

A population study of the Asian shore crab, *Hemigrapsus sanguineus*, at Point Judith Pond, RI

The Asian shore crab, *Hemigrapsus sanguineus* (De Haan), has recently invaded the Atlantic coast of the United States. Its large populations and continued fecundity are indicative of its successful establishment. Competitive interaction with other coastal crab species has been a subject of many studies. For example, in *ex situ* experiments, *H. sanguineus* has been shown to be superior to a long-established invader: the green crab, *Carcinus maenas*. Because *H. sanguineus* has been found in such great density on some shorelines, it has been postulated that it poses an ecological threat due to its potential to disrupt native and established species. However, many investigators have noted the invasive crab's limiting habitat requirement for complex, rocky shorelines. After observation of Point Judith Pond, RI, we assessed whether there were enough rocky areas to support significant populations of *H. sanguineus* that might be disruptive to *C. maenas*. Using a photo-quadrat system alongside software analysis, transects were laid across areas of interest. *H. sanguineus* were collected and counted in each quadrat, allowing habitat metrics obtained from the photographs, such as rock size and cover, to be correlated with the density of crabs, their size, and sex. These data, paired with the observation that Point Judith Pond has ample habitat for *C. maenas* to be displaced to, led us to conclude that the *H. sanguineus* population in Point Judith Pond, RI, is likely not capable of causing severe disruption of the native *C. maenas* population as it currently stands, and that this trend may extend to other estuarine systems.

2

¹Nicholas J. Jouett & ²Cory W. Child3 ¹University of Rhode Island, College of Environmental and Life Sciences, Kingston, RI, USA4 ²Eckerd College, Marine Science, St. Petersburg, FL, USA5 *For correspondence. Email nicholas.jouett@bios.edu

6 **INTRODUCTION:** *Carcinus maenas* has been established in New England for approximately
7 two centuries (Kraemer et al. 2007). Subsequently, it has become an integral part of the ecology
8 in estuarine environments, such as Point Judith Pond, Rhode Island, where it now cohabitates
9 with the blue crab, *Callinectes sapidus* and several other crustaceans across rocky shorelines, salt
10 marshes, and various benthic substrata (Mosknes & van Montefrans 1998). The preferred habitat
11 of *C. maenas* appears to be rocky shores (Epifanio et al. 1998). In the late 1980s, the Asian shore
12 crab, *Hemigrapsus sanguineus*, was able to establish a foothold in New England, and it has since
13 expanded its distribution and population along rocky shorelines from Pamlico Sound, North
14 Carolina, to Cape Cod, Massachusetts (Williams & McDermott 1990; McDermott 1991; Lafferty
15 & Kuris 1996). *H. sanguineus* is highly mobile as well as reproductively successful (Fukui 1998;
16 McDermott 1998); it can thus spread aggressively. In some areas, it has become the most
17 abundant intertidal crab (Ahl & Moss 1998; Lohrer & Whitlatch 1997), reaching densities of
18 >300 individuals/ m² in extreme cases (McDermott 1998). *H. sanguineus* strongly prefers rocky
19 substrate (MacDonald et al. 2007; Lohrer et al. 2000; McDermott 1998; Ledesma & O'Connor
20 2001), so much so that it displaces *C. maenas* from beneath cover (Jensen et al. 2002). This
21 exploitative competition exposes *C. maenas* to predators as well as harsher abiotic conditions. *H.*
22 *sanguineus* appears to be much less plastic in its tolerance for alternative habitats, though recent
23 observations have found them in marsh environments (Peterson et al. 2014).

24 Additionally, laboratory manipulations have demonstrated that *H. sanguineus* will win a
25 competition over a food item against *C. maenas* (Jensen et al. 2002). The fact that the larger
26 constituents of both crabs' diets are the mussel *Mytilus edulis* and algae, such as *Enteromorpha*
27 and *Ulva*, further suggests that *H. sanguineus* could have an influence on *C. maenas* (Ropes
28 1968; Brousseau & Baglivo 2005; Bourdeau & O'Connor 2003). The *in-situ* confrontations are
29 likely non-agonistic, as it has been shown that green crabs that coexist with *H. sanguineus* have
30 adapted subordinate behavior (Jensen et al. 2002). This means that *C. maenas* must continue
31 foraging, expend more energy, and possibly lose out on food items. Additionally, *H. sanguineus*
32 often co-occurs with juvenile *C. maenas* (Lohrer & Whitlatch 1997; McDermott 1998), which

33 closes the gap in size difference, thereby conferring *H. sanguineus* further advantage.

34 When these points are considered, it may seem as if *C. maenas* is bound to be negatively
35 influenced by the invasive crab. However, at some sites, like Point Judith Pond, rocky shores are
36 limited, and *C. maenas* has other habitats in the vicinity within which they do not face
37 competition with *H. sanguineus*. Beyond conducting a population survey and correlating crabs to
38 rock metrics, we tested the hypothesis that an estuary with few rocky shores cannot sustain *H.*
39 *sanguineus* in great enough numbers to significantly adversely influence the *C. maenas*
40 population, due to the alternative habitats for *C. maenas* offered by an estuary.

41 A unique aspect of this study is the inclusion of a photo-quadrat system paired with image
42 analysis. Our study used the software photoQuad (Trygonis & Sini 2012), which is for advanced
43 image processing of 2D photographic quadrat samples. This provides a much more exact degree
44 of measuring rock metrics and correlating them to *H. sanguineus* populations. Previous studies
45 (Ledesma & O'Connor 2001) measured rock cover by eye estimation. The methods in this study
46 create more rigorous and set definitions while beginning to point towards a predictive model for
47 *H. sanguineus* populations, as well as possibly other intertidal species dependent on rock metrics.

