

***Hemigrapsus sanguineus* in Long Island Salt Marshes: Experimental Evaluation of the Interactions Between an Invasive Crab and Resident Ecosystem Engineers**

The invasive Asian shore crab, *Hemigrapsus sanguineus*, has recently been observed occupying salt marshes, a novel environment for this crab species. As it invades this new habitat, it is likely to interact with a number of important salt marsh species. To understand the potential effects of *H. sanguineus* on this ecosystem, interactions between this invasive crab and important salt marsh ecosystem engineers were examined. Laboratory experiments demonstrated competition for burrows between *H. sanguineus* and the native fiddler crab, *Uca pugilator*. Results indicate that *H. sanguineus* is able to displace an established fiddler crab from its burrow. Feeding experiments revealed that the presence of *H. sanguineus* has a significantly negative impact on the number as well as the biomass of ribbed mussels (*Geukensia demissa*) consumed by the green crab, *Carcinus maenas*, although this only occurred at high predator densities. In addition, when both crabs foraged together, there was a significant shift in the size of mussels consumed. These interactions suggests that *H. sanguineus* may have long-term impacts and wide-ranging negative effects on the saltmarsh ecosystem.

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9 | **Introduction**

10 Marine systems that have suffered from a high level of human disturbance are more
11 susceptible to successful invasion by non-indigenous species. Anthropogenic disturbances such
12 as predator removal, land-use changes, and eutrophication may alter an environment to the extent
13 that native species lose their locally-adapted advantages. If this happens, non-native species
14 benefit from the disruption of ecosystems and may be able to establish themselves in the
15 community (Byers 2002). Once established, invasive species can have an array of negative
16 effects on the communities they invade: they may compete with native species for food and other
17 resources, introduce pathogens that infect humans or native species, reduce the recreational or
18 commercial value of the area, and ultimately alter biodiversity, potentially causing native species
19 to become drastically reduced or extirpated (Ruiz et al. 1997). Southern New England has
20 suffered from the invasion of many plant and animal species (e.g. the common reed, *Phragmites*
21 *australis*, and the green crab, *Carcinus maenas*), some of which have significantly changed the
22 structure of communities where they were introduced (see Angradi et al. 2001 (*P. australis*);
23 Grosholz and Ruiz 1996 (*C. maenas*)). One recently introduced species of concern in New
24 England is the Asian shore crab, *Hemigrapsus sanguineus*.

25 The Asian shore crab is believed to have been introduced to the northwest Atlantic once or
26 multiple times by ballast water discharged from ocean-going ships (Epifanio et al. 1998). The
27 crab was first observed in the United States in 1988, in Townsend Inlet, New Jersey (McDermott
28 1991). It was soon found in Long Island Sound and has since spread north to Maine and as far
29 south as North Carolina (Park et al. 2004). *Hemigrapsus sanguineus* is now well established on
30 the northeast coast of the United States, where densities rival or exceed those in their native Asia
31 (Altieri 2010), and has displaced other crab species in rocky areas to become the dominant crab
32 in some communities (Ahl and Moss 1999; Gerard et al. 1999; Cassanova 2001).

33 *Hemigrapsus sanguineus* is a cryptic predator and relies on the shelter of rocks, shells, and
34 seaweed during low tide to help prevent desiccation, predation, and thermal stress (Brousseau et
35 al. 2002). The crab has been described as selectively inhabiting rocky areas rather than sandy
36 coastal or estuarine habitats, seagrass beds, or marshes (Ledesma and O'Connor 2001). Recently,
37 however, it has been observed in several Long Island and Connecticut salt marshes using
38 macroalgae (*Ascophyllum*, *Fucus*) rather than rocks for shelter (Fig. 1) (Brousseau et al. 2003,
39 Fournier 2007). Brousseau et al. (2003) found Asian shore crabs, that are unable to excavate
40 burrows themselves, occupying burrows dug by fiddler crabs (*U. pugnax*) at the edge of a
41 Connecticut salt marsh, suggesting the native fiddler crab may be facilitating the invasion of *H.*

42 *sanguineus* into a new environment. If *H. sanguineus* is in fact able to exploit this new
43 environment, its range along the Atlantic coast may expand beyond its present boundaries.
44 Concomitantly, Asian shore crab abundance could increase in areas within its current range as
45 novel habitat becomes populated, which could have important consequences for a number of salt
46 marsh resident species.

47 An important and characteristic marsh resident is the fiddler crab, *Uca* sp. Fiddler crabs have
48 a facultative mutualism with cordgrass. In muddy marsh sediments, cordgrass roots help stabilize
49 the mud and provide structural support for crab burrows. The burrowing behavior of crabs, in
50 turn, facilitates the growth of cordgrass by oxygenating dense marsh soils, improving drainage,
51 and increasing the decomposition of underground plant debris in an otherwise anoxic
52 environment (Montague 1982). In sandy sediments, the presence of fiddler crabs may also
53 increase nutrient availability to cordgrass (Holdredge et al. 2010). In this way, fiddler crabs play
54 an important role in determining the primary productivity and structure of the salt marsh and may
55 influence the rate of marsh accretion and succession (Bertness 1985). The Asian shore crab has
56 been found to utilize burrows dug by fiddler crabs; this could cause a change in *Uca* burrowing
57 behavior or drive fiddler crabs from the area. In addition, fiddler crab mating, which occurs
58 inside burrows, may be limited in the presence of *H. sanguineus*; this also could potentially
59 reduce *Uca* populations in areas where Asian shore crabs are present.

60 In New England salt marshes, another species of particular importance that might be affected
61 by this new invasion is the ribbed mussel (*Geukensia demissa*), an important salt marsh engineer.
62 Mussels are limited by attachment sites and benefit from the stability provided by cordgrass
63 stems and root mass. As they filter water, ribbed mussels take up particulate nitrogen and convert
64 it to ammonia, dissolved organic nitrogen, and semi-solid biodeposits, the bulk of which are
65 excreted and quickly utilized by other marsh residents (Jordon and Valiela 1982). Cordgrass,
66 which is nitrogen-limited, benefits from the nutrient enrichment caused by ribbed mussels; where
67 mussels are associated with cordgrass, the plants productivity is higher (Bertness 1984). In
68 addition, mussels produce proteinaceous byssal threads, which further stabilize the substrate and
69 trap sediments.

70 Although *H. sanguineus* might not have a strong direct impact on mussel populations – they
71 are relatively small and capable of consuming only small mussels (Bourdeau and O’Connor
72 2003) – a more significant impact might arise with their interactions with a major salt marsh
73 predator, the green crab (*Carcinus maenas*), a long established invader. As *H. sanguineus* comes
74 into the marsh in greater numbers, competitive interactions between the crabs will likely increase.

75 This may indirectly affect mussel populations; despite being a potential shared prey for both crab
76 species, the presence of multiple predators rarely has an additive effect on prey (Griffen 2006).
77 Rather, when multiple predators forage together, risk of predation on the shared prey is often
78 either enhanced (greater than expected) or reduced (less than expected), known as emergent
79 effects (Sih et al 1998). Aggressive interactions between the two crab species could increase,
80 shifting behavior from feeding to antagonism, and ultimately having an impact on mussel
81 populations. Understanding if the two predators foraging together have an emergent effect on
82 ribbed mussels is important for fully understanding the impacts of marsh invasion by *H.*
83 *sanguineus*.

