

Temporal and spatial refugia modify predation risk for invasive crabs in rocky intertidal habitats

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Populations of the invasive Asian shore crab, *Hemigrapsus sanguineus*, now dominate the rocky intertidal of southern New England. High abundances suggest the recent invader may have experienced enhanced success as a result of enemy release. While larvae and juveniles may serve as a food source for ecologically important species, little is known about predation of mature *H. sanguineus*, or the influence of habitat on predation pressure. To assess natural predation rates of adult *H. sanguineus*, crabs were tethered in the intertidal at Clarks Cove in New Bedford, MA. Crabs were left *in situ* for half of a daytime or nighttime tidal cycle then observed for signs of predation. Results of separate high and low tide trials show adult crabs were preyed upon at both high and low tide, though at a significantly higher rate during high tide during both daytime and nighttime, suggesting predation by aquatic species is greater than that by terrestrial species. To investigate the role of habitat as refuge from predation, a laboratory experiment manipulated the complexity of habitat provided to crabs in the presence of native fish predators. Results indicate better refuge is provided by more complex shelter. Together, findings suggest fish, crabs, and/or diving birds are important predators for *H. sanguineus* in the invaded range and that habitat refuge acts to reduce predation pressure.

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12

13 Abstract

14 Populations of the invasive Asian shore crab, *Hemigrapsus sanguineus*, now dominate
15 the rocky intertidal of southern New England. High abundances suggest the recent invader may
16 have experienced enhanced success as a result of enemy release. While larvae and juveniles may
17 serve as a food source for ecologically important species, little is known about predation of
18 mature *H. sanguineus* the influence of habitat on predation pressure. To assess natural
19 predation rates of adult *H. sanguineus*, crabs were tethered in the intertidal at Clarks Cove in
20 New Bedford, MA. Crabs were left *in situ* for half of a daytime or nighttime tidal cycle then
21 observed for signs of predation. Results of separate high and low tide trials adult crabs
22 were preyed upon at both high and low tide, though at a significantly higher rate during high tide
23 during both daytime and nighttime, suggesting predation by aquatic species is greater than that
24 by terrestrial species. To investigate the role of habitat as refuge from predation, a laboratory
25 experiment manipulated the complexity of habitat provided to crabs in the presence of native fish
26 predators. Results indicate better refuge is provided by more complex shelter. Together, findings
27 suggest that, crabs, and/or diving birds are important predators for *H. sanguineus* in the invaded
28 range and that habitat refuge acts to reduce predation pressure.

29 Introduction

30 A prominent factor thought to facilitate the proliferation of invasive populations is enemy
31 release (Heger & Jeschke, 2018), wherein non-native species benefit from a reduction in natural
32 predators, competitors, and parasites in the naïve systems they invade (Colautti et al., 2004).
33 While enemy release may confer an advantage to non-native species (Antonini et al., 2019;
34 Roznik et al., 2020), invasion success is dependent on a myriad of ecological and environmental
35 interactions within native communities (Weis, 2010; Prior et al., 2015).

36 Across taxa and environments, the availability of temporal and spatial refuge can act to
37 constrain predation risk (Prugh & Golden, 2014; Palmer et al., 2022; Suraci et al., 2022). Habitat
38 structure, the arrangement of biotic and abiotic substrate that supports plant and animal
39 communities (Carvalho & Barros, 2017), can mediate interactions between predators and

40 prey by providing spatial refuge in which prey can more easily avoid capture (Warfe & Bermuta
41 2004; Lei, Lin & Zhang, 2014; Mendez, Schwindt & Bortolus 2015; Pozzebon, Loeb & Duso,
42 2015). In addition to habitat-specific structural refuge, predation risk can change over time
43 (Sperry et al., 2008). For example, risk and refuge for prey can exhibit diel variation (Clark, Ruiz
44 & Hines, 2003). More to the point, the availability of refuge is a consequential determinant of
45 predation risk (Smith et al., 2019), but rarely explored as a factor influencing enemy release
46 (Soifer & Ackerman, 2019).

47 Evidence suggests a recent invader to the rocky shores of the North American Atlantic
48 coast, the Asian shore crab, *Hemigrapsus sanguineus*, may have experienced enhanced success
49 as a result of enemy release. The abundance of *H. sanguineus* in invaded habitats can far exceed
50 densities found along the native Asian-Pacific region (Takahashi et al., 1985; Lohrer et al.,
51 2000). Today, Asian shore crabs are the most abundant intertidal crab species in southern New
52 England and Long Island Sound (Kraemer et al., 2007; O'Connor, 2014) and can reach densities
53 of >300 crabs m⁻² at some locations (O'Connor, 2018). The species' success since its
54 introduction to the northeast US in the 1980s is thought to be explained, in part, by reduced
55 impact of natural enemies compared to the populations in native habitats (Pushchina &
56 Panchenko, 2002; Brousseau et al., 2008).

57 Invasive Asian shore crabs benefit from significantly lower prevalence of parasitic
58 infection (Lohrer, 2001; Blakeslee et al., 2009), out-compete resident crab species, and may have
59 fewer crab competitors along the eastern US (Sakai, 1976; Jensen, McDonald & Armstrong,
60 2002; Kraemer et al., 2007; Hobbs, Cobb & Thornber, 2017). In other systems, native predators
61 can act as biological resistance against the growth of invasive populations, with several examples
62 including non-native crabs (Noé et al., 2017; Tiralongo, Messina & Lombardo, 2021). The
63 relationship between the invasive Asian shore crab and native predators, however, remains
64 ambiguous in the absence of direct field experimentation and laboratory tests with adult crabs.
65 Additionally, factors that modify predator-prey relationships, like spatial and temporal refuge,
66 should be more fully explored to clarify the factors influencing enemy release in invaded
67 systems.

68 For benthic aquatic species, the availability of refuge can have a strong effect on survival
69 (Coull & Wells, 1983; Scharf, Manderson & Fabrizio, 2006; Nunes, Sampaio & Barros, 2015)
70 and community structure (Margiotta et al., 2016; Hesterberg et al., 2017). Habitat structure can
71 provide spatial refuge from predation by limiting the ability of predators to access prey (Toscano
72 & Griffen, 2013). Asian shore crabs inhabit highly complex rocky intertidal habitats (Gilman &
73 Grace, 2009); if predator-prey dynamics can be modified by habitat refuge then invasive
74 populations across different coastal habitats may experience different degrees of enemy release.

75 Intertidal environments are particularly unique because they can be accessed by fish only
76 during the high tide period of the tidal cycle, providing a substantial temporal refuge from
77 marine predators at low tide. In contrast, predator-prey dynamics during periods of low tide are
78 underexplored. Despite serving as an important link between marine and terrestrial ecosystems,
79 coastal mammalian and avian predators have been largely overlooked by research on intertidal

80 systems (Quammen, 1984; Wootton, 1992; Carlton & Hodder, 2003). Terrestrial mammals
81 including rats, minks, skunks (Amos, 1966), shrews (Churchfield, 1990), raccoons (Ricketts et
82 al., 1985), mice (Drever et al., 2000), and even foxes (Fay & Stephenson, 1989) are all observed
83 to feed on intertidal invertebrates. Similarly, coastal birds, like gulls, are apex predators that can
84 affect the distribution of intertidal organisms and impact the density of species like crabs (Dumas
85 & Witman, 1993; Ellis et al., 2007). Yet the impact of bird predation is rarely considered in
86 studies of New England's rocky intertidal zone, particularly in relation to highly mobile prey
87 (Menge, 1976; Edwards, Conover & Sutter, 1982). In addition, most intertidal studies have been
88 conducted during daytime. Thus, our knowledge of predator activity during low tide and
89 nocturnal times is severely limited. The influence of habitat structure, and relative predation
90 throughout the tidal and diel cycle, should be considered when assessing a species' risk or
91 release from enemies.

92 In its native range, *H. sanguineus* is known to be consumed by two species of sculpins,
93 *Myoxocephalus stelleri* and *M. brandti* (Pushchina & Panchenko, 2002). Species thought to prey
94 on invasive *H. sanguineus* include those that utilize the rocky intertidal zone to forage, and
95 species that are adapted to eating hard-shelled benthic invertebrate prey, including fish and likely
96 bird species (Epifanio, 2013). Of the potential predators of invasive Asian shore crabs present
97 throughout its range in northeast North America, only predation by fish on juveniles has been
98 examined. Native coastal fish including tautog (*Tautoga onitis*), cunner (*Tautogolabrus*
99 *adspersus*), scup (*Stenotomus chrysops*), and grubby (*Myoxocephalus aeneus*) are all
100 documented to consume *H. sanguineus* megalopae in the laboratory (Rasch & O'Connor, 2012).
101 Striped killifish (*Fundulus majalis*) also readily consumed planktonic larval stage (megalopae)
102 *H. sanguineus* in the lab but did not feed on small (sexually immature) crabs (Kim & O'Connor,
103 2007). However, little is known about predation on larger, sexually mature *H. sanguineus*.

104 Tautog, *Tautoga onitis*, is a temperate reef fish that plays an important role in the
105 structure of nearshore marine communities as a specialized predator of hard-shelled benthic
106 invertebrates including crabs (Liem & Sanderson, 1986; Clark et al., 2006). Tautog is a major
107 component of recreational catch and a valuable commercial fishery resource from Massachusetts
108 to Virginia (Steimle & Shaheen, 1999). The species occurs in coastal environments from Nova
109 Scotia to South Carolina and is most abundant from Cape Cod to Chesapeake Bay (Dorf &
110 Powell, 1997; Steimle & Shaheen, 1999), occurring throughout the North American invasive
111 range of *H. sanguineus*.