48 **MATERIALS & METHODS:** Two sites were sampled on Point Judith Pond in Rhode Island
49 over the course of July and August 2013. Point Judith Pond is a brackish estuary, with salinity
50 varying from approximately 26 ppt at the northern end to oceanic levels at the southern portion,
51 which connects to the ocean past an artificial harbor (for more on the pond, see Stout 2006). The
52 sites sampled were Gardner Island and Beach Island (41° 24' 22.83" N, 71° 30' 21.40" W). The
53 two islands at their closest points are 100 meters from each other, whereas the sample sites were
54 no further than 300 m from each other. Both sites have rocky shores; these were where transects
55 were laid because *H. sanguineus* was not found in the sandy areas, as is noted by both personal
56 observation and other investigators. Both islands were easily accessible via pontoon boat from
57 Camp Fuller, the main base of the study. Each time an area was sampled, time and date was
58 recorded as well as height up from the waterline.

59 Collecting fully submerged crabs was not carried out; upon investigation, these crabs were
60 sparse, if at all present, and would have been near impossible to collect in a consistent and
61 reliable fashion (McDermott 1998). This was of little concern, however, as the crabs are only
62 reported to be subtidal in the winter months (Takahashi et al. 1985). Distance up from the
63 waterline varied from 3-12 feet, depending on the slope of the shoreline, but modally was 3 feet.

64 The camera used for photo acquisition was a Nikon D40 (Nikon, Chiyoda, Tokyo). The
65 photographs were analyzed using the software photoQuad (Trygonis & Sini 2012). The photo-
66 quadrat system was mounted on a tripod, and a ½ meter PVC quadrat was used. One hundred
67 foot transects were laid out along the shoreline at an appropriate height, between 3 and 12 feet up
68 from the water line. Each transect was carried out while the tide was low but still receding.
69 Quadrats were laid every five feet. The quadrat's picture was taken first, and then the rocks were
70 flipped over in the quadrat. Crabs were collected by hand and placed in a bucket to be processed.
71 Large rocks that were partially (1/3rd or more) in the quadrat were flipped; any rocks outside this
72 were not turned over, and any crabs outside the quadrat were not counted.

73 Once collected, we measured the carapace width of each crab with vernier calipers to the nearest
74 millimeter. *H. sanguineus* has three anterolateral teeth on each side of the carapace; the width of
75 each crab was measured from the middle teeth. Previous work validated the need to only measure

76 carapace width, as both weight and carapace length are related in a near exact fashion to the
77 width (McDermott 1998). The crabs are sexually dimorphic and therefore could be easily and
78 reliably sexed visually. Males possess a fleshy bulb at the base of the dactyl of the cheliped and
79 the claws are larger than those of females (Sakai 1976). The crabs were then be moved to another
80 bucket and released at the conclusion of the transect, so that no crabs could be counted twice.

81 **RESULTS:** A total of 268 *H. sanguineus* crabs were collected over the month-long period of
82 sampling (see Table 1). The population was found to have a sex ratio of 1:1. Sexual dimorphism
83 in the current sampling was limited only to apron shape and cheliped size, as the average width of
84 both males and females was not significantly different. The difference between gravid females
85 and non-gravid females, however, was noticeable. On average, a gravid female was 2.27 mm
86 wider than a given female, which likely reflects the required energetic cost of carrying eggs.
87 Another interesting point regarding gravidity was the identification of *H. sanguineus*' egg bearing
88 period. Not a single gravid female was found in July; all were found in August (Tables 2a & 2b).

89 The crab density did correlate positively with the different metrics of rock cover (Figs. 1-4). Out
90 of all the quadrats, the greatest density of crabs/ half meter² was 14 individuals, found on three
91 occasions. These quadrats had a significant amount of large rock cover. In no instance were crabs
92 found in an exclusively sandy area.

93 Other measurements of note included that the largest female collected was 28 mm wide, while
94 the largest male was significantly larger at 36 mm. *H. sanguineus* rarely attains carapace sizes
95 wider than 40 mm (Fukui 1998, pers. obs., Jouett). The widest found at the current locale, but not
96 included in the data, was 40.5 mm. The smallest gravid, and therefore mature, crab was 11 mm
97 wide.

98 The photoQuad analysis involved five different methods of analysis. Crabs were compared to: the
99 number of cobble sized rocks (defined as having an area ≥ 68 cm²) (Fig. 1); the area of the largest
100 rock in an individual quadrat (Fig. 2); the area of the average rocks size in the quadrat (of rocks
101 that were larger than 16 cm²) (Fig. 3); and the total coverage of rocks in the quadrat (also of rocks
102 ≥ 16 cm²) (Fig. 4). The strongest correlation among these individual components was seen when
103 crabs were measured as a function of the total coverage. It was found that the smallest rock that
104 had a crab underneath it had an area of 68 cm² (this was the justification for determining the
105 definition of cobble sized rocks). The correlation shows that the larger the rock is past this
106 threshold, the more crabs there are likely to be. The maximum amount of crabs found in any one
107 quadrat was 14, which was on three occasions. For these quadrats, the smallest largest rock was
108 236 cm², which describes the highest *possible* observed density of the crabs. There were only two
109 other cobble sized rocks in this particular quadrat, making it likely that most, if not all, crabs
110 came from beneath this rock, as the next biggest rock was 84 cm². As far as density is concerned,
111 the current study's quadrat size was half a square meter. If this is scaled up to a square meter, the
112 highest density of *H. sanguineus* that the current study found was 56 individuals/ m².

113 Using a multiple linear regression in the statistical software package PAST (Version 3.02,
114 Hammer et al. 2001), a more exact relationship linking all of the rock metrics to the abundance of
115 crabs was found (see Table 3), demonstrating that multivariate analysis better describes the
116 relationship of crabs to rock metrics than the analysis of any individual components.