84 The primary objectives of this study were: 1) to experimentally examine whether competition
85 for burrows occurs between this invasive crab and the native fiddler crab, *Uca pugilator*; and 2)
86 to investigate the emergent effects of multiple predators – the green crab, *Carcinus maenas* and
87 the new invader, *Hemigrapsus sanguineus* – on ribbed mussel predation.

88 **Methods**

89 ***Burrow Competition Experiment***

90 *Hemigrapsus sanguineus* were collected by hand along the shore of Stony Brook Harbor,
91 Long Island, NY, and maintained in an indoor saltwater aquarium, filled with rocks to provide
92 shelter, for no more than one month prior to use in trials. Crabs were fed Wardley Algae Discs
93 (Hartz Mountain Corp., Secaucus, NJ) supplemented with fresh algae, *Ulva lactuca*. *Uca*
94 *pugilator* were collected by hand from Flax Pond and Scallop Pond, Long Island, NY, and kept in
95 a tank built to mimic natural conditions: a sloping layer of sifted beach sand leading to a pool of
96 salt water approximately 4 cm deep on one end of the tank. The crabs were able to submerge
97 themselves, forage on the dry sand surface, or excavate burrows down to moist bottom sand.
98 *Uca* crabs were kept no more than one month prior to use in trials and were fed a ground mixture
99 of Wardley Algae Discs and Tetrafauna Hermit Crab Cakes (Tetra Holdings, Blacksburg, VA).
100 Male and female crabs of both species were used, and each crab was used in only one trial. Equal
101 number of males and females of each species were used to determine whether there was a
102 difference based on the sex of either crab. In addition, carapace width was recorded to determine
103 if size affected the outcome between the crabs. The average female carapace width of *U.*
104 *pugilator* was 18.6 ± 0.61 mm and ranged in size from 17.5-19.2 mm. The male size range was
105 16.9 – 21.2 mm and averaged 19.41 ± 1.32 mm. In comparison, the average size of *H.*

106 *sanguineus* females was 15.8 ± 2.0 mm and ranged in size from 12.0 – 19.2 mm. The average
107 male sizes were 17.9 ± 2.4 mm and ranged from 13.7 – 21.2 mm.

108 For each experiment, an arena was set up in a 19-liter bucket filled with damp beach sand,
109 sifted with 1 mm mesh, to a depth of approximately 20 cm and smoothed flat, resulting in a ~616
110 cm² surface area arena. Near the arena edge, an artificial burrow 2.3 cm in diameter and 6 cm
111 deep was made. A 125-watt heat lamp was positioned 22 cm from the sand surface, providing
112 thermal stress to promote the fiddler crab's burrowing response and increasing desiccation stress
113 for *H. sanguineus* (Fig. 2). During the experimental runs, the temperature at the sand surface
114 averaged 27° C while the temperature inside the burrow averaged 21° C, thus reflecting normal
115 summer temperatures of the natural habitat. One randomly selected fiddler crab was placed in
116 the arena and given sufficient time to occupy the burrow. Then a randomly selected *H.*
117 *sanguineus* was added opposite the burrow. After 20 minutes, the burrow occupant was recorded,
118 and any new burrowing activity was noted. Video recordings were made of eighteen trials to
119 examine the behavior of the crabs during the experiment.

120 To compare the competitive interactions of *U. pugilator* with conspecifics to its behavior with
121 the invasive crab, additional trials were performed as above, but with a second *U. pugilator* in the
122 place of *H. sanguineus*. Crabs were labeled with small (5 mm square) vinyl number tags,
123 attached to the carapace with cyanoacrylate glue. This was done to provide a means of
124 distinguishing the original crab from the one added. These experiments were conducted in such a
125 way to compare differences of the success of *H. sanguineus* in possessing a burrow based on crab
126 size (CW) and sex of the *U. pugilator* defender.

127 To control for laboratory artifacts, these experiments were conducted in the field as well.
128 Experiments were performed at the beach on Scallop Pond, Southampton NY using resident
129 fiddler crabs and *H. sanguineus* collected from Old Ponquogue Marine Park, Southampton NY.
130 Arenas were created using the top half of a 19-liter bucket driven into the sand approximately 3-5
131 cm. As in the laboratory experiments, an artificial burrow 2.3 cm in diameter and 6 cm deep was
132 made in the arena. One randomly selected fiddler crab was placed in the arena and given
133 sufficient time to occupy the burrow, then a randomly selected *H. sanguineus* was added opposite
134 the burrow. After 20 minutes, the burrow occupant was recorded and any new burrowing activity
135 noted. Conspecific trials, using two *U. pugilator* crabs, were performed in the same fashion.

136 *Mussel Feeding Experiment*

137 To determine the emergent effects of *H. sanguineus* and the green crab, *Carcinus maenas*, on
138 ribbed mussels, a feeding experiment was performed using a fixed number of ribbed mussels and
139 6 different combinations of *H. sanguineus* and *C. maenas* crabs. The treatments were i) one *H.*
140 *sanguineus*; ii) one *C. maenas*; and iii) one *H. sanguineus* plus one *C. maenas*; iv) two *H.*
141 *sanguineus*; v) two *C. maenas*; and vi) two *H. sanguineus* plus two *C. maenas* (1Cm, 1Hs,
142 1Cm+1Hs; 2Cm, 2Hs, 2Cm+2Hs). The use of these different density combinations allowed both
143 the impact of increasing density of conspecifics on mussel consumption as well as interspecific
144 effects. *Hemigrapsus sanguineus* and *Carcinus maenas* were collected from Old Ponquogue
145 Bridge Marine Park, Southampton, NY. Additional *C. maenas* were collected by trawl within
146 Shinnecock Bay (NY). Sizes of *H. sanguineus* ranged from 18–24 mm carapace width (CW),
147 with an average CW of 21.0 mm, while the sizes of *C. maenas* ranged from 53–76 mm CW and
148 averaged 62.1 mm CW, within sizes commonly observed in marine habitats around Long Island
149 and similar to sizes used in other studies (Griffen 2006, Griffen et al. 2008). Soft-shelled, gravid
150 females and crabs with missing or damaged chelipeds were not used in the experiment. All crabs
151 were starved 24 h prior to use in each experiment.

152 A large clump of approximately 800 individual ribbed mussels (*Geukensia demissa*) was
153 collected from Red Creek Pond, Southampton, NY. The mussels were measured and classed by
154 size, from < 1.0 to 6.5 cm in 0.5-cm increments, then counted. This was done to utilize the
155 natural size distribution of ribbed mussels in the field (supplemental Fig. 1). The mussels were
156 then divided into 18 identical sets of 39 mussels each, reflecting the natural size distribution
157 observed. Each set was allowed to attach via byssal threads to 12.5 cm plexiglass circles in a
158 flow-through seawater system for 48 hours before being used in experimental trials. Prior to the
159 experiment, mussels were able to feed on phytoplankton present in the unfiltered seawater but
160 were not given additional food.

