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RETURN OF THE NATIVE: HISTORICAL COMPARISON OF INVASIVE AND INDIGENOUS CRAB POPULATIONS NEAR THE MOUTH OF DELAWARE BAY

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ABSTRACT An invasive population of the Asian shore crab *Hemigrapsus sanguineus* was discovered in 1988 near the mouth of Delaware Bay, and populations now occur from North Carolina to Maine. The shore crab *H. sanguineus* competes with indigenous species and has displaced resident crabs throughout its invasive range. However, there have been few studies that document changes in populations of *H. sanguineus* after the species has become established. We compare sympatric populations of the Asian shore crab and a native mud crab (*Panopeus herbstii*) that were monitored initially in 2001 and again in 2011 and 2012. The historical study was conducted in a rocky habitat near Cape Henlopen at the southern terminus of Delaware Bay (38.793° N, 75.158° W). Results showed large differences in the relative abundance of the two species throughout the duration of the study. The Asian shore crab *H. sanguineus* accounted for 75% of total crab abundance in 2001, but abundance had decreased to less than 25% in both 2011 and 2012. Similar results were obtained when we compared the two species in terms of biomass. Additional sampling in 2012 showed comparable low values for *H. sanguineus* when compared with *P. herbstii* at two stations about 25 km and 50 km farther south along the coast. In contrast, *H. sanguineus* was strongly dominant at a station 50 km north of the historical sampling site. Percentage rock cover and size of rocks varied little among sampling locations, and all sites were proximal to the coastal ocean. However, basal sediment at the northern station was coarser than sediments at the other sites, which may have restricted the occurrence of mud crabs. Overall results of the study indicate a resurgence of native mud crabs at sites where sedimentary characteristics provide adequate habitat.

KEY WORDS: invasive species, Asian shore crab, *Hemigrapsus sanguineus*, mud crab, *Panopeus herbstii*

INTRODUCTION

The Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) is native to the east coast of Asia and was first observed in North America at Townsends Inlet near the mouth of Delaware Bay in 1988 (Williams & McDermott 1990, Ai-Yun & Yang 1991, McDermott 1991). The crab spread rapidly after its introduction, and invasive populations now extend from Maine to North Carolina (Delaney et al. 2008, Griffen 2011). The Asian shore crab *H. sanguineus* also occurs on the Atlantic coast of Europe, where invasive populations extend from Lower Saxony in Germany to the Cotentin Peninsula in France (Breton et al. 2002, Dauvin et al. 2009). Laboratory and field studies indicate that *H. sanguineus* is a generalist predator with potential for large effects on sympatric populations of molluscs and crustaceans (see Epifanio (2013) for a review).

Throughout the northern part of its American range, *Hemigrapsus sanguineus* coexists with a previously established bio-invader, the European green crab *Carcinus maenas* (Linnaeus, 1758). Very high densities of *H. sanguineus* have been reported throughout this region, along with a steep decline in the abundance of green crabs (Lohrer & Whitlatch 2002a, Griffen 2011, O'Connor 2013). This decline implies competition between the two species, and results of previous investigations support this idea (e.g., Jensen et al. 2002, Lohrer & Whitlatch 2002b, MacDonald et al. 2007, Griffen 2011, Epifanio 2013).

In the southern part of its American range, *Hemigrapsus sanguineus* co-occurs with the native Atlantic mud crab *Panopeus herbstii* H. Milne Edwards, 1834, and is common on structured

hard bottom throughout this region in both intertidal and shallow subtidal habitats (Ryan 1956, McDonald 1982, Williams 1984). Juvenile *P. herbstii* consume a variety of small invertebrates (Dame & Patten 1981, McDonald 1982), whereas adults often prey on co-occurring bivalve molluscs (McDermott 1960, Meyer 1994). In high abundance, *P. herbstii* has important effects on bivalve fisheries and mariculture (Whetstone & Eversole 1981, Lin 1990, Abbe & Breitburg 1992).

Before introduction of the Asian shore crab, *Panopeus herbstii* shared its intertidal habitat primarily with two other species of mud crab, *Dyspanopeus sayi* and *Eurypanopeus depressus* (McDonald 1982, Meyer 1994, McDermott 1998). Within 15 y of its introduction, *D. sayi* and *E. depressus* had largely disappeared from the intertidal habitat, and the abundance of *P. herbstii* had declined substantially (McDermott 1998, Ahl & Moss 1999, Kopin et al. 2001). There have been no published studies of the dynamics of co-occurring populations of *H. sanguineus* and *P. herbstii* since that time.

