1   **TITLE: Habitat complexity and benthic predator-prey interactions in Chesapeake Bay**

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23 **ABSTRACT**

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25   In Chesapeake Bay, the soft-shell clam *Mya arenaria* (thin-shelled, deep-burrowing)

26 exhibits population declines when predators are active and persists at low densities. In contrast,

27 the hard clam *Mercenaria mercenaria* (thick-shelled, shallow-burrowing) has a stable population

28 and age distribution. We examined the potential for habitat and predators to control densities and

29 distributions of bivalves in a field caging experiment (*Mya* only) and laboratory mesocosm

30 experiments (both species). In the field, clams exposed to predators experienced 76.3% greater

31 mortality as compared to caged individuals, and blue crabs were likely responsible for most of

32 the mortality of juvenile *Mya*. In mesocosm experiments, *Mya* had lower survival in sand and

33 seagrass than in shell hash or oyster shell habitats. However, crabs often missed one or more

34 prey in seagrass, shell, and oyster shell habitats. Predator search times and encounter rates

35 declined when prey were at low densities, likely due to the added cost of inefficient foraging;

36 however, this effect was more pronounced for *Mya* than for *Mercenaria*. *Mercenaria* had higher

37 survival than *Mya* in mesocosm experiments, likely because predators feeding on *Mercenaria*

38 spent less time foraging than those feeding on *Mya*. *Mya* may retain a low-density refuge from

39 predation even with the loss of structurally complex habitats, though a loss of habitat refuge may

40 result in clam densities that are not sustainable. A better understanding of density-dependent

41 predator-prey interactions is necessary to prevent loss of food-web integrity and to conserve

42 marine resources.

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44 **KEY WORDS**: bivalve, seagrass, functional response, density-dependent predation, optimal

45 foraging

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46   **INTRODUCTION**

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48   Predators exhibit top-down control on communities, influencing the abundance, size

49   structure, and distribution of prey by restricting their survival or activity in time and space [1–3].

50   Predators also influence community function by preying upon dominant species [4–6]. To

51   understand the structure and function of a community, it is important to consider the impact of

52   the predators. Prey populations experience the effects of predation differently depending on how

53   abundant the prey species is and, for actively foraging predators, how quickly the predator can

54   find and consume prey [7]. The degree to which a predator can reduce prey abundance is a

55   function of the probability of encountering a prey item, and the probability that the prey item will

56   be eaten, given that it has been encountered. Both factors depend on the characteristics of the

57   prey, the predator, and other environmental factors [6].

58   Bivalve mollusks exhibit a number of morphological and behavioral characteristics to

59   defend against predators. Armor and aggregation decrease rates of predation, allowing predators

60   and prey to coexist in the same space. For example, the infaunal, shallow-burrowing, hard-shell

61   clam *Mercenaria mercenaria* (hereafter, *Mercenaria*) has a relatively thick shell that protects it

62   from predation by blue crabs *Callinectes sapidus*; clams larger than 40 mm cannot be crushed

63   and therefore coexist with crabs [8]. Other bivalves must avoid predators to survive; the shell of

64   a soft-shell clam *Mya arenaria* (hereafter, *Mya*) is thin and has a permanent gape, indicating that

65   for this species, shell thickness is not an important mode of protecting against attack by predators

66   [9]. To avoid predation, large individuals of *M. arenaria* achieve a non-coexistence refuge by

67   burrowing 25-30 cm deep in the sediment, out of range of foraging predators, which rarely

68   consume clams buried deeper than 10 cm [10].

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69   Habitat also plays an important role in predator defense strategies of marine bivalves.

70   Predators in habitats that are not complex have a greater effect on prey than those in complex

71   habitats [11,12]. Vegetated or shell habitat provides a refuge from predation for many prey

72   [12,13], and increased sediment grain size allows infaunal species to avoid predators more

73   effectively than in fine sediments [10,14,15]. Complex habitats increase metabolic costs

74   associated with foraging, and as these costs become too high, predators may opt to conserve

75   energy or forage elsewhere [16,17].