161 The feeding experiments were performed at the Stony Brook-Southampton Marine Lab. Each
162 of the 6 experimental treatments had 3 replicates; all were run in 18 separate polypropylene
163 containers (33cm x 20 cm x 12 cm deep) haphazardly arranged in a 3-tiered, flow-through sea
164 table with unfiltered seawater. Water was directed into each individual container, and allowed to
165 flow over the top for water exchange. The water level in the sea table was kept at 9cm deep,
166 enough to help maintain constant temperature but preventing water exchange between different
167 containers, thus keeping them independent (Figure 3). All crabs were measured and sexed before
168 use. Only adult males of both species were used in these experiments. To begin, a pre-made

169 mussel clump was placed in each container, and then the randomly-assigned crab treatment was
170 added. The experiment was run for 48 h.

171 After completion of the experimental run, total prey consumption was measured by removing
172 the mussels from each bin and counting how many remained from each size class. The consumed
173 mussel count was converted into an approximate biomass value for each bin and treatment using
174 a regression equation,

$$y = 0.025x^{2.16}$$

175 where x = mussel shell length in centimeters and y = whole tissue dry weight in grams ($p < 0.001$;
176 $r^2 = 0.97$; Fig. 4). This relationship was calculated by collecting tissue dry weights of 50
177 individual mussels from each size class and regressing biomass (dry weight) to shell length.
178

179 *Statistical Analysis*

180 In total, this study consisted of two manipulative experiments: a burrow competition
181 experiment and a mussel feeding experiment. Results in all comparisons were considered to be
182 significant when $p < 0.05$.

183 For the burrow competition experiment, statistical comparisons of the final burrow occupant were
184 made via Chi-square tests. To determine whether an emergent multiple predator effect occurred,
185 log transformed prey survivorship data was analyzed with a two-way ANOVA with the presence /
186 absence of each predator species treated as a separate factor (Sih et al. 1998, Griffen 2006). A
187 significant interaction term between the two factors indicates the presence of an emergent effect
188 of combining the two predator species. In addition, we compared the observed proportion of
189 mussels consumed to values predicted by the multiplicative risk model (Sih 1998, Wong et al.
190 2010):

$$E_{C,H} = P_C + P_H - (P_C P_H)$$

191 where $E_{C,H}$ is the predicted proportion of the mussels consumed by *Carcinus* and *Hemigrapsus*
192 when foraging together, P_C is the observed proportion of mussels consumed by *Carcinus* in
193 isolation and P_H is the observed proportion of mussels consumed by *Hemigrapsus* in isolation.
194 Transformations were not necessary to meet assumptions of normality. The multiplicative risk
195 model is used to predict how many mussels should be eaten by both predators together based on
196 individual foraging rates, and therefore divergence from expected also illustrates an emergent
197 effect, and also the direction of the effect (risk enhancement, risk reduction). $P_C P_H$ is a correction
198 factor for mussels that can't be consumed twice. Both the two-way interaction approach and the
199

200 multiplicative risk model have been used separately in previous studies examining multiple
201 predator affects. We chose to use both approaches to identify whether an emergent effect
202 occurred and determine the direction of the effect. These statistical analyses were conducted
203 using the Sigma Plot 11.0 statistical software package.

204 **Results**

205 ***Burrow Competition Experiment***

206 There was a statistically significant difference in the crab species occupying the burrow after
207 20 min ($p < 0.001$). After a total of 38 trials, the burrow was occupied by *H. sanguineus* alone 14
208 times, by *Uca pugilator* alone 4 times, and by both crabs 20 times. In no trial was the burrow
209 unoccupied at the end of 20 min. The success of *H. sanguineus* in the trials was not dependent
210 upon the size (CW) ($p = 0.545$), nor sex ($p = 0.633$) of *U. pugilator*. Neither was it dependent on
211 the size (CW) ($p = 0.592$), nor sex ($p = 0.504$) of *H. sanguineus*.

212 The behavior of *U. pugilator* in response to *H. sanguineus* varied from trial to trial. On some
213 occasions, *H. sanguineus* would simply enter the burrow occupied by *U. pugilator* and both crabs
214 would remain together for the length of the experiment without any outward displays of
215 aggression. Other times, *U. pugilator* would leave the burrow upon entry of *H. sanguineus*, then
216 actively attempt to re-take it using aggressive behaviors and territorial displays such as acoustical
217 sound production by vibration of the major chelae (in males) and repeated approaches to the
218 burrow (both sexes). On two occasions, *U. pugilator* males were observed using their dominant
219 claw to pry *H. sanguineus* out of the burrow. In two trials, *U. pugilator* excavated a new burrow
220 after being displaced from the original burrow by *H. sanguineus*.

221 The behavior of *H. sanguineus* would also be aggressive when *U. pugilator* defended or
222 attempted to re-occupy the burrow. *H. sanguineus* would often approach an occupied burrow
223 with claws raised; if already inside the burrow, it could be seen stretching its chelipeds to occupy
224 as much space as possible. On several occasions, it was observed that *H. sanguineus* would use
225 its claws as pinchers to deflect attempts by *U. pugilator* to re-enter the burrow.

226 In the outdoor trials with *H. sanguineus* and *U. pugilator*, the same behaviors witnessed in the
227 lab trials were observed in the field. In 20 trials, the burrow was occupied by *H. sanguineus* 11
228 times (55%), by *U. pugilator* 5 times (25%), and by both crabs 4 times (20%). These results of
229 the field trials were not significantly different from those in the laboratory ($p = 0.40$).

230 *Mussel Feeding Experiment*

231 When foraging alone, *Carcinus maenas* consumed 17% of the mussels offered to them, while
232 only 8% were consumed by *Hemigrapsus sanguineus* foraging alone, likely due to a size
233 threshold of the prey. When one of each species was present together, the combined consumption
234 was 14%. However, the proportion of mussels consumed did not vary significantly across
235 predator treatments at low predator density ($p=0.801$). Increasing from single predators to
236 conspecific pairs of *C. maenas* more than doubled the number of mussel prey consumed (62%
237 consumed), but had no effect on *H. sanguineus* (5% consumed; Fig. 5). Two *C. maenas* together
238 consumed significantly more mussels than both two *H. sanguineus* and the mixed treatment with
239 two of each species ($p<0.001$ for both).

240 There was not a significant emergent effect on prey survival when single individuals of the
241 two predator species foraged together based on the additive experimental design (*C. maenas* x *H.*
242 *sanguineus* interaction, $p = 0.294$; Table 1, Figs. 5,6). The lack of an emergent effect was
243 confirmed by comparing our observed values to those predicted by the multiplicative risk model
244 ($p = 0.646$; Table 2). When applying the additive design to high predator densities (2Cm, 2Hs,
245 2Cm+2Hs), there was a significant interaction, suggesting an emergent effect ($p<0.001$; Table 1).
246 This emergent effect was also apparent when comparing the actual consumption observed to that
247 predicted by the multiplicative risk model ($p < 0.001$; Table 2, Figs.5,6).