117 **DISCUSSION:** McDermott's 1991 study reported a mean carapace width of 17.2 mm for males
118 and 17.6 mm for females. The current study reports a mean carapace width of 15.4 ± 5.26 mm for

119 males and 15.5 ± 4.95 mm for females. This is smaller than McDermott's study; however, when
120 only the crabs collected in August from the current study are considered, the mean increases to
121 19.6 mm for males and 17.9 mm wide for females. These notable differences are likely
122 attributable to the variations in locale and timing; this can be said with confidence because the
123 size ranges of the current study were drastically different. The maxima for both males and
124 females of McDermott's 1991 study were no larger than 24.5 mm, whereas the maxima for males
125 and females in the current study were 36 mm and 28 mm, respectively.

126 *H. sanguineus* rarely attains carapace sizes wider than 40 mm (Fukui 1998, pers. obs., Jouett).
127 The widest found at the current locale, but not included in the data, was 40.5 mm. The smallest
128 gravid, and therefore mature, crab was 11 mm wide. This is significantly smaller than the
129 smallest mature female in McDermott's 1991 study, which was 15.2 mm. However, the 2001
130 study by Ledesma & O'Connor was carried out in several, more proximal locales of southeastern
131 Massachusetts and Rhode Island, and the smallest mature female that they found was 12 mm,
132 which is much closer to this study's finding. This measurement is also corroborated by later
133 findings, where 12 mm is approximated to be the smallest possible size of maturity. It was
134 determined that sexual maturity in *H. sanguineus* is attained at 14 mm wide (Fukui 1998);
135 however, this was for Japanese shorelines, and it is clear that this size is smaller for New England
136 shores. Comparing Pacific and Atlantic shores is useful, and it is important to note the
137 differences. *H. sanguineus*' range currently is thought to be no further south than North Carolina,
138 and it has consistently been found to be no further north than Cape Cod (McDermott 1998). This
139 makes its latitudinal distribution a fifth of its Pacific range. It is thought that, provided the
140 necessary substrate, *H. sanguineus* therefore has the potential to expand further south.

141 In August, the percent of gravid crabs out of the entire female population sampled was 66% (n=
142 44/56). In Japan, *H. sanguineus*' native range, the period of egg bearing in the north is from
143 March to October, with the peak being in May-June (Fukui 1998). In the south of Japan, however,
144 the egg bearing period is shortened to 3 months (Takahashi et al. 1985). It has been suggested that
145 the period is dependent on water temperature, and the period in New Jersey has been found to last
146 from late April to September (McDermott 1991 & 1998). Other studies describe New England as
147 facilitating a 4 month period for egg bearing (Epifanio et al. 1998). Though the current study did
148 not span this long, all gravid crabs were found in August, while none were found in July. This
149 curiously was also the case in McDermott (1991); this may be because the time of sampling was
150 between broods in both instances, suggesting great similarity in the environments sampled.

151 Ledesma & O'Connor (2001) linearly correlated rock cover, estimated via eye by two observers,
152 to *H. sanguineus* abundance. The R^2 value of their results was 0.534. While this is a strong
153 relationship and does accurately describe what is found *in-situ*, it could be described in a better
154 way, though far more difficult to calculate. Percent cover of rocks is not the most important
155 factor; rather, it is the space between the rocks that the rocks create. This is referred to as
156 structural complexity (Lohrer et al. 2000). The space between rocks helps reduce desiccation
157 (also asserted by Grant & McDonald 1979), which is important for *H. sanguineus*. It also allows
158 for mobility to different areas and evasion of predators, likely increasing foraging proficiency
159 (Lohrer et al. 2000). More importantly, small shelters also serve as a buffer against temperature
160 changes (Taylor 1981; Abele et al. 1986), to which *H. sanguineus* is sensitive (Epifanio et al.
161 1998). However, measuring structural complexity is difficult to do in the field, and thus
162 measuring rock cover has been developed as a proxy for structural complexity. Our study shows
163 that this has its faults, as we did not produce as tight a correlation as has been found previously
164 while using a more precise method (Ledesma & O'Connor 2001). The multiple linear regression

165 produced an adjusted R^2 value of 0.29992, which is stronger than any relationship generated with
166 our univariate linear comparisons. Additionally, the ANOVA's p value (5.7169E-11) strongly
167 suggests that the trends observed are not due to random sampling. Therefore, it appears that this
168 study's analysis is not only objective (free of estimation), but also relatively robust and may have
169 applications to other intertidal species dependent on rock metrics.

170 In terms of density, although potential estimates have put maximum *H. sanguineus*/ m^2 at 320
171 individuals (McDermott 1998), this is likely an overestimation. The current results are the same
172 as actual previous results (Takahashi et al. 1985; McDermott 1998).

173 As far as competition with *C. maenas* is concerned, at both sites sampled in the current study, few
174 *C. maenas* were observed. While some individuals present were indeed juveniles, as could be
175 predicted by previous studies (MacDonald et al. 2007; Lohrer & Whitlatch 1997; McDermott
176 1998), no clear affiliation between site and size was observed. By personal observation, *C.*
177 *maenas* is very abundant in Point Judith Pond; however, it seems to thrive in epibenthic
178 environments and is less often found emerged. In fact, *C. maenas*' biggest competitor may be
179 itself; the species is cannibalistic, and this causes a constant juvenile bottlenecking pressure.
180 Juvenile *C. maenas* are more successful at surviving to adulthood when in a nursery habitat, such
181 as eelgrass (Mosknes & van Montfrans 1998). Due to the crab's cannibalism, this also makes
182 eelgrass meadows ideal habitats for adults. Point Judith Pond has an extensive bed of eelgrass in
183 the middle of the main body of the pond as a result of dredging out the channel. The deposits
184 were simply displaced to the center of the pond, and the decreased depth allowed eelgrass to
185 grow in large beds (Stout 2006). When searching through these beds of eelgrass, *C. maenas* is
186 found in abundance (pers. obs. Jouett).

