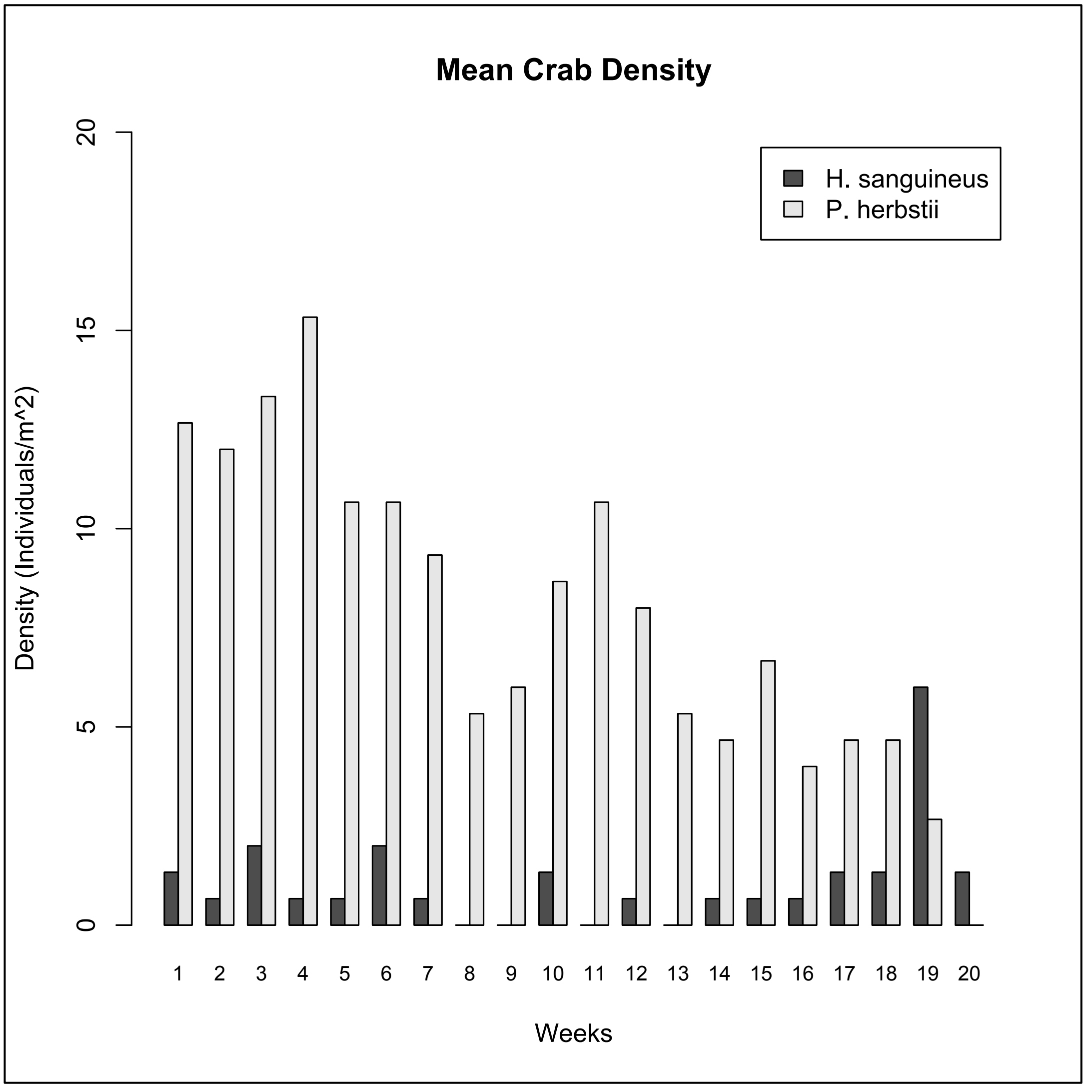

Figure 2.3: Mean Density of Crabs in Middle Intertidal Zone at the UD Harbor Station. Bars show values over 20 weeks of sampling from June through October, 2011.

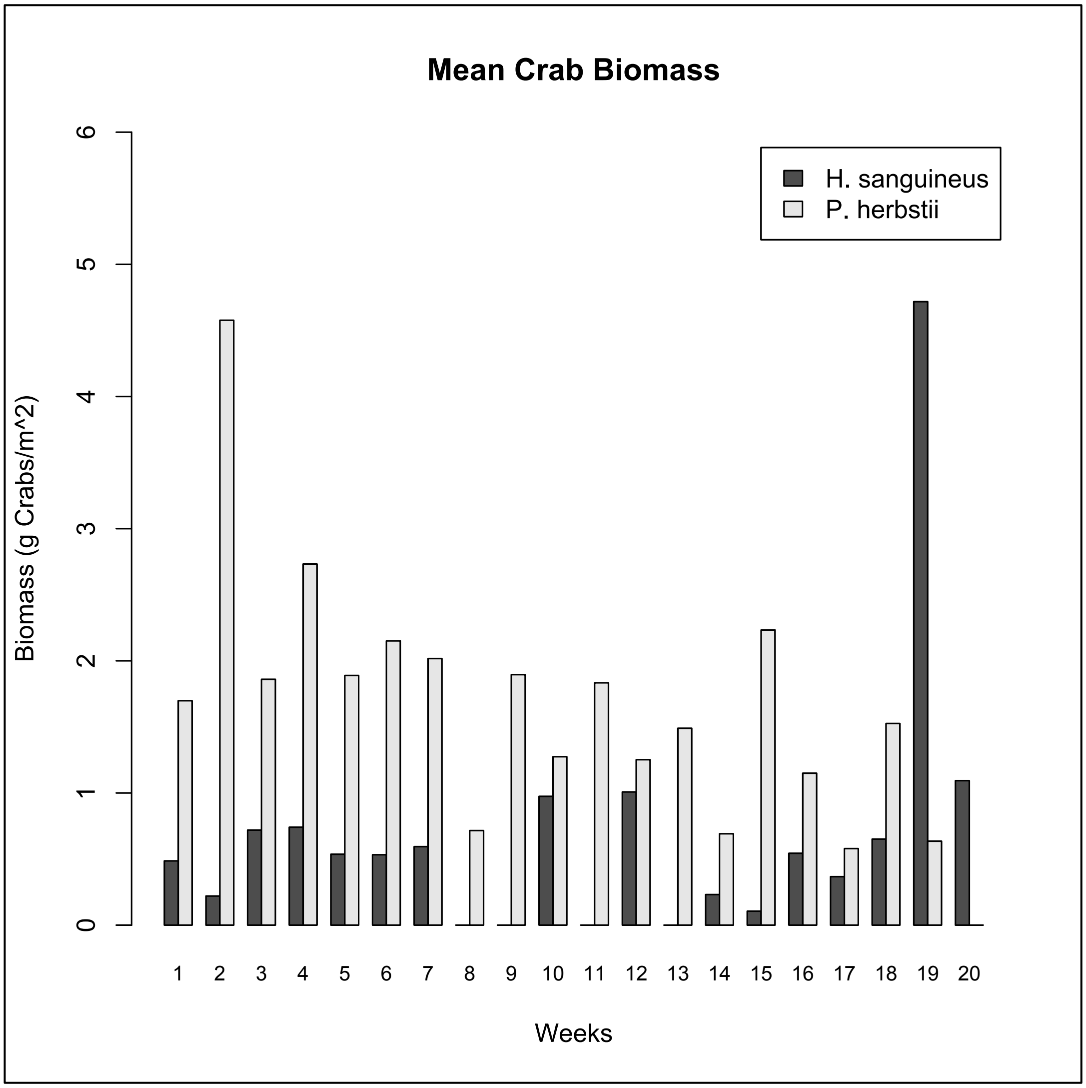

Figure 2.4: Mean Biomass of Crabs in the Middle Intertidal Zone at the UD Harbor Station. Bars show values over 20 weeks of sampling from June through October, 2011.