248 In addition to a change in the number of mussels consumed, the mean size of ribbed mussels
249 eaten shifted from larger to smaller mussels when both predators foraged together (Fig. 7). When
250 foraging alone, *C. maenas* consumed mussels ranging from the smallest size class (<1.0 cm) to a
251 length of 5.5 cm, while *H. sanguineus* consumed the smallest size range of mussels, from <1.0 to
252 2.0 cm in length. In treatments when both predators foraged together, the lack of consumption on
253 the larger mussel size classes was dramatic (Fig.7). A Mann-Whitney rank sum test was
254 performed on the data and showed that the median values for the two groups (*C. maenas* alone
255 and with *H. sanguineus*) were significantly different ($p < 0.001$), with smaller mussels being
256 consumed in heterospecific groupings. While this was affected by the increased consumption of
257 the smaller size classes by *H. sanguineus*, it also demonstrates that *C. maenas* did not consume
258 the larger individuals when *H. sanguineus* was present.

259 Finally, when considering the impact of mussel predation on removing biomass instead of
260 prey density, the effects of both predators foraging together are even more dramatic. High
261 density predator treatments of *C. maenas* consumed a significantly higher biomass of ribbed
262 mussels than the low density *C. maenas* treatment. When *H. sanguineus* was present there was

263 significantly less biomass consumed than when *C. maenas* was alone at the highest densities ($p =$
264 0.002, Fig.8).

265 Discussion

266 The purpose of this study was to examine the potential impact an invading crab may have on
267 two ecosystem engineers within the salt marsh community. The Asian shore crab, *Hemigrapsus*
268 *sanguineus*, is now common on rocky shores from Virginia to Maine and has recently begun to
269 invade salt marsh ecosystems in New York (Fornier 2007) and Connecticut (Brousseau et al.
270 2003). This can have serious consequences for the salt marsh ecosystem through both direct and
271 indirect interactions. Burrow competition experiments showed that the shore crabs can utilize
272 fiddler crab burrows and are capable of displacing the native species. Additionally, the presence
273 of *H. sanguineus* can significantly affect the amount, size, and biomass of mussels consumed by
274 an important marsh predator.

275 The burrow competition experiments performed in this study revealed that *H. sanguineus*
276 will utilize burrows created by *U. pugilator* and is able to displace an established crab from its
277 burrow. In the trials, *H. sanguineus* occupied the burrow alone or with *U. pugilator* significantly
278 more often (89% of the time) than did *U. pugilator* alone (11% of the time). The outcome of
279 these competition arena experiments were similar with respect to *H. sanguineus* occupancy in
280 both the lab and in the field experiments (80% of field burrows were occupied by *H. sanguineus*).
281 However, how the occupancy occurred was slightly different. In the lab arenas, *H. sanguineus*
282 occupied the burrow alone ~37% of the time, while it co-occupied the burrow in ~53% of the
283 trials. In the field, this pattern was almost opposite, which *H. sanguineus* in 55% of the burrows
284 alone compared to sharing the burrow 20% of the time. While it is unclear why the lab and field
285 arenas differed in how the burrow occupancy occurred, possibly due to behavioral differences
286 between lab adapted and resident crabs used in the different experiments, the results show that *H.*
287 *sanguineus* is able to use burrows created by *U. pugilator*. Therefore, fiddler crabs (*Uca*
288 *pugilator* and *U. pugnax*) may act as facilitators to *H. sanguineus* invasion by providing a
289 suitable desiccation refuge for the invaders.

290 It is not known what impact, if any, the presence of *H. sanguineus* will have on *Uca* sp.
291 However, the presence of *H. sanguineus* in burrows may cause an emigration of *Uca* sp. from
292 areas within the marsh, reduce the density of burrows, or interfere with reproductive activity
293 known to occur within burrows. Any of these scenarios could negatively impact the salt marsh,
294 as the importance of fiddler crab burrows to salt marsh functioning is well documented (*see*

295 Montague 1982 and Bertness 1985). However, if the benefit of *Uca* sp. to saltmarsh grasses is
296 via nutrient deposition, as is the case on sandy shores (Holdredge et al. 2010), it is possible *H.*
297 *sanguineus* could replace this function assuming suitable habitats remain to prevent dessication.
298 Regardless, any potential disruptions to the mutualistic fiddler crab – cordgrass relationship are
299 reasons for concern.

300 In addition, the feeding experiments suggested the possibility of an interaction between the
301 competing predators. When one of each predator was present, there was no emergent predator
302 effect, suggesting that the predators do not interfere with each other. However, when two of each
303 predator was present, there was a significant emergent effect, leading to a risk reduction of their
304 shared prey (Sih et al. 1998). While we were unable to use the substitutive design at high
305 predator densities, and thus cannot eliminate the possibility that the emergent effect was due to
306 predator density in general (Griffen 2006), the observed effect is likely due to interactions
307 between the species and not within species. First, video recordings of the two different crabs
308 interacting indicate a reduction in feeding by *C. maenas* which was likely due to an increased
309 amount of time spent interacting with the smaller shore crabs and second, when both crabs were
310 present, the size class consumed shifted toward smaller mussels, a behavior which was not
311 observed when green crabs were housed together. This experiment suggests that an emergent
312 effect in numbers or proportion of prey consumed is not necessarily the only indicator of a
313 multiple predator effect.

314 During this experiment, no traditional emergent effect was observed when individual *C.*
315 *maenas* and *H. sanguineus* were foraging together, that is, the proportion of mussels consumed
316 was as expected based on foraging of the individual crabs alone. Closer investigation of which
317 mussels were consumed, however, did suggest a potential emergent effect. The size range of
318 mussels consumed by green crabs were from <1mm to 5.5mm. However, when *C. maenas* and
319 *H. sanguineus* foraged together, the largest mussel consumed was in the 3.0-3.5mm size class and
320 the bulk of the consumption was between the <1 and 1.5-2mm size classes; therefore, despite the
321 expected amount of consumption when both foraged together, the significant and dramatic shift
322 in the size classes consumed suggest an emergent effect and can have important ecological
323 consequences. These results at the very least suggest looking beyond the typical “proportion
324 consumed” for investigating multiple predator effects.

325 These results are consistent with established foraging ecology of these two crab species on
326 other mussel prey (*Mytilus edulis*; Lohrer and Whitlatch 2002, Griffen 2006). In this study, the
327 observed emergent effect of the two predators when foraging together was dependent on the

328 predator density – only when two of each predator were foraging together was an effect observed.
329 Prey survival was greater than expected based on the additive experimental design at high
330 predator densities. The detection of risk reduction with the additive experimental design implies
331 that predation interference occurred between the two species, decreasing predation rates below
332 those observed when individuals of each species foraged independently. The shift in prey size
333 structure consumed by the predators when foraging together is likely another indication of
334 interference. This may have a positive impact on the larger size classes of *Guekensia demissa*.
335 Due to the competitive interference between the two species, it is likely that *C. maenas* might not
336 be afforded time to be a selective feeder, shifting its ‘preferred’ prey size down to smaller size
337 classes in presence of interspecifics (Wong et al 2010).