We compare sympatric populations of *Hemigrapsus sanguineus* and *Panopeus herbstii* that were monitored initially in 2001 and again in 2011 and 2012. The historical study was conducted in a rocky habitat near Cape Henlopen at the southern terminus of Delaware Bay, and comparative data were collected from locations within 50 km of the historical site. The investigation was designed to test the hypothesis that invasive populations of *H. sanguineus* are well established in the Middle Atlantic region and continue to dominate native crab species. We examined the following questions concerning this hypothesis: (1) Have the overall abundance and biomass of *H. sanguineus* and *P. herbstii* changed at the historical study site? (2) Is there a difference in proportional abundance and biomass? (3) Are the populations at the historical site similar to those at nearby locations?

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MATERIALS AND METHODS

Description of Study Sites

The historical comparison of *Hemigrapsus sanguineus* and *Panopeus herbstii* was conducted in the University of Delaware (UD) Harbor (38.793° N, 75.158° W), about 200 m from Roosevelt Inlet near the mouth of Delaware Bay (Fig. 1). The inlet receives discharge from the Broadkill River, a secondary estuary that drains extensive areas of salt marsh and freshwater wetlands before flowing into the main body of the bay (DeWitt & Daiber 1973, Petrone et al. 2005). Tides are semidiurnal at the study site with a mean vertical range of 1.2 m (NOAA Tides & Currents; <http://tidesandcurrents.noaa.gov/tides10/tab2ec2b.html>). The intertidal zone at the site is protected from direct wave impact and consists of muddy sand (Coastal and Marine Ecological Classification Standard Catalog of Units) overlain with riprap constructed from quarry rocks of various sizes. The maximum angle of descent of the intertidal region is approximately 10 deg from the horizontal plane. We measured surface temperature and salinity in open water immediately adjacent to the study site coincident with each collection (YSI Model 30/10 FT). Temperature varied seasonally and ranged from approximately 20°C in spring and autumn to about 29°C in midsummer. Salinity varied with runoff from the Broadkill and ranged from approximately 24–30‰.

Geographical comparisons south and north of Delaware Bay were made at Ocean City Inlet, MD (38.235° N, 75.090° W); Indian River Inlet, DE (38.610° N, 75.057° W); and Townsends Inlet, NJ (39.127° N, 74.711° W). Sampling sites at these stations have free connection to the coastal ocean, but are located inside the respective inlets and are protected from direct wave exposure. Tides are semidiurnal at all three stations. Mean tidal range is 0.6 m at Ocean City, 0.8 m at Indian River,

and 1.2 m at Townsends Inlet (NOAA Tides & Currents). The intertidal zone at each location is armored with quarry rock similar to that at the UD harbor. Underlying substratum at Indian River and Ocean City is muddy sand, whereas that at Townsends Inlet consists of coarse sand. The angle of descent varies from less than 5 deg at Townsends Inlet to approximately 10° at Ocean City and Indian River. During the course of this study, values for surface water temperature were similar at the three coastal stations and ranged seasonally from around 22–27°C. Salinity reflected conditions in the adjacent coastal ocean and varied from 30–32‰.

Benthic Sampling

Our sampling techniques were generally similar to those used in earlier investigations of Asian shore crab populations in Long Island Sound and southern New England (Ledesma & O'Connor 1991, Ahl & Moss 1999, Lohrer et al. 2000). These techniques exploit the fact that *Hemigrapsus sanguineus* and *Panopeus herbstii* seek shelter under rocks when their intertidal habitat is exposed (Ryan 1956, McDermott 1998, Lohrer et al. 2000). This behavior allows quantitative sampling near the time of low tide by cordoning an area of bottom and turning over all rocks within the restricted perimeter. Thus, our sampling always occurred within 1 h of low tide, and collections always included placement of quadrats (0.5 m² in 2001, and 0.25 m² in 2011 and 2012) at locations with at least 70% rock cover.

Collections in UD harbor were made along transects extending approximately 10 m landward from the apparent low-tide shoreline on each day of sampling. We sampled quadrats along 3 replicate transects on each day in 2001 and 5 replicates on each day in 2011 and 2012. Transects were divided into three equal segments (upper, middle, and lower intertidal zones), and one quadrat was sampled from each segment along each replicate transect (Fig. 2). The temporal pattern of sampling

