Community shelter use in response to two benthic decapod predators in the Long Island Sound

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Abstract

To investigate community shelter effects of two invasive decapod species, *Hemigrapsus sanguineus* and *Carcinus maenas*, in the Long Island Sound (LIS), we deployed artificial shelters in the intertidal and immediate subtidal zones. These consisted of five groups during the summer: a control, a resident *H. sanguineus* male or female group, and a resident *C. maenas* male or female group. We quantified utilization of the shelters at 24 hours by counting crabs and fish present. We found significant avoidance of *H. sanguineus* in the field by benthic hermit crabs (*Pagurus* spp.) and significant avoidance of *C. maenas* by the seaboard goby (*Gobiosoma ginsburgi*). The grubby (*Myoxocephalus aeneus*) avoided neither treatment, probably since it tends to be a predator of invertebrates. *H. sanguineus* avoided *C. maenas* treatments, whereas *C. maenas* did not avoid any treatment. Seasonal deployments in the subtidal indicated cohabitation of a number of benthic species in the LIS, with peak shelter use corresponding with increased
predation and likely reproductive activity in spring and summer for green crabs (*C. maenas*),
hermit crabs (*Pagurus* spp.), seaboard gobies (*G. ginsburgi*), and grubbies (*Myoxocephalus aenaeus*).

Introduction

In marine systems, the availability of shelter and risk avoidance when choosing shelter has a profound effect for many animals on growth rates, survival, avoidance of predators, and particularly mating systems for decapod crustaceans (Atema, 1986; Perkins-Visser, Wolcott & Wolcott, 1996; Beck, 1997; Wieters et al., 2009). As shelter is often at a premium (O’Neill & Cobb, 1979), conferral of group defense can be beneficial. For example, juvenile spiny lobsters in the Florida Key exhibit cohabitation within and among species within the same shelter (Childress & Herrnkind, 2001a; Childress & Herrnkind, 2001b; Jordan, 2010). As this can result in negative competitive interactions, this requires the animal to evaluate the risk associated with cohabitation (Jordan, 2010). Many marine species have to select new shelter when they migrate into, out of, and within estuaries seasonally or with changes in abiotic factors such as dissolved O$_2$ or salinity (Pörtner, 2001; Ortiz-León, de Jesus-Navarrete & Sosa Cordero, 2007). Shelter use by different benthic species varies by season, since the specific shelter challenges faced by resident species with the presence of migratory species or influence of non-native species can vary by time of year and competition between animals (Perkins-Visser, Wolcott & Wolcott, 1996; Childress & Herrnkind, 2001a). In this study, we show Long Island Sound (LIS) benthic species not only modify their shelter use by season, but also by the presence of invasive decapod predators or competitors.
Decapod crustacean populations can be limited by sufficient access to shelter (Perkins-Visser, Wolcott & Wolcott, 1996; Childress & Herrnkind, 2001a). Particularly, decapod crustaceans, especially crabs and lobsters, are known to utilize benthic habitat differently depending on the sex of the individual (Hines, Lipcius & Haddon, 1987; Karnofsky, Atema & Elgin, 1989), and can behaviorally respond to the presence of only one individual in a shelter (Cowan & Atema, 1990). Shelter’s importance is also evident since mortality in the losing group can increase when interspecific and intraspecific competition in marine systems for quality shelter limits its accessibility (O’Neill & Cobb, 1979; Cobb, 1981; Richards & Cobb, 1986; Grove & Woodin, 1996; Brousseau, Kriksciun & Baglivo, 2003; Jordan, 2010). In the LIS intertidal and subtidal zones, both the European green crab, *Carcinus maenas* (Linnaeus, 1758), and the Asian shore crab, *Hemigrapsus sanguineus* (De Haan, 1835) are invasive species. These species are competitors for space and food with native species (MacDonald et al., 2007; Griffen, Guy & Buck, 2008), requiring the identification of those finfish and crustacean species that may also utilize the same shelter and are likely to be affected in currently-invaded areas in order to predict likely future effects on community members.

The invasion of *H. sanguineus* to the western North Atlantic Ocean supplanted the earlier invader, *C. maenas*, and *H. sanguineus* is currently invading Europe along with its congener, *Hemigrapsus takanoi* (Lohrer & Whitlatch, 2002; Asakura & Watanabe, 2005; van den Brink, Wijnhoven & McLay, 2012; Gothland et al., 2013; Gothland et al., 2014). The Asian shore crab, *H. sanguineus*, was first found on the U.S. east coast in New Jersey in 1988 (Williams & McDermott, 1990). Since then, it became the most dominant crab in the intertidal zone of the northwest Atlantic Ocean, with densities up to 300 individuals/m² (McDermott, 1998; Lohrer & Whitlatch, 2002; Kraemer et al., 2007). It is found subtidally, but in lower densities (pers. obs.).
H. sanguineus is a generalist omnivore and can survive in a wide range of salinities (Depledge, 1984; Hudson, 2011). It prefers rocky substrate to sand and settles in the presence of conspecific adult olfactory cues (Lohrer et al., 2000; Steinberg, Epifanio & Andon, 2007; Hudson, 2011; Rasch & O’Connor, 2012). In the intertidal zone, predation occurs from both terrestrial and marine sources, which makes H. sanguineus a vigorous intertidal competitor for space and shelter due to its avoidance of risk during shelter choice and aggression toward smaller interspecific competitors (Jones & Shulman, 2008; Wieters et al., 2009; Rasch & O’Connor, 2012; Peterson et al., 2014). As such, we wanted to see if the presence of this species impacted the use of shelter by LIS community members in the field.

The previous intertidal resident invader, the European green crab, C. maenas, is still seen in the intertidal and subtidal zone in the Long Island Sound, though in lower densities than in its home range (Amaral et al., 2009). The arrival of C. maenas occurred sometime pre-1817 (Say, 1817) and that of H. sanguineus in the late 1980s (Williams and McDermott, 1990). However, C. maenas itself is still a potent invasive species worldwide and on the North American continent (Freeman & Byers, 2006; Darling et al., 2008). As benthic animal survival is so tied to the availability and ability to maintain shelter (O’Neill & Cobb, 1979; Cobb, 1981; Richards & Cobb, 1986; Grove & Woodin, 1996; Brousseau, Kriksciun & Baglivo, 2003; Jordan, 2010), our main focus for this work was to elucidate the sublethal choice effect that these two species have on the use of shelter by native fauna in the LIS. This information can be used in areas where both of these species are still relatively new invaders, to allow for an informed management strategy of native species.

Our main objectives for this study were to: (1) capture any sexual variability in shelter use by decapods, as described above for other decapods, which was accomplished through a field
experiment with empty PVC artificial shelters as a control, and a male and female treatment for each of the two types of crab (*H. sanguineus* and *C. maenas*), for a total of five treatments; and (2) use these deployments and complementary laboratory studies (to better explain any effects of *C. maenas* and *H. sanguineus* on one another) to predict which LIS community species found in our shelters will be most affected by the presence of one of these invaders.

