LONG-TERM CHANGES IN AN ESTUARINE MUD CRAB COMMUNITY: EVALUATING THE IMPACT OF NON-NATIVE SPECIES

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ABSTRACT

Along the US Atlantic coast, oyster reefs support a large number of estuarine species including ecologically important and abundant mud crabs. Multiple factors including environmental conditions, the introduction of non-native species, parasites, and interspecific competition can change the structure of these communities over time. To examine long-term changes in mud crab communities, crabs were sampled quarterly for ten years in a mixed oyster/mud habitat in a northeast Florida estuary. A total of 6935 individuals comprised of 10 species were collected, including two non-native crab species: *Petrolisthes armatus* (Gibbes, 1850) and *Charybdis hellerii* (Milne-Edwards, 1867). Three species (*Panopeus herbstdi* Milne Edwards, 1834, *P. armatus*, and *Eurypanopeus depressus* (Smith, 1869)) made up 97.3% of adult specimens collected, and were observed throughout the study period in varying abundances. Non-metric multi-dimensional scaling (MDS) conducted on species abundances revealed that the community underwent significant long-term, rather than cyclical seasonal, changes. Most noteworthy were the similarities in community assemblages observed in the years prior to, and soon after, the introduction of a non-native parasite, *Loxothylacus panopaei* (Gissler, 1884), which preferentially infects *E. depressus*. The significance of the presence/absence of the parasite on the community structure was confirmed through an analysis of similarities test (ANOSIM). While *E. depressus* abundance declined in the early years of the study after the introduction of *L. panopaei*, and never recovered, abundance of *P. herbstdi* did not significantly change. Temperature and salinity likely only briefly impacted individual species on a seasonal or yearly basis including *P. armatus*, whose abundance reached an all-time low in the winter of 2010-2011 along with extreme winter temperatures.

KEY WORDS: invasive species, *Loxothylacus panopaei*, mud crab, parasitic castrator, rhizocephalan barnacle

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INTRODUCTION

Along the Atlantic coast of North America, reefs composed of *Crassostrea virginica* (Gmelin, 1791) (the eastern oyster) support a high diversity of algae, invertebrates, and vertebrates (Kennedy et al., 1996; Lenihan and Peterson, 1998). One of the most conspicuous and abundant taxonomic groups inhabiting these estuarine habitats are mud crabs, which are important in maintaining community structure as they feed on, and therefore control numbers of, molluscs and other crustaceans on reefs (Ryan, 1956; McDermott, 1960; McDonald, 1982; Lee and Kneib, 1994; Meyer, 1994). Two common co-occurring species of native mud crabs, *Panopeus herbstdi* Milne Edwards, 1834 and *Eurypanopeus depressus* (Smith, 1869), are both able to tolerate a wide range of environmental conditions (Williams, 1965, 1984; McDonald, 1982), but environmental factors could affect other species and additional factors such as intraspecific competition and the introduction of non-native species to oyster reefs may alter community dynamics.

Non-native species are regularly introduced into marine and estuarine systems (Ruiz and Carlton, 2003), where their introduction often has significant negative impacts (Carlton and Geller, 1993; Ruiz et al., 1997). In particular, non-native species can adversely affect oyster reefs and the diversity they support by disrupting natural trophic cascades (Kimbro et al., 2009). Often, the transportation of oysters themselves introduces new fauna that may be detrimental to a system (Andrews, 1980). In North America, crustaceans are the most prevalent taxonomic group of non-native marine and estuarine invaders (Ruiz et al., 2011), and crabs, in particular, can have significant effects on native communities in introduced habitats (Griffen and Byers, 2009; Ruiz et al., 2011).

Several crab species including *Petrolisthes armatus* (Gibbes, 1850) and *Charybdis hellerii* (Milne-Edwards, 1867) have recently invaded estuarine waters along the southeastern US Atlantic coast (Lemaitre, 1995; Knott et al., 2000). *Petrolisthes armatus* was first reported north of Cape Canaveral, FL in 1994 (Knott et al., 2000), while its native range includes shallow habitats of more tropical and sub-tropical latitudes, including coastal Brazil, the central and northern Gulf of Mexico, the Caribbean islands, the central eastern Pacific Ocean, and the west coast of Africa (Oliveira and Masunari, 1995; Hollebone and Hay, 2007).
Charybdis helleri was introduced from the Indo-Pacific and first recorded in the continental US in 1995 in the Indian River Lagoon, FL (Lemaitre, 1995). Because of the relative recentness of these introductions, little is known about the long-term effects these crab species may have on native crab populations (but see Dineen et al., 2001; Hollebone and Hay, 2007).