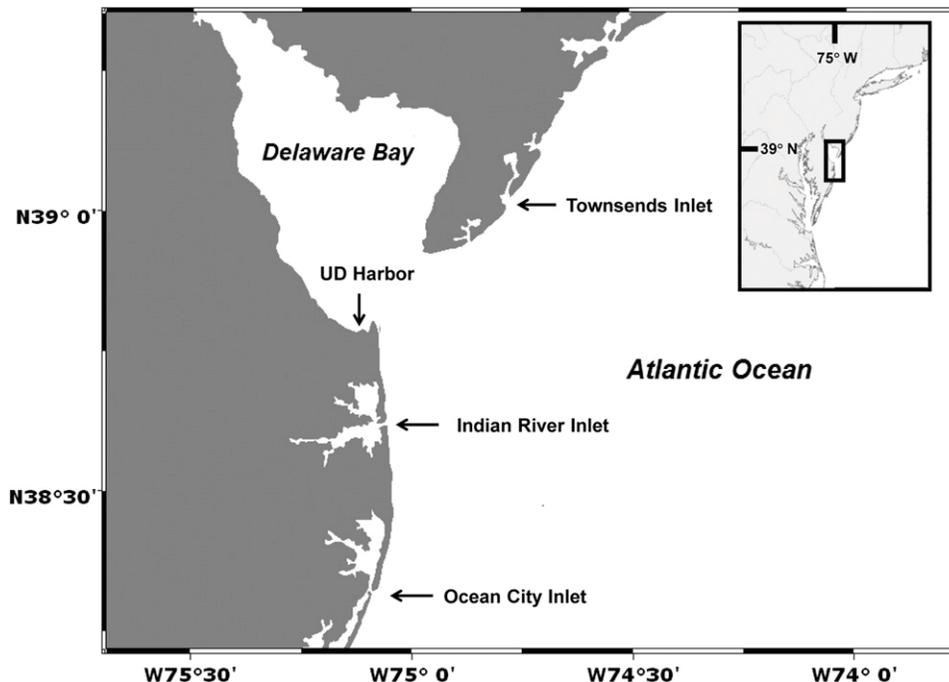


Figure 1. Location of study sites near the mouth of Delaware Bay. Inset shows the location of Delaware Bay in the Middle Atlantic Bight on the east coast of the United States.

varied somewhat throughout the course of the investigation and included (1) weekly collections from mid September through mid November in 2001, (2) biweekly collections from mid July through October in 2011, and (3) biweekly collections from mid June through September in 2012.

After collection, we transported all crabs to our nearby laboratory, where they were measured (carapace width) and identified to species using accepted morphological characters (Gosner 1971, Epifanio 2013). Crabs with carapace widths less than 10 mm were excluded from the analysis because of inefficiency in the collection of tiny juveniles and uncertainty in the taxonomic identification of very small specimens. To minimize effects of sampling, we replaced all rocks carefully after each sampling event and eventually released all crabs in the area where they had been captured.

To estimate biomass within the populations, we collected 35 crabs of each species for dry weight analysis. Collections were haphazard with regard to apparent size. Analysis consisted of initial measurement of carapace width with calipers, after which specimens were dried at 50°C for 72 h. We then determined dry weight of each specimen with a top-loading balance. We derived relationships between carapace width and dry weight to determine biomass for each species via regression analysis. In both species, the dry weight of individual crabs increased exponentially with increasing carapace width. For *Hemigrapsus sanguineus*, the relationship between dry weight and carapace width was $W = 0.04e^{0.17C}$, where W is dry weight and C is carapace width, and the R^2 value of the relationship was 0.91. For *Panopeus herbstii*, the relationship was $W = 0.04e^{0.16C}$, and the R^2 value was 0.96.

Geographical comparisons of populations north and south of UD harbor were carried out in 2012 and used similar techniques. Frequency of collection was monthly at Ocean City and Townsends Inlet and biweekly at Indian River Inlet. We sampled five replicate transects on each day of collection at each station, and we determined carapace width onsite rather than in the laboratory. Rocks were again replaced in their original positions, and crabs were released alive at the collection sites.

Statistical Analysis

We assessed the status of *Hemigrapsus sanguineus* and *Panopeus herbstii* populations by comparing respective values for abundance, biomass, and carapace width. We used nonparametric

techniques (2-sample Mann-Whitney-Wilcoxon's test) 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). Significance for all statistical tests was determined at $\alpha \leq 0.05$.

We calculated aggregate means for both absolute and proportional values of abundance and biomass. A separate analysis was conducted for each location in all 3 y. We used aggregate means for these two variables to provide a sense of variation among quadrats and across time. Determination of aggregate means for each species was a 2-step process. In the first step, we calculated a date-specific mean value (DSM) that considered all 3 intertidal zones and all transects for any day of sampling. For example, each DSM for abundance in UD harbor in 2011 was based on crab counts from each of 15 quadrats (3 zones \times 5 transects). The DSM for this case was calculated as

$$\bar{M}_{DSM} = \frac{(Q_1 + Q_2 + Q_3 \dots Q_n)}{n},$$

where \bar{M}_{DSM} is the date-specific mean, Q is abundance in each quadrat, and n is the number of quadrats ($n = 15$) sampled on a given day.

During the second step, we calculated an aggregate mean value based on the sum of all DSMs in any given year. This aggregate mean is essentially the average of all DSM values and can be represented as

$$\bar{M}_a = \frac{(DSM_1 + DSM_2 + DSM_3 \dots DSM_n)}{n},$$

where \bar{M}_a is the aggregate mean, DSM is the date-specific mean for each sampling day, and n is the number of sampling days. For the example in UD Harbor in 2011, there were 8 sampling days ($n = 8$).