187 However, there appears to be no doubt that *H. sanguineus* is having some effect on *C. maenas*. In
188 its native waters, juvenile *C. maenas* often occur under rocks and shells in the intertidal zone
189 (Crothers 1968; Klein-Breteler 1976; Thiel & Darnedde 1994). In Maine, which is too far north
190 for *H. sanguineus*, *C. maenas* are also found under rocks in the intertidal zone (Epifanio et al.
191 1998). This therefore appears to be their preferred habitat, but they are seemingly displaced by *H.*
192 *sanguineus* in New England rocky shores. Competitively inferior species may not necessarily be
193 found in their preferred habitat if they are displaced by competitive superiors (Lohrer et al. 2000).
194 However, *C. maenas* does not appear to be too adversely affected, as there are apparently
195 numerous other habitats that they can thrive in (pers. obs. Jouett; Moksnes & van Montfrans
196 1998).

197 Additionally, significant amounts of the black fingered mud crab, *Panopeus herbstii*, were found
198 to co-occur, in terms of proximity, with *H. sanguineus*. These individuals are significantly
199 smaller, especially at more northern latitudes (Hines 1989), and are often found embedded in the
200 mud underneath rocks. This proximity and habitat is described in the literature (Ledesma &
201 O'Connor 2001; Epifanio et al. 1998) and is agreed upon in regards to the current study. While
202 the overlap and competition between these two crabs cannot be commented on in the current
203 study in regards to foraging, it is possible that these two crabs are competitors. Rock and shell
204 substratum, as well as the presence of *Fucus vesiculosus*, is critical in the maturation of *P.*
205 *herbstii* megalopae (Weber & Epifanio 1996), and the megalopae could be vulnerable to the
206 various pressures of established *H. sanguineus*. Both crabs likely exploit the same benefits of the
207 habitat because *P. herbstii* has the same stringent temperature requirements for juvenile
208 development as *H. sanguineus* (Costlow et al. 1962). Additionally, it is well documented that *P.*
209 *herbstii* is vulnerable to desiccation (McDonald 1977).

210 After a review of the various literatures on the subject, attempting to define *H. sanguineus*
211 residence in terms of the tidal levels appears to be a fruitless task. The crab is, during the non-
212 winter months, certainly intertidal. Because the goal of the current study was to correlate *H.*
213 *sanguineus* individuals and their traits with rock metrics, areas of the shoreline could be selected
214 where it would be thought many crabs could be found. However, this is not to say that crabs were
215 not found significantly higher up. They could be found as high up as the tide went, though the
216 upper limits often had fewer members presumably due to the degree of desiccation. By personal
217 observation, these crabs were often larger (>25 mm) than their lower shoreline counterparts. All
218 in all, conflicting consensuses exist concerning *H. sanguineus*. It has been characterized as a high
219 intertidal crab in some studies (Takada & Kikuchi 1991; Lafferty & Kuris 1996; McDermott
220 1998) and as a low or mid-intertidal crab in others (Depledge 1984; Lohrer & Whitlatch 1997;
221 Saigusa & Kawagoye 1997). The crabs seem to be solely dependent on the rock cover, so long as
222 it is located within the intertidal zone (Hwang 1993; Lohrer et al. 2000). Finally, in accordance
223 with the authors' view, *H. sanguineus* is characterized as being present throughout the intertidal
224 (Lohrer & Whitlatch 1997). Wherever cobble sized rocks are deposited in the intertidal zone is
225 therefore where these crabs will be found.

226 We conclude that at the Point Judith Pond locale, there is not enough structurally complex rocky
227 shoreline available to support an amount of *H. sanguineus* that could be truly disruptive to *C.*
228 *maenas*. Additionally, Point Judith Pond's shoreline perimeter to area ratio appears to favor *C.*
229 *maenas*' relocation/displacement to shallow epibenthic areas. It seems that because an estuary has
230 numerous habitat types, such as eelgrass beds, salt marshes, rocky shorelines, sediment flats, and
231 sandy shorelines, competitive inferiors have many places to which they are able to relocate. In
232 our study, the areas that contain a high enough cobble sized rock cover are limited: there are the
233 two islands sampled, two other islands on the pond, and a few select portions of the shoreline,
234 which overall make up a small portion of the estuary.

235 For example, if *C. maenas* were living on a rocky shoreline that was exposed to a large body of
236 water, such as a large bay or the ocean, then *H. sanguineus*' effect would likely be much more
237 profound. In this instance, the only habitat *C. maenas* could relocate to is deeper water, where it
238 could be put into competition with *Cancer* or *Libinia* species. It may not be able to successfully
239 compete with these new pressures or cope with the environmental differences. As traditionally
240 noted, *C. maenas* may have its lower limit set by other crab species. Interestingly, this may also
241 be the case for its upper limit in rocky shoreline areas, as traditionally opposed to abiotic factors.
242 Upper and lower biotic limits are a widely studied phenomena in intertidal areas, and it would be
243 of no surprise if this concept applied heavily to sympatric crab species.

244 Future work should emphasize developing a method to identify areas of *H. sanguineus* refuge
245 from aerial imagery. By eye, it is relatively simple to (successfully) suppose where *H. sanguineus*
246 may be located. If a program or analysis could be developed that could determine this from mass
247 image data, population characteristics could be quickly deduced with relative accuracy. The
248 methods and results of this study could serve as a starting point and may have applications for
249 other intertidal species. These factors could then be compared to the amount of other habitats
250 available to *C. maenas*, and if the amount of displaceable habitat is too low, then it could be
251 postulated that *H. sanguineus* has the potential to adversely affect *C. maenas*. It is almost certain
252 that in the absence of other competitive crabs, *C. maenas* would spread throughout the intertidal,
253 epibenthic, and benthic environments. However, at Point Judith Pond, it is typically confined to
254 the epibenthic because of food sources, acceptable substrate, and competitive superiors such as

255 *H. sanguineus*.

256 **ACKNOWLEDGEMENTS:** The authors would like to thank Prentice K. Stout for his wisdom,
 257 Nikki Sabatino for assistance in the field, and Camp Fuller for its facilities and materials. The
 258 manuscript benefited greatly from the suggestions of Dr. Graham Forrester. Last but not least, the
 259 authors would also like to thank the eager young minds and hands of all the campers at Camp
 260 Fuller who assisted in field collection of specimens, especially Jaydon Gianfrancesco, who also
 261 took a majority of the photographs.