76   The functional response is a way to quantify predator foraging efficiency [7]. A

77   predator's functional response is the relationship between the number of prey consumed per

78   predator and prey density [18]. Predators that search for prey exhibit a density-dependent

79   functional response, because the encounter rate depends on prey density. In a type II density-

80   dependent response, handling rate and attack rate remain constant as prey density increases [7].

81   Prey consumed per predator increases with increasing prey density, but the rate of increase

82   declines to an upper asymptote. The asymptote is reached when the predator becomes satiated

83   and spends less time foraging, or when the predator is limited by the amount of time it takes to

84   consume prey [7]. A type III sigmoidal density-dependent response occurs when a predator

85   becomes more active as prey density rises, which means attack rate is a function of prey density

86   [7]. Type II and type III functional responses are very different biologically, since type III

87   functional responses create a refuge for prey at low densities, which may result in prey

88   persistence over time, even if a population is driven to low abundance [7,19,20].

89   The main parameters in a functional response model are encounter rate and handling time

90   [7], both of which change as a function of prey mortality, prey behavior, and habitat type. For the

91   purposes of this study, the encounter rate was defined as the number of encounters with prey

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92   divided by the amount of time a predator spends foraging, or actively looking for prey; and the

93   handling time was defined as the amount of time a predator spends manipulating or eating a prey

94   item. For thick-shelled bivalves, the consumption rate of their predators is determined more by

95   handling time than encounter rate; in this case, a type II functional response is more likely [14].

96   For burrowing, thin-shelled bivalves, encounter rate is more important than handling time for

97   their predators [2], which means that a density-dependent sigmoidal (type III) response is likely

98   [14]. The biological mechanism behind a type III response is that low encounter rates often lead

99   to low activity levels or predators emigrating from the area [21]. The functional response of a

100   predator-prey interaction can also be habitat specific. Reduced sediment penetrability [14] or

101   increased vegetative cover [22] may lead to decreased encounter rate, and this may change the

102   functional response by creating or strengthening a low-density refuge from predation. The

103   functional response also changes with ontogeny, as small bivalves may not have sufficiently

104   thick shells to impact predator handling time or burrow deeply enough to reduce encounter rate

105   with predators [23].

106   In the Chesapeake Bay, two commercially valuable clam species, the soft-shell clam *Mya*

107   and the hard clam *Mercenaria* have very different population dynamics. Adult and sub-adults of

108   *Mya* exist in the Bay at low abundance except immediately after spring recruitment, and

109   juveniles are nearly completely consumed by predators each year [24] (Fig 1). *Mercenaria* is

110   fairly abundant throughout the year, and all size classes persist in the Bay in all seasons [25] (Fig

111   1). The different dynamics of these species may be due to predator-prey dynamics, since the two

112   species exhibit different predator-avoidance strategies. Specifically, the persistence of *Mya* at

113   low abundance may be due to a low-density refuge, especially in complex habitats that prevent

114   efficient foraging by the species' main predators, the blue crab *Callinectes sapidus* [26,27] and

115   the cownose ray *Rhinoptera bonasus* [28].

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117   **Fig 1. Size frequency histograms of *Mercenaria mercenaria* (left) and *Mya arenaria* (right)**

118   **in lower Chesapeake Bay.** Samples were collected in spring (a-b), summer (c-d), and fall (e-f)

119   for two years starting in fall 2011. Sizes expressed are biomass (g AFDW) for *Mercenaria* [25]

120   and *Mya* [24].

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122   This study aims to examine the nature of blue crab-bivalve predator-prey interactions for

123   these two infaunal bivalves, including the role of structural refuge (in the form of complex

124   habitat) on these interactions, using both field and laboratory experiments. In field caging

125   experiments, we hypothesized the following: 1) blue crabs and cownose rays are both sources of

126   mortality for sub-adult *Mya* (evidenced as a significant difference in *Mya* survival among all

127   caging treatments); and 2) the presence of seagrass increases clam survival rates as compared to

128   sand and mud (for all plots without a complete cage). In laboratory mesocosm experiments, we

129   hypothesized the following: 1) predators on sub-adult *Mya* exhibit a type III functional response