Instead of an aggregate calculation of means for carapace width, we used ordinary mean values for this variable, which avoided the disproportionate influence of individual crabs in quadrats with low abundance compared with those with high abundance. Thus, each crab counted equally in determination of the annual mean carapace width. This calculation is represented as

$$\bar{M}_o = \frac{(C_1 + C_2 + C_3 \dots C_n)}{n},$$

where \bar{M}_o is the ordinary mean value for carapace width, C is the carapace width of an individual crab, and n is the total number

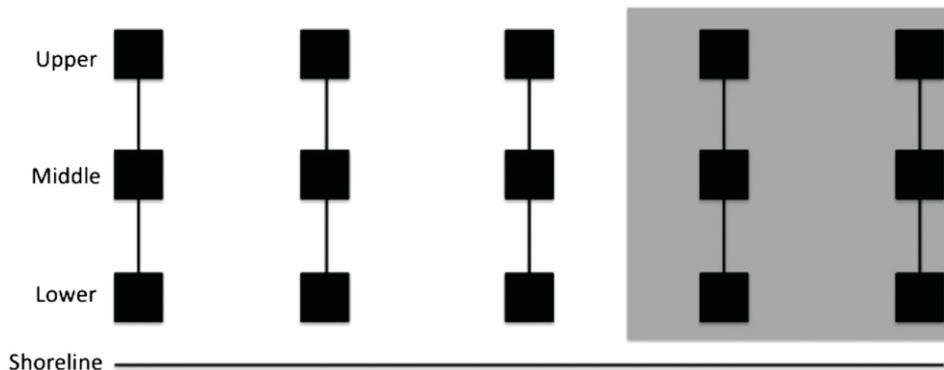


Figure 2. Conceptual view of the sampling design showing the location of the transects relative to the low-tide shore line (horizontal line at the bottom of the figure). Filled boxes show the location of the sampling sites in the upper, middle, and lower intertidal zones. Three transects (no shading) were sampled on each collection day in 2001. Five transects (shading and no shading) were sampled on each collection day in 2011 and 2012.

of crabs of a given species collected at any location in a sample year.

RESULTS

Historical Study in UD Harbor

Hemigrapsus sanguineus and *Panopeus herbstii* comprised by far the bulk of the crabs collected during each of the 3 y of sampling. Other crab species were caught in much smaller numbers and included the Atlantic rock crab *Cancer irroratus*, the European green crab *Carcinus maenas*, Say’s mud crab *Dyspanopeus sayi*, and the fiddler crab *Uca pugnax*. The Asian shore crab *H. sanguineus* was the numerically dominant crab species in UD harbor in 2001 and was significantly more abundant than *P. herbstii* (Table 1). This result was similar to findings of other researchers at various locations along the coast during the late 1990s and indicated that *H. sanguineus* had become well established in the Middle Atlantic region by the start of our investigation (McDermott 1998). Biomass in 2001 followed a similar trend in UD harbor, and there was, again, a significant difference between *H. sanguineus* and *P. herbstii* (Table 2). In contrast, there was no significant difference in the mean carapace width of the 2 species in 2001 (Table 3).

However, results from 2011 in UD harbor showed a large decline in abundance of *Hemigrapsus sanguineus* that was also observed in 2012 (Table 1). Mean abundance of *Panopeus herbstii* increased during the same period, and values for *P. herbstii* were significantly greater than *H. sanguineus* in both years. There was also a large decrease in biomass of the *H. sanguineus* population in 2011 and 2012, and biomass of the *P. herbstii* population was significantly greater than *H. sanguineus* in 2012, even though individual *H. sanguineus* were larger on average than *P. herbstii* (Tables 2 and 3). The changes in the UD harbor populations of *H. sanguineus* and *P. herbstii* during the course of the study are clearly apparent when the three annual data sets are presented as aggregate mean values of proportional abundance or biomass of each of the respective species (Figs. 3 and 4).

Geographical Survey

The crab *Panopeus herbstii* was significantly more abundant than *Hemigrapsus sanguineus* in 2012 at Indian River Inlet and Ocean City Inlet, and data for biomass followed the same

TABLE 1.

Mean abundance (number of crabs per square meter) of the Asian shore crab *Hemigrapsus sanguineus* and the Atlantic mud crab *Panopeus herbstii* at locations near the mouth of Delaware Bay (see text for latitude and longitude).