**Materials and Methods**

**Community Shelter Use**

To measure Long Island Sound (LIS) community shelter use differences in the field, we deployed a field shelter behavior assay. Benthic animals in the LIS are dependent on shelter for survival, so these shelter tubes imitate shelters that are unoccupied or occupied to test the potential for cohabitation with two important intertidal invaders in a shelter-limited area adjacent to habitat with ample shelter (small boulders). Replicates of the field apparatus (Figure 1B) were deployed during the summer of 2009 for approximately 24 hours in the immediate subtidal zone (~1 m depth) and intertidal zone (0.25 m above Mean Lower Low Water (MLLW), the lowest low tide daily) of the northwest end of Pine Island, Groton, CT USA (41°18’47.434” N, 72°3’36.216” W). The tubes were at least 1.5 meters apart, and were not attached to one another, but were all deployed along a uniform depth parallel to a shoreline with similar bottom characteristics along the length of the deployment. In cursory diving surveys, mobile animals seemed varied by species and fairly evenly distributed along the deployment location. This should have avoided the initial species approach phenomenon as much as possible. We operated under Connecticut Department of Environmental Protection Scientific Collector's Permits # SC-06040 and # SC-09015. Other researchers have quantified decapods’ responses artificial shelter
with conspecific presence (Nevitt et al. 2000, Childress & Herrnkind 2001a), so the apparatus was designed to fit the target species. The apparatuses were constructed with weathered (3+ years exposed to the elements) 5.08 cm PVC tubing, with two 30 cm sections connected by a PVC joint. Cages constructed of 0.5 cm plastic mesh were used to isolate the live treatment animal inside the tube. We saw some influence of individual presence on one another with different species in the laboratory, and the original idea was to pump (expensively) water over an individual in the field and into the tubes. We did not have sufficient funding for that design, so we were confident in using a single “bait” animal. Control tubes were deployed with an empty cage to provide internal structure, and all tubes were anchored with U-shaped steel rebar. After a 24-hour soak, divers capped each end, and deployed the next apparatus. The tubes were deployed over a two-week period with random assignment of treatments each day in groups of 20 to 25 tubes, until 60 replicates were reached for each treatment. Capped tubes were quantified each day for the presence of crab and arthropod species, and other macroinvertebrates and vertebrates.

Catch Per Unit Effort (CPUE) is reported here as percent of shelters used (%) calculated as the number of animals caught in each artificial shelter treatment, divided by the number of shelters for that treatment (60 per treatment). Data was analyzed in Systat 12.0 via one-way ANOVA, and Tukey’s Post-Hoc Test (alpha = 0.05).

We took two approaches: (1) to capture animals that may only be using subtidal shelters seasonally, we deployed the artificial shelters four times over the course of a year. (2) In order to gain a sense for the intertidal use of shelter, which is most used in the summer months in the LIS, we also deployed intertidal experimental artificial shelters during the summer.

Seasonal subtidal deployment
Due to dominance of *Hemigrapsus sanguineus* in the intertidal system, we wanted to see the overall effect on community shelter use across four seasons for this species in the subtidal zone. These shelters were deployed subtidally (~ 1 m depth) across four seasons in 2009, with control, and live male and female *H. sanguineus* bait treatments (total N=180 for each deployment).

*Summer subtidal and intertidal deployment*

In the summer months two additional treatments; live male and live female *Carcinus maenas* bait treatments were added. Thus, five treatments were used, along with the same control, live male and live female *H. sanguineus* treatments as already deployed in the seasonal deployment. We deployed the artificial shelters both in the subtidal and in the intertidal zone. As such, for summer experiments, each treatment was deployed in replicates of 60 both subtidally and intertidally (total N = 300 intertidal, N = 300 subtidal). A two-way ANOVA with tidal deployment and treatment was used to determine the interaction between treatment and tidal deployment, and size differences between subtidal and intertidal deployments were analyzed with Student’s t-test.

*Shelter interaction for *H. sanguineus* and *C. maenas***

To further determine size effects on dominance and shelter use of the two invaders, shelter competition experiments utilized size ratio for interspecific and intraspecific shelter dominance between *H. sanguineus* and *C. maenas*. Multiple carapace width ratios, approximately 3:1, 2:1, 1:1, 1:2, and 1:3 in replicates of 10, were used for a one-on-one laboratory shelter competition experiment that lasted 24 hours. We compared intraspecific (*H.*
sanguineus or C. maenas versus member of the same species) and interspecific (H. sanguineus versus C. maenas) competition trials. Shelter use frequency differences between competitors were analyzed using Fisher’s Exact Test. The effect of size ratio of competitors on “winner” and mortality was analyzed by a linear regression in R statistical software. Crabs were introduced to a plastic 18 cm x 31 cm arena with 2.5 cm of sand substrate and a 10 cm x 5.0 cm shelter made from 6.35 cm PVC pipe with a quarter of its circumference removed arranged in the container to have only one useable opening (Figure 1B). A clear piece of plexiglass was placed over the container to prohibit escape, and an airstone oxygenated the tank. Each competition experiment involved placing two individuals on opposite sides of the container, width-wise, while the shelter was opposite both of the individuals, length-wise. The two individuals in the container were then allowed to compete for the shelter over a 24-hour period, after which the positions of the crabs were noted as in the shelter or outside the shelter. Injuries to the claws or legs of each crab due to fighting were recorded. The plastic container, PVC pipe, and sand were cleaned with 10% bleach between replicates.

Results

Community Shelter Use

Four species commonly cohabitated in the subtidal artificial shelters: the green crab Carcinus maenas, hermit crabs Pagurus spp. (grouped by genus), the seaboard goby Gobiosoma ginsburgi, and the grubby Myoxocephalus aenaeus. Subtidal deployment caught very few Hemigrapsus sanguineus individuals (11 individuals in 960 replicates deployed). Seasonal change in shelter use (with no crabs present, or with H. sanguineus male, and H. sanguineus female present) occurred amongst the four most collected species (Fig. 2).
No significant difference (one-way ANOVA, $F = 1.394$, 4 d.f., $p = 0.236$, $N = 300$) was seen for *C. maenas* subtidal shelter preference by treatment. There is no indication of habitat partitioning by ontogeny for *C. maenas*, since carapace widths for summer subtidal and intertidal areas were not significantly different (mean = 25.4 mm for intertidal, mean = 25.64 mm for subtidal, Student’s t-test, $p = 0.95$). However, significant seasonal shelter usage changes were observed in *C. maenas* (one-way ANOVA, $F = 7.38$, 3 d.f., $p < 0.001$, $N = 721$). Spring shelter usage was nearly triple that of winter (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.001$), which then significantly (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.05$) dropped by 54% in the summer deployment (Fig. 2A). *C. maenas* also doubled its shelter use in autumn over the previous winter (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.05$ over winter values) (Fig. 2A). When all four seasons’ subtidal data are pooled, in which there were control, *H. sanguineus* male and *H. sanguineus* female treatments, *C. maenas* showed a trend for avoidance of the male *H. sanguineus* treatment over the control (one-way ANOVA, $F = 2.71$, 2 d.f., $p = 0.067$, $N = 721$, Tukey Post-Hoc $p = 0.068$, $p = 0.200$, for *H. sanguineus* male and *H. sanguineus* female treatments, respectively).