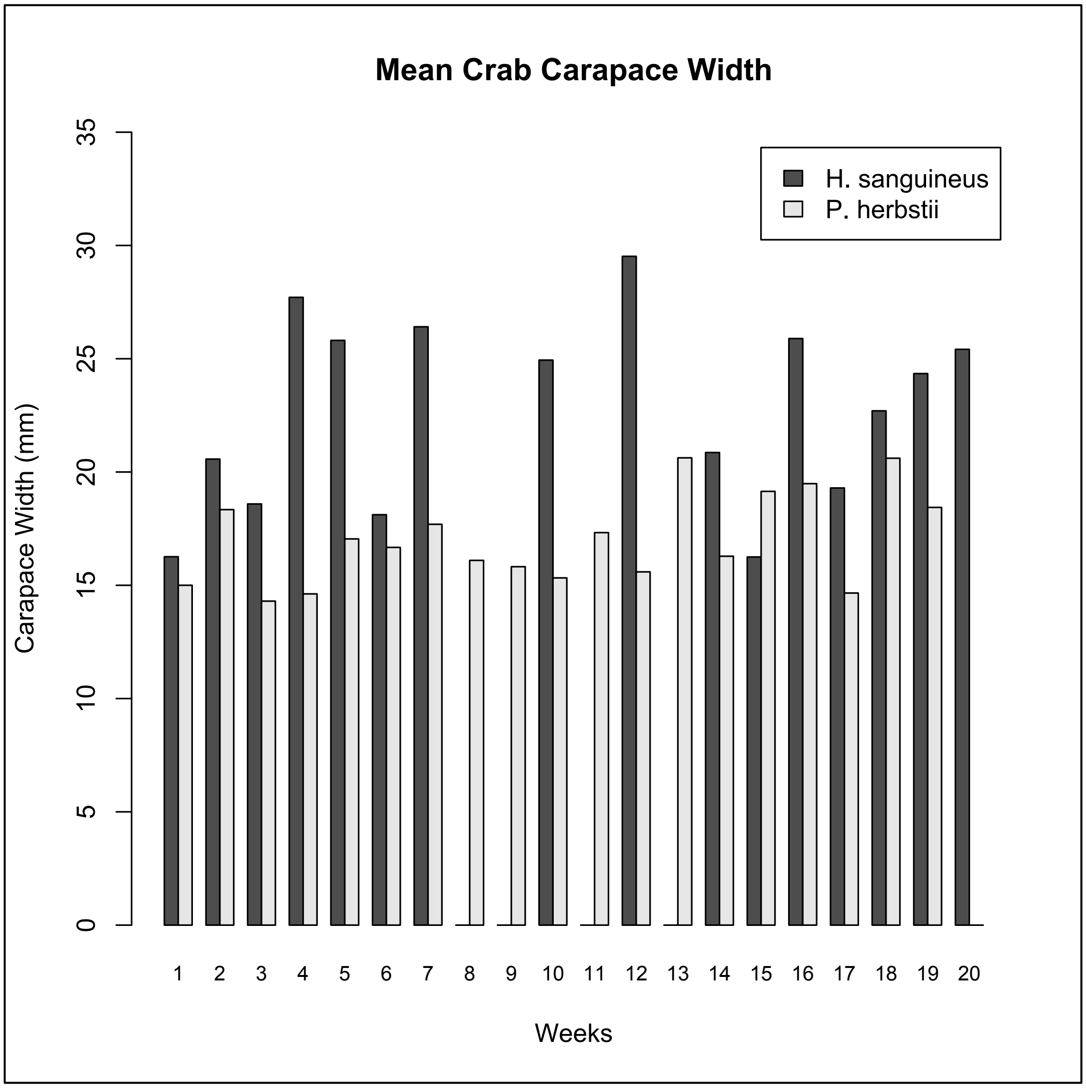

Figure 2.5: Mean Carapace Width of Crabs in the Middle Intertidal Zone at the UD Harbor Station. Bars show values over 20 weeks of sampling from June through October, 2011.

Horizontal benthic sampling during 2012 confirmed the differences observed above (Table 2.2). *P. herbstii* showed significantly higher mean densities than *H. sanguineus* ($p < 0.01$). Mean biomass was also significantly greater for *P. herbstii* than for *H. sanguineus* ($p < 0.01$). As seen in 2011, mean *H. sanguineus* carapace width was significantly greater than *P. herbstii* ($p < 0.01$). Overall, there were 261 *P. herbstii* caught and 83 *H. sanguineus*, which is over twice the number of crabs caught the previous year.

Table 2.2: Horizontal Benthic Sampling in UD Harbor in 2012. Top two values are totals and the remaining values are means of 17 weeks of sampling from June through September. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

Parameter	***H. sanguineus***	***P. herbstii***
Total Crabs Caught	83	261
Density*	3.3 (5.6)	10.2 (8.5)
Biomass*	6.4 (12.1)	6.8 (8.4)
Carapace Width*	19.9 (6.1)	14.6 (4.2)

Mean crab density and mean biomass decreased as the season progressed for *H. sanguineus* (Fig. 2.6 and Fig. 2.7). Observations yielded no consistent trend in mean density or biomass for *P. herbstii*. Mean carapace width was variable for *H. sanguineus*, showing higher values at the start and end of the investigation and lower values throughout mid-season (Fig. 2.8). Similar to density and biomass results, mean carapace width for *P. herbstii* showed no consistent trend (Fig. 2.8).

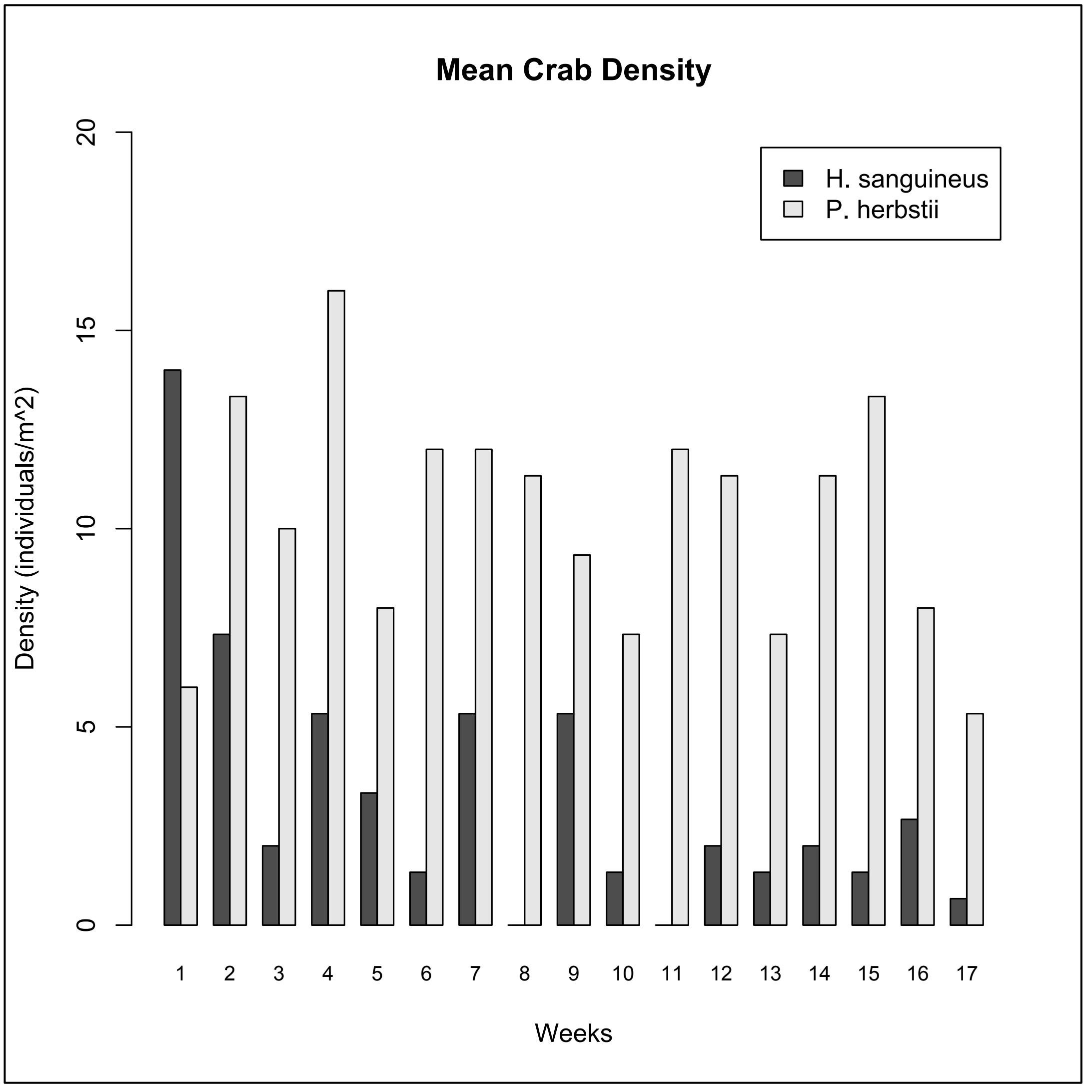

Figure 2.6: Mean Density of Crabs in Middle Intertidal Zone at the UD Harbor Station. Bars show values over 17 weeks of sampling from June through September, 2012.