The introduction of non-native parasites may also impact native mud crab communities. Loxothylacus panopaei (Gissler, 1884) is a widespread non-native parasite along the Atlantic coast of North America that is known to infect several species of mud crab (Kruse et al., 2012). This species castrates its host and feminizes males, which stops reproduction at the level of the individual and, if widespread, can potentially affect the health of the host species population (Dillon and Zwerner, 1966; O’Brien and Van Wyk, 1985; Alverez et al., 1995; Hooe, 1995; Hines et al., 1997).

It was thought to be introduced to the US Atlantic coast from the Gulf of Mexico, likely by crabs brought to Chesapeake Bay in oysters used to replenish ailing stocks (Van Engel et al., 1966; Kruse et al., 2012). Loxothylacus panopaei now occurs from Long Island Sound to northeast Florida, and infects nine species of mud crab, occurring at frequencies ranging from sporadic to as high as 93% throughout its introduced range (Daugherty, 1969; Hines et al., 1997; Kruse and Hare, 2007; Kruse et al., 2012; Freeman et al., 2013).

While studies have investigated the short-term (≤2 years) impacts of non-native species on crab communities (Hollebone and Hay, 2007, 2008; Griffen and Byers, 2009), and the effects of physical parameters on a single species (Stillman and Somero, 2000), potential long-term (decadal) impacts of multiple factors on communities have not been examined. Short-term studies are likely to only capture instantaneous effects of various physical or environmental factors, while long-term studies may elucidate chronic effects on mud crab communities and demonstrate the resilience of impacted species. To determine the long-term effects of non-native species and parasites on estuarine mud crab communities, we examined changes in the diversity and abundance of mud crabs over a 10-year period in a mixed oyster/mud habitat in a northeast Florida estuary.

**Materials and Methods**

**Crab Communities**

Sampling occurred at a single mixed oyster/mud habitat site within the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM NERR) located in northeast Florida (29.6708°N, 81.2159°W). The sample site, which was undisturbed throughout the study period, was within a mosaic of intertidal and subtidal flats and creeks adjacent to the main channel of the Matanzas River (Fig. 1). The Matanzas River is one of the main tributaries forming the Guana Tolomato Matanzas estuary, which is a well-mixed, high salinity (polyhaline) lagoonal estuary consisting of Spartina alterniflora-dominated marshes as well as mixed salt marsh-mangrove areas (Webb et al., 2007; Valle-Levinson et al., 2009; Williams et al., 2014).

Mud crabs were sampled using seven replicate habitat trays deployed 1 m apart among naturally-occurring oysters along the low tide line (at approximately the same depth), and were subtidal except during extreme low tides. Total tray coverage was less than 1% of the available reef habitat. Individual habitat trays consisted of ventilated plastic trays measuring approximately 63 L × 52 W × 12 H cm, lined with 4 mm plastic vexar screening and filled to the top of the tray with a loose mix of un-cleaned living and dead C. virginica clusters collected from nearby reefs at the sampling site (Fig. 1). Approximately 30-50% of the C. virginica in the trays throughout the study was living.

From fall 2002 through summer 2012, trays were sampled seasonally (quarterly: fall, winter, spring, summer) at low tide. During each seasonal sampling event, trays were quickly retrieved from approximately 0.5 m of water, crabs were examined, and then all trays were redeployed the same day. Trays were not cleaned after a sampling event and were allowed to be fouled, mimicking the proximal oyster habitat. Due to unexpected circumstances, some sampling events did not take place (fall and winter 2006; spring, fall, and winter 2007; fall 2008; spring 2009), so the actual number of seasons sampled (n = 33) during the ten-year period is slightly smaller than the balanced number (n = 40).

Trays were collected one-at-a-time and the contents of each tray were emptied into a large wood-framed sieve (5 mm mesh), rinsed, and sorted. Large crabs, including specimens of Menippe mercenaria (Say, 1818), Callinectes sapidus Rathbun, 1896, and C. similis Williams, 1966 were identified, measured (carapace width to the nearest 0.1 mm), sexed, assessed for presence of eggs or parasites, and released away from the sampling site. Specimens of the non-native species C. helleri and all other crab specimens were placed in containers labeled by tray number and either frozen or preserved in 70% EtOH to be examined and sorted later following the same protocol as that used for larger specimens in the field. Native mud crabs including P. herbstii and E. depressus are not reproductive until they reach approximately 6 mm or greater (Ryan, 1956; McDonald, 1982), therefore all crabs with a carapace of <6 mm were considered recruits and not identified to species in the early years of the study. Because not all crabs were saved, later re-identification of smaller specimens was not possible. For consistency, no crabs smaller than 6 mm were identified to species.