Other subtidal organisms showed changes in seasonal shelter use in our data. Pagurids changed their use of shelter (one-way ANOVA, $F = 19.399$, 3 d.f., $p < 0.001$, $N = 721$; all pairwise comparisons by Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.001$), with spring shelter usage 23 times that of winter, then a subsequent significant dip during the summer by about one third, and further dip from spring values during autumn to about 11 percent shelter use (Fig. 2B). The seaboard goby *Gobiosoma ginsburgi* (Fig. 2C) showed a significant seasonal signal as well (one-way ANOVA, $F = 32.425$, 3 d.f., $p < 0.001$, $N = 721$; Table 1B; all pairwise comparisons by Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.001$), with a significant increase in shelter use by
about 23 times from winter to spring, and a doubling of spring values during summer. Similarly, *Myoxocephalus aenaeus* (Fig. 2D) significantly (one-way ANOVA, $F = 5.061$, 3 d.f., $p = 0.002$, $N = 721$) increased its shelter use during summer versus winter and spring (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.005$) and decreased its shelter use in autumn (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.05$).

Organisms were only found in sufficient numbers to merit comparison by treatment in summer. As for subtidal summer shelter use, *Pagurus* spp. showed preference for treatments (one-way ANOVA, $F = 4.017$, 4 d.f., $p = 0.003$, $N = 300$), specifically avoiding both *H. sanguineus* male and female treatments (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.03$) in the subtidal (Fig. 3A) and using these shelters 1 to 2 times less often than others. The goby *G. ginsburgi* also showed preference for specific treatment shelters (one-way ANOVA, $F = 15.277$, 4 d.f., $p < 0.001$, $N = 300$) by avoiding completely (Tukey’s Post-Hoc Test, alpha 0.05, $p < 0.001$) both of the *C. maenas* treatments (Fig. 3B). The grubby *M. aenaeus* did not show preference (one-way ANOVA, $F = 0.823$, 4 d.f., $p = 0.511$, $N = 300$) for any treatments, and was found at lower catch rates (data are in attached supplemental data).

Only *C. maenas* and *H. sanguineus* were found in sufficient numbers in summer intertidal deployments to merit analysis by treatment. In those, *C. maenas* showed a significantly lower intertidal shelter use (one-way ANOVA, $F = 29.290$, $p < 0.001$, $N = 600$; Table 1C) than subtidal shelter use by a factor of about 3.6 times (Supplemental Fig. 1A). For summer deployments, no significant difference nor trend (one-way ANOVA, $F = 1.394$, $p = 0.236$, $N = 300$) was observed for subtidal shelter preference by treatment in *C. maenas* (Supplemental Fig. 1B, 1C). *H. sanguineus* exhibited the opposite pattern, with significantly lower (one-way ANOVA, $F = 30.88$, 1 d.f., $p < 0.001$, $N = 600$) subtidal shelter use (1% use at 3 crabs in 300 shelters) than
intertidal shelter use (14% use at 42 crabs in 300 shelters) (Supplemental Fig. 2). No comparison by treatment was possible for \textit{H. sanguineus} in subtidal treatments due to low catch rate, but catch efficiency was approximately 25 percent overall in the intertidal zone.

In the summer intertidal experiments, differences in male and female \textit{H. sanguineus} behavior were observed. \textit{H. sanguineus} males used shelters of any treatment 8.3% of the time (N = 301 shelters), but used intertidal treatments differently (one-way ANOVA, F = 3.46, 4 d.f., p = 0.0088, N = 301). Males displayed a lower (3.3% of treatment shelters) use of \textit{C. maenas} male (Tukey Post-Hoc, p = 0.029) and \textit{C. maenas} female (1.6% of total shelters) treatments (Tukey Post-Hoc, p = 0.011) when compared to the 16.9% use of \textit{H. sanguineus} female treatment shelters (Fig. 4A). Female \textit{H. sanguineus} crabs also differed significantly in use of intertidal shelters (one-way ANOVA, F = 2.577, 4 d.f., p = 0.038, N = 301), but across all treatments only used 4.65% of them (N=301 shelters). Female \textit{H. sanguineus} crabs (Fig. 4B) did not choose conspecific \textit{H. sanguineus} male treatment shelters (none were used, 0%) when compared with the control 11.7% usage rate (Tukey Post-Hoc, p = 0.018). There were no significant differences for other treatments, perhaps due to females’ low shelter usage rate.

When pooled regardless of sex or maturity, significant differences were found in use of intertidal treatments by \textit{H. sanguineus} (one-way ANOVA, F = 5.39, 4 d.f., p = 0.0003, N = 306). In intertidal treatments, \textit{H. sanguineus} showed no significant reduction in shelter use of either \textit{H. sanguineus} treatments over control (cage only) treatment (Tukey Post-Hoc, p > 0.05), sticking at 25% (15/60) use for control shelters, 8.33% (5/60) use for \textit{H. sanguineus} male treatments, and 25.4% (15/59) use for \textit{H. sanguineus} female treatments. The greater usage of \textit{H. sanguineus} female shelters over all other crab treatment shelters is significant (\textit{H. sanguineus} male, and both \textit{C. maenas} male and female treatments, Tukey Post-Hoc, p = 0.040, p = 0.006, p = 0.002,
respectively). However, *H. sanguineus* did significantly decrease use of *C. maenas* female treatment shelters to 4.84% (3/62) (Tukey Post-Hoc, p = 0.031), and trended (Tukey Post-Hoc, p = 0.064) to decrease (6.67%, or 4/60) use of *C. maenas* male treatment shelters (Fig. 4C). When subtidal and intertidal summer data are included together, these treatment differences still hold in *H. sanguineus* residency (two-way ANOVA, N= 600, Tidal Deployment: F = 32.83, 1 d.f., p < 0.0001, Treatment: F = 4.54, 4 d.f., p = 0.0012, Tidal Deployment*Treatment, F = 3.698, 4 d.f., p = 0.0055).