112 Tautog is a member of the Labridae family, named for their terminal protractile mouths
113 and jaw morphology associated with hard-prey diets (Liem & Sanders, 1986). The species
114 reaches a maximum size of 90 cm (about 6 kg) (Collette & Klein-MacPhee, 2002), and feeds
115 predominantly on mussels and other shellfish, including Atlantic rock crabs (*Cancer irroratus*),
116 Jonah crabs (*Cancer borealis*) and small American lobsters (*Homarus americanus*) (Smith,
117 1997; Steimle & Ogren, 1982; Richards, 1992). Cunner, *Tautogolabrus adspersus*, is another
118 Labrid fish which is abundant along the inshore temperate waters of the Gulf of Maine (Bigelow
119 & Schroeder, 1953) and consumes a wide variety of invertebrate prey, including crabs (Liem &

120 Sanderson, 1986; Bowman et al., 2000). Both Labrid species have high affinity for benthic
121 structure and aggregate around substrate like rocks and docks (Olla, Bejda & Martin, 1975;
122 Auster, 1989). Tautog and cunner begin foraging soon after sunrise and feed until evening
123 twilight (Olla, Bejda & Martin, 1975). They follow the flood tide up above low water levels to
124 forage in the intertidal zone and find their prey visually using a scan-and-pick foraging strategy
125 (Olla et al., 1974; Deacutis, 1982), then return to deeper water during the ebb tide (Bigelow &
126 Schroeder, 1953).

127 Limited studies on the gut contents of wild fishes, including tautog and *Fundulus spp.*
128 killifish, *F. majalis*, and mummichog, *F. heteroclitus*, since the establishment of the invasive
129 Asian shore crab provide evidence that *H. sanguineus* are consumed in nature, but at relatively
130 low frequencies compared to other food items (Clark et al., 2006; Brousseau et al., 2008). In one
131 laboratory choice experiment, tautog consumed juvenile *H. sanguineus*, but less often than native
132 prey species of mud crabs (family Panopeidae) and blue mussels, *Mytilus edulis* (Savaria &
133 O'Connor, 2013). Conversely, other laboratory experiments found cunner, tautog, and black sea
134 bass (*Centropristis striata*) preferentially preyed upon *H. sanguineus* when given the choice with
135 other local crab species (native mud crab *Panopeus herbstii*, and resident European green crab
136 *Carcinus maenas*), and that substrate influenced predator preference (Heinonen & Auster, 2012).
137 These native fish are well-equipped to influence the abundance of sexually mature *H.*
138 *sanguineus*. However, that dynamic has not yet been investigated and questions remain about the
139 role of spatial and temporal refuge as a potential mechanism to facilitate enemy release.

140 The purpose of this study was to measure predation of sexually mature Asian shore crabs
141 in the field to examine temporal refuge from predation risk and use laboratory experiments to
142 assess the influence of spatial refuge on predation. This investigation includes a series of field
143 tethering experiments to test relative predation of adult *H. sanguineus* at high tide and low tide,
144 during daytime and nighttime. Tethering is a useful method to compare relative predation
145 intensity (Moody & Aronson, 2007; Glazner, Ballard & Armitage, 2021). In addition, a series of
146 laboratory feeding trials were conducted to test the influence of high and low levels of habitat
147 refuge on predation of sexually mature *H. sanguineus* by the fish predator *T. onitis*.

148 **Materials & Methods**

149 **Field experiment**

150 *Crab collection and housing*

151 Male (n = 28) and female (n = 6) sexually mature *Hemigrapsus sanguineus* (15 - 22 mm
152 in carapace width, CW) used for tethering experiments were collected at the study site in Clark's
153 Cove, New Bedford, Massachusetts (41°35'40.33"N, 70°54'37.45"W) by hand at low tide and
154 outfitted with tethers 12 – 24 h prior to experimentation. Crabs were held individually in 113 L
155 aerated aquaria, with water sourced directly from Clark's Cove, and kept at ambient conditions
156 (temp 20.5 - 24.5 °C, salinity 33-34), housed adjacent to the field site at the University of
157 Massachusetts School for Marine Science and Technology Seawater Lab. Outfitting crabs with
158 tethers beforehand ensured that the tether was retained and did not impede mobility.

159 The tethering apparatus was constructed using 0.3 m of monofilament fishing line (6.8 kg

160 test strength) secured to the crab by looping around the transverse plane of the body between the
161 2nd and 3rd walking legs. The line was tied at the dorsal midline and the knot was secured with a
162 drop of cyanoacrylate glue. Crabs were reliably recovered using this tethering method and the
163 tether was not shown to cause damage to the crabs when subjected to simulated wave energy in
164 the lab.

165 *Field tethering procedure*

166 Field tethering experiments were conducted in the lower intertidal zone of Clark's Cove,
167 New Bedford, MA (41°35'40.33"N, 70°54'37.45"W) June 28 - August 26, 2020 (Table 1) at
168 +0.29 m above mean low water. Previous investigations at the study site showed crabs were most
169 abundant at that tidal elevation (Towne, Judge & O'Connor, 2023).

170 To prepare the field site for tethering experiments, all rocks and cobble were removed
171 from a 1 m diameter circle, so that only flat sandy substrate was available to the tethered crab. At
172 the time of experimentation, the free end of the tether line was attached to the top of a 10 cm
173 stake embedded in the sediment. Two experimental replicates (plot A and B) were established
174 >10 m apart. The experiments took place during low tide and high tide, during daytime (daylight
175 hours) and nighttime (after sunset). Tethered crabs were left in situ for half of a daytime or
176 nighttime tidal cycle (beginning three hours before low/high tide and ending three hours after
177 low/high tide). Crabs were considered to have been eaten by predators if missing at the end of
178 the trial. Each crab was used for a single trial, and surviving crabs were returned to the wild,
179 outside of the area where this work was performed.

180 *Field tethering analysis*

181 To test whether tide (high / low) and time (daytime / nighttime) influence predation of
182 adult crabs, predation was examined using binomial regression. The dependent variable
183 (predation) was coded as binary data (predation = 1; no predation = 0). The test determined the
184 probability that a crab would be eaten based on the independent variables tide (high / low), and
185 time (daytime / nighttime). The interaction between each of the independent variables (time and
186 tide) were not significant and therefore excluded from the final model. Other independent
187 variables including trial position (plot A or B), trial date, tide time, tidal height, crab sex, moon
188 phase, and their interactions were tested with an expanded binomial regression, and were not
189 found to significantly influence predation, so they were also excluded from the final analysis.
190 Significance of factors was evaluated with analysis of deviance using the `anova()` function of the
191 `car` v3.1-2 package in R (Fox and Weisberg 2019). All statistical analyses performed in this
192 study were done using R v4.0.0 (R Core Team, 2020).

193 **Laboratory experiment**

194 *Crab and fish collection*

195 The twenty-seven *Tautoga onitis* (25.5 – 37 cm total length) used in the laboratory
196 experiment were caught in New Bedford Harbor, MA using unbaited traps May 13 – June 4,
197 2021. Fish were collected during annual trap surveys conducted by the Massachusetts Division
198 of Marine Fisheries; traps were checked at least every three days. Fish were transported in a 50 L
199 insulated cooler with fresh seawater and continuous aeration. Fish were held in groups of < 10

200 for a two-week acclimation period ahead of experimentation. During acclimation, fish were fed
201 crabs and cracked clams to satiation. Fish and crabs were housed, and experiments were
202 conducted, in 1.8 m diameter tanks (tank floor area = 2.6 m²) continuously supplied with ambient
203 seawater from Clarks Cove, New Bedford (water temp 20.5 - 24.5 °C, salinity 33-34) and
204 artificially lit to match natural light-dark cycles. Tanks were cleaned daily. Fish were provided
205 pieces of large PVC pipe (10.2 cm diameter) for shelter during acclimation. Each fish was used
206 for a single trial, then returned to the wild.

207 The 720 *Hemigrapsus sanguineus* (14 – 20 mm) used in these tests were collected from
208 the rocky intertidal in Clark's Cove 12 - 24 h prior to experimentation. Crabs were held in one
209 tank in mesh-sided 0.5 L Tupperware containers in groups of <6 crabs. Crabs were not fed
210 during this time. Only non-gravid crabs with all ten limbs were used in this study. Each crab was
211 used for a single experiment.

212 *Lab experiment treatment construction*

213 Habitat structure provided during the lab experiment was constructed from concrete
214 pavers (L = 40 cm, W = 20 cm, H = 5 cm). The experiment included a No Refuge control
215 treatment without structure, as well as a control treatment without a fish predator. Low Refuge
216 Habitat consisted of two pavers laid flat on the bottom of the tank (Fig. 1). High Refuge Habitat
217 consisted of two pavers, modified with the addition of twelve quartzite river stones (2-3 cm)
218 glued to one long edge of the pavers using saltwater resistant Seachem cyanoacrylate Reef
219 Glue™ which created 1984 cm³ of refuge space under each paver (Fig. 1).

220 All materials were rinsed with fresh water and allowed >24 h to air dry before use. The
221 glue was given >24 h to cure. Stones remained glued in place throughout the duration of the
222 experiment.

223 Each tank was outfitted with a shelter for the fish made of three large PVC tubes (10.2
224 cm diameter), suspended 8 cm above the tank floor in the center of the tank (Fig. 1). Fish utilized
225 the inside and the outside of the PVC tubes as shelter. These PVC tubes were not accessible to
226 the crabs. Fish were maintained and housed under University of Massachusetts Dartmouth
227 Institutional Animal Care and Use Committee protocol # 21-02 approved July 19, 2021.