All specimens of E. depressus collected and preserved during the ten-year study were re-examined in 2012 after the presence of the parasitic rhizocephalan barnacle, L. panopaei, which targets and infects E. depressus, was detected. Because of the resemblance of L. panopaei to a gravid female’s egg sac, it was suspected that at least some crab specimens that had been recorded as gravid during the study were actually infected by the parasite. Not all crab specimens from the study were available (samples from winter 2002, summer 2004 and spring 2005 were not archived), therefore, only a subset of all E. depressus specimens could be re-examined. This subset was used for examining changes in the number of gravid and infected specimens (as indicated by the presence of externae) over time.

**Data Analysis**

Seasonal abundance for all species collected (individually and combined) was expressed as the mean number of crabs per tray (NPT) and its standard deviation. Mud crab communities were compared by year and season using non-parametric multi-dimensional scaling (MDS). A Bray-Curtis similarity matrix was constructed using the fourth root of mean NPT (n = 7) of all species per sample date, and was used for MDS and further analyses. The transformation reduced the weight of abundant
species, allowing less abundant species to contribute to the community classification. The similarity matrix was used to conduct one-way analysis of similarity (ANOSIM) on community separation based on season and year. Further analyses were conducted on the community separation based on the presence/absence of an introduced parasite. The importance of individual species in the overall community structure was determined using a BEST match permutation test on the transformed species abundance matrix. Effects of environmental parameters (temperature and salinity) on community composition were analyzed with BEST relating the species abundance matrix to the Euclidean distance matrix of environmental parameters (normalized 30-day pre-collection average). PRIMER 6.0 was used for all multivariate analyses.

Long-term trends in species abundance were examined through a seasonal Mann-Kendall’s test with a correction for covariance between seasons (R statistical package) on the NPT by season for the three most abundant species, E. depressus, P. herbstii, and P. armatus. Comparisons between individual species abundances by season were made using one-way analysis of variance (ANOVA) tests (R statistical package).

**Environmental Parameters**

Temperature and salinity were measured using a YSI handheld meter during sampling events from 2011-2012. In addition to these discrete measurements, temperature and salinity were measured continuously throughout the study period by a YSI datasonde deployed at a nearby GTM NERR System-Wide Monitoring Program station, Ft. Matanzas (29.7370’N, 81.2460’W) (NERRS, 2013). Because the measurements were taken 7.9 km away from the study site, a regression analysis was conducted to estimate conditions at the study site using a subset of paired measurements from the Ft. Matanzas datasonde and study site (38 temperature and 39 salinity measurements). The resulting equations for estimating conditions at the study site were: temperature = 0.9612x + 1.1725°C (R² = 0.9016) and salinity = 1.7926x – 31.6780 ppt (R² = 0.6081). Regression-estimated parameters were used to examine extreme environmental conditions during the study and were used in multivariate analyses on community composition.

**RESULTS**

**Crab Diversity**

A total of 6935 individuals of ten species of crab were collected over the course of the study including two species of non-native crabs: P. armatus, which was abundant, and C. hellerii, which was extremely rare (Table 1). Species collected included members of eight genera and five families: Grapsidae (shore crabs), Menippidae (includes stone crabs), Panopeidae (mud crabs), Porcellanidae (porcelain crabs) and Portunidae (swimming crabs). Three species dominated the catch (E. depressus, P. herbstii, and P. armatus), each accounting for at least 10.0% of the total number of crabs collected. The remaining catch was made up of seven species (C. sapidus, C. similis, C. helleri, Dyspanopeus sayi (Smith, 1869), M. mercenaria, Pachygrapsus gracilis (De Saussure, 1858) and Panopeus occidentalis (De Saussure, 1857)), which together comprised 25.2% of the crabs collected, and recruits (<6 mm carapace width), which comprised 9.9% of the crabs collected.