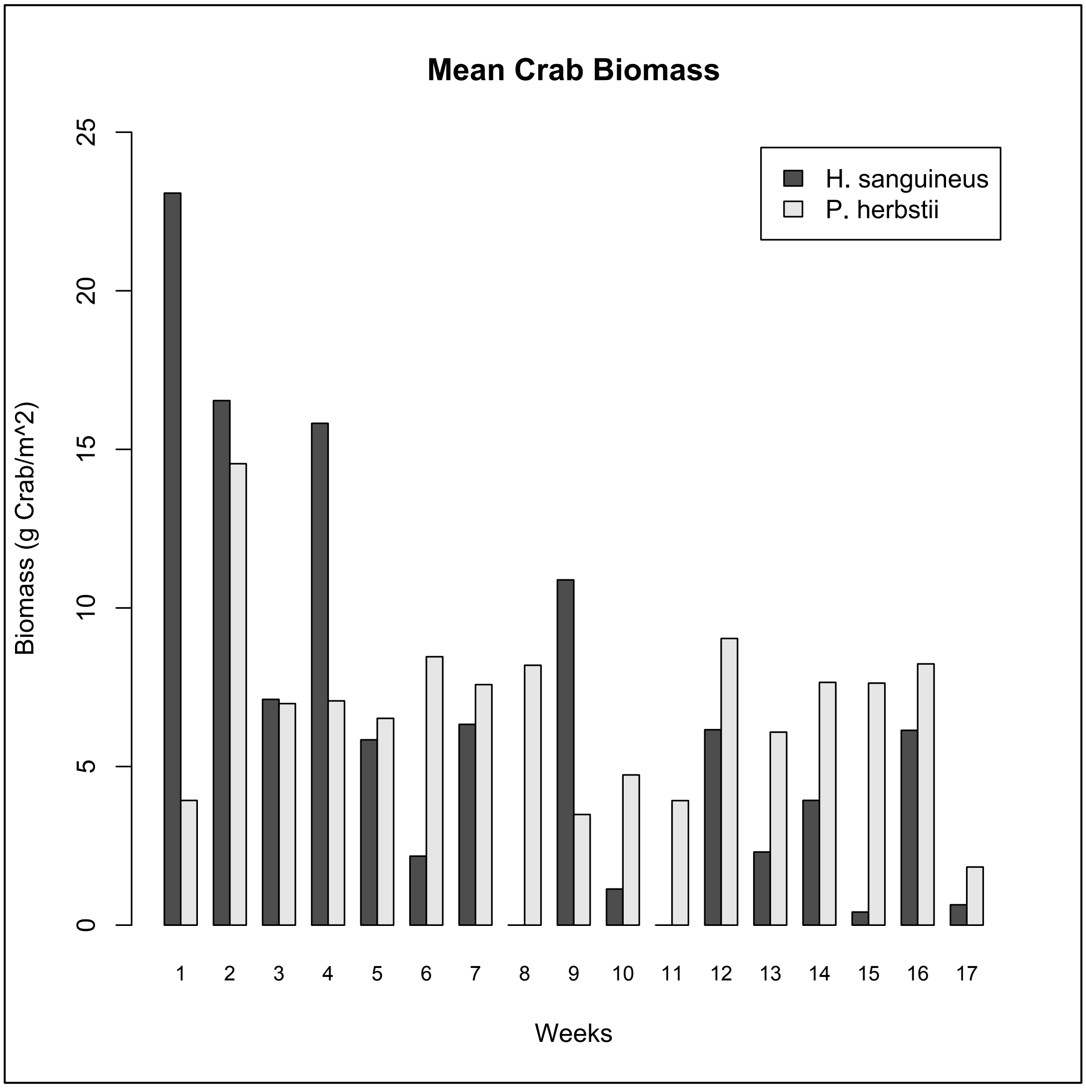

Figure 2.7: Mean Biomass of Crabs in the Middle Intertidal Zone at the UD Harbor Station. Bars show values over 17 weeks of sampling from June through September, 2012.

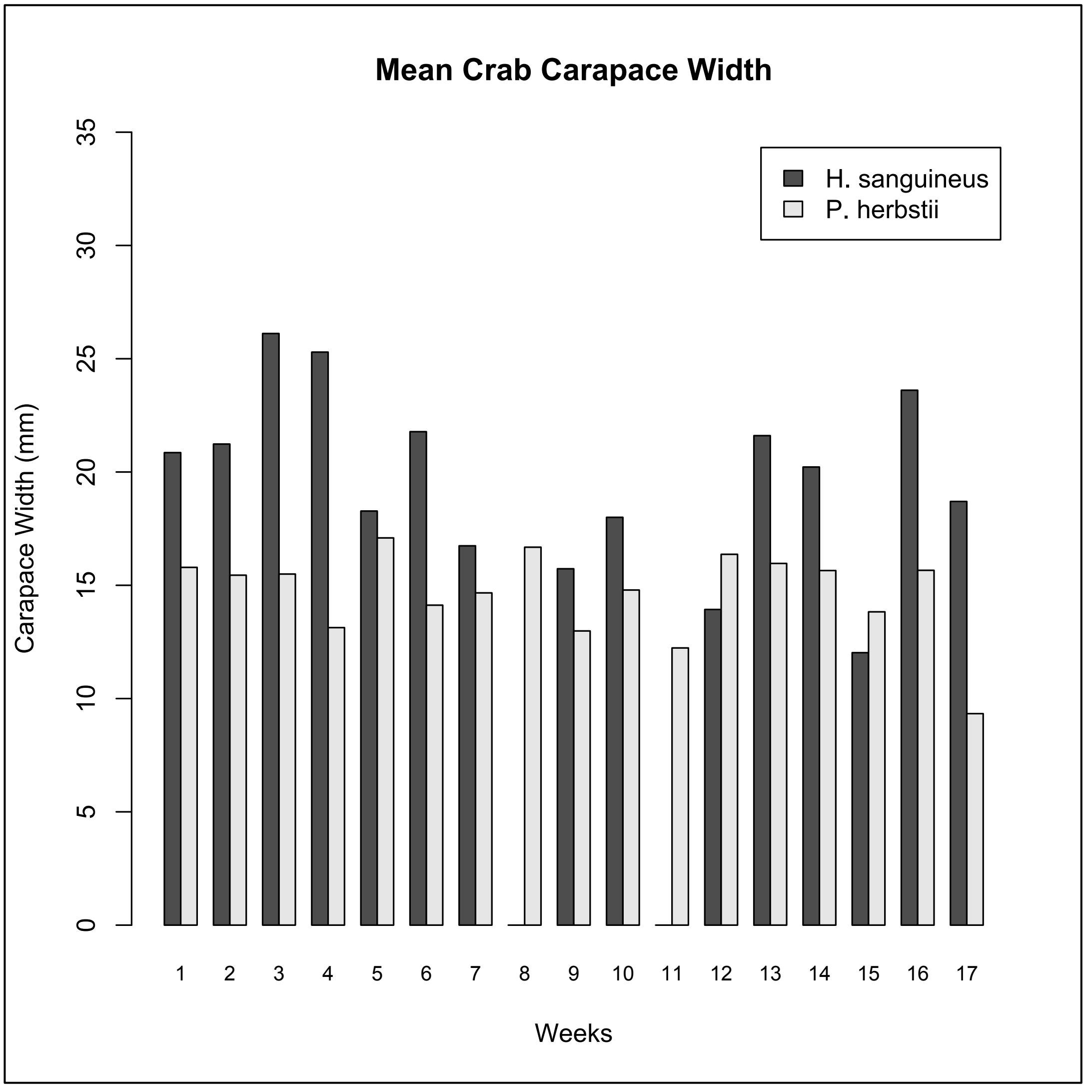

Figure 2.8: Mean Carapace Width of Crabs in the Middle Intertidal Zone at the UD Harbor Station. Bars show values over 17 weeks of sampling from June through September, 2012.

Vertical Benthic Sampling

Harbor Station

Vertical distributions within the intertidal zone differed between *Hemigrapsus sanguineus* and *Panopeus herbstii* at the Harbor Station in 2011 and 2012. In 2011, there were 154 *P. herbstii* and 49 *H. sanguineus* caught during the investigation. *P. herbstii* mean density was significantly greater at all three tidal elevations when compared with *H. sanguineus* (Table 2.3). Mean biomass of *H. sanguineus* was significantly greater than *P. herbstii* at the upper intertidal ($p = 0.02$); however there was no significant difference in mean carapace width ($p = 0.11$). Nonetheless, mean carapace width of *H. sanguineus* at both the middle and lower intertidal was significantly greater than *P. herbstii* ($p < 0.01$; $p = 0.02$).

Table 2.3: Vertical Benthic Sampling in UD Harbor in 2011. Values are means of biweekly sampling in each intertidal zone from June through October. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

UD Harbor Station 2011	Parameter	*H. sanguineus*	*P. herbstii*
Upper Intertidal Zone	Density*	2.6 (5.6)	4.8 (4.5)
	Biomass*	4.4 (9.7)	3.8 (4.0)
	Carapace Width	20.2 (5.4)	17.8 (3.6)
Middle Intertidal Zone	Density*	0.9 (2.8)	4.3 (4.1)
	Biomass*	2.5 (7.9)	3.4 (4.7)
	Carapace Width*	23.9 (4.3)	16.8 (3.9)
Lower Intertidal Zone	Density*	1.4 (2.5)	6.3 (5.4)
	Biomass*	2.0 (3.9)	6.3 (7.9)
	Carapace Width*	20.3 (3.9)	17.6 (3.8)

Results of the 2012 investigation were similar; however, there were 336 *P. herbstii* and 97 *H. sanguineus* caught, which is almost twice the number collected in 2011. Mean density for *P. herbstii* was significantly greater than *H. sanguineus* at all three tidal elevations (Table 2.4). *H. sanguineus* also had a significantly greater mean carapace width, but only at the middle and lower zones. Mean biomass for *P. herbstii* at the middle and lower intertidal zone was significantly greater than *H. sanguineus*.

Table 2.4: Vertical Benthic Sampling in UD Harbor in 2012. Values are means of biweekly sampling in each intertidal zone from June through September. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

UD Harbor Station 2012	Parameter	*H. sanguineus*	*P. herbstii*
Upper Intertidal Zone	Density*	4.4 (5.3)	10.1 (10.3)
	Biomass	5.9 (9.0)	6.7 (8.2)
	Carapace Width	16.4 (5.8)	15.9 (2.6)
Middle Intertidal Zone	Density*	3.7 (5.7)	11.3 (7.9)
	Biomass*	4.9 (8.1)	7.6 (7.1
	Carapace Width*	19.6 (3.9)	14.9 (4.8)
Lower Intertidal Zone	Density*	1.6 (4.0)	12.2 (8.3)
	Biomass*	3.9 (10.3)	12.4 (11.8)
	Carapace Width*	22.7 (2.8)	17.4 (4.8)

Canal Station

Observations of crab populations at the Canal Station yielded slightly different results (Tables 2.5 and 2.6). A total of 155 and 161 *Panopeus herbstii* and *Hemigrapsus sanguineus* were caught during the 2011 sampling season. The only significant differences present in 2011 were mean density and mean carapace width. Mean density of *P. herbstii* was significantly greater than *H. sanguineus* ($p = 0.04$) at the lower intertidal zone only. Also within this zone, *H. sanguineus* was significantly larger than *P. herbstii* ($p = 0.01$).