228 *Lab experimental procedure*

229 Experimental tanks were randomly assigned habitat treatments. Nine trials were
230 conducted for each habitat treatment (High Refuge, Low Refuge, No Refuge, and no fish
231 control). One fish was used per trial and allowed 24 h to acclimate in the experimental tank prior
232 to the experiment, during which time the fish was not fed. Tautog require 8 h to process and
233 evacuate food (Olla et al., 1974). To begin the experiment, habitat treatments were lowered into
234 the tanks (pavers placed >0.5 m away from each other and from tank walls) and 20 crabs were
235 added to the tank. A dip net was used to quarantine the fish for 15 min to allow the crabs to
236 acclimate to the experimental tank. Fish were then given 6 h to feed. Results of pilot work
237 showed, when starved for 24 h, a Tautog (35 cm total length) could consume between 20 and 30
238 *Hemigrapsus sanguineus* (10 mm - 18 mm CW) in 6 h. All trials were conducted during daylight
239 hours, approximately 0700 – 1300.

240 At the end of each trial, the surviving crabs were counted. Fish were returned to storage
241 tanks and observed for an hour after experimentation, then transported in a cooler with sea water
242 to Clark's Cove. No fish showed signs of illness or injury, and all 27 fish used in experiments
243 were released. Tanks were drained and cleaned following each experiment.

244 *Lab experimental analysis*

245 The proportion of crabs eaten was calculated for all trials. To test if habitat refuge
246 treatments influenced the proportion of crabs eaten, all habitat treatments were compared using a
247 one-way ANOVA. A Tukey post hoc test was then performed to determine any differences
248 among levels of habitat complexity. Other independent variables including fish size, water
249 temperature, and experimental tank (A, B, C, D) were tested using an expanded ANOVA model,
250 none of which had significant influence on the proportion of crabs eaten, so were excluded from
251 the final analysis. Data met the assumptions of normality and homogeneity of variance.
252 Significance of factors was evaluated with type-III sums of squares using the R package car (Fox
253 and Weisberg 2019).

254 **Results**

255 **Field tethering**

256 One male and one female crab were found damaged (lost multiple limbs) after
257 experiments, and although injuries were likely the result of predation attempts by a small
258 predator, injured crabs were excluded from the analysis. Of the remaining 32 crabs, seventeen
259 were missing and presumed eaten, and fifteen crabs were recovered unharmed. The proportion of
260 crabs missing during daytime high tides was 0.83 (n = 6); nighttime high tides was 0.89 (n = 9),
261 daytime low tides was 0.22 (n = 9), nighttime low tides was 0.25 (n = 8) (Fig. 2). There was a
262 significantly higher probability of predation at high tide compared to low tide (df = 30, $X^2 =$
263 30.330, $p < 0.001$), while daytime or nighttime did not influence the probability of predation (df
264 = 29, $X^2 = 30.245$, $p = 0.77$) (Table 2).

265 **Laboratory experiment**

266 In the control (no fish) treatment, all crabs survived without injury. Predation in
267 laboratory feeding trials varied significantly with habitat complexity ($p < 0.001$) (Fig. 3, Table
268 3). The proportion of crabs eaten was significantly lower in the presence of High Refuge Habitat
269 (mean = 0.18, SD = 0.13, median = 0.15) compared to both Low Refuge Habitat (mean = 0.64,
270 SD = 0.13, median = 0.70) ($p < 0.001$) and No Refuge (mean = 0.71, SD = 0.16, median = 0.65)
271 ($p < 0.001$). There was no difference in predation between the Low Refuge Habitat and No
272 Refuge treatments ($p = 0.63$) (Fig. 3, Table 4). One fish consumed all 20 crabs available in the
273 experiment (No Refuge, fish total length = 31 cm), and one fish consumed 20 crabs (High
274 Refuge Habitat, fish total length = 35.5 cm).

275 **Discussion**

276 Predation of *Hemigrapsus sanguineus* was influenced by tide (high tide / low tide) and not
277 affected by time (daytime / nighttime) in field experiments. Crabs had a higher probability of
278 being eaten during high tide than low tide. However, predation at high tide and predation at low
279 tide occurred at similar rates irrespective of time of day. The tethering experiment in the field

280 likely overstated actual predation risk, because the tether apparatus restricted the crabs' ability to
281 flee predators, and the experiment was conducted in the absence of refuge for the crab.
282 Nevertheless, results show predation of adult Asian shore crabs can occur during high tide and
283 low tide, and during daytime and nighttime, suggesting that diurnal as well as nocturnal marine
284 and terrestrial species can prey on the invasive Asian shore crab.

285 Tautog and cunner were likely the primary fish species responsible for predation at high
286 tide during this study. The native fishes are specialized for consuming hard-shelled invertebrates
287 in the intertidal zone during high tide (Olla et al., 1974), and are known to feed on crabs,
288 including *H. sanguineus* (Clark et al., 2006). At the study site, beach seines deployed during
289 daytime high tides in August 2020 found 5 species of fish (Table 5), of which tautog and cunner
290 were the only candidate species for preying on benthic adult crabs. Additionally, in >20 h of
291 video footage recorded of tethered crabs for pilot work (July 18 – August 23, 2020) there were
292 three predation attempts observed during daytime high tides and all appeared to involve tautog
293 and/or cunner (pers. obs.). Other species, that are unlikely to prey on adult crabs, including the
294 American puffer and Alewife were observed in footage, and found in beach seines, but were not
295 seen interacting with crabs (Table 5; pers. obs.).

296 When predation occurred during high tide field experiments, the free end of tether line
297 was found broken and masticated, which is consistent with feeding morphology of Labrid fishes
298 that masticate prey with knob-like teeth lining their mouth and pharynx (Liem & Sanderson,
299 1986, Collette & Klein-MacPhee, 2002). Most crabs in the field experiments were entirely
300 consumed, most likely by Tautog which can swallow small crustaceans whole and use their
301 pharyngeal teeth to crush larger prey (Collette & Klein-MacPhee, 2002). Two crabs in the
302 tethering experiment were found alive but missing limbs after the trial. Those incidences better
303 reflect the feeding strategy of a smaller fish predator like cunner which use their highly evolved
304 jaw morphology to shear and crush food items (Collette & Klein-MacPhee, 2002).

305 Higher probability of predation during high tide may, in part, be explained by what is
306 known about the behavior of the Asian shore crab. Both male and female *H. sanguineus* are
307 highly mobile and can travel up to 16 m over a single day (Brousseau et al., 2002). Thought to be
308 most active at high tide, laboratory experiments conducted during daytime found crabs were
309 more likely to move under and out from under shelter when submerged in water (Towne, Judge
310 & O'Connor, 2023). Activity at high tide may expose crabs to visual predators, like tautog and
311 cunner, which use a scan-and-pick foraging strategy to feed in the intertidal zone (Dew, 1976;
312 Deacutis, 1982) where the crabs occur (Brousseau et al., 2002; Epifanio, 2013; Towne, Judge &
313 O'Connor, 2023).

314 Given greater relative predation at high tide, periods of low tide appear to offer, to some
315 extent, temporal refuge from predation. While at lower levels, predation did occur during field
316 tethering experiments at low tide, demonstrating that species that are not strictly aquatic also
317 pose a predation risk to adult *H. sanguineus*. Other invertebrate species could have been
318 responsible for the predation observed in this study at high tide or low tide. European green
319 crabs, *Carcinus maenas*, Atlantic rock crabs, *C. irroratus*, and blue crabs, *Callinectes sapidus*,

320 co-occur with Asian shore crabs on the US east coast (DeRivera et al., 2005). Additionally, other
321 resident crab species have been found in intertidal surveys conducted at the location of these
322 field experiments (Z. Towne, 2020, pers. comm.). The European green crab avoids competitive
323 interactions with Asian shore crabs (Hobbs, Cobb & Thornber, 2017). Blue crabs, however, are
324 known to exert biotic resistance to limit the density and distribution of other invasive
325 invertebrate species like European green crabs (DeRivera et al. 2005), as well as zebra mussels
326 (Molloy, Powell & Ambrose, 1994), and whelks (Harding 2003). Blue crabs are expanding their
327 range northward due to increasing water temperature in the Gulf of Maine (Johnson, 2015) and
328 increasingly overlap with the invasive range of *H. sanguineus* in North America. The
329 antagonistic interactions between Asian shore crabs and blue crabs (MacDonald et al., 2007)
330 deserve further exploration to understand *H. sanguineus* as prey under current and future
331 conditions. Large Asian shore crabs are also known to cannibalize sub-adult conspecifics (Crane
332 & O'Connor, 2021), and while not the dynamic under focus in this study, predation threats for
333 Asian shore crabs are known to change across ontogeny (Kim & O'Connor, 2007), which further
334 complicates questions about enemy release.

335 Benthic species in rocky intertidal communities are commonly prey for birds (Edwards et al.
336 al., 1982; Wootton, 1992). Previous experiments that have excluded avian predators from rocky
337 intertidal habitat found the absence of bird predation caused a significant increase in the density
338 of intertidal crabs like *Cancer borealis* (Ellis et al., 2007). Predation of invasive *H. sanguineus*
339 specifically by avian predators has not been well documented but merits additional investigation.
340 Several species of shorebirds were noted at the site where field tethering experiments were
341 conducted; cormorants (family Phalacrocoracidae) and gulls (family Laridae) were observed
342 feeding in the intertidal during daytime low tides but none were seen consuming crabs (A.
343 Marcelino, 2020, pers. comm.). Similarly, the relationship between Asian shore crabs and coastal
344 mammals has yet to be investigated. Animals like rats, skunks, and racoons are known to
345 consume intertidal organisms (Carlton & Hodder, 2003) and have been observed at the
346 experimental location (pers. obs.), and so may be responsible for the low tide predation observed
347 here. Further research should include field studies that specifically measure the impact of non-
348 fish predators and the variation in predation risk and refuge throughout the tidal cycle, which
349 could have an effect on the degree of enemy release experienced by invasive Asian shore crabs.