Year	Station	<i>H. sanguineus</i>	<i>P. herbstii</i>	P value
2001	UD harbor	13.0* (4.3)	4.5(2.9)	<0.001
2011	UD harbor	1.6 (2.1)	4.9* (1.7)	0.012
2012	UD harbor	2.7 (1.8)	9.2* (1.8)	0.001
2012	Indian River Inlet	1.0 (0.6)	9.5* (2.7)	0.012
2012	Ocean City Inlet	6.1 (2.6)	15.5* (4.1)	0.029
2012	Townsend's Inlet	31.3 (11.5)	0.0	NA

* Significant differences between respective mean abundance of *H. sanguineus* and *P. herbstii*. Values in parentheses are SDs. NA, not applicable; UD, University of Delaware.

TABLE 2.

Mean dry weight biomass (in grams per square meter) of populations of the Asian shore crab *Hemigrapsus sanguineus* and the Atlantic mud crab *Panopeus herbstii* at locations near the mouth of Delaware Bay.

Year	Station	<i>H. sanguineus</i>	<i>P. herbstii</i>	P value
2001	UD harbor	14.1* (4.1)	5.5 (4.6)	0.002
2011	UD harbor	3.0 (3.3)	4.5 (1.6)	0.270
2012	UD harbor	4.9 (3.9)	8.7* (2.1)	0.049
2012	Indian River Inlet	0.9 (0.9)	7.0* (2.7)	0.008
2012	Ocean City Inlet	3.1 (1.2)	9.4* (3.5)	0.029
2012	Townsend's Inlet	19.4 (9.6)	0.0	NA

* Significant differences between respective mean biomasses of *H. sanguineus* and *P. herbstii*. Values in parentheses are SDs. NA, not applicable; UD, University of Delaware.

pattern (Tables 1 and 2). Likewise, there was no significant difference in mean carapace widths of the 2 species at Indian River, but *P. herbstii* was significantly larger at Ocean City (Table 3). However, crabs of both species were generally smaller at the two southern stations than at the UD harbor site.

Overall results from Townsend's Inlet were very different from Indian River and Ocean City. There, *Hemigrapsus sanguineus* occurred at a very high density and biomass, and *Panopeus herbstii* was entirely absent from the samples (Tables 1 and 2). A few other crab species (*Cancer irroratus*, *Carcinus maenas*, *Dyspanopeus sayi*) were collected at Townsend's Inlet, but always in very low abundance compared with *H. sanguineus*.

DISCUSSION

Our study demonstrates a decadal change in relative abundance and biomass of invasive Asian shore crabs and native Atlantic mud crabs in rocky habitat near the mouth of Delaware Bay. Results of sampling in 2001 indicated that *Hemigrapsus sanguineus* was well established at this site and accounted for approximately 75% of overall crab abundance and biomass when compared with *Panopeus herbstii*. However, follow-up sampling at the same location showed that abundance of *H. sanguineus* had declined nearly 5-fold by 2012, with a 3-fold decrease in mean biomass. Meanwhile, abundance of *P. herbstii*

TABLE 3.

Mean carapace width (in millimeters) of the Asian shore crab *Hemigrapsus sanguineus* and the Atlantic mud crab *Panopeus herbstii* at selected locations near the mouth of Delaware Bay.

Year	Station	<i>H. sanguineus</i>	<i>P. herbstii</i>	P value
2001	UD harbor	19.6 (4.8)	19.6 (5.7)	0.497
2011	UD harbor	21.1* (4.5)	18.0 (4.1)	<0.001
2012	UD harbor	20.6* (3.0)	17.9 (1.1)	<0.001
2012	Indian River Inlet	16.4 (3.4)	16.9 (1.4)	0.282
2012	Ocean City Inlet	13.8 (1.5)	15.5* (1.0)	<0.001
2012	Townsend's Inlet	14.1 (0.7)	—	NA

* Significant differences between respective mean carapace widths of *H. sanguineus* and *P. herbstii*. Values in parentheses are SDs. NA, not applicable; UD, University of Delaware.