130   and predators on sub-adult *Mercenaria* exhibit a type II functional response (evidenced as a

131   significant species-density interaction); 2) complex (as compared to unstructured) habitats

132   increase the extent of the low-density refuge for species using density as a refuge, which

133   manifests as increased proportional survival in complex habitats as compared to sand, but only

134   for *Mya* (evidenced as a significant species-habitat interaction); 3) *Mercenaria*'s armor leads to

135   increased handling time compared to *Mya* (evidenced as a significant main effect of species on

136   handling time); 4) low densities, complex habitat, and deep-burrowing prey result in decreased

137   blue crab search time, due to the added cost of inefficient foraging (evidenced as a 3-way

138   interaction between species, density, and habitat), and 5) there is a decreased encounter rate at

139   low densities of *Mya* compared to high densities (evidenced as a significant species-density

140   interaction).

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142   **MATERIALS AND METHODS**

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144   **Field caging experiment**

145   A caging study was conducted in patchy seagrass, sand, and mud near-shore habitats

146   (1.5-2 m depth mean high water) in May 2014 near the mouth of the York River, VA (between

147   37.258323, -76.428047 and 37.275197, -76.370150). These habitat types represented decreasing

148   habitat complexity from seagrass to mud; compared to mud, sand provides additional habitat

149   complexity for infaunal bivalves such as *Mya*, altering the functional response [29]. Ten replicate

150   0.25 m^2 plots were randomly assigned one of three caging treatments in each habitat: full cage,

151   stockade, or uncaged. Full cages were constructed of 13-mm galvanized wire mesh with PVC

152   frames (0.6 m height, 0.5 m width, 0.5 m length) and were sunk into the sediment approximately

153   10 cm and secured with PVC legs sunk an additional 30-40 cm. Stockades were constructed by

154   placing 8 10-ft PVC poles around an otherwise unprotected plot at 25-cm intervals. Stockades

155   kept cownose rays out of the plots, while still allowing for crab and fish predation. Uncaged plots

156   were marked with two PVC poles on the diagonals.

157   Juvenile soft-shell clams (*Mya*) 20-40 mm shell length (mean 28.48 ± 4.41 mm SD) were

158   collected from the York River and held in flow-through tanks until experimentation. Clams were

159   marked individually with permanent marker and transplanted towards the center of the plot at

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160   densities of 12 clams per plot (48 m^{-2}) [30]. A cage was placed over all transplanted clams to

161   allow them to acclimate overnight and achieve a stable burrowing depth as in previous laboratory

162   experiments under similar temperatures [21], and acclimation cages were removed from stockade

163   and uncaged treatments. After 5 d, the contents of all plots were collected to a depth of 40 cm

164   using a suction sampler [20]. Remaining bivalves were counted and shell fragments were noted

165   as evidence of crab predation. Partial cages were not used to control for caging artifacts due to

166   the short nature of this study and the tendency for partial cages to attract blue crabs. Given the

167   relatively large aperture of the cage mesh (13 mm), we would not expect notable differences in

168   cage artifacts among habitat types over the 5-day trial. Only one density was used in this study

169   due to the presence of wild *Mya* in the area, and the consequent logistical difficulties associated

170   with creating reliable densities.

171   Proportional survival data were Box-Cox transformed ($\lambda = 0.51$) to achieve normality and

172   homogeneous variance (assessed using quantile-quantile and residual plots), and analyzed using

173   two-way ANOVA, with cage type (3 levels: full cage, stockade, and uncaged) and habitat (3

174   levels: mud, sand, and seagrass) as fixed factors, with $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for

175   interaction terms [31]. Post-hoc pairwise comparisons were done using Tukey honest significant

176   difference (HSD) tests. From a pilot caging experiment in 2012, we used a simulation of

177   resampled data to determine that our sample size of n = 10 resulted in the following estimates of

178   statistical power: 1.00 for the main effect of cage type, 0.42 for the main effect of habitat, and

179   0.87 for the interaction effect.