338 *Hemigrapsus sanguineus* consumed a greater number of smaller ribbed mussels than did *C.*
339 *maenas*, likely because of its smaller size. Within existing populations of ribbed mussels, the
340 largest individuals should benefit from the reduced predation pressure from *C. maenas* as salt
341 marsh populations of *H. sanguineus* increase. However, both smaller mussels and mussel
342 recruitment will likely be negatively impacted over time. Experimental treatments of *H.*
343 *sanguineus* consumed more mussels in <1.0 cm size range than either of the other treatments, an
344 observation also made in other studies (Bourdeau and O’Connor 2003). As densities of *H.*
345 *sanguineus* increase, wild populations of ribbed mussels within this size class will be most
346 affected. This can have especially dire consequences for mussel populations – as *H. sanguineus*
347 populations rise to replace the biomass of predators they are displacing (O’Connor et al. 2008,
348 Hudson 2011), they can replace the feeding pressure exerted by *C. maenas*. However, this feeding
349 pressure would be specifically targeting the recruiting classes of mussels, potentially leading to
350 recruitment failure and population decline (O’Connor et al 2008).

351 Previous surveys show that *Hemigrapsus sanguineus* is present in salt marshes throughout
352 coastal Long Island (Fournier 2007), and these experiments demonstrate that *H. sanguineus*
353 interacts with two of the most important marsh engineers in ways that may have detrimental
354 effects on the ecosystem. While densities of *H. sanguineus* in the salt marsh at present appear
355 low, it is apparent that these crabs have found a habitable niche in this environment and are
356 reproducing there (*pers. obs.*). The ecological consequences of this for the salt marshes of Long
357 Island and elsewhere are as of yet unknown.

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362 Island, and who has been a great source of ideas and assistance with this project. The authors
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Table 1 (on next page)

ANOVA Table of the mussel predation experiment

Results of ANOVAs used to compare observed predation by *Carcinus maenas* and *Hemigrapsus sanguineus* to expected predation based on the additive design and method described by Griffen (2006). Crab predation was measured as the proportion of mussels consumed over the 48 hour experiments in the presence/absence of each predator.

Source	<i>df</i>	SS	F	P
Test of additive for low density (two-way ANOVA)				
<i>C. maenas</i>	1	0.0430	1.858	0.210
<i>H. sanguineus</i>	1	0.00197	0.0853	0.778
<i>C. maenas</i> x <i>H. sanguineus</i>	1	0.00789	0.341	0.575
Error	8	0.185		

Source	<i>df</i>	SS	F	P
Test of additive design for high density (two-way ANOVA)				
<i>C. maenas</i>	1	0.444	253.125	<0.001
<i>H. sanguineus</i>	1	0.0877	50.000	<0.001
<i>C. maenas</i> x <i>H. sanguineus</i>	1	0.148	84.500	<0.001
Error	8	0.0140		

Table 2 (on next page)

ANOVA Table of the multiplicative risk model

Results of One-Way ANOVAs used to compare observed predation by *Carcinus maenas* and *Hemigrapsus sanguineus* together to expected predation calculated by using the multiplicative risk model as described by Wong et al (2010). Predation was measured as the proportion of mussels consumed over 48 hr. experiments.

Source	<i>df</i>	SS	F	P
Low predator density				
Between Groups	1	0.0110	0.245	0.646
Error	4	0.180		

Source	<i>df</i>	SS	F	P
High predator density				
Between Groups	1	0.266	92.663	<0.001
Error	4	0.0115	0.00287	

Figure 1

Long Island salt marshes invaded by *Hemigrapsus*

Sites of *Hemigrapsus sanguineus* presence/absence surveys on Long Island, NY. 1) Crab Meadow Beach; 2) West Meadow Creek; 3) Flax Pond; 4) Mt. Sinai Harbor; 5) Goose Creek; 6) Dune Road Marsh; and 7) Fireplace Neck.

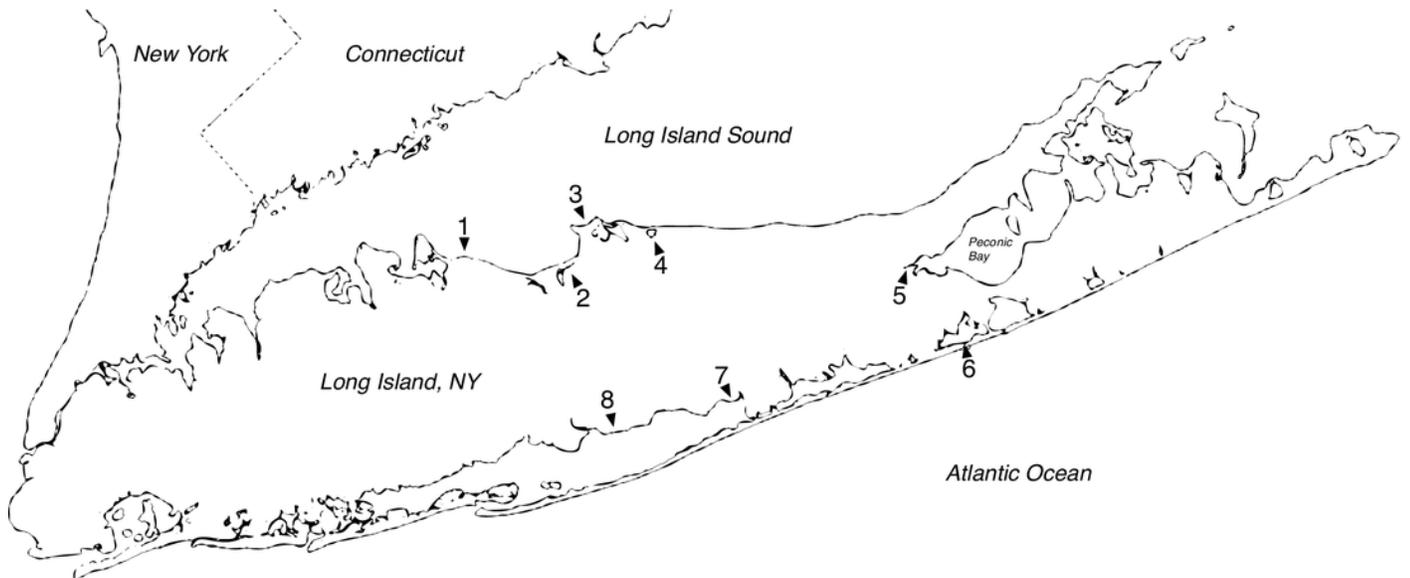


Figure 2

Arena set-up for burrow competition experiment

Arena set-up for the burrow competition experiment, showing the 19l bucket and the position of the heat lamp.