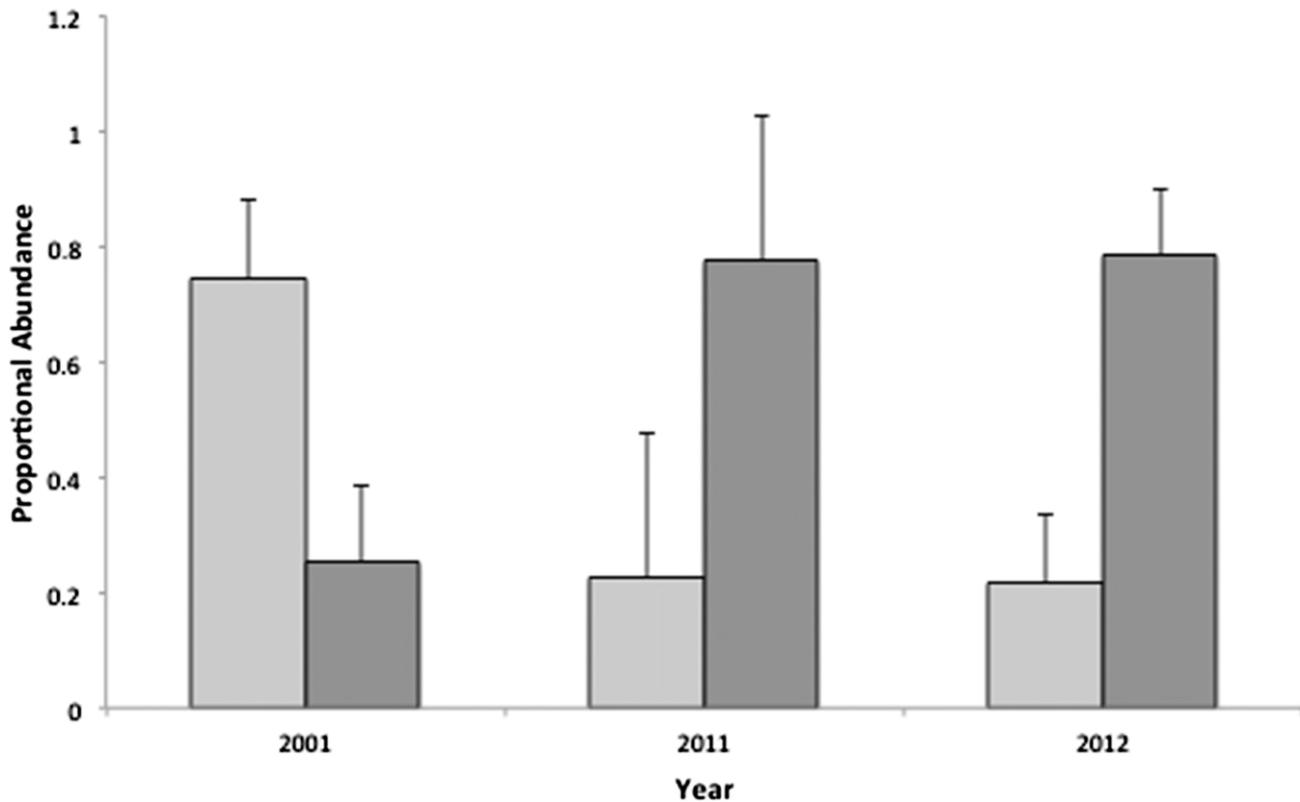


Figure 3. Changes in mean proportional abundance of invasive Asian shore crabs *Hemigrapsus sanguineus* (light shading) and native Atlantic mud crabs *Panopeus herbstii* (dark shading) in the University of Delaware Harbor (see Fig. 1) over a 12-y period from 2001 to 2012. Abundance was originally expressed as number of crabs per square meter. Proportional abundance is nondimensional. Error bars are SDs.

had increased by a factor of approximately 2, and this species now accounted for almost 80% of total crab abundance. Additional sampling in 2012 showed comparable low values for *H. sanguineus* when compared with *P. herbstii* at two stations about 25 km and 50 km farther south along the coast. In contrast, *H. sanguineus* was strongly dominant at Townsends Inlet, a location 50 km north of the Delaware Bay site. (Townsends Inlet was the site of the original observation of *H. sanguineus* in North America.) Percentage rock cover and size of rocks varied little among sampling locations, and all sites were proximal to the coastal ocean. However, basal sediment at Townsends Inlet was coarser than sediments at the other sites, which may have restricted the occurrence of mud crabs.

Changes in mean size of the two species over time and space are more difficult to explain. There was no significant difference in carapace width in UD harbor in 2001, but *Hemigrapsus sanguineus* was significantly larger than *Panopeus herbstii* at this site in 2011 and 2012. In contrast, *P. herbstii* was the larger species at Ocean City Inlet in 2012, and there was no difference in size at Indian River Inlet. Crabs of both species were generally larger at the Delaware Bay site than farther south or north along the coast, regardless of sampling year. Reasons for these differences are not apparent from our data, but results suggest dissimilarities in recruitment or predation at the various stations.

Previous investigations at other locations along the east coast of the United States have documented the rapid spread of *Hemigrapsus sanguineus* and the concurrent decline of resident

crab species (Epifanio 2013). Results of these studies have attributed the success of *H. sanguineus* to factors such as high annual fecundity (McDermott 1998), superior competition for shelter (Jensen et al. 2002), release from parasitism (Blakeslee et al. 2009), direct predation on co-occurring crab species (Lohrer & Whitlatch 2002a), or a combination of factors (Griffen 2011). However, these research threads typically end when *H. sanguineus* has become well established at a given location, and there has been little focus on the subsequent changes in established populations of *H. sanguineus* and the diminished populations of endemic crabs.