In laboratory direct interspecific and intraspecific individual competition, *H. sanguineus* is more likely to use shelter than *C. maenas* (Fisher’s Exact Test, p = 0.0020, N = 64) (Fig. 5A). In interspecific competition experiments, *H. sanguineus* utilized (“won”) shelter 32.8% of the time, whereas *C. maenas* only utilized shelter 9.1% of the time. While this comparison is interesting on its surface, intraspecific competition puts this in context. When *C. maenas* competes against an individual *C. maenas*, one of the crabs utilizes the shelter 20.1% of the time (N = 29), which is not significantly different than its 9.1% shelter from when it was competing against *H. sanguineus* (Fisher’s Exact Test, p = 0.1818, N = 93). The same result is observed for *H. sanguineus*, which uses shelter at 33.3% rate (N = 39) when competing against another *H. sanguineus*, which is also not significantly different in its shelter use from when it was competing against *C. maenas* (Fisher’s Exact Test, p = 0.3019, N = 103). When analyzed by the effect of competitor size (Fig. 5A), *H. sanguineus* had a significant linear regression for shelter use (\(y = -0.1835x + 0.5728\), \(R^2 = 0.7449\), p = 0.0027), but *C. maenas’* use of shelter was not significant by linear regression (p = 0.49). When crabs of the same approximate size are compared (1:1 ratio group, N = 17), *H. sanguineus* is significantly more likely to end up in the shelter than *C. maenas* in interspecific trials (Fisher’s Exact Test, p = 0.0024, N = 17). However,
neither is more likely to be injured or die when evenly matched by size. In interspecific trials, both *H. sanguineus* and *C. maenas* were killed more often when they were smaller than the opposing crab (Fig. 5B), and linear regressions explain a large amount of the variation of death rates in both species. Competitor size explains 96% of the variation in death rates of *H. sanguineus* ($y = -0.3459x - 0.1805$ ($R^2 = 0.9607$, $p = 3.555 \times 10^{-6}$)), and 67% of that in *C. maenas* death rates ($y = -0.3101x + 0.8744$ ($R^2 = 0.6704$, $p = 0.0069$)). *C. maenas* and *H. sanguineus* both exhibit cannibalism when large differences in carapace width exist (see supplemental data), and readily prey upon interspecific individuals.

**Discussion**

All collected species showed an increased use of shelter during warmer months, probably correlated with the increased predation in this system with increasing seasonal temperature (Clark, 1968; O’Neill & Cobb, 1979) and increased need for seasonal mating and reproduction. Specifically, *Myoxocephalus aenaeus* and *Pagurus* spp. shelter competition with these decapods may have a greater impact during spring and summer months. Decapods *Carcinus maenas* and the *Pagurus* spp. complex showed peak shelter use in the spring deployments, and both of the fish species (*Gobiosoma ginsburgi* and *M. aenaeus*) peaked during summer. Other *Gobiosoma* spp. exhibit seasonal patterns in shelter use, primarily with an increase in use of seagrass shelter in July and October (King & Sheridan, 2006). Shelter competition could further pressure *G. ginsburgi* as *C. maenas* invades further into Canada in the North Atlantic (Roman & Darling, 2007), and this shelter competition will likely affect congener *Gobiosoma* species in areas other than the Long Island Sound (LIS) at risk of *C. maenas* invasion.
Some species were collected in these shelters during this work, but not in sufficient numbers for seasonal or treatment analysis. The effects on the following species could not be assessed (see supplemental data): the oyster drill *Nucella lapillus* (6 collected), shrimp *Palaemontes* spp. (11 collected), *Crangon septemspinosa* (5 collected), *Cancer irroratus* (5 collected), *Panopeus herbstii* (21 collected), *Dyspanopeus sayi* (9 collected), Xanthid crab settlers (8 collected), *Pholis gunnelus* (1 collected), *Anguilla rostrata* (4 collected), *Littorina littorea* (17 collected), and the cunner *Tautogolabrus adspersus* (17 collected). These collected species could just be in lower numbers, not typically use shelter (not likely for the crab species), or be adversely affected by the presence of the two crabs. Determining the proximal cause requires further comparative work, but in the Gulf of Maine, both *Hemigrapsus sanguineus* and *C. maenas* make intertidal shelter maladaptive for native species (Griffen & Riley, 2015). If there is any intraguild predation interference on other community members as Griffen and Byers (2006; 2009) found between *H. sanguineus* and *C. maenas*, this merits additional investigation with respect to shelter. It is also typically difficult to dislodge a resident decapod from a shelter, but some species are able to do this, such as the invasive *Eriocheir sinensis* (Gilbey, Attrill & Coleman, 2008), and in *H. sanguineus* and *Hemigrapsus oregonensis* (Jensen, McDonald & Armstrong, 2002; Lohrer & Whitlatch, 2002). If LIS shelter-using species cannot dislodge *H. sanguineus* or *C. maenas*, they may just avoid the shelter altogether, resulting in our undersampling of those species.

Species within the LIS community also responded to the treatments in our experiments. *Pagurus* spp. avoided *H. sanguineus* treatments, perhaps indicating previous individual experience with them as a predator. This was observed with induced responses to *C. maenas* predators in *Mytilus edulis* mussels (Freeman & Byers, 2006), and underscores how changes in
dominance by each crab species could impact LIS community members, especially bivalve populations. *C. maenas* consistently consumes more blue mussels than *H. sanguineus* and per capita predation on mussels decreases with interspecific and intraspecific interference between and within *H. sanguineus* and *C. maenas* (Griffen, 2006). Prior to this work, *Pagurus* spp. was not specifically documented as potential prey of *H. sanguineus* (Brousseau and Baglivo, 2005), but crustacean parts were found in the stomachs of *H. sanguineus* (Ledesma & O’Connor, 2001).

Seaboard gobies, *G. ginsburgi*, actively avoided *C. maenas* treatments, indicating likely predation, but showed no aversion to *H. sanguineus* present in shelters, likely since interactions with this species are unlikely in the subtidal. Congener *Gobiosoma* spp. in non-invaded areas would be expected to experience the same risk and respond in the same way. Newly-invaded communities are negatively impacted by *C. maenas* (Walton et al., 2002), and it likely had a similar impact upon its invasion to eastern North America (Freeman et al., 2014; Griffen & Riley, 2015). Although not much is known about *G. ginsburgi*’s specific behavior, congeners prefer woody debris as shelter (Everett & Ruiz, 1993), and males guard eggs even through near-lethal levels of hypoxia (Breitburg, 1992). There is high tidal flow at our study site, which are the preferred conditions for congener *Gobiosoma* spp. (Tolley et al., 2006), but there may also be a population that moves up the estuary (Schultz et al., 2003) that merits investigation. *Gobiosoma robustum* chooses sand over seagrass shelter in the presence of a predator (Schofield, 2003); therefore, a similar pattern in *G. ginsburgi* would mean a greater use of sand, and thus greater exposure to finfish predators in areas where *C. maenas* is present.

No treatment was preferred by the grubby *M. aenaeus*, but it is known to be a predator of small decapods (van der Meeren, 2000). The area where we deployed these shelters does not have much vegetation and therefore is not a likely nursery habitat for *M. aenaeus* (Lazzari,
Sherman & Kanwit, 2003), but it did still show seasonal shelter use in this system. Use of these
shelters may be due to the slower escape response accelerations and velocities found in this
genus than other teleosts (Jordan, Herbert & Steffensen, 2005), along with their role as an active
winter predator of small lobsters (van der Meeren, 2000). The lack of correlation of *M. aenaeus*
shelter use with treatments in our experiments demonstrated no interaction with *C. maenas* and
*H. sanguineus*.