350 In the field experiments conducted here, the probability of predation was similar during
351 daytime and nighttime. This is counter to the hypothesis that predation risk would be constrained
352 to the daytime period of the diel cycle, because of the propensity of high tide predators to restrict
353 their activity to daytime. For example, tautog cease feeding at night (Dew, 1976; Deacutis, 1982;
354 Collette & Klein-MacPhee, 2002).

355 Predation during nighttime high tides indicates consumption by nocturnal piscine or crab
356 predators. The American eel, *Anguilla rostrata*, feeds at night (Collette & Klein-MacPhee, 2002)
357 and is ubiquitous in coastal habitats throughout the Gulf of Maine (Sheppard & Block, 2013).
358 While notorious for being an indiscriminate predator and scavenger of animal food items, large
359 eels are known to feed on crustaceans (Ogden, 1970) which may explain the predation measured

360 during nighttime high tides. Potentially increased nighttime activity by *H. sanguineus*, which
361 feed more actively during dark conditions (Spilmont, Gothland & Seuront, 2015), could
362 contribute to predation occurring at night.

363 Predation at nighttime may have been enhanced because of the proximity of the field
364 experiment to a lighted dock. The dock could have encouraged aggregation of tautog and cunner
365 which are known to affiliate with structures like docks (Olla et al., 1975). Illumination from
366 lights on the dock at night could improve the predators' ability to see prey and forage throughout
367 nighttime, particularly on a dark night, like under cloudy skies or during a new or crescent moon
368 (Table 1). Nevertheless, man-made structures like the dock described here are increasingly
369 common in coastal habitats (Ruiz et al., 2000), and such human influence does affect predation
370 efficiency and prey choice in nearshore ecosystems (Montalvo, 2020).

371 In the laboratory study detailed here, High Refuge Habitat significantly reduced the
372 proportion of crabs eaten by *Tautoga onitis*. In addition, there was no difference in the
373 proportion of crabs eaten when provided Low Refuge Habitat and when provided No Refuge.
374 Asian shore crabs are most abundant in mid and lower intertidal zone where there is high
375 structural complexity (Ledesma & O'Connor, 2001; Brousseau et al., 2002; Gilman & Grace,
376 2009; Epifanio, 2013). A limitation of this study is an under-representation of the true
377 complexity of the rocky intertidal zone, which is more often composed of multiple layers of
378 rocks and cobble that could provide more spatial refuge to further minimize the risk from
379 predators (Hesterberg et al., 2017). Nevertheless, evidence presented here demonstrates that *T.*
380 *onitis* will readily consume adult (sexually mature) *H. sanguineus*, and that the availability of
381 structural refuge modifies the risk of predation.

382 The availability of spatial refuge from predation greatly impacts predator-prey
383 interactions across marine ecosystems. Other studies of benthic marine communities have
384 demonstrated that prey survivorship increases significantly with habitat that provides refuge
385 (Scharf, Manderson & Fabrizio, 2006). Local site-level differences in habitat quality best
386 explained variation in predation risk along the range of another invasive crab, the green porcelain
387 crab (*Petrolisthes armatus*) (Kinney, Pintor & Byers, 2019). Similarly, physical-biological
388 interactions like the effect of refuge on predation tested here appear to enhance the degree of
389 enemy release experienced by Asian shore crabs.

390 Given the high density of invasive Asian shore crabs, relative to other intertidal crab
391 species (O'Connor 2014, 2018), *H. sanguineus* appears particularly adept at avoiding predation.
392 The high abundance of *H. sanguineus* in many coastal communities throughout the invaded
393 range suggests that predators do not strongly impact the population size of this species, perhaps,
394 in part, because of the temporal and spatial refuge within rocky intertidal habitats. Unlike other
395 resident crabs, *H. sanguineus* has a high tolerance for sharing refuge with conspecifics (Hobbs,
396 Cobb & Thornber, 2017) and is more active than other resident crab species (Saxton et al. 2020).
397 These characteristics, combined with cryptic coloration and anti-predatory behaviors (Kim &
398 O'Connor, 2007; Savaria & O'Connor, 2013), may confer an advantage against predation, even
399 at high densities.

400 Adult *Hemigrapsus sanguineus* can be eaten throughout the diurnal and tidal cycles in the
401 rocky intertidal zone, although refuge strongly modifies predation threat by a common fish
402 predator, *Tautoga onitis*. Not all the predation observed in field studies can be explained by
403 diurnal fish predation; other predators like nocturnal fish or terrestrial mammals could also prey
404 on the invasive crab. This study suggests invasive Asian shore crab predation risk can be
405 modified by habitat refuge, and therefore populations across different coastal habitats may
406 experience different degrees of enemy release by different suits of predator. Subsequent research
407 could combine the factors examined here, predation and refuge, to directly test if predation
408 pressure experienced by adult *H. sanguineus* populations is different among coastal habitats with
409 varying structural complexity.

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417 References


- 418 Amos W. 1966. *Life on the Seashore*. Toronto: New York, Published in cooperation with the
419 World Book Encyclopedia, McGraw-Hill.
- 420 Antonini Y, Lobato DNC, Norte AC, Ramos JA, Moreira P de A, Braga EM. 2019. Patterns of
421 avian malaria in tropical and temperate environments: Testing the “*The enemy release*
422 *hypothesis*.” *Biota Neotropica* 19:e20180716. DOI: [10.1590/1676-0611-BN-2018-0716](https://doi.org/10.1590/1676-0611-BN-2018-0716).
- 423 Auster PJ. 1989. *Species Profiles: Life Histories and Environmental Requirements of Coastal*
424 *Fishes and Invertebrates (North Atlantic and Mid-Atlantic): Tautog and Cunner*. No. 4. The
425 Service.
- 426 Bigelow HB, Schroeder WC. 1953. *Fishes of the Gulf of Maine*. Washington, United States
427 Government Printing Office.
- 428 Blakeslee A, Keogh C, Byers J, Kuris A, Lafferty K, Torchin M. 2009. Differential escape from
429 parasites by two competing introduced crabs. *Marine Ecology Progress Series* 393:83–96.
430 DOI: [10.3354/meps08225](https://doi.org/10.3354/meps08225).
- 431 Bowman R, Stillwell C, Michaels W, Grosslein M. 2000. *Food of northwest Atlantic fishes and*
432 *two common species of squid*. National Oceanic and Atmospheric Administration National
433 Marine Fisheries Service.
- 434 Brousseau DJ, Baglivo JA, Filipowicz A, Segó L, Alt C. 2002. An experimental field study of
435 site fidelity and mobility in the Asian shore crab, *Hemigrapsus sanguineus*. *Northeastern*
436 *Naturalist* 9:381–390. DOI: [10.2307/3858551](https://doi.org/10.2307/3858551).
- 437 Brousseau DJ, Murphy AE, Enriquez NP, Gibbons K. 2008. Foraging by two estuarine fishes,
438 *Fundulus heteroclitus* and *Fundulus majalis*, on juvenile Asian shore crabs (*Hemigrapsus*
439 *sanguineus*) in western Long Island Sound. *Estuaries and Coasts* 31:144–151. DOI:
440 [10.1007/s12237-007-9006-7](https://doi.org/10.1007/s12237-007-9006-7).