The same trend was also seen in the 2012 sampling season; however, the results from this season additionally showed a significantly greater mean biomass for *H. sanguineus* compared to *P. herbstii* ($p < 0.01$), as well as a significantly greater mean density of *H. sanguineus* at the upper intertidal zone ($p < 0.01$). A total of 679 *P. herbstii* and 744 *H. sanguineus* were collected in 2012, a substantially greater number of crabs than what was observed in 2011.

Table 2.5: Vertical Benthic Sampling at Canal Station in 2011. Values are means of biweekly sampling in each intertidal zone from June through October. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

Canal Station 2011	Parameter	*H. sanguineus*	*P. herbstii*
Upper Intertidal Zone	Density	7.2 (11.9)	4.1 (4.0
	Biomass	4.0 (6.3)	1.8 (2.2)
	Carapace Width	14.3 (3.0)	14.1 (3.0)
Middle Intertidal Zone	Density	7.9 (9.9)	6.1 (5.0)
	Biomass	5.6 (8.5)	2.7 (2.3)
	Carapace Width	14.4 (3.7)	14.3 (2.2)
Lower Intertidal Zone	Density*	6.4 (9.4)	10.4 (12.1)
	Biomass	6.2 (9.1)	5.3 (7.0)
	Carapace Width*	17.7 (3.9)	13.6 (3.5)

Table 2.6: Vertical Benthic Sampling at Canal Station in 2012. Values are means of biweekly sampling in each intertidal zone from June through September. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

Canal Station 2012	Parameter	*H. sanguineus*	*P. herbstii*
Upper Intertidal Zone	Density*	31.5 (23.9)	14.2 (15.0)
	Biomass*	14.9 (19.0)	5.1 (5.6)
	Carapace Width	12.7 (3.2)	12.2 (2.7)
Middle Intertidal Zone	Density	11.2 (13.8)	19.5 (13.3)
	Biomass	22.4 (18.4)	8.3 (6.6)
	Carapace Width	12.7 (3.3)	13.2 (2.6)
Lower Intertidal Zone	Density*	19.5 (17.2)	34.2 (17.1)
	Biomass	22.5 (22.9)	16.3 (9.5)
	Carapace Width*	17.1 (4.2)	13.8 (2.4)

2.4 Discussion

The investigations during 2011 and 2012 characterized the distributions of co-occurring Asian shore crabs (*Hemigrapsus sanguineus*) and native mud crabs (*Panopeus herbstii*) in rocky habitat near the mouth of Delaware Bay. The study showed clear patterns in crab density, biomass, and size at three elevations within the intertidal zone. Because the two-year investigation spanned more than four months per season and was conducted during peak activity for the two species, the results provide a general portrayal of these crab populations near the mouth of the bay. *P. herbstii* always showed greater density than *H. sanguineus* within the UD Harbor, and horizontal benthic sampling showed abundances of 7.1 and 3.1 times those of *H. sanguineus* during 2011 and 2012, respectively. Vertical distributions of the two species followed this trend at the Harbor Station, but proportional density values were somewhat higher for *H. sanguineus* at the Canal Station.

The distribution of biomass within the intertidal zone closely reflected what was observed for mean densities. Highest biomass for *P. herbstii* was observed in the lower intertidal 100% of the time, while maximum biomass for *H. sanguineus* often occurred in the upper intertidal. However, mean biomass for *H. sanguineus* in 2012 at the Canal Station was greater in the lower intertidal, despite the higher densities of the species in the upper intertidal zone. This discrepancy can be explained by size distributions mentioned below.

Regardless of habitat, *H. sanguineus* individuals were larger than *P. herbstii* on average. However, the Canal Station showed a vertical gradient in the size distribution of *H. sanguineus,* and smaller individuals were more common in the upper and middle intertidal zones, leading to the idea of these smaller individuals being out-competed in the lower intertidal. This size-dependent distribution pattern was also seen at the Harbor Station, but only in 2012. There was no clear trend in mean carapace width for *P. herbstii* within the intertidal, as the mean size of individuals fluctuated within zones, between stations, and between sampling years. However, the Canal Station generally possessed smaller individuals of both species when compared to the Harbor Station.

Other differences in crab distributions between stations were discovered as well. The population of *P. herbstii* at the Harbor Station showed proportionally greater density when compared to the Canal Station. This may reflect closer proximity of the Canal Station to Roosevelt Inlet, which is the source of recruitment for the two populations. Therefore, newly recruited individuals would most likely encounter this habitat before the Harbor Station. However, there is little information in the literature concerning movement of newly settled juveniles of either species in benthic habitat (Epifanio, 2013).

Variation in grain-size of sediments composing the substratum beneath rocks at the two stations also may have contributed to the observed differences between stations. UD Harbor was designed and constructed to minimize currents and waves and to provide safe harbor for ships and boats. Because of this low-energy environment, sediment at the Harbor Station consisted of fine-grained mud. In contrast, the Canal Station is exposed to occasional storm waves and daily periods of strong current associated with tidal flow. Accordingly, the substratum consists of courser, pebbly sediment, which is more attractive to *H. sanguineus* than the finer sediment seen at the Harbor Station (Lohrer et al., 2000).

Another observation to help explain differences between the two stations is food source, since food availability is a major factor controlling crab populations (Lohrer et al., 2000). *P. herbstii* relies heavily on *Geukensia demissa* as a primary food source (Seed, 1980), and there were personal observations of high abundance of this mussel species at the Harbor Station. In contrast, the Canal Station contained a large population of the blue mussel, *Mytilus edulis*, which is a primary food source for *H. sanguineus* (McDermott, 1998).

Results also showed a much larger number of crabs caught in the 2012 sampling season, which is striking considering the shortened investigation during 2012. Greater collection efficiency during 2012 may account for some of this;

however, the difference more likely reflects natural variation in the size of the populations between the two years. This variation may be the outcome of higher recruitment during 2011 and high survival of that cohort into the 2012 sampling season. Hurricane Irene occurred near the end of the 2011 sampling and may have contributed to the possible high level of recruitment. This event produced a substantial amount of landward advection, which would have aided in the transport of recruits from the open ocean to coastal habitat (Epifanio and Garvine, 2001).

Horizontal benthic sampling yielded no temporal trend in density or biomass for *H. sanguineus* over the four-month collection period in either 2011 or 2012. Although there was an obvious decline in density of *P. herbstii* over the study period in 2011, this trend was not evident during 2012. The two crab species often move into subtidal habitat or deep in the rocky shelter during the winter months to avoid harsh weather (McDermott, 1998). If the investigations had included the winter months, temporal trends may have been more evident. In addition, my sampling methods were not effective in collecting very small juveniles (< 4mm), and accurate monitoring of newly settled individuals would likely have shown pulses in abundance related to recruitment processes.

Overall results of my investigation were very different from earlier studies examining the invasion of *H. sanguineus* in the Middle Atlantic region. For example, McDermott (1998) showed *H. sanguineus* densities as high as 320 individuals/m^2 during his six-year survey along the New Jersey coast, from 1989-1995. Likewise, Park et al. (2005) discovered a numerical dominance of *H. sanguineus* (13.0 individuals/m2) compared to *P. herbstii* (4.5 individuals/m^2) during their 2001 investigation at UD Harbor. Another study by Brown (2005) was conducted in nearby habitat, at Indian River Bay, DE and showed mean *H. sanguineus* densities of 22.7 individuals/m^2 compared to 16.0 individuals/m^2 for *P. herbstii*. It is difficult to identify the exact mechanisms causing the proportional decline in *H. sanguineus* that was observed in my study; however, marine invasive populations can sometimes decline, following a persistence stage of their invasion (Attrill et al., 1996; Veldhuizen and Stanish, 1999; Dittel and Epifanio, 2009). New dynamics between co-occurring species can lead to new equilibria in population sizes, which is one explanation for a recovering native population. Agents important in these new dynamics could include physical factors, such as less severe winters and generally warming waters, or biological factors, such as intraspecific competition or increased incidence of disease and parasitism in dense populations of newly invasive species (Epifanio, 2013). Also, food resources initially utilized by newly invasive species and enabling population growth could have been depleted, leading to population declines (Nalepa et al., 2000; Nalepa et al., 2006; Watkins et al., 2007; Wiklund et al., 2008).

Studies in the Middle Atlantic region during the early years of the invasion showed *H. sanguineus* distributions mainly in the upper intertidal (McDermott, 1992, 1998b). Studies further north in Long Island Sound and New England showed *H. sanguineus* populations distributed in the middle and lower intertidal zone, with extensions into subtidal habitat (Ledesma and O'Connor, 2001; Gilman and Grace, 2009). Moreover, these studies showed that the occurrence of *H. sanguineus* was more closely related to availability of shelter than to elevation within the intertidal zone (Lohrer et al., 2000). In contrast, my investigations of *H. sanguineus* populations showed a preference for the upper intertidal at both stations, especially among smaller individuals, even though the amount of rock shelter was virtually identical throughout the intertidal. An important observation was higher densities of *P. herbstii* in the lower intertidal at both stations. Interspecific competition may exist in these locations, and *P. herbstii* could be driving smaller *H. sanguineus* to higher tidal elevations (Steinberg and Epifanio, 2011). There could also be size-related intraspecific competition among *H. sanguineus* populations. Finally, it is possible for the habitats in Long Island Sound and New England to possess different interactions between crab species. Specifically, *P. herbstii* is the main competitor of *H. sanguineus* in the Middle Atlantic, while the green crab *Carcinus maenas* plays this role in Long Island Sound and New England (Epifanio, 2013). Therefore, interspecific competition could result in different responses of *H. sanguineus* at these locations.