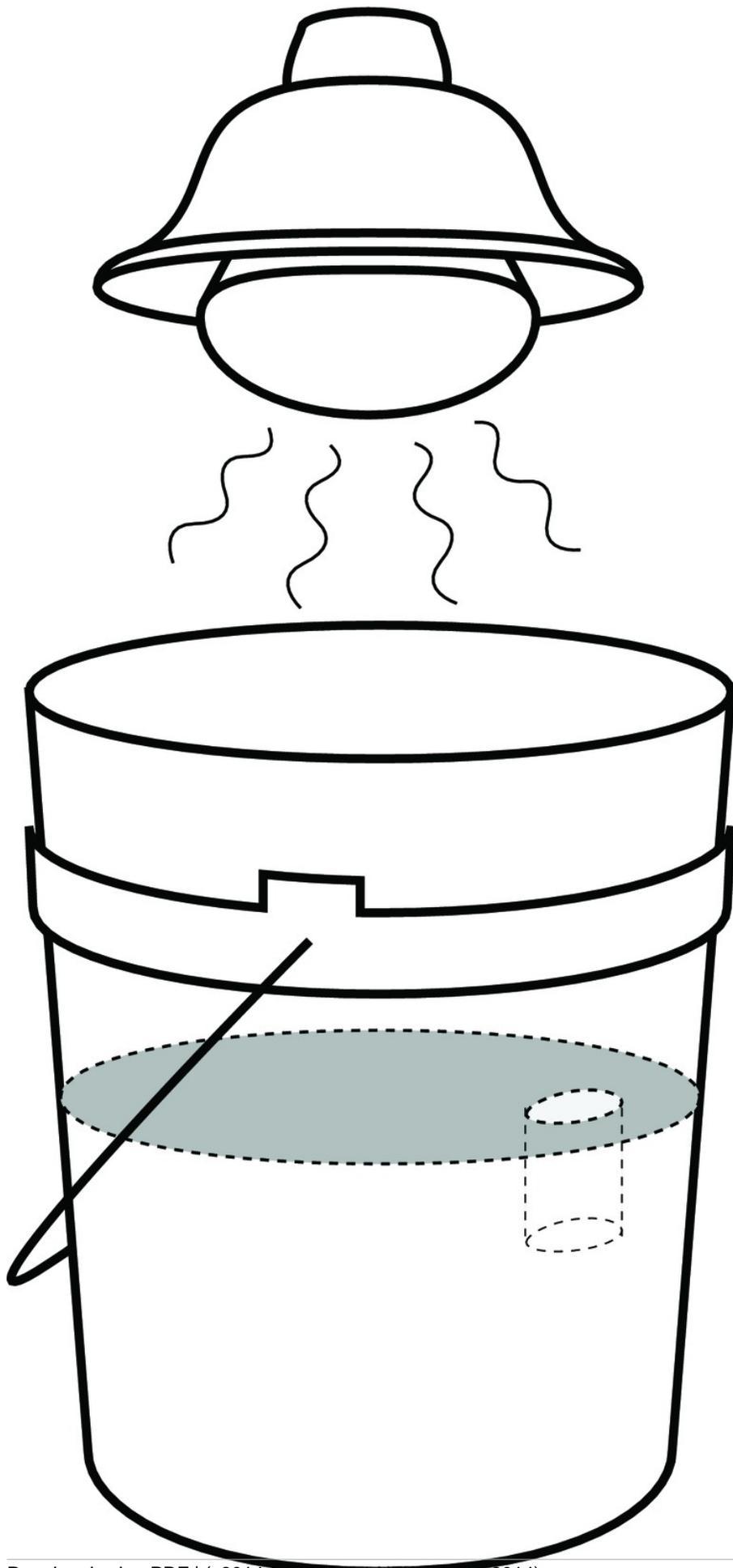
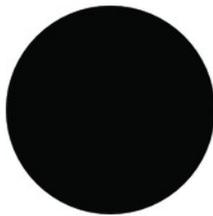


Figure 3

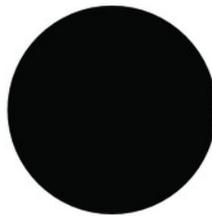
Experimental set-up for the mussel predation experiment

Diagram of the experimental set-up for the multiple predator experiments between *Hemigrapsus sanguineus* and *Carcinus maenas* feeding on shared mussel prey, illustrating the 6 different treatment combinations – A. 1 Hs; B. 1 Cm; C. 1Hs + 1Cm; D. 2 Hs; E. 2 Cm; F. 2Hs + 2 Cm.

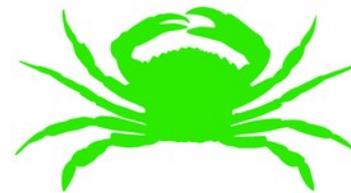
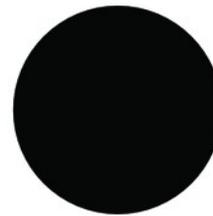
A



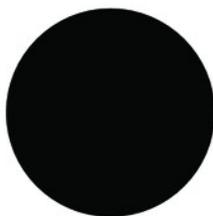
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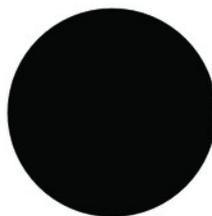
C



D



E



F

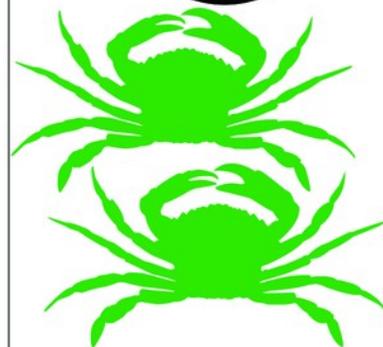
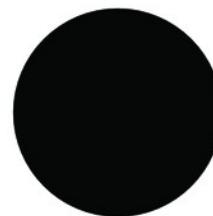


Figure 4

Mussel biomass versus shell length regression

Mussel biomass vs. shell length regression; equation: $y = 0.025x^{2.1561}$, where y is the tissue dry weight in g and x = mussel shell length in cm.