262 Literature Cited

- 263 Ahl, Robert S., and Susan P. Moss. (1999). Status of the nonindigenous crab, *Hemigrapsus*
 264 *sanguineus*, at Greenwich Point, Connecticut. *Northeastern Naturalist*: 221-224.
- 265 Bourdeau, P. E., and N. J. O'Connor. (2003). Predation by the Nonindigenous Asian Shore Crab
 266 *Hemigrapsus Sanguineus* on Macroalgae and Molluscs. *Northeastern Naturalist* 10, no. 3: 319–
 267 334.
- 268 Brousseau, D. J., and J. A. Baglivo. (2005). Laboratory Investigations of Food Selection by the
 269 Asian Shore Crab, *Hemigrapsus Sanguineus*: Algal Versus Animal Preference. *Journal of*
 270 *Crustacean Biology* 25, no. 1: 130–134.
- 271 Brousseau, D. J., K. Kriksciun, and J. A. Baglivo. (2003). Fiddler Crab Burrow Usage by the Asian
 272 Crab, *Hemigrapsus Sanguineus*, in a Long Island Sound Salt Marsh. *Northeastern Naturalist* 10,
 273 no. 4: 415–420.
- 274 Costlow JD, Bookhout CG, Monroe R. (1962). Salinity-temperature effects on the larval
 275 development of the crab, *Panopeus herbstii* Milne-Edwards, reared in the laboratory".
 276 *Physiological Zoology* 35: 79-93
- 277 Crothers, J.H. (1968). The biology of the shore crab *Carcinus maenas* (L.) The life of the adult
 278 crab. *Field Studies* 2(5): 579-614.
- 279 Depledge, M. H. (1984). Disruption of circulatory and respiratory activity in shore crabs *Carcinus*
 280 *maenas* exposed to heavy metal pollution. *Comparative Biochemistry and Physiology Part C:*
 281 *Comparative Pharmacology* 78.2: 445-459.
- 282 Epifanio, C. E., A. I. Dittel, S. Park, S. Schwalm, and A. Fouts. (1998). Early Life History of
 283 *Hemigrapsus Sanguineus*, a Non-Indigenous Crab in the Middle Atlantic Bight (USA)." *Marine*
 284 *Ecology Progress Series* 170, no. 23: 1–238.
- 285 Fukui, Y. (1998). Comparative studies of the life history of the Grapsid crabs (Crustacea:
 286 Brachyura) inhabiting intertidal cobble and boulder shores". *Publications from the Seto Marine*
 287 *Biological Laboratory* 33: 121-162.
- 288 Grant, J., McDonald, J. (1979). Desiccation tolerance of *Eurypanopeus depressus* (Smith)
 289 (Decapoda: Xanthidae) and the exploitation of microhabitat." *Estuaries* 2: 172-177
- 290 Hammer, Ø., Harper, D.A.T., and P. D. Ryan. (2001). PAST: Paleontological Statistics Software
 291 Package for Education and Data Analysis. *Palaeontologia Electronica* 4(1): 9pp.
- 292 Jensen, G. C., P. S. McDonald, and D. A. Armstrong. (2002). East Meets West: Competitive
 293 Interactions Between Green Crab *Carcinus Maenas*, and Native and Introduced Shore Crab
 294 *Hemigrapsus Spp.* *Marine Ecology Progress Series* 225: 251–262.
- 295 Klein-Breteler, WCM. (1976). Settlement, growth and production of the shore crab, *Carcinus*
 296 *maenas*, on tidal flats in the Dutch Wadden Sea. *Netherland Journal of Sea Research* 10: 354-376
- 297 Kraemer, G. P., Sellberg, M., Gordon, A., and Main, J. (2007). Eight-Year Record of *Hemigrapsus*
 298 *Sanguineus* (Asian Shore Crab) Invasion in Western Long Island Sound Estuary." *Northeastern*
 299 *Naturalist* 14, no. 2: 207–224.