In this part of the LIS, *C. maenas* utilized artificial shelters far more in the subtidal than
the intertidal, which is a reflection of its higher subtidal abundance, but this exclusively subtidal-
use phenomenon has not been observed in other *C. maenas*-invaded areas, nor in its native
European range (Amaral et al., 2009). The dominance of competing *H. sanguineus* in the
intertidal zone of the LIS likely decreases the availability of these shelters for native species as it
does in the Gulf of Maine (Griffen & Riley, 2015). However, our field experiments do not
provide evidence of a *H. sanguineus*-mediated decrease in the *C. maenas* utilization of artificial
shelters in the intertidal nor subtidal, even though we saw a difference in sheltering patterns
between these two in the laboratory when pitted against one another. Ultimately, there is no
evidence from these data that *H. sanguineus* drive the difference in abundance of *C. maenas*
between subtidal and intertidal zones. This is consistent with work in Dutch estuaries where both
*H. sanguineus* and *H. takanoi* are invading and competing with *C. maenas* (van den Brink,
Wijnhoven & McLay, 2012), but the decline in *C. maenas* seems to be due to overall decline in
environmental quality. However, a difference could arise if *C. maenas* cannot readily use shelter
as easily, and *H. sanguineus* was clearly the shelter winner in similar-sized crabs in our
laboratory trials. This could feed into the probable negative impact *H. sanguineus* has on early
settlement survival for this population of *C. maenas* crabs. Work done by Lohrer and Whitlatch
(2002) corroborates this fact, as zero-year *C. maenas* were not found as often in field enclosures with *H. sanguineus*. From these data and the literature, we can postulate that adult *C. maenas* will shelter where it wants regardless of conspecific or heterospecific presence, and the intertidal/subtidal pattern is likely due to interactions early in ontogeny (Lohrer & Whitlatch 2002).

It is clear that both *C. maenas* and *H. sanguineus* avoided each another. While *C. maenas* does not avoid shelter regardless of presence of a competitor in summer data, it does show a trend for avoidance of *H. sanguineus* when all seasonal data is pooled. In fact, same-size *C. maenas* are inferior shelter competitors to *H. sanguineus* in laboratory experiments. One would expect a strong signal for avoidance of aggressive male crabs of conspecifics and heterospecifics to avoid injury, but only *H. sanguineus* showed an avoidance of conspecific males, and it also avoided shelters with either male or female *C. maenas* (Fig. 4C and Supplemental Figure 1).

That *C. maenas* does not show stronger avoidance of the heterospecific *H. sanguineus* shelters of either sex makes them more likely to be negatively affected in the way we observed in the direct competition studies, whereas *H. sanguineus* seems to avoid this negative interaction.

When *H. sanguineus* is the same size as its competitor or larger, it is not only more likely to inhabit the shelter, but also more likely to kill its competitor, in this case *C. maenas*. *C. maenas* will do the same to a smaller *H. sanguineus*, but we saw that when competing against a conspecific *C. maenas* it is less likely to use shelter in the first place. *H. sanguineus* is likely to avoid potential competitors in the field, but these data are size-dependent, consistent with earlier work (Lohrer & Whitlatch, 2002). Thus, one can conclude that this inherent lower use of shelter by *C. maenas*, combined with the agonistic interaction with *H. sanguineus*, results in an increased exposure of *C. maenas* to predation and desiccation in the intertidal zone and partially
results in *H. sanguineus* dominance of this zone. The limited use of the subtidal zone by *H. sanguineus* in seasonal and summer subtidal shelter deployments means that in this particular system, it does not often interact with *C. maenas* in the subtidal. Although *H. sanguineus* is sometimes found in large numbers subtidally, this has been in marinas not along rocky shorelines (Gilman & Grace, 2009). This adds a critical dynamic to interspecific interaction for *H. sanguineus* in the intertidal zone: as it establishes in a new area, it will consume all likely competitors, dominate shelter use, and result in greater exposure of competitors to both terrestrial and marine predation (at high tide).

Shelter use data for *H. sanguineus* shows avoidance of potentially dangerous heterospecifics (*C. maenas* of both sexes) and conspecific male shelters and a preference for conspecific female shelters and unoccupied control shelters. This may enhance *H. sanguineus*’ survival and reproduction through avoidance of antagonistic interactions like predation and competition, and indicates it can detect and use conspecific and heterospecific presence as an adult in addition to as a megalopa (Steinberg, Epifanio & Andon, 2007). In the laboratory direct competition individual match-ups, adult male *H. sanguineus* were more likely to take over vacant shelter. It is common in lobsters (O’Neill & Cobb, 1979) and pea crabs (Grove & Woodin, 1996) to use the presence of conspecifics to determine its use of shelter, but this avoidance behavior runs counter to the communal denning seen in lobster species (Zimmer-Faust & Spanier 1987), which is often due to ontogeny (Childress & Herrnkind 1996) or reproduction (Bushman & Atema 1997). In the subtidal, other decapods seem to avoid *H. sanguineus* treatments over the other three treatments, underscoring how the presence of this species deters other decapods. Adult olfactory cues were implicated in metamorphosis and settlement of *H. sanguineus* (Steinberg, Epifanio & Andon, 2007; Rasch & O’Connor, 2012) near conspecifics,
and now we can conclude that adult presence also has an impact upon small-scale spatial
patterns, by indicating evaluation and mediation of risk by the adult animal.
From our data and the literature, changes in the abundances of these two invaders will
clearly result in changes to LIS community shelter use. *C. maenas* does not compete for shelter
as well as *H. sanguineus*, and the effects that the presence of each crab has on other community
members’ use of shelter means there are different effects of each on those populations’ risk of
predation. As such, changes in abundances of each of these two species may have different
shelter and seasonal effects on different LIS community members, especially as they impact
potential survival of *G. ginsburgi* and the *Pagurus* spp. complex, not to mention the potentially
negative effects of the presence of these *H. sanguineus* and *C. maenas* have on each other.

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References

Amaral V, Cabral HN, Jenkins S, Hawkins S, Paula J. 2009. Comparing quality of estuarine and nearshore intertidal habitats for Carcinus maenas. Estuarine, Coastal and Shelf Science 83:219-226. DOI: 10.1016/j.ecss.2009.03.029

Asakura A, Watanabe S. 2005. Hemigrapsus takanoi, new species, a sibling species of the common Japanese intertidal crab H. penicillatus (Decapoda: Brachyura: Grapsoidea). Journal of Crustacean Biology 25(2):279-292. DOI: 10.1651/C-2514

Atema J. 1986. Review of sexual selection and chemical communication in the lobster, Homarus americanus. Canadian Journal of Fisheries and Aquatic Sciences 43:2283-2290. DOI: 10.1139/f86-279

Beck M. 1997. A test of the generality of the effects of shelter bottlenecks in four stone crab populations. Ecology 78:2487-2503. DOI: 10.1890/0012-9658(1997)078[2487:ATOTGO]2.0.CO;2