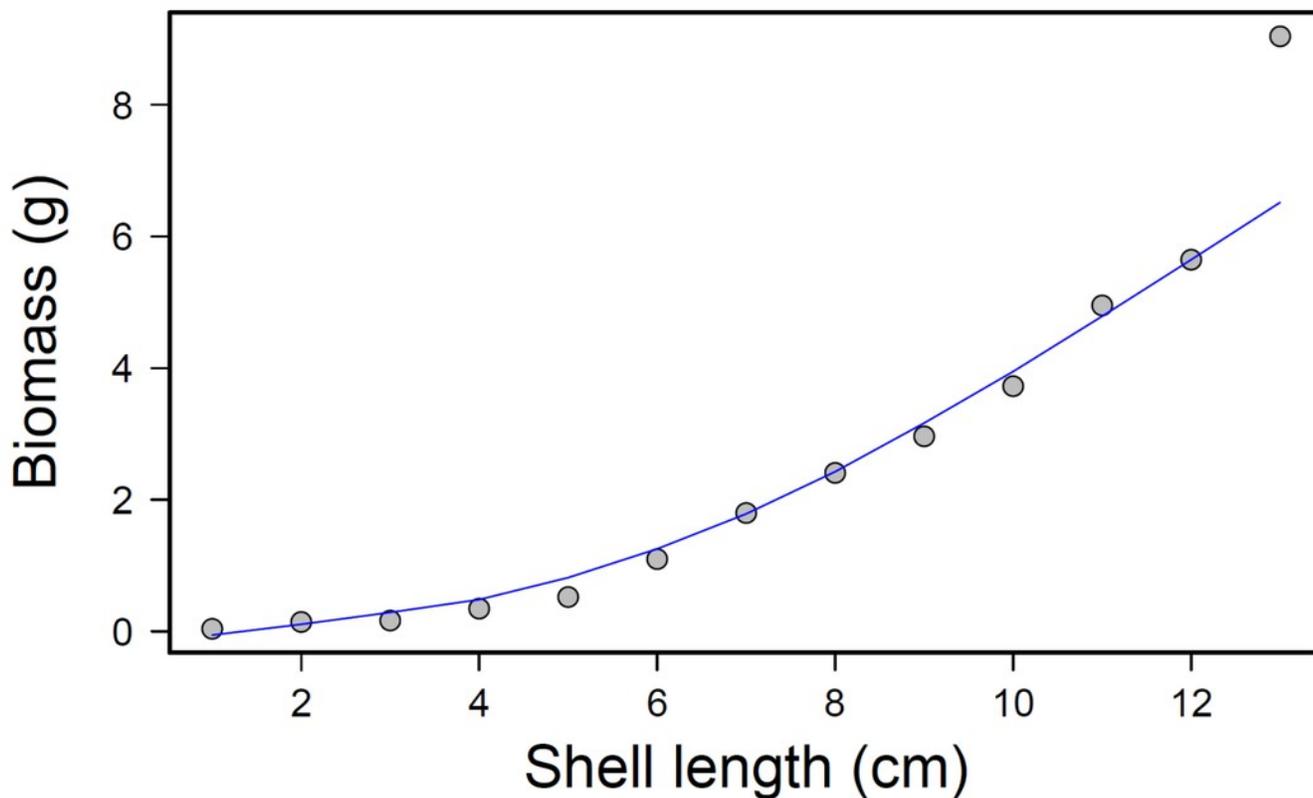


Figure 5

Crab predation of mussels as individuals and heterospecific and conspecific pairs

Proportion of mussel prey consumed (mean \pm SE, $n = 3$) foraging as single individuals and in heterospecific and conspecific pairs. Low predator density refers to one individual or one of each in the mixed trial. High predator density refers to two individuals or two of each in the mixed trial.

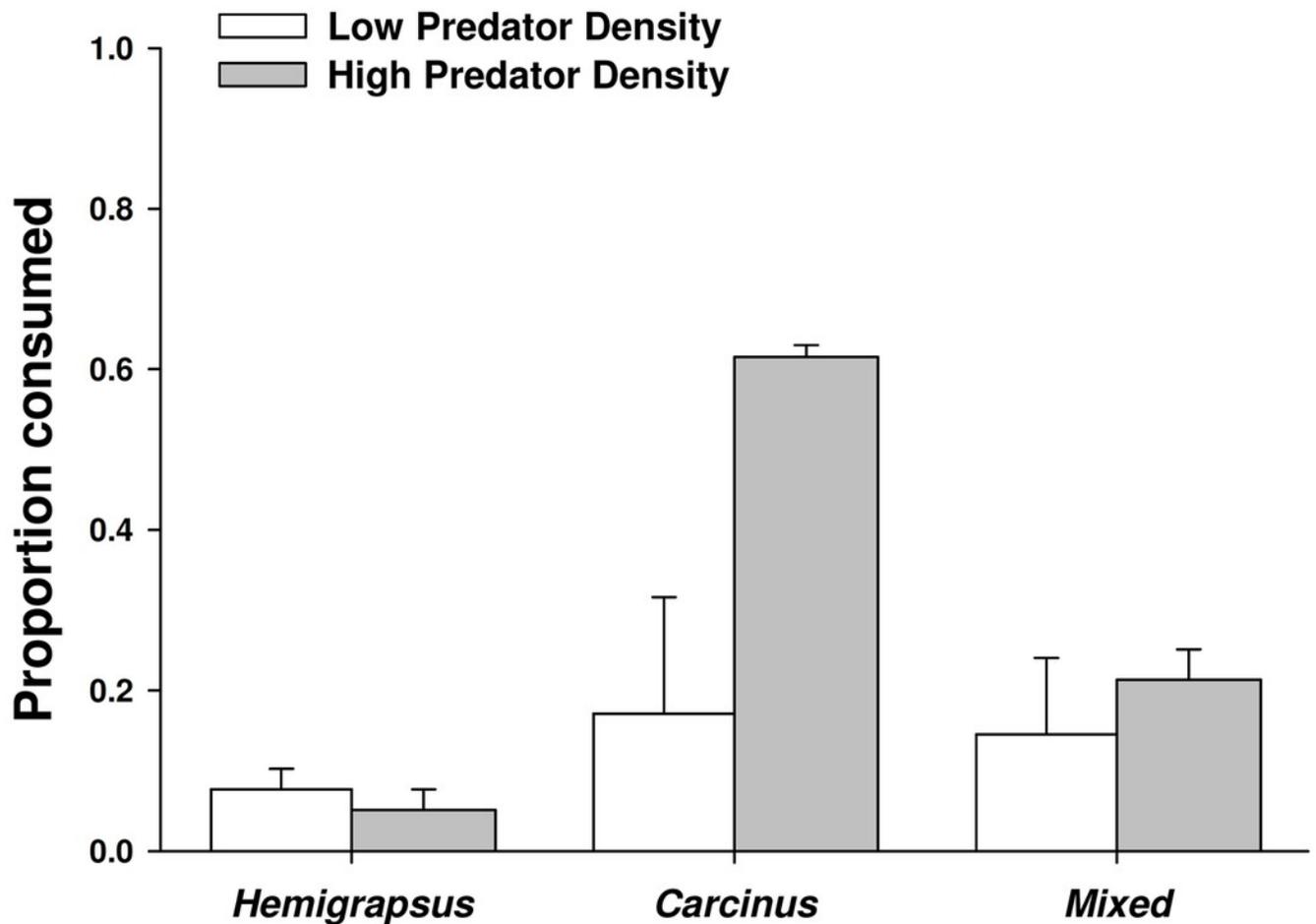


Figure 6

Proportion of mussels surviving in low versus high crab densities

Observed and expected mussel prey survival when predators foraged together at low (one of each species) and high (two of each species) predator densities (mean \pm SE, $n = 3$).

Expected survival was calculated using the multiplicative risk model $E_{C,H} = P_C + P_H - (P_C P_H)$, where P_C is the proportion of the mussels consumed by *Carcinus maenas* and P_H is the proportion of mussels consumed by *Hemigrapsus sanguineus* when foraging along. Low predator densities are the observed and expected survival of mussels when 1 individual of each species foraged together. High predator densities are the observed and expected survival of mussels when 2 individuals of each species foraged together. * when $p < 0.05$.