- 441 Carlton JT, Hodder J. 2003. Maritime mammals: Terrestrial mammals as consumers in marine
442 intertidal communities. *Marine Ecology Progress Series* 256:271–286. DOI:
443 [10.3354/meps256271](https://doi.org/10.3354/meps256271).
- 444 Carvalho LRS, Barros F. 2017. Physical habitat structure in marine ecosystems: The meaning of
445 complexity and heterogeneity. *Hydrobiologia* 797:1–9. DOI: [10.1007/s10750-017-3160-0](https://doi.org/10.1007/s10750-017-3160-0).
- 446 Churchfield S. 1990. *The Natural History of Shrews*. Comstock Publishing, Cornell University
447 Press, Ithaca, New York.
- 448 Clark PE, Pereira JJ, Auker LA, Parkins CJ, Vinokur LM. 2006. Size-Related variation in the
449 diet of juvenile tautogs from Long Island Sound. *Transactions of the American Fisheries*
450 *Society* 135:1361–1370. DOI: [10.1577/T05-313.1](https://doi.org/10.1577/T05-313.1).
- 451 Clark KL, Ruiz GM, Hines AH. 2003. Diel variation in predator abundance, predation risk and
452 prey distribution in shallow-water estuarine habitats. *Journal of Experimental Marine*
453 *Biology and Ecology* 287:37–55. DOI: [10.1016/S0022-0981\(02\)00439-2](https://doi.org/10.1016/S0022-0981(02)00439-2).
- 454 Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ. 2004. Is invasion success explained by
455 the enemy release hypothesis? *Ecology Letters* 7:721–733. DOI: [10.1111/j.1461-0248.2004.00616.x](https://doi.org/10.1111/j.1461-0248.2004.00616.x).
- 457 Collette BB, Klein-Macphree G. 2002. *Bigelow and Schroeder's Fishes of the Gulf of Maine,*
458 *Third Edition*. Washington, DC: Smithsonian Books.
- 459 Coull BC, Wells JBJ. 1983. Refuges from fish predation: Experiments with phytal meiofauna
460 from the New Zealand rocky intertidal. *Ecology* 64:1599–1609. DOI: [10.2307/1937513](https://doi.org/10.2307/1937513).
- 461 Crane LC, O'Connor NJ. 2021. Cannibalism as a potential factor affecting recruitment of the
462 invasive Asian shore crab *Hemigrapsus sanguineus*. *Marine Biology* 168:46. DOI:
463 [10.1007/s00227-021-03849-4](https://doi.org/10.1007/s00227-021-03849-4).
- 464 Deacutis CF. 1982. *Feeding behavior of red hake and tautog, and responses to oil-tainted food.*
465 *[Urophycis chuss; Tautoga onitis]*. Univ. of Rhode Island, Kingston, RI (USA). 3447-3447.
- 466 DeRivera CE, Ruiz GM, Hines AH, Jivoff P. 2005. Biotic resistance to invasion: Native predator
467 limits abundance and distribution of an introduced crab. *Ecology* 86:3364–3376. DOI:
468 [10.1890/05-0479](https://doi.org/10.1890/05-0479).
- 469 Dew CB. 1976. A contribution to the life history of the cunner, *Tautogolabrus adspersus*, in
470 Fishers Island Sound, Connecticut. *Chesapeake Science* 17:101–113. DOI:
471 [10.2307/1351052](https://doi.org/10.2307/1351052).
- 472 Dorf BA, Powell JC. 1997. Distribution, abundance, and habitat characteristics of juvenile
473 Tautog (*Tautoga onitis*, Family Labridae) in Narragansett Bay, Rhode Island, 1988-1992.
474 *Estuaries* 20:589–600. DOI: <https://doi.org/10.2307/1352617>.
- 475 Drever MC, Blight L, Hobson K, Bertram D. 2000. Predation on seabird eggs by Keen's mice
476 (*Peromyscus keeni*): Using stable isotopes to decipher the diet of a terrestrial omnivore on a
477 remote offshore island. *Canadian Journal of Zoology-revue Canadienne De Zoologie - CAN*
478 *J ZOOLOG* 78:2010–2018. DOI: [10.1139/cjz-78-11-2010](https://doi.org/10.1139/cjz-78-11-2010).
- 479 Dumas JV, Witman JD. 1993. Predation by Herring Gulls (*Larus argentatus* Coues) on two
480 rocky intertidal crab species [*Carcinus maenas* (L.) & *Cancer irroratus* Say]. *Journal of*

- 481 *Experimental Marine Biology and Ecology* 169:89–101. DOI: [10.1016/0022-](https://doi.org/10.1016/0022-0981(93)90045-P)
482 [0981\(93\)90045-P](https://doi.org/10.1016/0022-0981(93)90045-P).
- 483 Edwards DC, Conover DO, Sutter F. 1982. Mobile predators and the structure of marine
484 intertidal communities. *Ecology* 63:1175–1180. DOI: [10.2307/1937256](https://doi.org/10.2307/1937256).
- 485 Ellis JC, Shulman MJ, Wood M, Witman JD, Lozyniak S. 2007. Regulation of intertidal food
486 webs by avian predators on New England rocky shores. *Ecology* 88:853–863. DOI:
487 [10.1890/06-0593](https://doi.org/10.1890/06-0593).
- 488 Epifanio CE. 2013. Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: A
489 review. *Journal of Experimental Marine Biology and Ecology* 441:33–49. DOI:
490 [10.1016/j.jembe.2013.01.010](https://doi.org/10.1016/j.jembe.2013.01.010).
- 491 Fay FH, Stephenson RO. 1989. Annual, seasonal, and habitat-related variation in feeding habits
492 of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. *Canadian Journal*
493 *of Zoology* 67:1986–1994. DOI: [10.1139/z89-283](https://doi.org/10.1139/z89-283).
- 494 Fox J, Weisberg S. 2019. *An R Companion to Applied Regression*. Thousand Oaks, CA.
- 495 Gilman M, Grace SP. 2009. Use of subtidal habitat by the Asian shore crab *Hemigrapsus*
496 *sanguineus* in Long Island Sound. *Northeastern Naturalist* 16:481–487. DOI:
497 [10.1656/045.016.n314](https://doi.org/10.1656/045.016.n314).
- 498 Glazner R, Ballard J, Armitage AR. 2021. Predation refuge values of marsh and mangrove
499 vegetation for the marsh periwinkle *Littoraria irrorata*. *Marine Ecology Progress Series*
500 672:153–162. DOI: [10.3354/meps13785](https://doi.org/10.3354/meps13785).
- 501 Harding JM. 2003. Predation by blue crabs, *Callinectes sapidus*, on rapa whelks, *Rapana venosa*:
502 Possible natural controls for an invasive species? *Journal of Experimental Marine Biology*
503 *and Ecology* 297:161–177. DOI: [10.1016/j.jembe.2003.07.005](https://doi.org/10.1016/j.jembe.2003.07.005).
- 504 Heger T, Jeschke JM. 2018. Enemy release hypothesis. *Invasion Biology: Hypotheses and*
505 *Evidence*: 92–102. DOI: [10.1079/9781780647647.0092](https://doi.org/10.1079/9781780647647.0092).
- 506 Heinonen KB, Auster PJ. 2012. Prey selection in crustacean-eating fishes following the invasion
507 of the Asian shore crab *Hemigrapsus sanguineus* in a marine temperate community. *Journal*
508 *of Experimental Marine Biology and Ecology* 413:177–183. DOI:
509 [10.1016/j.jembe.2011.12.011](https://doi.org/10.1016/j.jembe.2011.12.011).
- 510 Hesterberg SG, Duckett CC, Salewski EA, Bell SS. 2017. Three-dimensional interstitial space
511 mediates predator foraging success in different spatial arrangements. *Ecology* 98:1153–
512 1162. DOI: [10.1002/ecy.1762](https://doi.org/10.1002/ecy.1762).
- 513 Hobbs N-VS, Cobb JS, Thornber CS. 2017. Conspecific tolerance and heterospecific
514 competition as mechanisms for overcoming resistance to invasion by an intertidal crab.
515 *Biological Invasions* 19:765–772. DOI: [10.1007/s10530-016-1290-3](https://doi.org/10.1007/s10530-016-1290-3).
- 516 Jensen GC, McDonald PS, Armstrong DA. 2002. East meets west: Competitive interactions
517 between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus*
518 *spp.* *Marine Ecology Progress Series* 225:251–262. DOI: [10.3354/meps225251](https://doi.org/10.3354/meps225251).

- 519 Johnson DS. 2015. The savory swimmer swims North: A Northern range extension of the Blue
520 Crab *Callinectes Sapidus*? *Journal of Crustacean Biology* 35:105–110. DOI:
521 [10.1163/1937240X-00002293](https://doi.org/10.1163/1937240X-00002293).
- 522 Kim A, O'Connor NJ. 2007. Early stages of the Asian shore crab *Hemigrapsus sanguineus* as
523 potential prey for the striped killifish *Fundulus majalis*. *Journal of Experimental Marine*
524 *Biology and Ecology* 346:28–35. DOI: [10.1016/j.jembe.2007.01.011](https://doi.org/10.1016/j.jembe.2007.01.011).
- 525 Kinney KA, Pintor LM, Byers JE. 2019. Does predator-driven, biotic resistance limit the
526 northward spread of the non-native green porcelain crab, *Petrolisthes armatus*? *Biological*
527 *Invasions* 21:245–260. DOI: [10.1007/s10530-018-1821-1](https://doi.org/10.1007/s10530-018-1821-1).
- 528 Kraemer GP, Sellberg M, Gordon A, Main J. 2007. Eight-year record of *Hemigrapsus*
529 *sanguineus* (Asian shore crab) invasion in western Long Island Sound estuary. *Northeastern*
530 *Naturalist* 14:207–224. DOI: [10.1656/1092-6194\(2007\)14\[207:EROHSA\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2007)14[207:EROHSA]2.0.CO;2).
- 531 Ledesma ME, O'Connor NJ. 2001. Habitat and diet of the non-native crab *Hemigrapsus*
532 *sanguineus* in Southeastern New England. *Northeastern Naturalist*: 63. DOI:
533 [10.2307/3858263](https://doi.org/10.2307/3858263).
- 534 Lei C, Lin Z, Zhang Q. 2014. The spreading front of invasive species in favorable habitat or
535 unfavorable habitat. *Journal of Differential Equations* 257:145–166. DOI:
536 [10.1016/j.jde.2014.03.015](https://doi.org/10.1016/j.jde.2014.03.015).
- 537 Liem KF, Sanderson SL. 1986. The pharyngeal jaw apparatus of labrid fishes: A functional
538 morphological perspective. *Journal of Morphology* 187:143–158. DOI:
539 [10.1002/jmor.1051870203](https://doi.org/10.1002/jmor.1051870203).
- 540 Lohrer AM. 2001. The invasion by *Hemigrapsus sanguineus* in eastern North America: A
541 review. *Aquatic Invaders* 12:1–11. DOI: [DOI:10.1016/j.jembe.2013.01.010](https://doi.org/10.1016/j.jembe.2013.01.010).
- 542 Lohrer AM, Fukui Y, Wada K, Whitlatch RB. 2000. Structural complexity and vertical zonation
543 of intertidal crabs, with focus on habitat requirements of the invasive Asian shore crab,
544 *Hemigrapsus sanguineus* (de Haan). 244:203–217. DOI: [https://doi.org/10.1016/S0022-](https://doi.org/10.1016/S0022-0981(99)00139-2)
545 [0981\(99\)00139-2](https://doi.org/10.1016/S0022-0981(99)00139-2).
- 546 MacDonald JA, Roudez R, Glover T, Weis JS. 2007. The invasive green crab and Japanese shore
547 crab: Behavioral interactions with a native crab species, the blue crab. *Biological Invasions*
548 9:837–848. DOI: [10.1007/s10530-006-9085-6](https://doi.org/10.1007/s10530-006-9085-6).
- 549 Margiotta AM, Shervette VR, Hadley NH, Plante CJ, Wilber DH. 2016. Species-specific
550 responses of resident crabs to vertical habitat complexity on intertidal oyster reefs. *Journal*
551 *of Experimental Marine Biology and Ecology* 477:7–13. DOI:
552 [10.1016/j.jembe.2016.01.007](https://doi.org/10.1016/j.jembe.2016.01.007).
- 553 Mendez M, Schwindt E, Bortolus A. 2015. Differential benthic community response to increased
554 habitat complexity mediated by an invasive barnacle. *Aquatic Ecology* 49:441–452. DOI:
555 [10.1007/s10452-015-9536-1](https://doi.org/10.1007/s10452-015-9536-1).
- 556 Menge BA. 1976. Organization of the New England rocky intertidal community: Role of
557 predation, competition, and environmental heterogeneity. *Ecological Monographs* 46:355–
558 393. DOI: [10.2307/1942563](https://doi.org/10.2307/1942563).