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Laboratory mesocosm experiment

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182 *Mya* (thin-shelled, deep infaunal) and *Mercenaria* (thick-shelled, shallow infaunal) were

183 exposed to blue crab *C. sapidus* predation in mesocosm tanks of 0.87 m diameter and 0.59 m

184 height, which were partitioned with corrugated plastic to form a rectangular experimental arena

185 (40 cm x 70 cm). Sand was added to the tank to 25 cm depth, and an additional 25 cm of the tank

186 was filled with filtered water from the York River. An aquarium heater held tank temperature

187 constant at 26-27 °C, typical of shallow York River water in the summer months [32], and the

188 water was aerated by air stones placed outside the experimental arena. Trials were randomly

189 assigned one of four habitat treatments: sand alone, sand/shell hash, sand/oyster shell, or

190 sand/seagrass. For trials receiving shell or oyster shell, a constant volume of 0.5-L crushed shell

191 hash (lightly crushed Baltic clam *Macoma balthica*, ribbed mussel *Geukensia demissa*, and

192 *Mercenaria* shell halves) or oyster shell halves was added to the center of the mesocosm tank.

193 Eelgrass (*Zostera marina*) and widgeongrass (*Ruppia maritima*) shoots and rhizomes were

194 collected from the York River and used to construct seagrass mats for use in trials receiving

195 seagrass. Seagrass mats were constructed with 0.5 liter of natural seagrass blades tied onto

196 plastic 1-cm Vexar mesh meant to simulate a rhizome mat. Holes measuring approximately 25

197 cm^2 were cut approximately every 10 cm to allow crabs to forage for clams buried under the

198 simulated seagrass mat. The mesh and attached seagrass roots were placed in the center of the

199 tank and completely covered with sand.

200 Juvenile *Mya* 20-40 mm shell length were collected from the York River and held in

201 flow-through tanks until experimentation. Hard clams *Mercenaria* 30-40 mm shell length were

202 obtained from Cherrystone Aqua-Farms in Virginia. Only hard clams with shell lengths < 40 mm

203 were used in the study, because blue crabs are able to consume clams of this size [33]. Bivalves

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204   were placed in the sediment siphon up, away from the edge of the tank to avoid edge effects, and

205   allowed 24 h to achieve a stable burial depth [21]. Each species was transplanted at two densities

206   as determined from the literature, one low and one medium density. When number of prey

207   consumed is converted to proportion of prey eaten per predator, two densities (low and medium)

208   are sufficient to determine whether a low-density refuge exists (positive relationship between

209   proportional mortality and prey density, indicating at type III functional response) or does not

210   exist (negative relationship between proportional mortality and prey density, indicating at type II

211   functional response, as in previous studies [21,34]. Low densities for both species were 4 clams

212   per tank, and medium densities were 11 clams per tank for *Mercenaria* and 16 clams per tank for

213   *Mya* [16,34].

214   *Callinectes sapidus* were collected from the York River via baited crab pot. All crabs

215   were acclimated to the lab for 1 week or longer and fed fish or clam meat three times per week.

216   At the start of the experiment, one adult male blue crab with a carapace width ≥ 100 mm was

217   added to each tank receiving a predator treatment. Bivalves were exposed to blue crab predation

218   for 48 h, as is common for similar mesocosm studies [20]. Remaining bivalves were excavated

219   and counted upon termination of the experiment. There were six replicates of each

220   habitat/density combination, as well as an equal number of mesocosms set up without predators,

221   which served as controls (though only 0.6% of clams died in predator-free controls and they are

222   not analyzed or discussed further).

223   Proportional survival data were Box-Cox transformed (λ = -0.14) to achieve normality

224   and homogeneous variance (assessed using quantile-quantile and residual plots), and they were

225   analyzed using three-way ANOVA, with density (2 levels: low and medium), species (2 levels:

226   *Mya* and *Mercenaria*) and habitat (4 levels: sand, shell hash, oyster shell, and seagrass) as fixed

227 factors, with $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms [31]. Effect size and

228 standard error estimates from a previously conducted mesocosm experiment [21] were used to

229 calculate power to see a significant main effect of density, which was 0.95 for n = 6. Post-hoc

230 pairwise comparisons were done using Tukey HSD tests.