Breitburg D. 1992. Episodic hypoxia in Chesapeake Bay: Interacting effects of recruitment, behavior, and physical disturbance. Ecological Monographs 62:525-525-546. DOI: 10.2307/2937315
Brousseau DJ, Baglivo JA. 2005. Laboratory investigations of food selection by the Asian shore crab, *Hemigrapsus sanguineus*: algal versus animal preference. *Journal of Crustacean Biology* 25(1):130-134. DOI: 10.1651/C-2530

Brousseau DJ, Kriksciun K, Baglivo JA. 2003. Fiddler crab burrow usage by the Asian crab, *Hemigrapsus sanguineus*, in a Long Island Sound salt marsh. *Northeastern Naturalist* 10(4):415-420. DOI: 10.1656/1092-6194(2003)010[0415:FCBUBT]2.0.CO;2

Bushmann PJ, Atema J. 1997. Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*. *Canadian Journal of Fisheries and Aquatic Sciences* 54:647-654. DOI: 10.1139/f96-302

Childress MJ, Herrnkind WF. 1996. The ontogeny of social behavior among juvenile Caribbean spiny lobsters. *Animal Behaviour* 51:675-687. DOI: 10.1006/anbe.1996.0071

Childress MJ, Herrnkind WF. 2001a. The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behaviour* 62:465-472. DOI: 10.1006/anbe.2001.1760

Childress MJ, Herrnkind WF. 2001b. Influence of conspecifics on the ontogenetic habitat shift of juvenile Caribbean spiny lobsters. *Marine and Freshwater Research* 52:1077-1084. DOI: 10.1071/MF01047
Clark, J. 1968. Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. *Transactions of the American Fisheries Society* 97(4):320-343. DOI: 10.1577/1548-8659(1968)97[320:SMOSBC]2.0.CO;2

Cobb JS. 1981. Behaviour of the Western Australian Spiny Lobster, *Panulirus cygnus* George, in the Field and Laboratory. *Australian Journal of Marine and Freshwater Research* 32(3):399-409. DOI: 10.1071/MF9810399

Cowan DF, Atema J. 1990. Moult staggering and serial monogamy in American lobsters, *Homarus americanus*. *Animal Behaviour* 39(6):1199-1206. DOI: 10.1016/S0003-3472(05)80792-4

Darling J, Bagley M, Roman J, Tepolt C, Geller J. 2008. Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. *Molecular Ecology* 17:4992-4992-5007. DOI: 10.1111/j.1365-294X.2008.03978.x

Depledge MH. 1984. Cardiac activity in the intertidal crab *Hemigrapsus sanguineus* (De Haan). *Asian Marine Biology* 1:115-123.

Everett R, Ruiz G. 1993. Coarse woody debris as a refuge from predation in aquatic communities. An experimental test. *Oecologia* 93:475-475-486. DOI: 10.1007/BF00328954
Freeman AS, Byers JE. 2006. Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations. *Science* 313:831-833. DOI: 10.1126/science.1125485

Freeman AS, Dernbach E, Marcos C, Koob E. 2014. Biogeographic contrast of *Nucella lapillus* responses to *Carcinus maenas*. *Journal of Experimental Marine Biology and Ecology* 452:1-8. DOI: 10.1016/j.jembe.2013.11.010

Gilbey V, Attrill MJ, Coleman RA. 2008. Juvenile Chinese mitten crabs (*Eriocheir sinensis*) in the Thames estuary: distribution, movement, and possible interactions with the native crab *Carcinus maenas*. *Biological Invasions* 10:67–77. DOI: 10.1007/s10530-007-9110-4

Gilman M, Grace SP. 2009. Use of Subtidal Habitat by the Asian Shore Crab *Hemigrapsus sanguineus* in Long Island Sound. *Northeastern Naturalist* 16(3):481-487. DOI: 10.1656/045.016.n314

Gothland M, Dauvin JC, Denis L, Jobert S, Ovaert J, Pezy JP, Spilmont N. 2013. Additional records and distribution (2011–2012) of *Hemigrapsus sanguineus* (De Haan, 1835) along the French coast of the English Channel. *Management of Biological Invasions* 4(4):305-315. DOI: 10.3391/mbi.2013.4.4.05

Gothland M, Dauvin JC, Denis L, Dufossé F, Jobert S, Ovaert J, Pezy JP, Rius AT, Spilmont N. 2014. Biological traits explain the distribution and colonisation ability of the invasive shore crab
525 Hemigrapsus takanoi. *Estuarine, Coastal and Shelf Science* 142:41-49. DOI:
526 10.1016/j.ecss.2014.03.012
527
528 Griffen BD. 2006. Detecting emergent effects of multiple predator species. *Oecologia*
529 148(4):702-709. DOI: 10.1007/s00442-006-0414-3
530
531 Griffen BD, Byers JE. 2006. Partitioning mechanisms of predator interference in different
532 habitats. *Oecologia* 146:608-614. DOI: 10.1007/s00442-005-0211-4
533
534 Griffen BD, Guy T, Buck JC. 2008. Inhibition between invasives: a newly introduced predator
535 moderates the impacts of a previously established invasive predator. *Journal of Animal Ecology*
536 77:32-40. DOI: 10.1111/j.1365-2656.2007.01304.x
537
538 Griffen BD, Byers JE. 2009. Community impacts of two invasive crabs: the interactive roles of
539 density, prey recruitment, and indirect effects. *Biological Invasions* 11:927–940. DOI:
540 10.1007/s10530-008-9305-3
541
542 Griffen BD, Riley ME. 2015. Potential impacts of invasive crabs on one life history strategy of
543 native rock crabs in the Gulf of Maine. *Biological Invasions* 17:2533–2544. DOI:
544 10.1007/s10530-015-0890-7
545
546 Grove MW, Woodin SA. 1996. Conspecific Recognition and Host Choice in a Pea Crab, *Pinnixa*
547 *chaetopterana* (Brachyura: Pinnotheridae). *Biological Bulletin* 190:359-366.
Hines A, Lipcius R, Haddon A. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Marine Ecology Progress Series* 36:55-64.

Hudson DM. 2011. Characteristics Contributing to Invasiveness of the Asian Shore Crab, *Hemigrapsus sanguineus*. PhD dissertation, University of Connecticut, Storrs, CT.

Jensen GC, McDonald PS, Armstrong DA. 2002. East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Marine Ecology Progress Series* 225:251-262. DOI: 10.3354/meps225251

Jones PL, Shulman MJ. 2008. Subtidal-intertidal trophic links: American lobsters [*Homarus americanus* (Milne-Edwards)] forage in the intertidal zone on nocturnal high tides. *Journal of Experimental Marine Biology and Ecology* 361:98-103. DOI: 10.1016/j.jembe.2008.05.004

Jordan A, Herbert N, Steffensen J. 2005. Escape performance in three teleosts from West Greenland. *Polar Biology* 28:164-167. DOI: 10.1007/s00300-004-0679-0

Jordan TS. 2010. The role of behavioral temperaments on the ecology of the Caribbean reef octopus, *Octopus briareus*. Masters thesis, Clemson University, Clemson, SC.
Karnofsky EB, Atema J, Elgin RH. 1989. Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. *The Biological Bulletin* 176(3):239-246.