- 559 Molloy D, Powell J, Ambrose P. 1994. Short-term reduction of adult zebra mussels (*Dreissena*
560 *polymorpha*) in the Hudson River near Catskill, New York: An effect of juvenile blue crab
561 (*Callinectes sapidus*) predation? *Journal of Shellfish Research* 13:367–371.
- 562 Montalvo C. 2020. Predation efficiency and prey choice of estuarine organisms under varying
563 anthropogenic light types and intensities. Master's thesis. Nova Southeastern University.
564 Retrieved from NSUWorks (535).
- 565 Moody RM, Aronson RB. 2007. Trophic heterogeneity in salt marshes of the northern Gulf of
566 Mexico. *Marine Ecology Progress Series* 331:49–65. DOI: [10.3354/meps331049](https://doi.org/10.3354/meps331049).
- 567 Noè S, Gianguzza P, Trapani FD, Badalamenti F, Vizzini S, Fernández TV, Bonaviri C. 2017.
568 Native predators control the population of an invasive crab in no-take marine protected
569 areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28:1229–1237. DOI:
570 [10.1002/aqc.2921](https://doi.org/10.1002/aqc.2921).
- 571 Nunes JDA, Sampaio CL, Barros F. 2015. The influence of structural complexity and reef habitat
572 types on flight initiation distance and escape behaviors in labrid fishes. *Marine Biology*
573 162:493–499. DOI: [10.1007/s00227-014-2578-4](https://doi.org/10.1007/s00227-014-2578-4).
- 574 O'Connor NJ. 2014. Invasion dynamics on a temperate rocky shore: From early invasion to
575 establishment of a marine invader. *Biological Invasions* 16:73–87. DOI: [10.1007/s10530-](https://doi.org/10.1007/s10530-013-0504-1)
576 [013-0504-1](https://doi.org/10.1007/s10530-013-0504-1).
- 577 O'Connor NJ. 2018. Changes in population sizes of *Hemigrapsus sanguineus* (Asian shore crab)
578 and resident crab species in southeastern New England (2010–2016). *Northeastern*
579 *Naturalist* 25:197–201. DOI: [10.1656/045.025.0202](https://doi.org/10.1656/045.025.0202).
- 580 Ogden JC. 1970. Relative abundance, food habits, and age of the American Eel, *Anguilla*
581 *rostrata* (LeSueur), in certain New Jersey streams. *Transactions of the American Fisheries*
582 *Society* 99:54–59. DOI: [10.1577/1548-8659\(1970\)99<54:RAFHAA>2.0.CO;2](https://doi.org/10.1577/1548-8659(1970)99<54:RAFHAA>2.0.CO;2).
- 583 Olla BL, Bejda AJ, Martin AD. 1975. Activity, movements, and feeding behavior of the cunner,
584 *Tautoglabrus adspersus*, and comparison of food habits with young tautog, *Tautoga onitis*,
585 off Long Island, New York. *Fish. Bull.; (United States)* 73:4. 
- 586 Olla BL, Studholme AL, Bejda AJ, Samet C, Martin AD. 1974. Effect of temperature on activity
587 and social behavior of the adult tautog *Tautoga onitis* under laboratory conditions. *Marine*
588 *Biology* 45:369–378. DOI: [10.1007/BF00391823](https://doi.org/10.1007/BF00391823).
- 589 Palmer MS, Gaynor KM, Becker JA, Abraham JO, Mumma MA, Pringle RM. 2022. Dynamic
590 landscapes of fear: Understanding spatiotemporal risk. *Trends in Ecology & Evolution*
591 37:911–925. DOI: [10.1016/j.tree.2022.06.007](https://doi.org/10.1016/j.tree.2022.06.007).
- 592 Pozzebon A, Loeb GM, Duso C. 2015. Role of supplemental foods and habitat structural
593 complexity in persistence and coexistence of generalist predatory mites. *Scientific Reports*
594 5:14997. DOI: [10.1038/srep14997](https://doi.org/10.1038/srep14997).
- 595 Prior KM, Powell THQ, Joseph AL, Hellmann JJ. 2015. Insights from community ecology into
596 the role of enemy release in causing invasion success: The importance of native enemy
597 effects. *Biological Invasions* 17:1283–1297. DOI: [10.1007/s10530-014-0800-4](https://doi.org/10.1007/s10530-014-0800-4).

- 598 Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals
599 divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*
600 83:504–514. DOI: [10.1111/1365-2656.12148](https://doi.org/10.1111/1365-2656.12148).
- 601 Pushchina OI, Panchenko VV. 2002. Feeding of Sculpins *Myoxocephalus stelleri* and *M. brandtii*
602 (Cottidae) in the Coastal Zone of Amur Bay in the Sea of Japan. *Journal of*
603 *Ichthyology/Voprosy Ikhtiologii* 42. DOI: [10.1134/S0032945213040085](https://doi.org/10.1134/S0032945213040085).
- 604 Quammen ML. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal
605 mudflats: An experimental test. *Ecology* 65:529–537. DOI: [10.2307/1941415](https://doi.org/10.2307/1941415).
- 606 Rasch JA, O'Connor NJ. 2012. Development and behavior of megalopae of the non-native crab
607 *Hemigrapsus sanguineus* in response to chemical cues from coastal fishes. *Journal of*
608 *Experimental Marine Biology and Ecology* 416:196–201. DOI:
609 [10.1016/j.jembe.2011.12.012](https://doi.org/10.1016/j.jembe.2011.12.012).
- 610 Richards RA. 1992. Habitat selection and predator avoidance: Ontogenetic shifts in habitat use
611 by the Jonah crab *Cancer borealis* (Stimpson). *Journal of Experimental Marine Biology*
612 *and Ecology*: 180–197. DOI: [https://doi.org/10.1016/0022-0981\(92\)90245-6](https://doi.org/10.1016/0022-0981(92)90245-6).
- 613 Ricketts EF, Calvin J, Hedgpeth JW, Phillips DW. 1985. *Between Pacific tides*. Stanford
614 University Press.
- 615 Roznik EA, Surbaugh KL, Cano N, Rohr JR. 2020. Elucidating mechanisms of invasion success:
616 Effects of parasite removal on growth and survival rates of invasive and native frogs.
617 *Journal of Applied Ecology* 57:1078–1088. DOI: [10.1111/1365-2664.13634](https://doi.org/10.1111/1365-2664.13634).
- 618 Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH. 2000. Invasion of coastal marine
619 communities in North America: Apparent patterns, processes, and biases. *Annual Review of*
620 *Ecology and Systematics* 31:481–531. DOI: [10.1146/annurev.ecolsys.31.1.481](https://doi.org/10.1146/annurev.ecolsys.31.1.481).
- 621 Sakai T. 1976. *Crabs of Japan and the Adjacent Seas*. Tokyo, Japan: Kodansha Ltd.
- 622 Savaria MC, O'Connor NJ. 2013. Predation of the non-native Asian shore crab *Hemigrapsus*
623 *sanguineus* by a native fish species, the cunner (*Tautoglabrus adspersus*). *Journal of*
624 *Experimental Marine Biology and Ecology* 449:335–339. DOI:
625 [10.1016/j.jembe.2013.10.003](https://doi.org/10.1016/j.jembe.2013.10.003).
- 626 Saxton NA, Vernier AD, Jebe MT, Griffen BD. 2020. Startle response of the invasive Asian
627 shore crab under different environmental conditions. *Journal of Ethology* 38:281–288. DOI:
628 [10.1007/s10164-020-00649-z](https://doi.org/10.1007/s10164-020-00649-z).
- 629 Scharf FS, Manderson JP, Fabrizio MC. 2006. The effects of seafloor habitat complexity on
630 survival of juvenile fishes: Species-specific interactions with structural refuge. *Journal of*
631 *Experimental Marine Biology and Ecology* 335:167–176. DOI:
632 [10.1016/j.jembe.2006.03.018](https://doi.org/10.1016/j.jembe.2006.03.018).
- 633 Sheppard J, Block S. 2013. Monitoring response of diadromous populations to fish passage
634 improvements on a Massachusetts coastal stream. *Journal of Environmental Science and*
635 *Engineering. A* 2:71. 
- 636 Smith HM. 1907. *The Fishes of North Carolina*. E.M. Uzzell & Company.