One investigation that has addressed this issue is the work of Kraemer et al. (2007) at a location in western Long Island Sound (40.981° N, 73.684° W), about 250 km north of Delaware Bay. Field and analytical protocols in that study were similar to our investigation, and direct comparison with our findings is reasonable. Asian shore crabs were first observed in Long Island Sound in 1994 (McDermott 1998), and the study by Kraemer et al. (2007) monitored abundance and biomass of *Hemigrapsus sanguineus* and the flat back mud crab *Eurypanopeus depressus* during an 8-y period from 1998 to 2005. Results showed that *H. sanguineus* and *E. depressus* accounted for about 99% of all crabs collected at the study site in both 1998 and 1999, and the respective abundance of the two species was approximately equal for those 2 y. However, the following year saw a precipitous decline in the mud crab population, and proportional abundance of *E. depressus* never exceeded 1% for the remaining 6 y of the investigation.

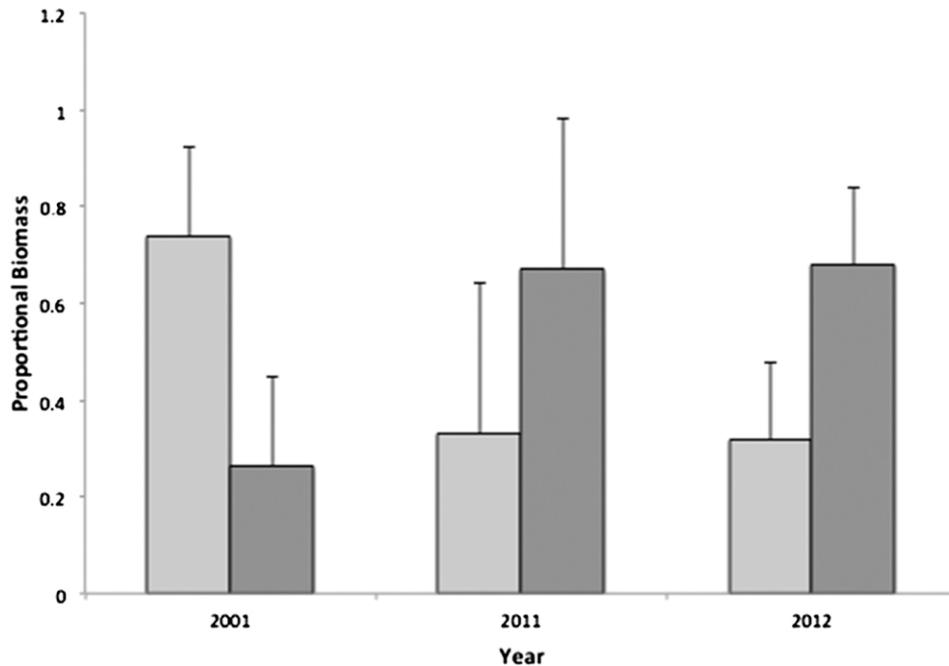


Figure 4. Changes in mean proportional biomass of invasive Asian shore crabs *Hemigrapsus sanguineus* (light shading) and native Atlantic mud crabs *Panopeus herbstii* (dark shading) in the University of Delaware Harbor (see Fig. 1) over a 12-y period from 2001 to 2012. Biomass was originally expressed as grams of dry weight per square meter. Proportional biomass is nondimensional. Error bars are SDs.

A similar study by O'Connor (2013) examined the dynamics of sympatric populations of Asian shore crabs and resident mud and green crabs over time periods as long as 12 y at several locations along the coast of southern New England. Collection techniques were similar to our investigation, and direct comparison with our findings is again sensible. Results of the study by O'Connor (2013) identified three discrete stages during the bioinvasion process. During the early stage (1998 to 1999), *Hemigrapsus sanguineus* co-occurred with three species of mud crab (*Dyspanopeus sayi*, *Eurypanopeus depressus*, *Panopeus herbstii*) at locations in Vineyard Sound (41.553° N, 70.609° W) and Narragansett Bay (41.677° N, 71.266° W). Mean abundance of mud crabs in Narragansett Bay was more than 10 times that of *H. sanguineus* during the early stage, and reached levels approaching 50 crabs/m². Abundance of mud crabs declined to less than 10 crabs/m² during the short mid stage of the invasion (2000), and was similar to the abundance of Asian shore crabs at that time. The ensuing late stage of the invasion (2001 to 2010) was characterized by a sharp increase in numbers of *H. sanguineus*, and within a decade, the abundance of Asian shore crabs was nearly 200 crabs/m² compared with less than 5 crabs/m² for mud crabs. Results from a location farther north in Massachusetts Bay (42.092° N, 70.706° W) documented a similar dynamic between *H. sanguineus* and the resident green crab *Carcinus maenas*.