Overall, my 2-year investigation of the distribution of *H. sanguineus* and *P. herbstii* near the mouth of the Delaware Bay has provided important new information about the abundance, biomass, and size of crabs comprising these populations. Results were clearly different from previous work in the Middle Atlantic and indicate that proportional abundance and biomass of *H. sanguineus* have declined when compared to co-occurring native crabs like *P. herbstii*. My results also differ from earlier work in Long Island Sound and New England, and indicate that *H. sanguineus* may respond differently to the ambient communities in these respective regions. Furthermore, my work suggests a new equilibrium between populations of the invasive *H. sanguineus* and the native *P. herbstii* in habitat adjacent to the Delaware Bay, supporting the idea of a recovering native species.

Chapter 3

GEOGRAPHICAL SURVEY OF *HEMIGRAPSUS SANGUINEUS* AND *PANOPEUS HERBSTII* DISTRIBUTIONS WITHIN THE INTERTIDAL ZONE IN THE MIDDLE ATLANTIC

3.1 Introduction

Invasive species have been shown to dramatically impact native communities, often leading to displacement of indigenous taxa. *Hemigrapsus sanguineus*, the Asian shore crab, is a marine invasive, first discovered near Townsends Inlet, New Jersey, in 1988 (Williams and McDermott, 1990; McDermott, 1991). Since the initial discovery of *H. sanguineus*, most studies have demonstrated the numerical dominance of the species within the intertidal zone when compared to native species (Kraemer et al., 2007). *H. sanguineus* has been shown to flourish in regions with plentiful shelter, while complete absence occurs when no shelter is available (Lohrer et al., 2000; Ledesma and O'Connor, 2001). The rocky New England coasts provide extensive natural shelter, and studies have shown the numerical dominance of established populations there, with greatest abundances in the middle and lower intertidal zone (Ledesma and O'Connor, 2001). More recent work in southern New England has shown the range of *H. sanguineus* to include the whole intertidal, extending into subtidal habitat (Gilman and Grace, 2009). Greater abundances in the lower intertidal zone are also acknowledged in its native range (Fukui and Wada, 1983; Takada and Kikuchi, 1991). However, initial studies in the Middle Atlantic region had shown a preference for the upper intertidal zone (McDermott, 1992, 1998b). Although the Middle Atlantic lacks natural rocky habitat, there are many man-made structures, such as riprap and jetties, which contain established populations of *H. sanguineus* (McDermott, 1992, 1998b; Park et al., 2005; Brown 2005).

The Middle Atlantic region is home to a native mud crab, *Panopeus herbstii*, which is a primary space competitor of *H. sanguineus* (Epifanio, 2013 and see *Chapter 2*). Park et al. (2005) and Brown (2005) performed population assessments of both species at the University of Delaware Harbor (UD Harbor Station) and at a location 25 km south of Delaware Bay, respectively, and results of their studies had shown clear numerical dominance of *H. sanguineus* over native species. In contrast, my 2011 and 2012 investigations at the UD Harbor Station and an adjacent location along the Lewes-Rehoboth Canal (Canal Station) have shown a distinct reversal in this trend and indicate that native mud crab populations are beginning to recover (see Chapter 2). These investigations also revealed a greater abundance of *H. sanguineus* in the upper intertidal zone, while *P. herbstii* existed mostly in the lower intertidal zone.

Because results of my 2011 investigations indicated a recovery of native mud crabs in UD Harbor, I designed and executed a corollary study in 2012 to determine if the recovery of *P. herbstii* populations extended to similar habitats within 50 km of Delaware Bay. This chapter summarizes the expansion of my investigations and gives results of crab-population assessments at Townsends Inlet, New Jersey, Ocean City Inlet, Maryland, and Indian River Inlet, Delaware during the summer and fall of 2012. The study consisted of measurements of abundance (density), biomass, and carapace width in the upper, middle, and lower intertidal zones at each of the three study stations.

3.2 Methodology

Vertical Benthic Sampling

Vertical benthic sampling was employed to assess populations of *Hemigrapsus sanguineus* and *Panopeus herbstii* from June through September during 2012. Monthly sampling was done within protected areas at Townsends Inlet, New Jersey (39° 6'51.43"N, 74°42'50.33"W) and Ocean City Inlet, Maryland (38°19'33.88"N, 75° 5'26.63"W), which are approximately equidistant, north and south, from the original investigation station at UD Harbor. Bi-weekly sampling was also performed at a protected area previously chosen by Brown (2005) for crab population assessments, connected to Indian River Inlet, Delaware (38°36'58.19"N, 75° 4'22.52"W) from June through September. Sampling protocol was identical to that described for vertical sampling in UD Harbor in *Chapter 2*. Prior to each sampling event, water temperature and salinity were measured (YSI Model 30/10 FT) in open water adjacent to each sampling station, and a 12-m line was placed along the mid-intertidal zone, parallel to the shoreline. Five vertical transects were then placed perpendicularly along the line at 3-m intervals and each transect extended from the lower to the upper intertidal (Fig. 2.1).

Once the design layout was complete, crab collections consisted of placing a 0.25-m^2 quadrat on the substratum, removing all rocks and stones, and collecting all crabs taking shelter within the quadrat area. Collections occurred along each transect at the upper, middle, and lower intertidal zone. There were 5 replicated collections at each intertidal zone and rock cover (at least 70%) and vertical distance between zones for each station remained constant. All rocks and stones were carefully replaced and all crabs were released where they were originally caught after every collection event to limit sampling effects. Carapace width was measured using calipers, and biomass for each species was calculated using equations shown in Chapter 2. Statistical procedures were identical to those described in Chapter 2.

3.3 Results

Townsends Inlet, New Jersey

Vertical benthic sampling at Townsends Inlet, New Jersey showed a crab assemblage dominated by *Hemigrapsus sanguineus*. There were no *Panopeus herbstii* caught during the investigation, but the green crab, *Carcinus maenas*, and the mud crab, *Dyspanopeus sayi*, were occasionally collected. There was a clear pattern in the distribution and biomass of *H. sanguineus*, with highest mean values in the lower intertidal that decreased as vertical elevation increased. There was no apparent trend in mean carapace width.

Table 3.1: Vertical Benthic Sampling at Townsends Inlet in 2012. Values are means of monthly sampling in each intertidal zone from June through September. Values in parentheses are standard deviations. *Panopeus herbstii* did not occur at this station.

Townsend Inlet 2012	Parameter	*H. sanguineus*
Upper Intertidal Zone	Density	35.2 (35.2)
	Biomass	14.5 (15.6)
	Carapace Width	12.3 (3.0)
Middle Intertidal Zone	Density	53.2 (33.6)
	Biomass	23.0 (23.4)
	Carapace Width	11.7 (3.1)
Lower Intertidal Zone	Density	64.8 (33.6)
	Biomass	29.1 (20.1)
	Carapace Width	12.0 (2.2)

Indian River Inlet

Distributions of crab species at Indian River Inlet yielded different results. *P. herbstii* was present, and there was a clear trend in density and biomass within the intertidal zone for the species. Mean density of *P. herbstii* was significantly greater than *H. sanguineus* at the middle ($p=0.04$) and lower ($p<0.01$) intertidal zones. Mean biomass of *P. herbstii* was also inversely related to tidal elevation and was significantly greater than *H. sanguineus* at the middle and lower intertidal zones ($p=0.048$ and $p<0.01$, respectively). Mean carapace width for *P. herbstii* varied little with tidal height. However, there was a trend in mean carapace width for *H.*

sanguineus, and size increased going from the upper to the lower intertidal zone (Table 3.2). The same trend was observed for mean biomass and there was no apparent trend in mean density.

Table 3.2: Vertical Benthic Sampling at Indian River Inlet in 2012. Values are means of monthly sampling in each intertidal zone from June through September. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

Indian River Inlet 2012	Parameter	*H. sanguineus*	*P. herbstii*
Upper Intertidal Zone	Density	1.0 (1.7)	1.9 (3.7)
	Biomass	0.4 (1.0)	1.3 (2.7)
	Carapace Width	11.3 (6.0)	16.5 (4.2)
Middle Intertidal Zone	Density*	1.9 (2.0)	5.9 (6.7)
	Biomass*	1.1 (2.0)	4.1 (5.2)
	Carapace Width	12.4 (6.3)	16.6 (3.5)
Lower Intertidal Zone	Density*	1.4 (2.0)	22.2 (12.0)
	Biomass*	1.3 (3.1)	16.0 (9.9)
	Carapace Width	15.6 (5.9)	16.4 (1.8)

<u>Ocean City Inlet</u>

Investigations at Ocean City Inlet, Maryland during 2012 showed similar results to those seen at Indian River Inlet. Mean density for *P. herbstii* was greatest at the lower intertidal and was also significantly greater than *H. sanguineus* at this elevation ($p<0.01$) (Table 3.3). Mean biomass for *P. herbstii* was significantly greater than *H. sanguineus* at the lower intertidal ($p<0.01$). Mean carapace width of *P. herbstii* was significantly greater than *H. sanguineus* at all intertidal zones, but showed no vertical trend. Mean density of *H. sanguineus*, however, showed a clear trend and values decreased going from the upper to the lower intertidal zone (Table 3.3). Mean biomass for the species reflected the same trend.