- 300 Lafferty, K. D., & Kuris, A. M. (1996). Biological control of marine pests. *Ecology*, 1989-2000.
- 301 Ledesma, M. E., & O'Connor, N. J. (2001). Habitat and diet of the non-native crab *Hemigrapsus*
302 *sanguineus* in southeastern New England. *Northeastern Naturalist*, 8(1), 63-78.
- 303 Lohrer, A. M., and R. B. Whitlatch. (2002). Relative Impacts of Two Exotic Brachyuran Species
304 on Blue Mussel Populations in Long Island Sound. *Marine Ecology Progress Series* 227: 135–
305 144.
- 306 Lohrer, A. M., Fukui, Y., Wada, K., & Whitlatch, R. B. (2000). Structural complexity and vertical
307 zonation of intertidal crabs, with focus on habitat requirements of the invasive Asian shore crab,
308 *Hemigrapsus sanguineus* (de Haan). *Journal of Experimental Marine Biology and Ecology*,
309 244(2), 203-217.
- 310 Lohrer, A. M., R. B. Whitlatch, and N. Balcom. (1997). Ecological studies on the recently
311 introduced Japanese shore crab (*Hemigrapsus sanguineus*), in eastern Long Island Sound."
312 *Proceedings of the Second Northeast Conference on Nonindigenous Aquatic Nuisance Species*,
313 *Burlington, VT, 18-19 April 1997*. Connecticut Sea Grant College Program.
- 314 MacDonald, J. A., Roudez, R., Glover, T., & Weis, J. S. (2007). The invasive green crab and
315 Japanese shore crab: behavioral interactions with a native crab species, the blue crab. *Biological*
316 *Invasions*, 9(7), 837-848.
- 317 McDonald J. (2007). The comparative intertidal ecology and niche relations of the sympatric mud
318 crabs, *Panopeus herbstii* (Milne Edwards) and *Eurypanopeus depressus* (Smith), at North Inlet,
319 South Carolina, USA (Decapoda: Brachyura: Xanthidae). Ph.D. Dissertation, University of South
320 Carolina, Columbia, South Carolina.
- 321 McDermott, J. J. (1991). A breeding population of the western Pacific crab *Hemigrapsus*
322 *sanguineus* (Crustacea: Decapoda) established on the Atlantic coast of North America." *Biology*
323 *Bulletin* 181: 195-198
- 324 McDermott, J. J. (1998). The Western Pacific Brachyuran (*Hemigrapsus Sanguineus*: Grapsidae),
325 in Its New Habitat Along the Atlantic Coast of the United States: Geographic Distribution and
326 Ecology. *ICES Journal of Marine Science: Journal Du Conseil* 55, no. 2: 289–298.
- 327 McDermott, J. F. Schram, and J. V. Klein. (1999). The western Pacific brachyuran *Hemigrapsus*
328 *sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: feeding,
329 cheliped morphology and growth." *Crustaceans and the biodiversity crisis. Proceedings of the*
330 *Fourth International Crustacean Congress, Amsterdam, the Netherlands, 20-24 July 1998*.
- 331 Moksnes, P. O., L. Pihl, and J. Van Montfrans. (1998). Predation on Postlarvae and Juveniles of the
332 Shore Crab *Carcinus Maenas*: Importance of Shelter, Size and Cannibalism." *Marine Ecology*
333 *Progress Series* 166: 211–225.
- 334 Peterson, B. J., Fournier, A. M., Furman, B. T., & Carroll, J. M. (2014). *Hemigrapsus sanguineus* in
335 Long Island salt marshes: experimental evaluation of the interactions between an invasive crab
336 and resident ecosystem engineers. *PeerJ*, 2, e472.
- 337 Ropes, J. W. (1968). The Feeding Habits of the Green Crab, *Carcinus maenas*. *Fishery Bulletin* 67,
338 no. 2: 183–203.
- 339 Saigusa, M., and O. Kawagoye. (1997). Circatidal rhythm of an intertidal crab, *Hemigrapsus*
340 *sanguineus*: synchrony with unequal tide height and involvement of a light-response mechanism.
341 *Marine Biology* 129.1: 87-96.
- 342 Sakai T. (1976). Crabs of Japan and the adjacent seas." *Kodansha Ltd*. Tokyo
- 343 Stout, P. K. (2006). A Place of Quiet Waters: The History and Natural History of Rhode Island's
344 Point Judith Pond and the Harbor of Refuge. Wakefield, RI: Limulus Book.
- 345 Takahashi, K., T. Miyamoto, Y. Mitzutori, and I. Masaichi. (1985). Ecological study on rocky-shore
346 crabs in Oshoro Bay. *Scientific Reports of the Hokkaido Fisheries Experimental Station* 27: 71-
347 89.

- 348 Thiel M, Darnedde T. (1994). Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel
349 clumps as an important refuge for juveniles.” *Helgolander Meeresunters* 48: 321-332
- 350 Trussell, G. C., & Smith, L. D. (2000). Induced defenses in response to an invading crab predator:
351 an explanation of historical and geographic phenotypic change. *Proceedings of the National*
352 *Academy of Sciences*, 97(5), 2123-2127.
- 353 Trygonis, V., & Sini, M. (2012). photoQuad: A dedicated seabed image processing software, and a
354 comparative error analysis of four photoquadrat methods. *Journal of Experimental Marine*
355 *Biology and Ecology*, 424, 99-108.
- 356 Weber J.C., C.E. Epifanio. (1996). Response of mud crab (*Panopeus herbstii*) megalopa to cues
357 from adult habitat.” *Marine Biology*, 126, pp. 655–661
- 358 Williams, A. B. and McDermott, J. J. (1990) An eastern United States record for the western Indo-
359 Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae). *Proceedings of the*
360 *Biological Society of Washington*, 103: 108–109

Table 1 (on next page)

Table 1 - Data for all *H. sanguineus* sampled

Data grouping all crabs logged. Measurements are in millimeters. See Tables 2a and 2b for temporal differences

Table 1	Non-Gravid	Gravid	All Females	Males	All
Mean	14.39326	17.79545	15.5188	15.43704	15.47761
Mode	11	15	15	14	15
Std. Dev.	4.564233	3.897403	4.627981	5.259827	4.947237
Range	21	16	21	30	30
Min	7	11	7	6	6
Max	28	27	28	36	36
Total Count	89	44	133	135	268

Table 2 (on next page)

Table 2a - Data for *H. sanguineus* in July

Temporal data for crabs in July. Measurements are in millimeters. No gravid females were found

Table 2a	Females July	Males July	All July
Mean	13.75325	12.90476	13.31056
Mode	11	14	14
Std. Dev.	4.280174	3.137872	3.740381
Range	19	19	20
Min	7	6	6
Max	26	25	26
Total Count	77	84	161

Table 3 (on next page)

Table 2b - *H. sanguineus* data for August

Temporal data for crabs in August. Measurements are in millimeters

Table 2b	Non-Gravid Aug	Gravid Aug	All Females Aug	Males Aug	All Aug
Mean	18.5	17.79545	17.94643	19.60784	18.73832
Mode	16	15	15	18	18
Std. Dev.	4.337993	3.897403	3.965394	5.41139	4.760958
Range	17	16	17	23	25
Min	11	11	11	13	11
Max	28	27	28	36	36
Total Count	12	44	56	51	107

Table 4 (on next page)

Table 3 - ANOVA of multiple linear regression

Multiple linear regression with crab count per quadrat as the dependent variable and rock metrics as the independent variables.

N	N=155
Multiple R	0.54765
Multiple R ²	0.29992
Multiple R ² adjusted	0.28125
ANOVA	
F	16.065
df1, df2	4,150
p	5.7169E-11

Figure 1

Crabs versus cobble

Number of crabs as a function of cobble sized rocks. "Cobble sized rocks" were defined as rocks that had an area of 68 cm² or higher in photoQuad analysis.