Mud crab communities were most similar depending on the phase (pre, early, and post) of the parasitic L. panopaei invasion in 2004, with samples separating out by year, regardless of season (Fig. 2). A one-way ANOSIM of the Bray-Curtis resemblance matrix confirmed that year was a significant factor (p < 0.01), while season was not (p = 0.08). The species that best described the changes in the overall community (correlation = 0.970) included (in no particular order): C. sapidus, D. sayi, E. depressus, M. mercenaria, P. armatus, P. herbstii, and P. occidentalis. Callinectes similis, C. helleri, and P. gracilis did not have a significant effect on the overall community during the study period. Sampling without replacement likely did not influence study results, as no abnormal increases in species abundances were observed after missed sampling events; in fact abundances for some species (P. armatus) even decreased in such instances (Fig. 3).

More detailed analyses focus on changes that occurred in the three most common species that comprised 87.6% of the total catch (97.3% of the adult crabs) collected during the ten-year study period: P. herbstii, P. armatus, and E. depressus.

**Eurypanopeus depressus.**—At the initiation of the study E. depressus was the third most abundant species (maximum density was 53.6 m⁻²), but its numbers declined during the fall of 2004 and did not increase for the remainder of the study period (Tau = −0.721, slope = −2.733 NPT/year, p < 0.01) (Fig. 3). Specimens of E. depressus collected at the start of the study, during the winter of 2002 thru the winter 2003, did not contain the parasitic rhizocephalan barnacle L. panopaei. The first collection of a parasitized crab occurred during spring 2004 (one of 62 crabs was parasitized). Of the archived specimens we were able to re-examine, only one female (from the summer of 2007) was found to be gravid (and unparasitized) after the presence of L. panopaei was first recorded. That female was within one standard deviation of all previously collected ovigerous females. Regardless of season, after L. panopaei was first detected; most specimens collected after spring 2004 were of similar size, but parasitized (Table 2). The presence of the parasite had a significant effect on the overall community structure. A one-way ANOSIM of the species abundance resemblance matrix and the presence of the parasite (pre/post introduction) demonstrated the significant (p = 0.04) impact of the species’ presence on the crab community.

**Panopeus herbstii.**—Abundances of P. herbstii at the study site were more consistent than for other species throughout the study, and the species was collected with a maximum density of 58.9 m⁻². There was no significant change in the number of P. herbstii collected per tray during the study (Tau = 0.112, slope = 1.125 NPT/year, p = 0.48) (Fig. 3). More crabs were collected during the fall (likely reflecting summer recruitment); however, NPT by season was not significantly different (p = 0.54).

**Petrolisthes armatus.**—The number of P. armatus per tray was high during the first five years of the study (highest density was 89.8 m⁻²), but decreased during early 2008 and remained low (lowest density was 3.1 m⁻²) until 2011, when the number collected began to increase again (Fig. 3). Overall, there was no significant trend in P. armatus abundances over the study period (Tau = −0.287, slope = −6.575 NPT/year, p = 0.15). More crabs were collected during the fall, but the NPT did not differ significantly by season (p = 0.42). The smallest gravid specimen of P. armatus collected was 4.8 mm. The bopyrid isopod Aporobopyrus curtatus (Richardson, 1904) was detected in specimens of P. armatus throughout the course of the study (as noted by a bulge in the posterolateral carapace), with a mean infection rate of P. armatus by A. curtatus of 1.8%.
Environmental Parameters

The BEST analysis demonstrated that temperature and salinity were not significant factors in determining the overall crab community structure ($p = 0.32$, correlation = 0.064). Nonetheless, several instances of extreme environmental conditions may have had brief impacts on individual crab species during the study period. Extreme low temperatures occurred during the 2009-2010 and 2010-2011 winters when water temperatures fell below 10°C in January of each season (Fig. 4). During this period, a reduction in the number of *P. armatus* species was observed (Table 1). Additionally, animals were exposed to salinities of less than 5 ppt in September of 2004 during Hurricane Frances and May of 2009 due to heavy rainfall (Fig. 4). However, these brief periods of reduced salinity did not appear to affect the number of the three dominant species at the study site (Table 1).