King S, Sheridan P. 2006. Nekton of New Seagrass Habitats Colonizing a Subsided Salt Marsh in Galveston Bay, Texas. *Estuaries and Coasts* 29:286-296. DOI: 10.1007/BF02781997

Kraemer GP, Sellberg M, Gordon A, Main J. 2007. Eight-year record of *Hemigrapsus sanguineus* (Asian Shore Crab) invasion in Western Long Island Sound estuary. *Northeastern Naturalist* 14(2):207-224. DOI: 10.1656/1092-6194(2007)14[207:EROHSA]2.0.CO;2

Lazzari M, Sherman S, Kanwit J. 2003. Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. *Estuarine, Coastal and Shelf Science* 56:73-73-84. DOI: 10.1016/S0272-7714(02)00122-1

Ledesma ME, O’Connor NJ. 2001. Habitat and diet of the non-native crab *Hemigrapsus sanguineus* in southeastern New England. *Northeastern Naturalist* 8(1):63-78. DOI: 10.1656/1092-6194(2001)008[0063:HADOTN]2.0.CO;2

Lohrer AM, Whitlatch RB. 2002. Interactions among aliens: Apparent replacement of one exotic species by another. *Ecology* 83(3):719-732. DOI: 10.1890/0012-
Lohrer AM, Whitlatch RB, Wada K, Fukui Y. 2000. Home and away: comparisons of resource utilization by a marine species in native and invaded habitats. *Biological Invasions* 2:41-57. DOI: 10.1023/A:1010069327402

MacDonald JA, Roudez R, Glover T, Weis JS. 2007. The invasive green crab and Japanese shore crab: behavioral interactions with a native crab species, the blue crab. *Biological Invasions* 9:837–848. DOI 10.1007/s10530-006-9085-6

McDermott JJ. 1998. The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology. *ICES Journal of Marine Science* 55:289-298. DOI: 10.1006/jmsc.1997.0273

Nevitt G, Pentcheff ND, Lohmann KJ, Zimmer RK. 2000. Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecific odors in the field. *Marine Ecology Progress Series* 203:225-231. DOI: 10.3354/meps203225

O'Neill DJ, Cobb JS. 1979. Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). *Marine Behaviour and Physiology* 6(1):33-45. DOI: 10.1080/10236247909378551

Ortiz-León HJ, de Jesus-Navarrete A, Sosa Cordero E. 2007. Temporal and spatial distribution of the crab *Callinectes sapidus* (Decapoda : Portunidae) in Chetumal Bay, Quintana Roo, Mexico. *Revista de Biología Tropical* 55:235-245.
Perkins-Visser E, Wolcott TG, Wolcott DL. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology* 198:155-173. DOI: 10.1016/0022-0981(96)00014-7

Peterson BJ, Fournier AM, Furman BT, Carroll JM. 2014. *Hemigrapsus sanguineus* in Long Island salt marshes: experimental evaluation of the interactions between an invasive crab and resident ecosystem engineers. *PeerJ* 2:e472. DOI: 10.7717/peerj.472

Pörtner HO. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenshaften* 88:137-146. DOI: 10.1007/s001140100216

Rasch, JA, O’Connor NJ. 2012. Development and behavior of megalopae of the non-native crab *Hemigrapsus sanguineus* in response to chemical cues from coastal fishes. *Journal of Experimental Marine Biology and Ecology* 416-417:196-201. DOI: 10.1016/j.jembe.2011.12.012

Richards RA, Cobb JS. 1986. Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size. *Canadian Journal of Fisheries and Aquatic Sciences* 43(11):2250-2255. DOI: 10.1139/f86-276

Roman J, Darling JA. 2007. Paradox lost: genetic diversity and the success of aquatic invasions. *TRENDS in Ecology and Evolution* 22(9):454-464. DOI: 10.1016/j.tree.2007.07.002
Say T. 1817. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 1:57-63.

Schofield P. 2003. Habitat selection of two gobies (*Microgobius gulosus, Gobiosoma robustum*): influence of structural complexity, competitive interactions, and presence of a predator. *Journal of Experimental Marine Biology and Ecology* 288:125-137. DOI: 10.1016/S0022-0981(03)00004-2

Schultz ET, Lwiza KMM, Fencil MC, Martin JM. 2003. Mechanisms promoting upriver transport of larvae of two fish species in the Hudson River estuary. *Marine Ecology Progress Series* 251:263-277. DOI: 10.3354/meps251263

Steinberg MK, Epifanio CE, Andon A. 2007. A highly specific chemical cue for the metamorphosis of the Asian shore crab, *Hemigrapsus sanguineus*. *Journal of Experimental Marine Biology and Ecology* 347:1-7. DOI: 10.1016/j.jembe.2007.02.005

Tolley S, Volety A, Savarese M, Walls L, Linardich C, Everham E. 2006. Impacts of salinity and freshwater inflow on oyster-reef communities in Southwest Florida. *Aquatic Living Resources* 19:371-387. DOI: 10.1051/alr:2007007

van den Brink AM, Wijnhoven S, McLay CL. 2012. Competition and niche segregation following the arrival of *Hemigrapsus takanoi* in the formerly *Carcinus maenas* dominated Dutch delta. *Journal of Sea Research* 73:126-136. DOI: j.seares.2012.07.006
van der Meeren GI. 2000. Predation on hatchery-reared lobsters released in the wild. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1794-1803. DOI: 10.1139/f00-134

Walton WC, MacKinnon C, Rodriguez LF, Proctor C, Ruiz GM. 2002. Effect of an invasive crab upon a marine fishery: green crab, *Carcinus maenas*, predation upon a venerid clam, *Katelysia scalarina*, in Tasmania (Australia). *Journal of Experimental Marine Biology and Ecology* 272:171-189. DOI: 10.1016/S0022-0981(02)00127-2

Wieters EA, Salles E, Januario SM, Navarrete SA. 2009. Refuge utilization and preferences between competing intertidal crab species. *Journal of Experimental Marine Biology and Ecology* 374:37-44. DOI: 10.1016/j.jembe.2009.04.006

Williams AB, McDermott JJ. 1990. An eastern United States record for the western Indo-Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae). *Proceedings of the Biological Society of Washington* 103:108-109.

Zimmer-Faust RK, Spanier E. 1987. Gregariousness and sociality in spiny lobsters: implications for den habitation. *Journal of Experimental Marine Biology and Ecology* 105:57-71. DOI: 10.1016/S0022-0981(87)80029-1
Figure Legends

Fig. 1: Field and laboratory shelter setup. Over the course of several weeks, the diagrammed artificial shelter was deployed at the northwest side of Pine Island, USA (41°18’47.434” N, 72°3’36.216” W) by fixing it to the sediment for a 24-hour soak of the treatments described in the Methods. B) Shelter setup for direct shelter competition experiments between Hemigrapsus sanguineus and Carcinus maenas, which was completed in an 18 cm x 31 cm plastic box with sand substrate for 24 hours. A 10 cm x 5.0 cm shelter, made from 6.35 cm PVC pipe with a quarter of its circumference removed, was arranged in the container to have only one useable opening.