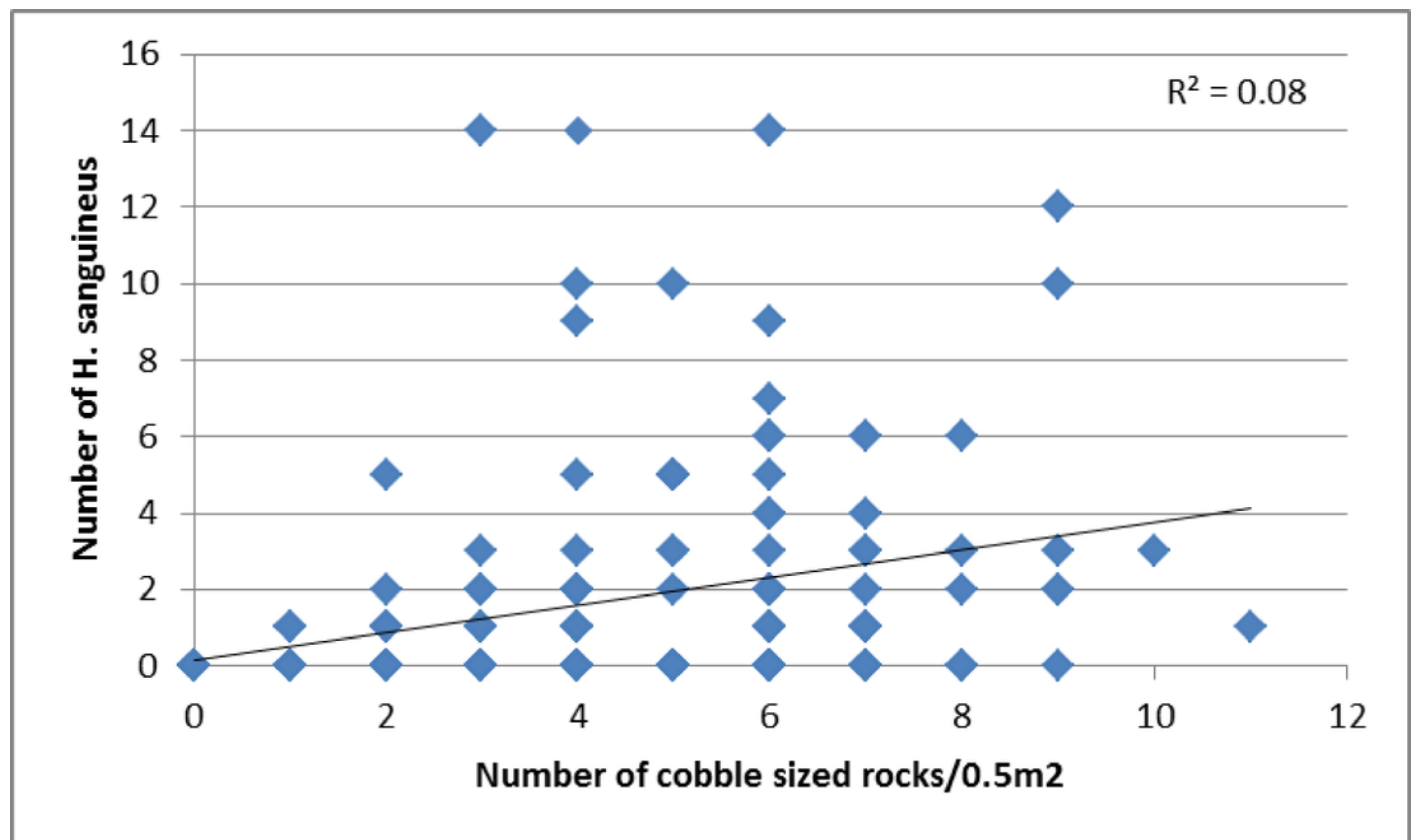


Figure 2

Crabs versus average rock

Number of crabs as a function of the average individual rock area.