**DISCUSSION**

Mud crab species composition in the mixed oyster/mud habitat investigated in this study was stable during the ten year period examined, however, the abundance ratios for some of the most frequently occurring species changed over the course of the study. Of these frequently occurring species, decreased abundance was observed for *E. depressus*, a slightly increased, although not significant, change in abundance was observed for *P. herbstii*, and a decline and re-

Table 1. Mean number of crabs per tray (NPT) and standard deviation (in parentheses) by season for all species with more than 10 individuals total ($n = 5$) and recruits. The remaining five less-abundant species (*Callinectes sapidus*, $n = 7$; *C. similis*, $n = 2$; *Charybdis hellerii*, $n = 7$; *Pachygrapsus gracilis*, $n = 1$; *Panopeus occidentalis*, $n = 3$) were included in the total numbers for each season ($n = 6935$ total). F, fall; W, winter; Sp, spring; Su, summer.
covery in abundance was observed for *P. armatus*. Thus, not surprisingly, these same three highly abundant and ubiquitous species (*E. depressus*, *P. herbstii*, and *P. armatus*) were also included in the group that best characterized changes in community structure over time. Less abundant and infrequently occurring species (7 of the 10 crab species) included members of Portunidae and Menippidae, which were typically larger than other species observed and likely rarely collected because of: 1) size constraints which limit the number of individuals occupying a tray, and 2) their ability to escape from the tray (rapidly in the case of the portunids) during retrieval of trays from the water. Only one specimen of *D. sayi* was collected during the first five years of the study, but sporadic collections occurred during the final years. Abiotic and biotic factors, including the presence of parasites, appeared to affect the overall crab community.

**Parasites**

Two species of introduced parasites, *A. curtatus* and *L. panopaei*, both of which are parasitic castrators, were found to infect *P. armatus* and *E. depressus* respectively. No individuals of other crab species collected had visible signs of parasitization. The bopyrid isopod *A. curtatus* co-occurs with its host in its native habitat (Oliveira and Masunari, 1998). The infection rate of *P. armatus* by *A. curtatus* was 1.8% during the ten-year study, which is lower than rates observed (9.5 and 3.1%) in previous studies in its native range of coastal Brazil (Oliveira and Masunari, 1998; Miranda and Mantelatto, 2010). One reason for the low parasite densities may be that presence/absence was determined visually (by existence of a carapace bulge) rather than through dissections, thus potentially leading to young parasites being overlooked. Despite varying levels of infection, previous studies have indicated no negative effects of this parasite for host crabs in their native range (Oliveira and Masunari, 1998; Miranda and Mantelatto, 2010).

An abrupt decrease in the number of *E. depressus* occurred in fall 2004, after which the population continued to decline with low densities consistently observed during the remaining eight years of the study. Specimens from the summer of 2004 were not available for re-examination, however, one crab (of 62 collected) was found to be parasitized by *L. panopaei* in the spring 2004 collection. Concurrently, a July 2004 study reported an absence of parasites in *E. depressus* in the same northeast Florida marsh and several sites south to Cape Canaveral (Kruse and Hare, 2007), while infected *E. depressus* specimens were found south of the sampling site in another study in 2006 (Kruse et al., 2012). It appears that *L. panopaei* was introduced to the study site near the spring of 2004 and that the introduction resulted in a population decline months later due to the impeded reproductive capabilities of infected crabs. The decline of *E. depressus* mirrors the collapses of local populations of mud shrimps *Upogebia* spp. along the US Pacific coast after the introduction of
the non-native bopyrid isopod *Orthione griffenis* Markham, 2004 (Chapman et al., 2012).

Laboratory experiments on larval *L. panopaei* have shown that the parasite is unable to successfully proliferate in salinities below 10 ppt (Reisser and Forward, 1991; Walker and Clare, 1994) and field experiments have shown that infection rates in *Panopeus obesus* Smith, 1869 were lower when salinities were reduced (Tolley et al., 2006). Although *E. depressus* can survive in salinities as low as 5 ppt (Gracés, 1987), salinities during the course of this study were rarely below 10 ppt, offering little to no refuge for the crabs. The decline in *E. depressus* may therefore be highly localized with infection rate being dependent on salinity. Further examination of crab densities and parasitization rates at sites with greater freshwater influence is necessary.

A high parasite load can greatly reduce the number of crabs and restructure the mud crab community as evidenced by the structuring of the crab community around the occurrence of *L. panopaei* in the present study. Based on sample separation using MDS, the early stage of *L. panopaei* introduction was determined to be from winter 2004 thru 2007, after which the crab community changed and did not return to its original composition. The most notable change in the community was the decline in abundance of *E. depressus*, which remained low through the completion of the study.

The decline of *E. depressus* at the study site mirrors the decline of the species in Virginia where the dominant species of mud crabs, *E. depressus* and *R. harrisii* (Gould, 1841), were replaced by *D. sayi*, a formerly rare species in that region, after the introduction of *L. panopaei* (Andrews, 1980). Although infected specimens of *D. sayi* have been reported (Hines et al., 1997), it appears to be less susceptible to infection than *E. depressus*, and no infected individuals of *D. sayi* were observed during our study.