Table 3.3: Vertical Benthic Sampling at Ocean City Inlet in 2012. Values are means of monthly sampling in each intertidal zone from June through September. Values in parentheses are standard deviations. Asterisks show significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii.*

Ocean City Inlet 2012	Parameter	*H. sanguineus*	*P. herbstii*
Upper Intertidal Zone	Density	21.4 (20.5)	19.4 (15.0)
	Biomass	6.6 (5.4)	12.5 (12.7)
	Carapace Width*	11.1 (4.2)	14.9 (3.2)
Middle Intertidal Zone	Density	11.6 (11.2)	13.6 (12.1)
	Biomass	3.8 (5.0)	6.4 (7.0)
	Carapace Width*	9.9 (2.5)	13.1 (3.0)
Lower Intertidal Zone	Density*	6.6 (6.4)	22.8 (11.0)
	Biomass*	2.1 (2.8)	10.2 (5.5)
	Carapace Width*	10.6 (1.9)	13.6 (2.1)

3.4 Discussion

The geographical survey employed in 2012 offered detailed assessments of co-occurring Asian shore crabs (*Hemigrapsus sanguineus*) and native mud crabs (*Panopeus herbstii*) extending from Townsends Inlet, New Jersey to Ocean City Inlet, Maryland, roughly 100 km of shoreline. Investigations were performed during peak population abundance for both species and offered an accurate representation of proportional crab populations. Results from stations south of Delaware Bay generally corroborated those seen at UD Harbor during the 2011 and 2012 investigations (see *Chapter 2*). Density and biomass of *P. herbstii* were significantly greater than *H. sanguineus* in the middle and lower intertidal zones at Indian River Inlet and in the lower intertidal at Ocean City Inlet. Mann-Whitney tests showed no significant differences in density and biomass between species throughout any of the remaining sampling locations. Previous studies (Brown, 2005) showed the numerical dominance of *H. sanguineus* at locations around the Delmarva Peninsula, only a decade ago, and results of my survey give the notion of a recovering native mud crab population. In contrast, results from Townsends Inlet, north of Delaware Bay, showed a population dominated by the Asian shore crab, and not a single *P. herbstii* was collected at this station during the course of the 2012 study. Townsends Inlet was the site of the original invasion of *H. sanguineus* in the early 1980's (McDermott, 1992) and it is interesting to observe the continued dominance of the species at this site for roughly 30 years.

Similarities and differences in vertical distributions of the respective species existed between Indian River and Ocean City Inlet. Mean density for *P. herbstii* was greatest in the lower intertidal at both Indian River and Ocean City Inlet, as seen at the UD Harbor and Canal Station (see *Chapter 2*). A clear trend in density was seen at Indian River Inlet for *P. herbstii*, and density increased approaching the lower intertidal. However, there was no apparent trend in density for *P. herbstii* at Ocean City Inlet. *H. sanguineus* density was greatest in the middle and upper intertidal, when *P. herbstii* was present, at Indian River and Ocean City Inlet, respectively. This trend was also observed in the investigations at the UD Harbor and Canal Station, where *P. herbstii* was the main competitor. Density trends for *H. sanguineus* were reversed at Townsends Inlet, and density increased going from the upper to the lower intertidal. This trend was seen in previous studies around New England (Ledesma and O'Connor, 2001; Gilman and Grace, 2009), however earlier work in Middle Atlantic showed different trends, with *H. sanguineus* more abundant in the upper intertidal (McDermott, 1992, 1998b).

Biomass distributions mimicked the density trends for *H. sanguineus* at Townsends Inlet and Ocean City Inlet. However, at Indian River Inlet highest biomass was recorded in the lower intertidal zone, even though density for the species was highest in the middle intertidal at this station. Size distributions discussed below will explain this lack of coherence. *P. herbstii* biomass increased with decreasing tidal height at Indian River Inlet, the same as its density distribution. There was no clear pattern in biomass of the species at Ocean City Inlet, and highest values were observed at the upper intertidal, a result that was not seen anywhere else throughout my investigations.

The geographical survey also yielded interesting results for carapace width of *H. sanguineus*. Overall, the species was smaller at all three sampling locations compared to sizes seen at UD Harbor and the Canal Station (see *Chapter 2*). Additionally, *H. sanguineus* was smaller than *P. herbstii* regardless of tidal height at Indian River and Ocean City Inlet and significantly smaller in all three zones at Ocean City Inlet. In contrast, *H. sanguineus* was almost always larger than *P. herbstii* during investigations at the UD Harbor and Canal Station.

Vertical trends in carapace width were also evident at Indian River Inlet for *H. sanguineus*, and smaller individuals were seen in the upper intertidal zone. Size increased going from the upper to the lower intertidal, a trend similar to observations at the Canal Station and 2012 results at the UD Harbor Station. This suggests that size-dependent competition for space may exist. Mean carapace width for *P. herbstii* remained fairly constant regardless of height in the intertidal zone at both Indian River Inlet and Ocean City Inlet. Likewise, there was little variation in mean carapace width for *H. sanguineus* at the Ocean City station.

Overall, the results of the survey showed that density, biomass, and carapace width varied depending on the composition of crab assemblages. As mentioned in *Chapter 2*, *H. sanguineus* may respond differently when confronted with different competitors. For example, values for density and biomass of Asian shore crabs were greatest in the middle and upper intertidal zones at Indian River and Ocean City Inlet where there were extensive populations of *P. herbstii*. However, at Townsends Inlet, where *P. herbstii* was absent, trends in density, biomass, and carapace were different for *H. sanguineus* and there were no size-related zonation patterns and density and biomass increased approaching the lower intertidal zone.

Another factor that may explain differences among stations is the substratum underlying the rocks. As mentioned in *Chapter 2*, variation in grain size has been shown to affect distributions of *H. sanguineus* (Lohrer et al., 2000). At Townsends Inlet, the substratum beneath the rocks consisted of coarse sand, while Indian River Inlet and Ocean City Inlet were composed of a fine sand-mud mixture. The former is more attractive of *H. sanguineus* (Lohrer et al., 2000), while the other is more attractive of the native mud crab, *P. herbstii*. Nevertheless, the fact that there were absolutely no *P. herbstii* caught at Townsends Inlet is puzzling, and it would be interesting to know the community composition before the invasion of *H. sanguineus*.

The results of my 2012 geographic exploration were substantially different from previous population studies of *H. sanguineus*. The Brown (2005) study at Indian River Inlet showed densities of 22.7 individuals/m^2 and 16.0 individuals/m^2 for *H. sanguineus* and *P. herbstii*, respectively. Pooled results of my study showed mean densities of 1.4 individuals/m^2 and 10.0 individuals/m^2 for the two species, illustrating a large decline in the invasive population at this location. Previous work around Townsends Inlet showed densities as high as 320 individuals/m^2 for *H. sanguineus* (McDermott, 1998) and results of my investigation showed a mean density of 51.1 individuals/m^2 when pooled across all tidal heights. *H. sanguineus* clearly remains the dominant species at this location, but the large decrease in density suggests that the population is starting to decline. Also, the distribution of *H. sanguineus* at Townsends Inlet showed a greater abundance in the lower intertidal. This is opposite of distributions observed during the nascent stages of the invasion, during the early to mid 1990's, when highest abundance of *H. sanguineus* occurred in the upper intertidal zone (McDermott, 1998).

In conclusion, the results of the 2012 survey provide evidence of declining populations of *H. sanguineus* over time, along roughly 100 km of coastline, from

Townsends Inlet, New Jersey to Ocean City Inlet, Maryland. Additionally, results support the idea of recovering populations of mud crabs along the coast of the Delmarva Peninsula south of Delaware Bay. In contrast, the Asian shore crab remains firmly established at the site of its original discovery near Townsends Inlet to the north of the bay. Continued work observing co-occurring populations of *H. sanguineus* and *P. herbstii* is needed to determine if the species are responding to new dynamics in competition, differences in substratum type, or a latitudinal gradient in ambient communities. As mentioned above, invasive species sometimes decline after becoming fully established, and my survey in 2012 has provided evidence of a decline phase in the invasion of *H. sanguineus* along the coastline of New Jersey, Delaware, and Maryland.

Chapter 4

HISTORICAL COMPARISON OF INVASIVE *HEMIGRAPSUS SANGUINEUS* AND NATIVE *PANOPEUS HERBSTII* POPULATIONS NEAR THE MOUTH OF THE DELAWARE BAY

4.1 Introduction

Invasive species can have serious effects on native ecosystems. Marine invasive species can reduce biodiversity of communities, which can facilitate spread of disease and impact the yield of native fisheries (Cox, 1999; MacDonald et al., 2007; Molnar et al., 2008). Observations of bio-invasions have led to the identification of certain stages of the process which include: 1) arrival; 2) settlement; 3) expansion; and 4) persistence (Schmidt et al., 2007; Mollison, 1986; Reise et al., 2006). It is also possible for populations to decline following the persistence stage, and research done on the Chinese mitten crab, *Eriocheir sinensis*, in Germany and other parts of Europe has documented this phenomenon (Panning, 1939; Attrill et al., 1996; Dittel and Epifanio, 2009). The Asian shore crab, *Hemigrapsus sanguineus*, invaded the Delaware Bay region along the east coast of the USA in the early 1980's (McDermott, 1992; Epifanio, 2013) and has been shown to possess competitive advantages when compared to native crab species (Epifanio, 2013). This has allowed rapid proliferation of the Asian shore crab, and its range currently extends from Cape Hatteras to central Maine (Griffen, 2011). *H. sanguineus* inhabits the intertidal zone, taking shelter under rocks and stones, and some studies have shown its extension into subtidal habitat (Gilman and Grace, 2009; McDermott, 1998b; Takahashi et al., 1985).