Fig. 2: Seasonal subtidal shelter use. Seasonal subtidal shelter use across seasons for all treatments for which there are seasonal data (control, Hemigrapsus sanguineus male, and H. sanguineus female) in catch per unit effort (CPUE, in number of animals per number of tubes (n = 180 tubes for each bar)) mean ± SE for: (A) Carcinus maenas, (B) Pagurus spp., (C) Gobiosoma ginsburgi, and (D) Myoxocephalus aenaeus. Significance between seasons indicated by brackets: “*” = p < 0.05, “**” = p < 0.01, “***” = p < 0.001.
Fig. 3: Summer subtidal shelter use in hermit crabs and gobies. Summer subtidal shelter use across treatments in catch per unit effort (CPUE, in number of animals per number of traps (n = 60 for each bar)) mean ± SE for (top graph) hermit crab *Pagurus* spp. and (lower graph) seaboard goby *Gobiosoma ginsburgi*. Treatments: NC = No Crab, HSM = *H. sanguineus* Male, HSF = *H. sanguineus* Female, CMM = *C. maenas* Male, and CMF = *C. maenas* Female. Bars with the same letter are statistically similar (p > 0.05).

Fig. 4: Summer shelter choice in *Hemigrapsus sanguineus*. Stated in catch per unit effort (CPUE, in number of animals caught per number of tubes (n = 60 tubes for each bar)) mean ± SE. Treatments were: HSm = *H. sanguineus* male, HSf = *H. sanguineus* female, CMm = *Carcinus maenas* male, CMf = *C. maenas* female. Results for shelter occupancy are shown for A) intertidal male *H. sanguineus*, B) intertidal female *H. sanguineus*, and C) overall intertidal *H. sanguineus*. Significance between treatments indicated by brackets: “*” = p < 0.05, “**” = p < 0.01, “***” = p < 0.001.

Fig. 5: Laboratory shelter competition between *Hemigrapsus sanguineus* and *Carcinus maenas*. A) Fraction of each species in shelter after 24 hours of direct shelter competition between an individual *H. sanguineus* and *C. maenas*. At the left side of the x-axis, *H. sanguineus* are larger by carapace width (CW), and on the right, *C. maenas* are larger. N is between 4 and 17 for each point. B) Fraction of each species dead after 24 hours of direct shelter competition between an individual *H. sanguineus* and *C. maenas*. At the left side of the x-axis, *H. sanguineus* are larger, and on the right, *C. maenas* are larger. N is between 4 and 17 for each point.
Supplemental Fig. 1: Summer use of shelter in *Carcinus maenas*. Catch per unit effort (CPUE, in number of animals caught per number of tubes (n = 60 tubes for each bar)) mean ± SE. A) *C. maenas* use of subtidally- and intertidally-deployed shelters. B) Summer intertidal deployment of multiple treatments (Treatments: NC = No Crab, HSM = *Hemigrapsus sanguineus* Male, HSF = *H. sanguineus* Female, CMM = *C. maenas* Male, and CMF = *C. maenas* Female). C) Summer subtidal deployment in *C. maenas*. Significance between treatments or deployment depth indicated by: ‘*’ = p < 0.05, ‘**’ = p < 0.01, ‘***’ = p < 0.001.

Supplemental Fig. 2: Summer overall shelter use in *Hemigrapsus sanguineus*. Stated in catch per unit effort (CPUE, in number of animals caught per number of tubes, n = 300 tubes for each bar) mean ± SE. Significance between deployment depth indicated by: ‘*’ = p < 0.05, ‘**’ = p < 0.01, ‘***’ = p < 0.001.
Figure 1

Field and laboratory shelter setup

Over the course of several weeks, the diagrammed an artificial shelter was deployed at the northwest side of Pine Island, USA (41°18’47.434” N, 72°3’36.216” W) by fixing it to the sediment for a 24-hour soak of the treatments described in the Methods. B) Shelter setup for direct shelter competition experiments between *Hemigrapsus sanguineus* and *Carcinus maenas*, which was completed in an 18 cm x 31 cm plastic box with sand substrate for 24 hours. A 10 cm x 5.0 cm shelter, made from 6.35 cm PVC pipe with a quarter of its circumference removed, was arranged in the container to have only one useable opening.
Figure 2

Seasonal subtidal shelter use

Seasonal subtidal shelter use across seasons for all treatments for which there are seasonal data (control, *Hemigrapsus sanguineus* male, and *H. sanguineus* female) in catch per unit effort (CPUE, in number of animals per number of tubes (n = 180 tubes for each bar)) mean ± SE for: (A) *Carcinus maenas*, (B) *Pagurus* spp., (C) *Gobiosoma ginsburgi*, and (D) *Myxocephalus aenaeus*. Significance between seasons indicated by brackets: “*” = p < 0.05, “**” = p < 0.01, “***” = p < 0.001.
Figure 3

Summer subtidal shelter use in hermit crabs and gobies

Summer subtidal shelter use across treatments in catch per unit effort (CPUE, in number of animals per number of traps (n = 60 for each bar)) mean ± SE for (top graph) hermit crab *Pagurus* spp. and (lower graph) seaboard goby *Gobiosoma ginsburgi*. Treatments: NC = No Crab, HSM = *H. sanguineus* Male, HSF = *H. sanguineus* Female, CMM = *C. maenas* Male, and CMF = *C. maenas* Female. Bars with the same letter are statistically similar (p > 0.05).
Figure 4

Summer shelter choice in *Hemigrapsus sanguineus*

Stated in catch per unit effort (CPUE, in number of animals caught per number of tubes (n = 60 tubes for each bar)) mean ± SE. Treatments were: HSm = *H. sanguineus* male, HSf = *H. sanguineus* female, CMm = *Carcinus maenas* male, CMf = *C. maenas* female. Results for shelter occupancy are shown for A) intertidal male *H. sanguineus*, B) intertidal female *H. sanguineus*, and C) overall intertidal *H. sanguineus*. Significance between treatments indicated by brackets: “*” = p < 0.05, “**” = p < 0.01, “***” = p < 0.001.
Laboratory shelter competition between *Hemigrapsus sanguineus* and *Carcinus maenas*.

A) Fraction of each species in shelter after 24 hours of direct shelter competition between an individual *H. sanguineus* and *C. maenas*. At the left side of the x-axis, *H. sanguineus* are larger by carapace width (CW), and on the right, *C. maenas* are larger. N is between 4 and 17 for each point. B) Fraction of each species dead after 24 hours of direct shelter competition between an individual *H. sanguineus* and *C. maenas*. At the left side of the x-axis, *H. sanguineus* are larger, and on the right, *C. maenas* are larger. N is between 4 and 17 for each point.