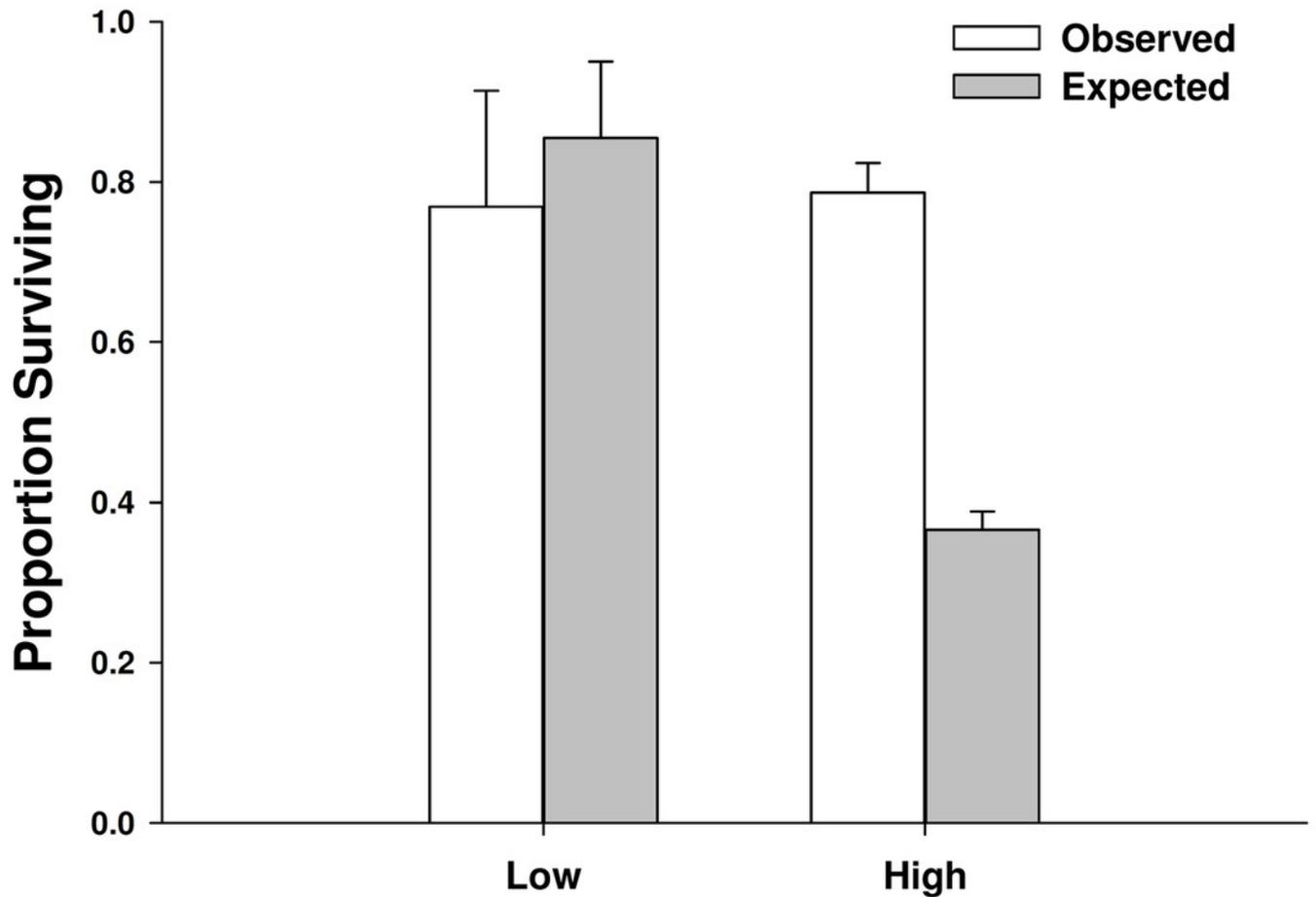


Figure 7

Impact of heterospecific predators on reducing the size of mussels being consumed

Proportion of mussels consumed in each size class for each predator alone and when foraging together. Prey consumption by both predator densities were combined. Shell length was measured across the longest shell axis.

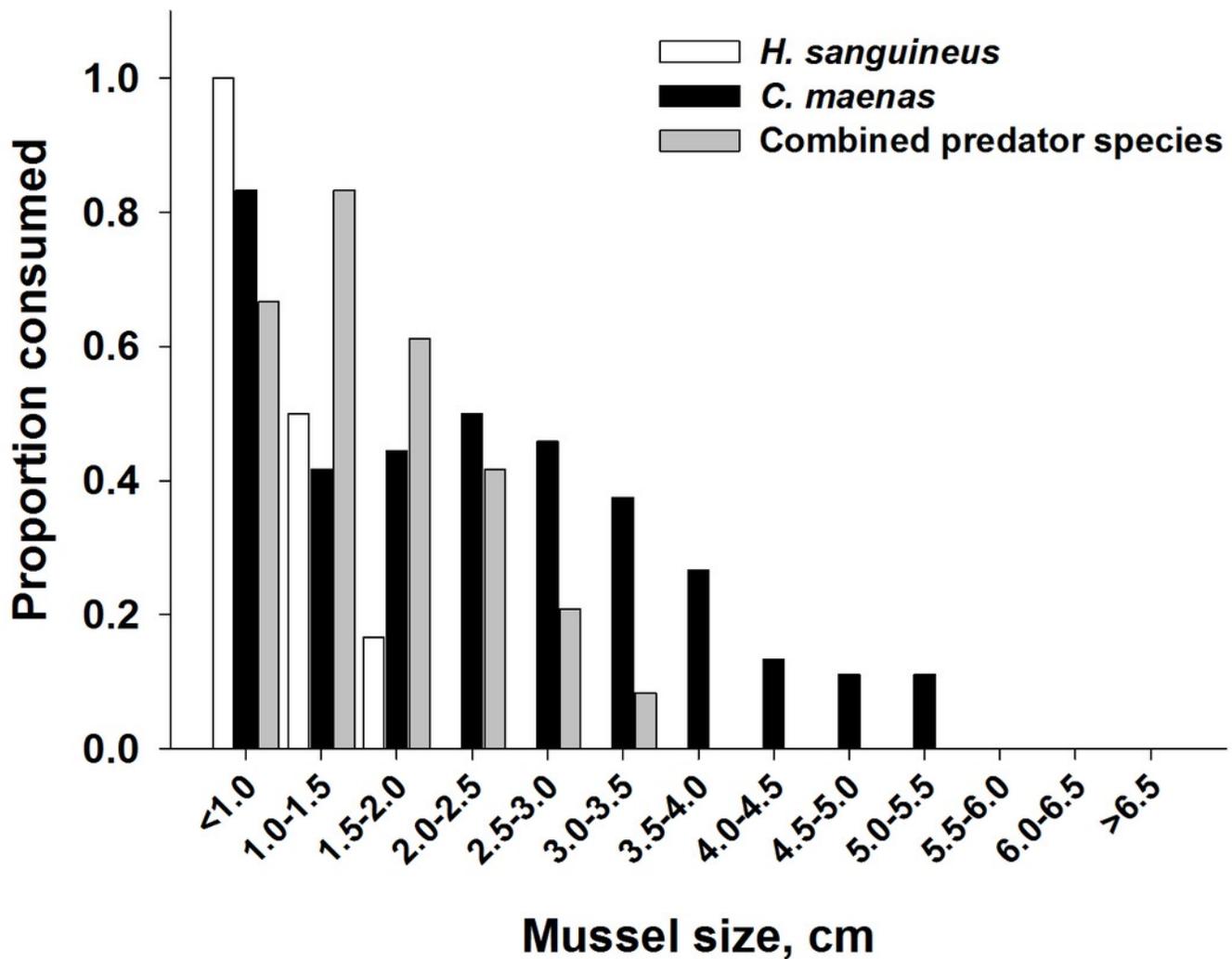


Figure 8

Dramatic increase in mussel biomass consumed by *Carcinus maenas* at high predator densities

Mussel biomass consumed by both predators individually and when foraging together (mean \pm SE). Low predator density refers to one individual or one of each in the mixed trial. High predator density refers to two individuals or two of each in the mixed trial.