- 637 Smith JA, Donadio E, Pauli JN, Sheriff MJ, Middleton AD. 2019. Integrating temporal refugia
638 into landscapes of fear: Prey exploit predator downtimes to forage in risky places.
639 *Oecologia* 189:883–890. DOI: [10.1007/s00442-019-04381-5](https://doi.org/10.1007/s00442-019-04381-5).
- 640 Soifer LG, Ackerman JD. 2019. Extremes of forest–urban gradient offer some refuge for alien
641 orchid invasion. *Biological Invasions* 21:2143–2157. DOI: [10.1007/s10530-019-01963-5](https://doi.org/10.1007/s10530-019-01963-5).
- 642 Sperry JH, Peak RG, Cimprich DA, Weatherhead PJ. 2008. Snake activity affects seasonal
643 variation in nest predation risk for birds. *Journal of Avian Biology* 39:379–383.
- 644 Spilmont N, Gothland M, Seuront L. 2015. Exogenous control of the feeding activity in the
645 invasive Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835). *Aquatic Invasions*
646 10:327–332. DOI: [10.3391/ai.2015.10.3.07](https://doi.org/10.3391/ai.2015.10.3.07).
- 647 Steimle FW, Ogren L. 1982. Food of fish collected on artificial reefs in the New York Bight and
648 off Charleston, South Carolina. *Marine Fisheries Review* 44:49–52.
- 649 Steimle FW, Shaheen PA. 1999. *Tautog (Tautoga Onitis) Life History and Habitat*
650 *Requirements*. U.S. Department of Commerce, National Oceanic and Atmospheric
651 Administration, National Marine Fisheries Service, Northeast Region, Northeast Fisheries
652 Science Center.
- 653 Suraci JP, Smith JA, Chamailé-Jammes S, Gaynor KM, Jones M, Luttbeg B, Ritchie EG, Sheriff
654 MJ, Sih A. 2022. Beyond spatial overlap: Harnessing new technologies to resolve the
655 complexities of predator–prey interactions. *Oikos* 2022:e09004. DOI: [10.1111/oik.09004](https://doi.org/10.1111/oik.09004).
- 656 Takahashi K, Miyamoto T, Mizutori Y, Ito M. 1985. Ecological studies on rocky shore crabs in
657 Oshoro Bay. *Scientific Reports of the Hokkaido Fisheries Research Institutes* 27:71–89.
- 658 Team RC. 2020. R Core Team R: A language and environment for statistical computing.
659 *Foundation for Statistical Computing*.
- 660 Tiralongo F, Messina G, Lombardo BM. 2021. Invasive species control: Predation on the alien
661 crab *Percnon gibbesi* (H. Milne Edwards, 1853) (Malacostraca: Percnidae) by the Rock
662 Goby, *Gobius paganellus* Linnaeus, 1758 (Actinopterygii: Gobiidae). *Journal of Marine*
663 *Science and Engineering* 9:393. DOI: [10.3390/jmse9040393](https://doi.org/10.3390/jmse9040393).
- 664 Toscano BJ, Griffen BD. 2013. Predator size interacts with habitat structure to determine the
665 allometric scaling of the functional response. *Oikos* 122:454–462. DOI: [10.1111/j.1600-0706.2012.20690.x](https://doi.org/10.1111/j.1600-0706.2012.20690.x).
- 667 Towne ZW, Judge ML, O’Connor NJ. 2023. Intertidal habitat complexity influences the density
668 of the non-native crab *Hemigrapsus sanguineus*. *PeerJ* 11:e15161. DOI:
669 [10.7717/peerj.15161](https://doi.org/10.7717/peerj.15161).
- 670 Warfe DM, Barmuta LA. 2004. Habitat structural complexity mediates the foraging success of
671 multiple predator species. *Oecologia* 141:171–178. DOI: [10.1007/s00442-004-1644-x](https://doi.org/10.1007/s00442-004-1644-x).
- 672 Weis JS. 2010. The role of behavior in the success of invasive crustaceans. *Marine and*
673 *Freshwater Behaviour and Physiology* 43:83–98. DOI: [10.1080/10236244.2010.480838](https://doi.org/10.1080/10236244.2010.480838).
- 674 Wootton JT. 1992. Indirect effects, prey susceptibility, and habitat selection: Impacts of birds on
675 limpets and algae. *Ecology* 73:981. DOI: <https://doi.org/10.2307/1940174>.

Figure 1

Low Refuge Habitat and High Refuge Habitat treatments in the laboratory experiment with concrete pavers.

Low Refuge Habitat and High Refuge Habitat treatments in the laboratory experiment with concrete pavers. Paver underside: dark gray area shows the underside of the 20 x 40 cm paver used to construct habitat; light gray circles represent individual quartzite river stones (2-3 cm) glued to the underside of the paver on one side. Experiment profile: dark gray represents habitat pavers and light gray represents space available to crabs underneath pavers.

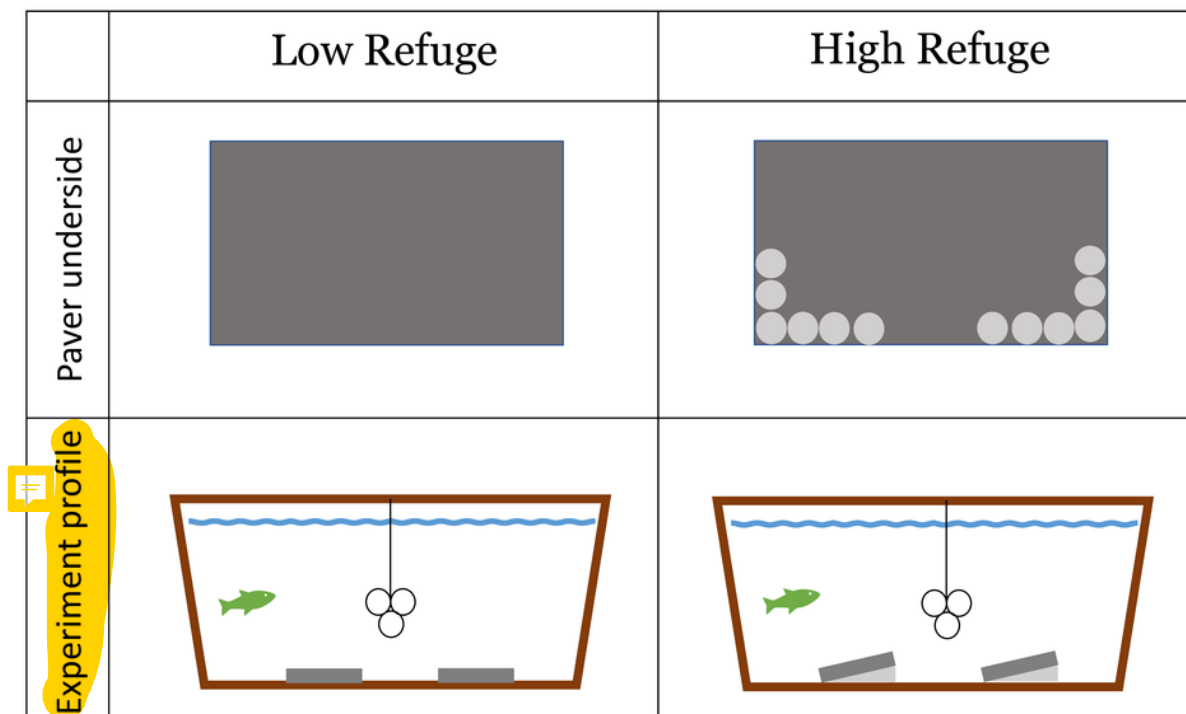


Figure 2

Results of tethering experiments in the field

Results of tethering experiments in the field. Proportion of crabs eaten during daytime high tide (n = 6), daytime low tide (n = 9), nighttime high tide (n = 9), and nighttime low tide (n = 8).