Historical monitoring of *H. sanguineus* in the University of Delaware (UD) Harbor at the mouth of Delaware Bay, via benthic sampling, was conducted in 2001 by Park et al. and later reported in 2005. The researchers performed density and biomass assessments to characterize the crab assemblage in the harbor and took samples throughout the whole intertidal. It was determined that the crab assemblage was dominated by *H. sanguineus*, and densities and biomass were significantly greater than its main competitor, the native mud crab *Panopeus herbstii* (Table 4.1). In *Chapter 2* of this thesis, I have described results of a recent survey of co-occurring Asian shore crabs and native mud crabs conducted at the UD Harbor Station during 2011 and 2012. Here in *Chapter 4*, I provide an explicit comparison of the results of the recent survey in UD Harbor and results of the historical survey that was done a decade earlier at the same location.

4.2 Methodology

Vertical benthic sampling was performed bi-weekly from mid-July through October during 2011 and from mid-June through September in 2012 in UD Harbor to assess *Hemigrapsus sanguineus* and *Panopeus herbstii* populations. Sampling protocol has already been described in *Chapter 2*, but data have been analyzed differently to allow explicit comparison with results of the historical survey conducted in 2001. This new analysis has calculated mean values for density, biomass, and carapace width of *H. sanguineus* and *P. herbstii* when data were pooled across all sampling dates and elevations within the intertidal zone. Inter-species comparison of each of the three parameters was done separately using the non-parametric, two-sampled Mann-Whitney-Wilcoxon test because the data did not meet the normality assumption for parametric analysis of variance after log, square root, or arc-sin transformation (Shapiro-Wilk normality tests). Separate analyses were conducted for data from 2011 and 2012. Averages for each variable were first calculated at each tidal height, and the three averaged values were then pooled to give one, bi-weekly average value for each sampling date. Bi-weekly averages were considered replicates and the mean of these averages was used for the Mann-Whitney-Wilcoxon test to compare differences in density, biomass, and carapace width between *H. sanguineus* and *P. herbstii*. All statistical analyses were performed using R (Version 2.14.1), a computational statistical software program.

4.3 Results and Discussion

Mean density and biomass values for *Panopeus herbstii* were significantly greater than *Hemigrapsus sanguineus* during both 2011 and 2012. However, *H. sanguineus* was significantly larger than *P. herbstii* during both 2011 and 2012 ($p < 0.01$ and $p < 0.01$, respectively).

Table 4.1: Historical Comparison of Crab Populations in UD Harbor, 2001-2012. Data were averaged over all tidal zones on each sampling date, and mean values were calculated over all sampling dates within each year. Asterisks indicate significant differences between *Hemigrapsus sanguineus* and *Panopeus herbstii* within each year.

Year	Density		Biomass		Carapace Width	
	H. sanguineus	*P. herbstii*	*H. sanguineus*	*P. herbstii*	*H. sanguineus*	*P. herbstii*
2012	3.2	11.2*	4.9	8.9	18.7*	16.1
2011	1.6	5.1*	3.0	4.5	21.1*	17.4
2001	13.0*	4.5	13.7	5.1	19.6	19.6

Comparing observations of recent surveys with those from 2001 gives strong and consistent evidence for a declining *H. sanguineus* population in the UD Harbor (Table 4.1). In addition, the comparison also suggests a simultaneous recovery of native mud crabs, and densities have more than doubled. There is a clear reversal in proportional values of *H. sanguineus* and *P. herbstii* abundance from 2001, and values from my recent survey further support the observed trend (Figure 4.1). Proportional biomass values over the decade separating the surveys followed the same pattern (Figure 4.2). However, there was little change in mean carapace width since 2001 (Figure 4.3), suggesting a constant population age structure of the two species during this time period.

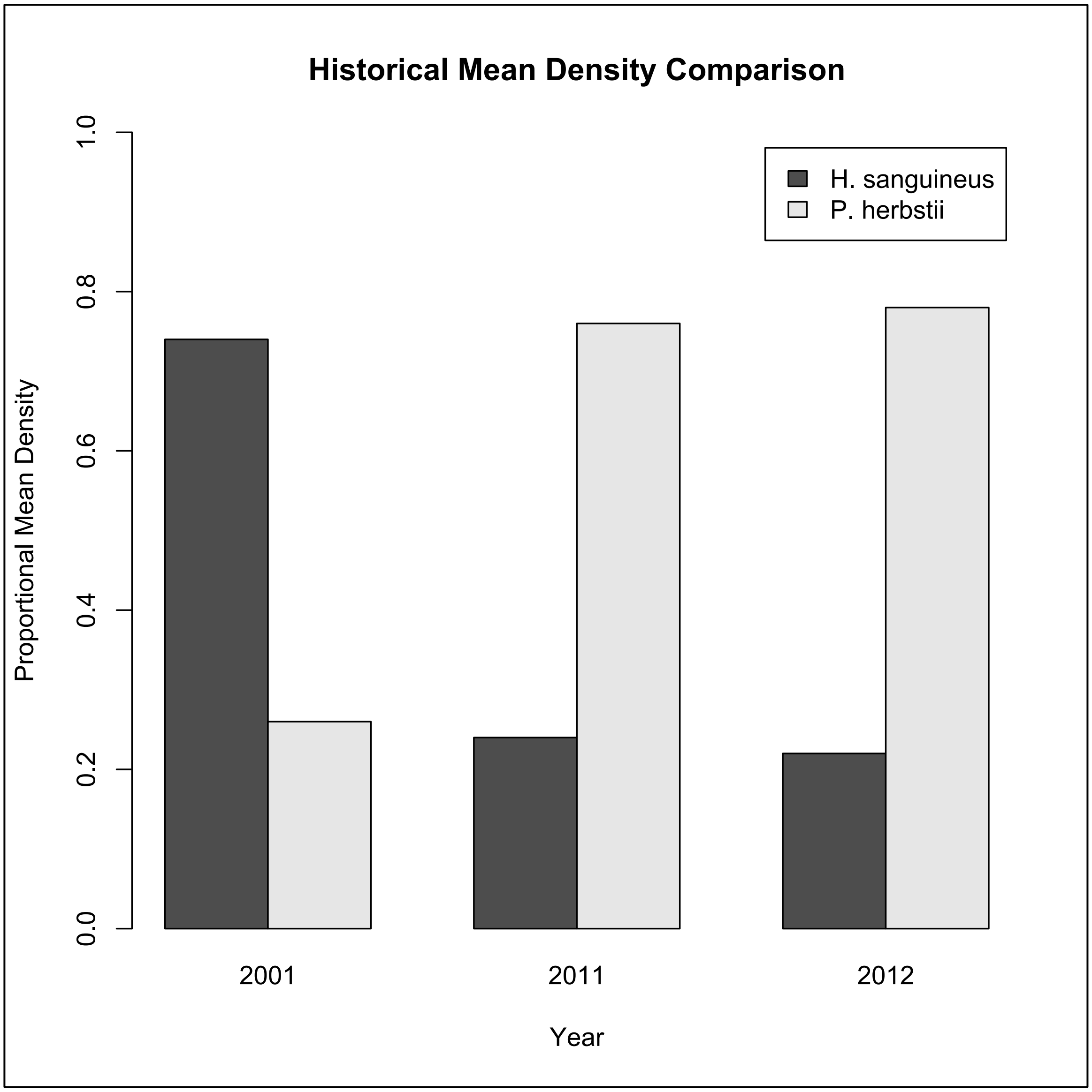

Figure 4.1: Proportional Density of Crabs in UD Harbor. Twelve-year historical comparison. Data were pooled over all tidal zones and sampling dates within each year.