Overall, it is evident that introduced species, such as *Hemigrapsus sanguineus*, are capable of explosive population growth in suitable alien habitats. However, invasive populations sometimes decline after a period of rapid expansion. For example, the Chinese mitten crab *Eriocheir sinensis* proliferated during the first 20 y after its introduction in northern Europe and then declined throughout the following decade (Panning 1939, Attrill et al. 1996). This boom-and-bust phenomenon for mitten crabs also occurred in other areas of Europe, and most recently in San

Francisco Bay on the west coast of the United States (Dittel & Epifanio 2009). In contrast, other invasive populations of *E. sinensis* have experienced delayed expansions that occurred many years after initial introduction. For example, *E. sinensis* was first reported in the Thames River in England in 1935; however, it was not until the early 1990s that populations began to grow rapidly (Ingle 1986, Gilbey et al. 2008).

Our own investigation provides clear evidence of a decline in abundance of Asian shore crabs near the mouth of Delaware Bay after a period of expansion from 1988 to at least 2001 (McDermott 1998, Andrews et al. 2001, Kopin et al. 2001). The *Hemigrapsus* population was well established in UD harbor at the beginning of our study in 2001, and the mud crab assemblage had been reduced to low numbers of a single species (*Panopeus herbstii*). This situation corresponds to the late invasive stage in the O'Connor scheme, and our proportional results for 2001 are similar to data from Kraemer et al. (2007) and O'Connor (2013) during the final years of their respective monitoring studies. A subsequent decline in Asian shore crabs, as observed at our UD harbor site, was not detected in the other two studies, and the generality of our own findings is not entirely clear. For example, we have no data for the period between 2001 and 2011, so the temporal pattern of the decline at UD harbor is unknown. Likewise, the historical data for Indian River Inlet are limited to a few observations, and there is no historical information for Ocean City Inlet at all (McDermott 1998, Brown 2005).

Nevertheless, we observed low abundance and low biomass of *Hemigrapsus sanguineus* in UD harbor during both 2011 and 2012, along with very similar patterns of abundance at nearby Indian River Inlet in 2012. Abundance at Ocean City Inlet, farther south along the coast, was somewhat higher, but was also depressed compared with data from 2001 in UD harbor. In

contrast, *H. sanguineus* remained the dominant intertidal crab farther north at Townsends Inlet (where the original invasion had been observed in 1988), but even at that site, abundance had declined compared with historical data (McDermott 1998).

It is difficult to determine causes of the apparent decline in Asian shore crabs from a purely observational study like ours. We have no information concerning disease, parasitism, or subtle changes in ambient habitat or community that might tip the competitive balance between *Hemigrapsus sanguineus* and *Panopeus herbstii*. Nevertheless, our results show clear resurgence in the populations of *P. herbstii* in and near UD harbor, which suggests a change in competitive dynamics over the 12 y encompassed by our study. Under some circumstances, the magnitude of larval supply is an important determinant of competitive outcomes (Hughes et al. 2000), and recent work has shown that *H. sanguineus* accounts for only a small percentage of overall crab larval abundance near the mouth of Delaware Bay (Epifanio et al. 2013). This is probably a result of the limited spawning stock of *H. sanguineus* in an area where adult habitat is restricted mainly to armored shorelines and anthropogenic structures such as jetties, groins, and breakwaters. In contrast, *P. herbstii* extends widely into subtidal habitats (where it does not compete with *H. sanguineus*), and the species comprises a much larger portion of the regional larval pool (Steppe & Epifanio 2006). This high abundance likely provides *P. herbstii* with greater insulation from density-independent factors (e.g., wind and estuarine outflow) that impact supply of larvae to adult populations (Epifanio & Garvine 2001). This circumstance affords a possible mechanism for rapid growth of mud crab populations during years of particularly diminished supply of *Hemigrapsus* larvae and suggests that differential larval supply, rather than postsettlement competition, is at play here.

In summary, our study has shown a decadal reversal in the proportional abundance and biomass of Asian shore crabs and Atlantic mud crabs in rocky habitat near the mouth of Delaware Bay. The reversal was stable for two annual sampling seasons, and similar patterns of proportional abundance were observed at locations as far as 50 km from the historical study site in UD harbor. Our results differed greatly from comparable monitoring studies conducted farther north in Long Island Sound and southern New England—both of which documented expansion of a newly established population of *Hemigrapsus sanguineus* and coincident displacement of a resident assemblage of mud crabs. In contrast, our investigation started with an established population of *H. sanguineus* and observed temporal changes in that population and a sympatric population of mud crabs. Much of the previous work on dynamics of invasive populations of *H. sanguineus* has been conducted under the tacit assumption that well-established populations of the species will remain stable through time. Results of our study bring that assumption into question.

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