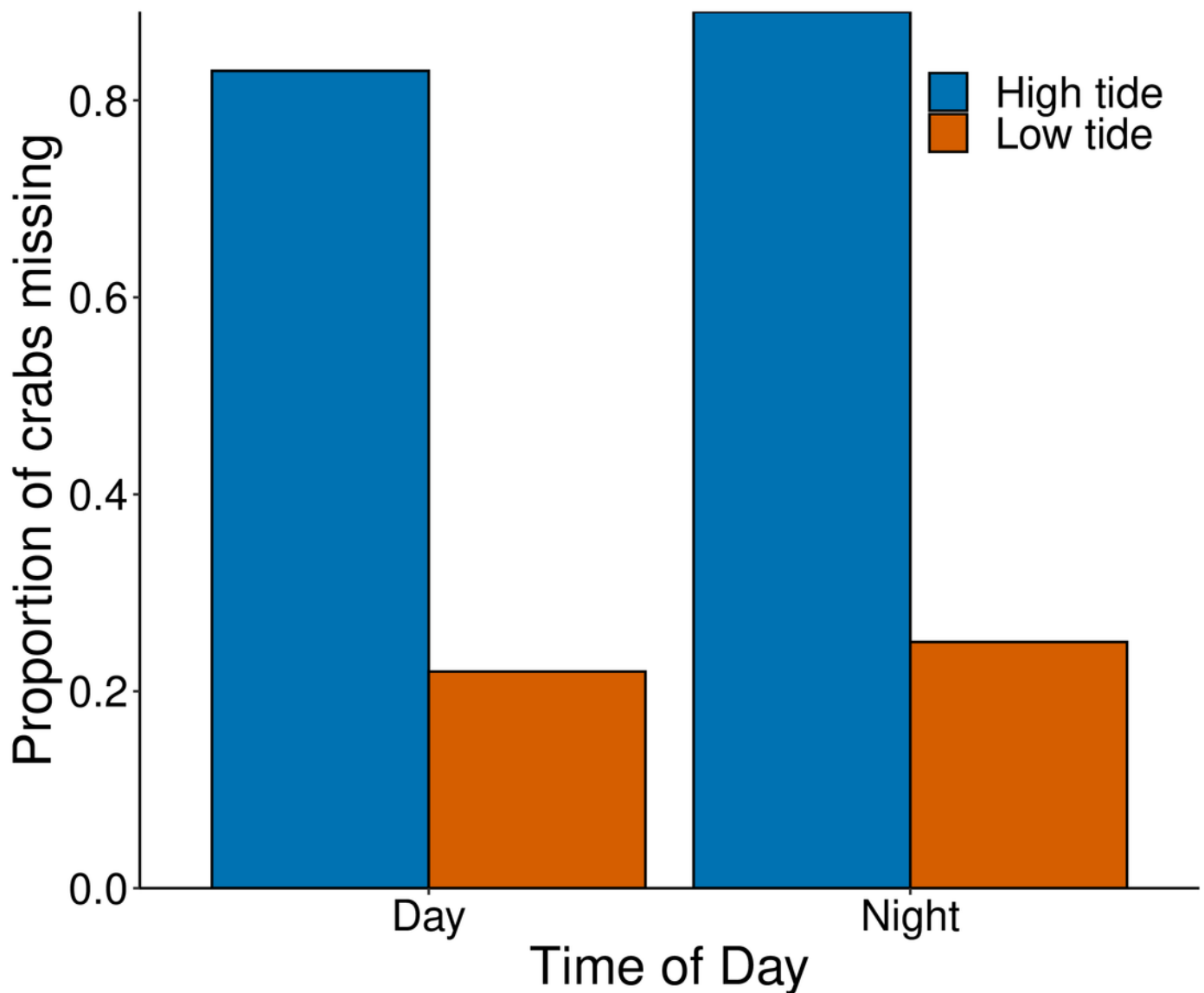


Figure 3

Results of habitat complexity experiments in the laboratory.

Results of habitat complexity experiments in the laboratory. Box and whisker plot showing the proportion of crabs missing with No Refuge, Low Refuge Habitat and High Refuge Habitat. Boxes indicate 25th percentile (Q1), median, and 75th percentile (Q3). Whisker lines extend to maximum and minimum values. Habitat treatments that share a letter were not significantly different (Tukey $p < 0.001$). Sample size was equal for all habitat treatments ($n = 9$).

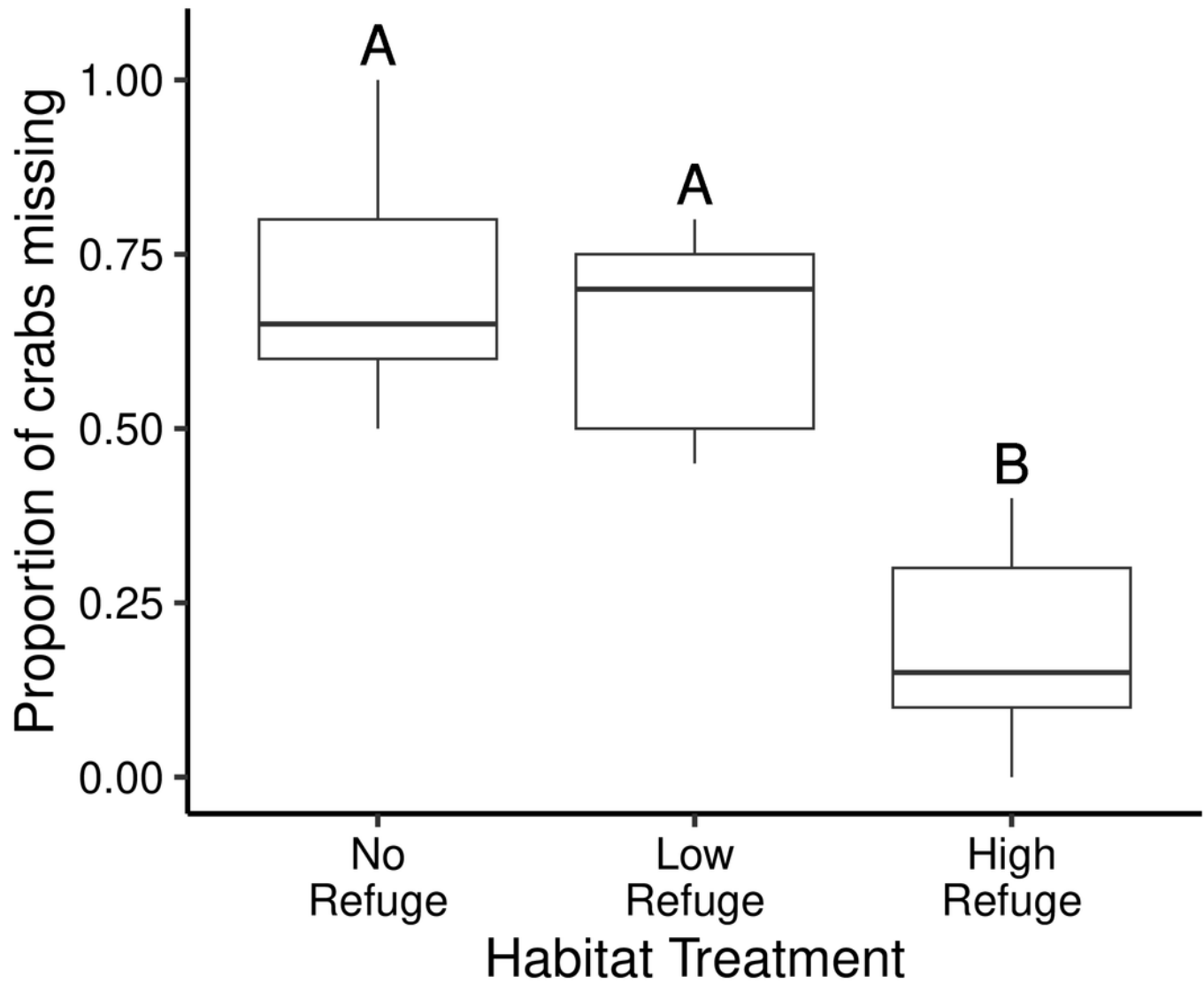


Table 1 (on next page)

Details of field experiment conditions.

Details of field experiment conditions. Dates experimental trials were conducted in 2020, the time (Day or Night), tide (High or Low), predicted tidal height (difference from mean low water level in meters, source: US Harbors Padanaram, South Dartmouth, MA), moon phase (jpl.nasa.gov/edu), and cloud cover (personal observation).

Trial #	Date	Time	Tide	Tidal Height	Moon Phase	Cloud Cover
1	28-Jul	Day	Low	0.1	N/A	Clear
2	28-Jul	Night	Low	0.2	Waxing Gibbous	Cloudy
3	29-Jul	Night	High	1.3	Waxing Gibbous	Clear
4	30-Jul	Day	High	1.0	N/A	Clear
5	3-Aug	Day	High	1.1	N/A	Clear
6	4-Aug	Day	High	1.1	N/A	Cloudy
7	12-Aug	Night	High	1.0	Waning Crescent	Cloudy
8	13-Aug	Day	Low	0.2	N/A	Cloudy
9	14-Aug	Day	Low	0.2	N/A	Clear
10	18-Aug	Night	Low	-0.1	Waning Crescent	Cloudy
11	19-Aug	Night	Low	-0.1	New Moon	Cloudy
12	19-Aug	Day	Low	-0.1	N/A	Cloudy
13	20-Aug	Night	Low	-0.2	Waxing Crescent	Clear
14	21-Aug	Day	Low	-0.2	N/A	Clear
15	24-Aug	Night	High	1.3	Waxing Crescent	Cloudy
16	25-Aug	Night	High	1.3	1st quarter	Cloudy
17	26-Aug	Night	High	1.2	Waxing Gibbous	Clear

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Table 2 (on next page)

Results of field experiment binomial regression.



Results of field experiment binomial regression testing the probability that a crab would be eaten based on the independent variables tide (high / low), time (daytime / nighttime).

Parameter	DF	Deviance Resid.	DF	Resid. Dev	Pr(>Chi)
Tide	1	13.91	30	30.33	< 0.01
Time	1	0.09	29	30.25	0.77

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Table 3 (on next page)

Results of laboratory experiment one-way ANOVA.

Results of laboratory experiment one-way ANOVA testing the effect of habitat complexity treatment on predation.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	2	1.43	0.72	35.99	< 0.001
Residuals	24	0.48	0.02		

1

Table 4(on next page)

Laboratory experiment post-hoc Tukey Test.

Laboratory experiment post-hoc Tukey Test to determine differences in crab predation among habitat complexity treatment.





Treatment	diff	lwr	upr	p adj
Low-High	0.46	0.29	0.63	< 0.001
None-High	0.52	0.35	0.69	< 0.001
None-Low	0.06	-0.11	0.23	0.63

1

Table 5 (on next page)

List of species found during beach seines at the field site in Clark's Cove, New Bedford August 2020.

List of species found during beach seines at the field site in Clark's Cove, New Bedford August 2020. Two hauls with a 10 m net, conducted  high tide, 9:50 am, +3.6ft predicted tidal height (difference from mean low water level  in feet, source: US Harbors Padanaram, South Dartmouth, MA), N is the total number of individuals collected.

Common Name	Species	N
Cunner	<i>Tautoglabrus adspersus</i>	1
Tautog	<i>Tautoga onitis</i>	2
Alewife	<i>Alosa pseudoharengus</i>	44
Atlantic silverside	<i>Menidia menidia</i>	56
Northern puffer	<i>Sphoeroides maculatus</i>	3

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