231   It was not possible to use a different crab for each trial due to space requirements, nor

232 was it possible to use each crab the same number of times due to losses throughout the

233 experiment. Crabs were used between one and five times, and crabs were randomly assigned to

234 trials so there was no bias inherent in the re-use of crabs. An ANCOVA including density,

235 species, habitat, individual crab identity (51 levels), number of times a crab was used

236 (continuous, 1-5), tank (4 levels), and day of the experiment (continuous, standardized using z

237 score transformation) as covariates indicated that there was no difference in proportion of

238 bivalves eaten based on crab identity ($F_{49, 24} = 1.23$, p = 0.30), number of times the crabs were

239 used ($F_{1, 24} = 1.56$, p = 0.22), tank ($F_{3, 24} = 0.48$, p = 0.70), or day of the experiment ($F_{1, 24} = 1.15$,

240 p = 0.29). These results provided no evidence that crabs exhibited learning behavior, and no

241 evidence for tank effects or trends through time; thus, each trial was treated as an independent

242 replicate.

243   For half of the trials (n = 3 for each treatment) predator behavior was recorded using an

244 infrared-sensitive camera system. A red spotlight was used to improve night-time video quality

245 without disrupting crab behavior [35]. Videos were used to calculate search time, encounter rate,

246 and handling time. Search time (h) was defined as the total time spent exhibiting foraging

247 behavior, such as probing the sediment with legs or claws or lifting items to mouthparts.

248 Encounter rate (hr^{-1}) was defined as the number of encounters (picking up bivalve) divided by

249 the search time. Handling time (h) was defined as the total time spent manipulating or eating a

250 bivalve, divided by the number of encounters. Handling time, search time, and encounter rate

251 were fourth-root transformed to achieve homogeneity and compared for the two bivalve species

252 in different habitat treatments and at different densities using three-way ANOVAs with the same

253 factors as were used for analysis of proportional survival. Post-hoc pairwise comparisons were

254 done using Tukey HSD tests.

255   All analyses were completed using R statistical software [36], and data and R code files

256 are available in the Knowledge Network for Biocomplexity (KNB) repository [37].

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258 **ETHICS STATEMENT**

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260 Virginia Institute of Marine Science is statutorily mandated as Virginia's scientific advisor on

261 marine- and coastal-related natural resources and exempt from having to obtain a scientific

262 collection permit for non-protected species in Virginia's waters.

263

264 **RESULTS**

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266 **Field caging experiment**

267   Over the 5-day caging experiment, mean water temperature at the nearby YKTV2

268 weather buoy was 18.76 °C ($\pm$ 1.63 SD). All replicates (n = 10) for the stockade and uncaged

269 plots lasted through the experiment and were subsequently sampled. At least one of the caged

270 plots was lost from each habitat, leaving n = 9 replicates in mud, n = 7 replicates in sand, and n =

271 8 replicates in seagrass.

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272   As compared to full cages, there was a decrease in proportional survival of 75.6% in

273   stockades and 77.0% in uncaged plots (Fig 2), but the effect of one main effect depended on the

274   conditions of the other (Table 1). Stockade and uncaged treatments had similar survival among

275   habitats (p = 1.0). Mud had significantly lower survival than sand (p = 0.002) or seagrass (p =

276   0.0002). Seagrass and sand had similar survival (p = 0.86). Due to a significant habitat x cage

277   interaction, main effects need to be interpreted with caution (Table 1). The significant habitat x

278   cage treatment interaction was driven by the full cage treatment, which had different patterns of

279   survival than the other caging treatments (Supp. Table 1). Survival of clams in stockades placed

280   in mud was lower than might be expected with just main effects of habitat and cage type (Supp.

281   Table 1).

282

283   Table 1. ANOVA summary table for field caging study proportional survival data.

284   Three types of caging treatments (full cage, stockade, and uncaged) were placed in three habitat

285   types (mud, sand, and seagrass); all were included in the ANOVA model as fixed factors. Data

286   were Box-Cox transformed ($\lambda = 0.51$) prior to analysis. Significant p values (at $\alpha = 0.05$ for main

287   effects and $\alpha = 0.20$ for interaction terms) are bolded.