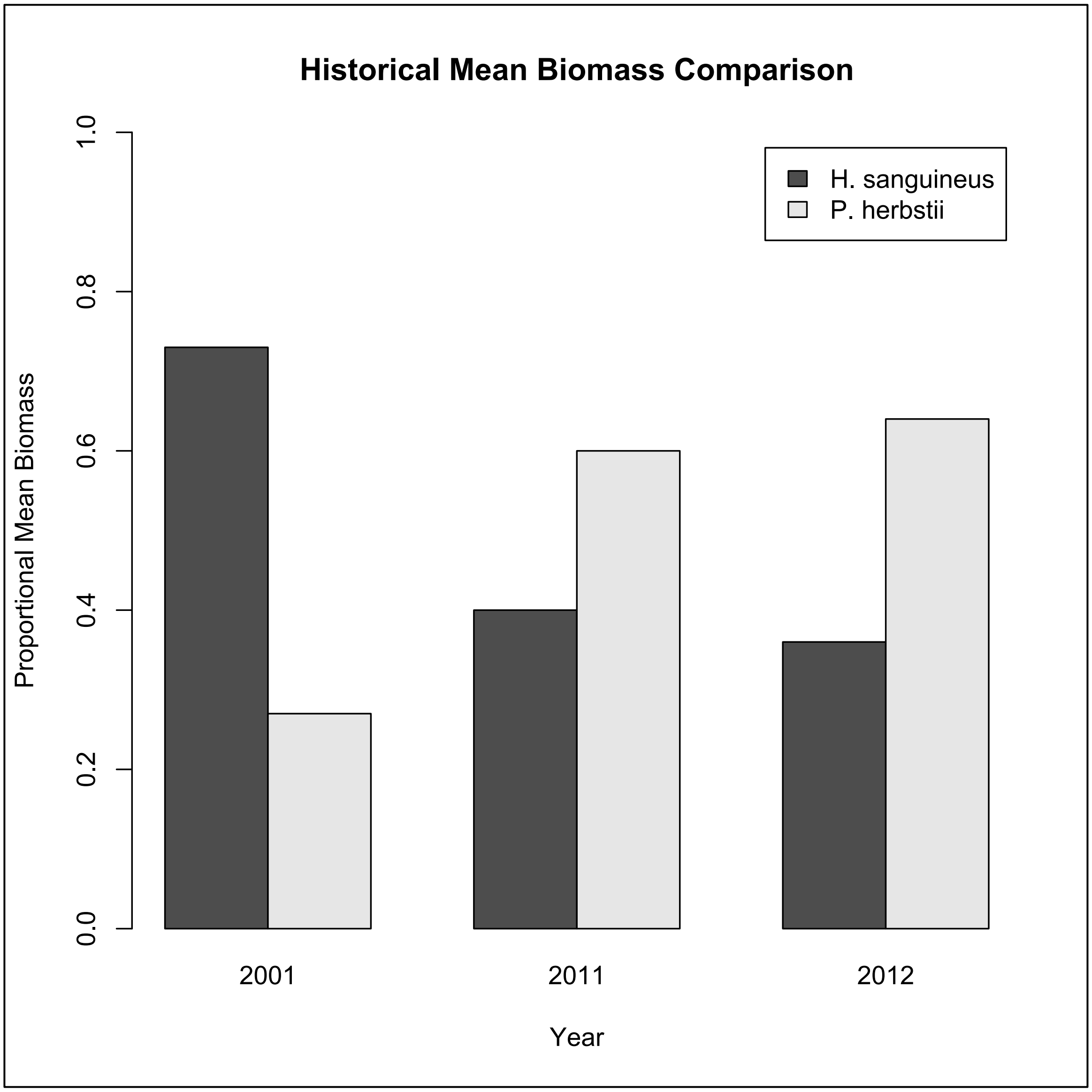

Figure 4.2: Proportional Biomass of Crabs in UD Harbor. Twelve-year historical comparison. Data were pooled over all tidal zones and sampling dates within each year.

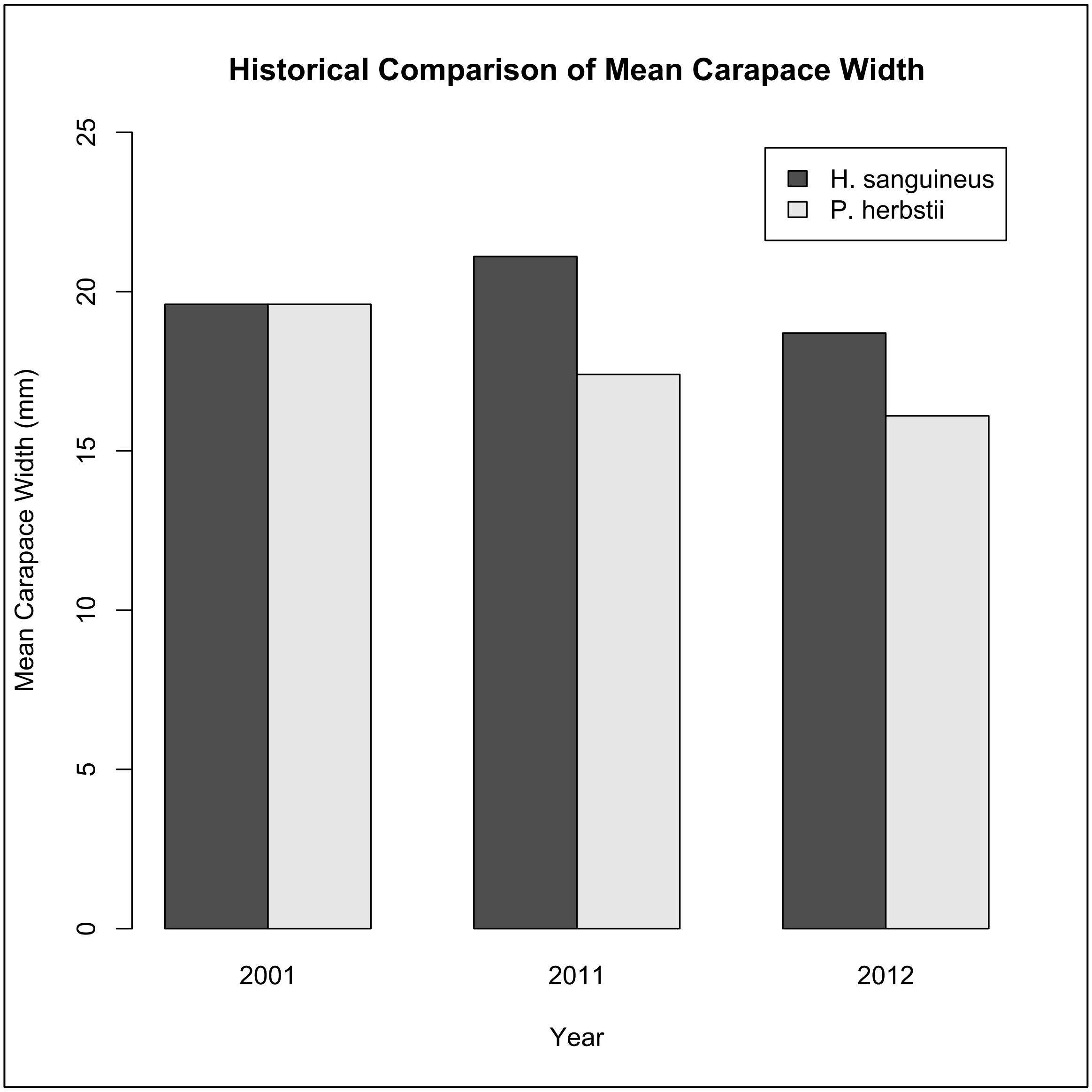

Figure 4.3: Mean Carapace Width of Crabs in UD Harbor. Twelve-year historical comparison. Data were pooled over all tidal zones and sampling dates within each year.

There have been no other studies showing a decline in *H. sanguineus* populations on the east coast of North America. Nonetheless, my results are similar to dynamics seen with the invasive Chinese mitten crab in European and Californian habitats (Panning, 1939; Attrill et al., 1996; Dittel and Epifanio, 2009). Possible explanations for the decline of *H. sanguineus* in the Middle Atlantic region could involve new dynamics between the species and relative competitors. Food limitations could also exist in the areas of my surveys, and the habitats may only be able to support smaller populations of *H. sanguineus*.

Overall, results of my 2011 and 2012 investigations show a new trend in crab assemblages. As previously mentioned, a decline phase has been associated with some bio-invasions and interactions between the co-occurring Asian shore crab and native mud crab could be yielding behavioral changes and subsequent changes in populations. Because my investigations generally followed procedures of the Park et al. (2005) study and were conducted during peak crab abundance for the two species, the data presented in my investigations provide strong evidence of a decline phase in the invasive *H. sanguineus* population and a recovering indigenous population at the UD Harbor Station, near the mouth of the Delaware Bay.

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Appendix

TEMPERATURE AND SALINITY DATA

2011 UD Harbor. Data are from horizontal benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/15/11	21.6	20.3
6/22/11	23.0	23.0
6/29/11	24.2	27.1
7/6/11	25.0	23.0
7/12/11	23.3	29.4
7/20/11	24.2	27.6
7/27/11	26.1	26.2
8/3/11	25.5	27.8
8/10/11	24.6	29.5
8/17/11	23.7	26.2
8/24/11	23.9	27.4
8/31/11	22.4	20.1
9/7/11	23.3	25.9
9/14/11	24.2	20.5
9/21/11	20.3	17.7
9/28/11	22.0	24.6

2011 UD Harbor. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
7/14/11	23.7	28.4
7/28/11	25.5	27.7
8/4/11	24.2	28.6
8/18/11	24.2	27.7
9/1/11	24.3	26.0
9/29/11	22.2	23.8

2011 Canal Station. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
7/28/11	27.2	26.9
8/18/11	24.6	30.0
9/1/11	24.3	26.0
9/29/11	22.5	26.5

2012 UD Harbor. Data are from horizontal benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/6/12	20.1	26.7
6/14/12	22.9	28.6
6/20/12	25.5	26.2
6/27/12	23.2	26.5
7/4/12	26.5	27.2
7/11/12	25.9	29.0
7/18/12	28.9	28.8
7/25/12	24.5	29.4
8/1/12	22.6	25.9
8/8/12	25.7	30.0
8/15/12	25.0	28.4
8/22/12	23.4	29.9
8/29/12	25.8	27.5
9/5/12	26.4	29.7
9/12/12	22.4	23.7
9/20/12	22.4	29.1
9/26/12	20.6	27.5

2012 UD Harbor. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/13/12	22.4	26.2
6/28/12	27.7	23.6
7/19/12	28.5	29.2
8/3/12	25.5	29.9
8/16/12	26.5	29.2
8/30/12	25.6	27.4
9/13/12	23.4	20.4

2012 Canal Station. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/7/12	20.2	26.2
6/21/12	27.2	28.4
7/5/12	29.9	28.1
7/26/12	25.1	29.4
8/9/12	26.2	29.6
8/23/12	23.8	29.7
9/7/12	24.2	14.2
9/20/12	22.9	30.4

2012 Townsends Inlet. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/19/12	23.3	31.0
7/3/12	24.7	31.2
8/2/12	27.6	30.4
9/17/12	23.0	31.4

2012 Indian River Inlet. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/12/12	22.9	31.1
6/29/12	26.5	29.7
7/10/12	26.7	30.1
7/24/12	24.6	30.8
8/7/12	25.4	31.3

2012 Ocean City Inlet. Data are from vertical benthic sampling.

Date	Water Temperature (°C)	Salinity (ppt)
6/12/12	21.9	31.9
7/10/12	25.3	30.9
8/1/12	27.7	31.1
9/19/12	23.1	31.3