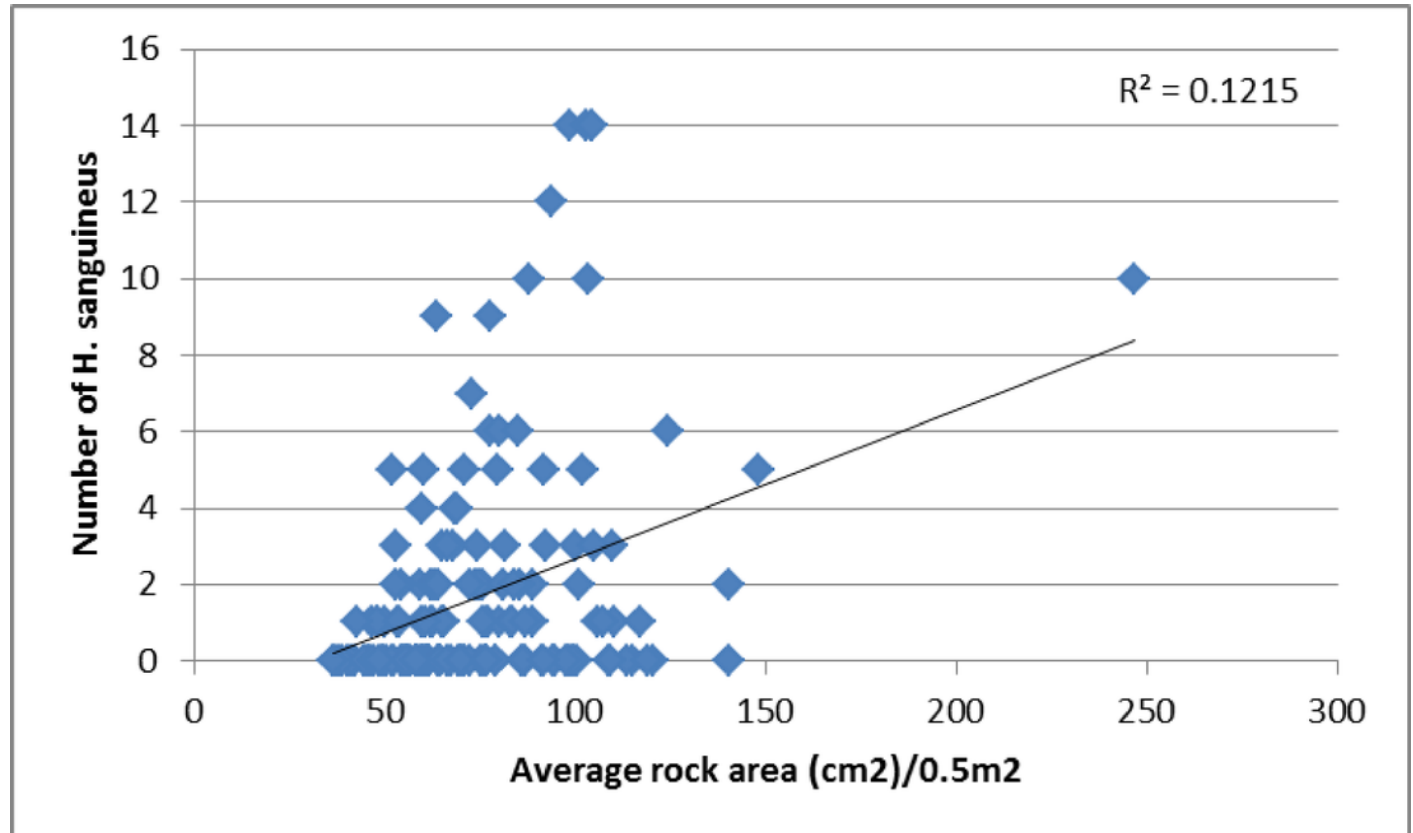


Figure 3

Crabs versus largest rock

Number of crabs as a function of the largest rock's area per quadrat.

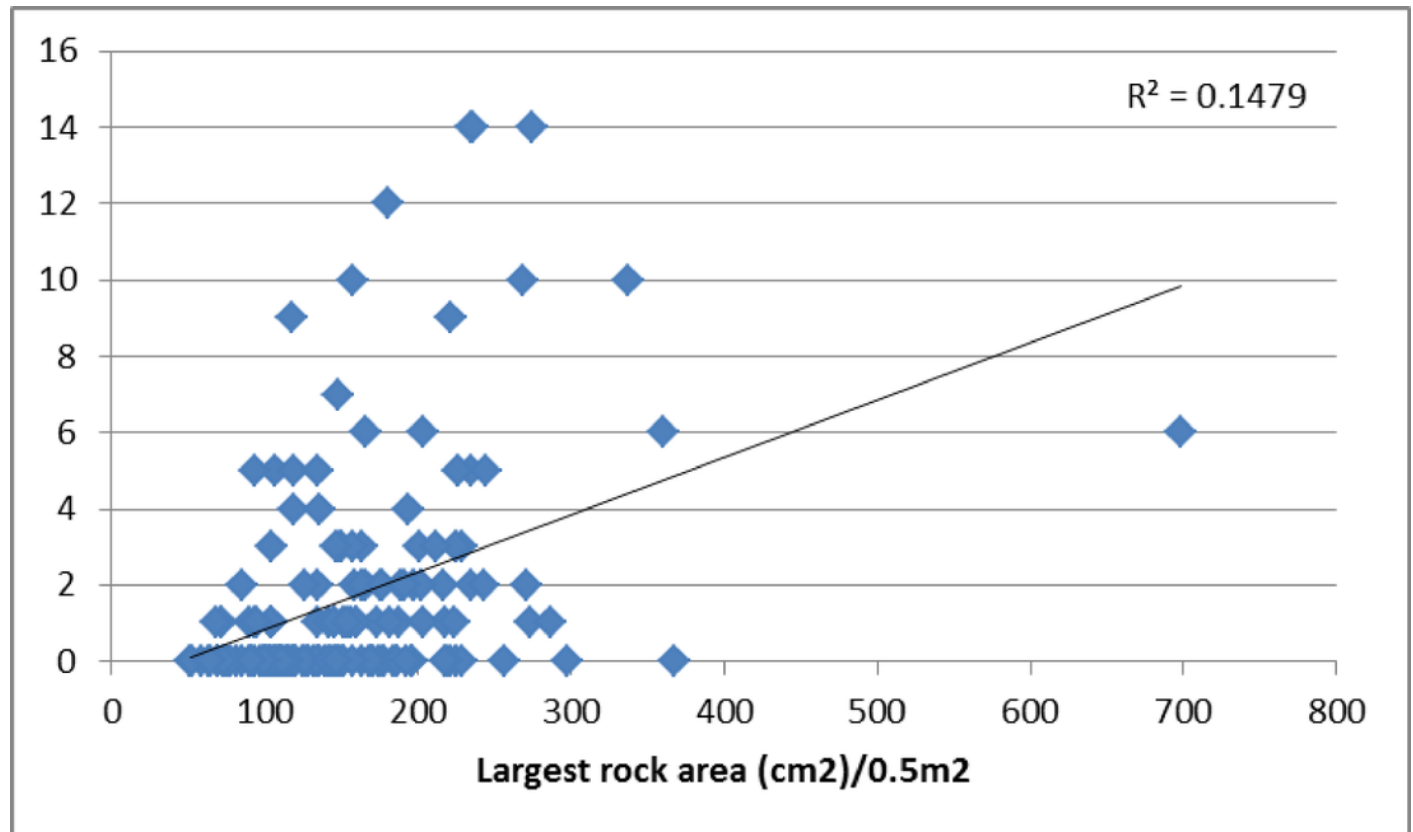


Figure 4

Crabs versus total coverage

Number of crabs as a function of the total rock coverage.