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	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Habitat	2	2.65	1.32	10.35	**0.0001**
Cage	2	20.29	10.14	79.28	**< 0.0001**
Habitat x Cage	4	2.59	0.65	5.05	**0.001**
Residuals	75	9.60	0.13		

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290 **Fig 2. Survival of transplanted juvenile *Mya arenaria* exposed to a natural suite of**

291 **predators near the mouth of the York River, VA.** Shown are mean proportional survival ($\pm$ 1

292 SE) after 5 d in the field. Bivalves were placed in full cages (full), stockades, or uncaged plots.

293 Plots were in different habitats (denoted by different color bars). There were n = 10 replicates for

294 the stockade and uncaged plots, and n = 9, 7, and 8 replicates for cages in mud, sand, and

295 seagrass, respectively.

296

297 On average, 39.3% of missing clams were recovered as crushed shells within the plots.

298 Mean recovery of crushed shells varied little among caging types and habitats. The highest

299 occurred in stockade plots in sand, with 49.2% ($\pm$ 28.7 SD) of missing clams recovered as

300 crushed shells, and lowest occurred in uncaged plots in mud, with 24.7% ($\pm$ 26.5 SD) of missing

301 clams recovered as crushed shells. Not all clams were recovered from caged plots because the

302 suction sampler used to retrieve clams missed some individuals.

303

304 **Laboratory mesocosm experiment**

305 In mesocosm experiments, mean proportional survival ranged from 0.27 (*Mya* in seagrass

306 at medium densities) to 1.00 (*Mercenaria* in seagrass at medium densities). Crabs ate at least one

307 *Mercenaria* in 18 out of 48 trials, and ate all offered *Mercenaria* in only one trial (low density in

308 shell). Predation of *Mya* was more common, with at least one *Mya* eaten in 27 out of 48 trials. In

309 the sand at low densities, crabs either ate all of the available *Mya* (occurred 3 times), or none of

310 them (occurred 3 times). In the more-complex habitats (shell hash, oyster shell, and seagrass),

311 crabs offered low densities of clams usually ate none of them (occurred 13 out of 18 trials); only

14

312   occasionally would a crab eat a portion of the total number of clams offered (1, 2, or 3 clams;

313   occurred 3 times) or all 4 of the clams (occurred 2 times).

314   *Mya* had significantly lower survival than *Mercenaria* (Fig 3; Table 2), but the effect of

315   one main effect depended on the conditions of the others. There was some evidence that bivalves

316   had lower proportional survival in trials with medium bivalve densities than in trials with low

317   bivalve densities (Table 2). There were no significant differences in survival by habitat type or

318   bivalve density (Table 2), but there were significant species x habitat interactions. *Mya* in

319   medium densities had lower survival than the other species x density combinations, driving a

320   significant species x density interaction (Supp. Table 2). In sand and seagrass, *Mya* had lower

321   survival than some other species x habitat combinations, driving a significant species x habitat

322   interaction (Supp. Table 3).

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Table 2. ANOVA results for mesocosm study proportional survival of juvenile clams, as well as handling time (HT), search time (ST), and encounter rate (ER) of blue crabs *Callinectes sapidus* feeding on juvenile clams. Two species (*Mya arenaria* and *Mercenaria mercenaria*) were offered to blue crabs *Callinectes sapidus* at two densities (low and medium) in tanks with four different habitats (sand, sand with shell hash, sand with oyster shell halves, and sand with live seagrass); all were included in the ANOVA model as fixed factors. Data were Box-Cox transformed ($\lambda = -0.14$; survival only) or fourth-root transformed (HT, ST, and ER) prior to analysis. Significant p values (at $\alpha = 0.05$ for main effects and $\alpha = 0.20$ for interaction terms) are bolded.