### Environmental Parameters

Although environmental parameters did not have a significant impact on the overall crab community composition, the dominant mud crab species displayed different responses to varying temperatures and salinities. Two species, *P. herbstit* and *E. depressus*, did not appear to be impacted by temperature or salinity variability. These crabs are native to southeastern US estuaries, and are able to tolerate a wide range of environmental conditions (Williams, 1965, 1984; McDonald, 1982). However, the brief fluxes in abundance observed for the introduced species, *P. armatus* may have been a result of extreme environmental variation.

*Petrolisthes armatus* can tolerate temperatures of up to 40.5°C (Stillman and Somero, 2000), which is above the maximum temperature recorded at our study site. These animals were observed in high densities north of our study site in Georgia (Hollebone and Hay, 2007), where winter temperatures are generally lower than those observed in northeast Florida. However, only 39% of crabs survived oscillating water temperatures of 5.3-14.4°C that mimicked temperatures along the southern US coast in January 2010 (Cunning-Cloade et al., 2011). Consequently, the fewest crabs were collected during the winters of 2009-2010 and 2010-2011 following the lowest recorded temperatures (<10°C) in the study area. The population was able to recover somewhat during the following year suggesting that their thermal minimum may be near 10°C and that low temperature tolerance currently limits their northern distribution. Despite occasional near-lethal extreme winter water temperatures, it appears that *P. armatus* can overwinter in introduced waters.

Unlike temperature, salinity did not appear to have an effect on the seasonal density of *P. armatus*. This is contrary to a study of crab densities in southwest Florida, which

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**Table 2.** Specimens of *Eurypanopeus depressus* re-examined to determine the percentage of gravid females and crabs parasitized by *Loxothylacus panopaei* by year. The percent of gravid females was calculated from re-examined female crabs, and the percent crabs parasitized was calculated from both male and female crabs that were re-examined. F, fall; Su, summer.

<table>
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<th>Year</th>
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<th>Examined/ Collected</th>
<th>% Females gravid</th>
<th>% Crabs parasitized</th>
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<td>1</td>
<td>F02-Su03</td>
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suggested that *P. armatus* is a stenohaline species that prefers high salinities (Shirley et al., 2004). Although higher salinities may be more preferable (Shumway, 1983), *P. armatus* occurs in high densities in its natural range at salinities of 6.7 to 31.5 ppt (Oliveira and Masunari, 1995). This suggests that *P. armatus* may be better classified as a euryhaline species and that salinity is unlikely to have a large effect on densities. To this end, in the present study there were no effects on *P. armatus* densities observed following periods of decreased salinity after storm events.

Non-Native Species

Over the long-term, the population of *P. herbstii* appears to be stable and has neither significantly decreased or increased despite the presence of introduced crab species. Previous studies have observed no negative effect on mud crab populations due to the presence of *P. armatus* (Hollebone and Hay, 2007), likely due to differences in feeding strategy. A slight, although statistically insignificant, increase in the number of *P. herbstii* collected during the course of the study (1.125 NPT/year) may be due to the large food source provided by the non-native *P. armatus*, which *P. herbstii* have been observed to preferentially feed on (Hollebone, 2006; Hollebone and Hay, 2008). Alternatively, the slight population increase observed for *P. herbstii* may be attributable to the decrease in competition for food and habitat following the decline of the smaller *E. depressus*. Although *E. depressus* is a smaller species and tends to be more omnivorous than adults of *P. herbstii*, young *P. herbstii* have a diet and habitat preference that is similar to adults of *E. depressus* (McDonald, 1977, 1982).

Non-native species can threaten the natural balance of native communities (Carlton and Geller, 1993), however, the intensity of their impact often varies. We observed little to no effect on native crab communities due to the presence of the non-native crab species *P. armatus* over a ten-year period. Although the density of *P. armatus* changed during the study, the species has persisted and has not appeared to negatively affect the native *P. herbstii* population, confirming earlier conclusions made by Hollebone and Hay (2007). In contrast, the non-native parasitic barnacle, *L. panopaei*, appears to have had a dramatic effect on the density of *E. depressus* and significantly influenced crab community structure over the ten-year study period. Additional studies targeting oyster reefs elsewhere in the region are necessary to determine if these changes are localized or more widespread. The impacts of the altered mud crab community on the oyster reef habitat and greater biological community, if the effects of the introduction are permanent, have yet to be determined.

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**REFERENCES**