	Survival	HT	ST	ER
Species	$\mathbf{F_{1,80} = 15.90, p = 0.0001}$	$F_{1,32} = 2.87, p = 0.10$	$F_{1,32} = 0.69, p = 0.41$	$F_{1,32} = 0.07, p = 0.79$
Density	$F_{1,80} = 3.68, p = 0.06$	$\mathbf{F_{1,32} = 4.28, p = 0.05}$	$\mathbf{F_{1,32} = 10.10, p = 0.003}$	$\mathbf{F_{1,32} = 6.46, p = 0.02}$
Habitat	$F_{3,80} = 1.86, p = 0.14$	$F_{3,32} = 1.23, p = 0.32$	$F_{3,32} = 0.31, p = 0.82$	$F_{3,32} = 1.19, p = 0.33$
Species x Density	$\mathbf{F_{1,80} = 7.17, p = 0.01}$	$F_{1,32} = 0.03, p = 0.88$	$\mathbf{F_{1,32} = 11.38, p = 0.002}$	$F_{1,32} = 0.95, p = 0.34$
Species x Habitat	$\mathbf{F_{3,80} = 2.19, p = 0.10}$	$\mathbf{F_{3,32} = 2.01, p = 0.13}$	$F_{3,32} = 1.13, p = 0.35$	$F_{3,32} = 0.65, p = 0.59$
Density x Habitat	$F_{3,80} = 0.65, p = 0.58$	$F_{3,32} = 0.91, p = 0.45$	$F_{3,32} = 1.47, p = 0.24$	$F_{3,32} = 1.27, p = 0.30$
Species x Density x Habitat	$F_{3,80} = 0.62, p = 0.61$	$F_{3,32} = 0.25, p = 0.86$	$\mathbf{F_{3,32} = 2.08, p = 0.12}$	$F_{3,32} = 0.54, p = 0.66$

330   **Fig 3. Density-dependent predation in different habitats.** Mean juvenile *Mya arenaria* and

331   *Mercenaria mercenaria* proportional survival (± 1 SE) in mesocosms when exposed to blue crab

332   predation in a) sand, b) shell hash, c) oyster shell, and d) seagrass. Solid black lines are mean

333   proportional survival for *Mya* at two initial densities of 4 and 16 per tank, and dashed black lines

334   are mean proportional survival for *Mercenaria* at two initial densities of 4 and 11 per tank.

335

336   Handling time was significantly lower in low-density trials than in medium-density trials

337   (Fig 4a, b; Table 2), but the effect of one main effect depended on the conditions of the others.

338   The two treatments with the longest mean handling times were *Mercenaria* at medium density in

339   shell hash (1.31 h) and *Mercenaria* at medium density in sand (0.76 h). All other treatments had

340   mean handling times of 0.30 h or less. The overall mean handling times for *Mercenaria* and *Mya*

341   were 0.18 h and 0.03 h, respectively. In shell hash, *Mercenaria* had longer handling times than

342   the rest of the species x habitat combinations, driving a significant species x habitat interaction

343   (Supp. Table 4).

344

345   **Fig 4. Behavior of blue crab *Callinectes sapidus* feeding on juvenile *Mya arenaria* and**

346   ***Mercenaria mercenaria*.** Shown are means (± 1 SE) of a) handling time (HT) for crabs feeding

347   on *Mya*, b) HT for crabs feeding on *Mercenaria*, c) search time (ST) for crabs feeding on *Mya*,

348   d) ST for crabs feeding on *Mercenaria*, e) encounter rate (ER) for crabs feeding on *Mya*, and f)

349   ER for crabs feeding on *Mercenaria*. Lines of different colors and patterns represent different

350   habitat types (shell = shell hash; oyster = oyster shell), and means were calculated from n = 3

351   trials.

352

17

353   Search time was shorter in low-density trials than in medium-density trials (Fig 4c, d;

354   Table 2), but the effect of one main effect depended on the conditions of the others. The two

355   treatments with the longest mean search times were *Mya* at medium density in seagrass (5.67 h)

356   and *Mya* at medium density in oyster shell (5.56 h). The overall mean search times for

357   *Mercenaria* at low and medium densities were 1.22 h and 1.91 h, respectively. The overall mean

358   search times for *Mya* at low and medium densities were 0.89 h and 4.16 h, respectively. *Mya* at

359   medium densities had longer search times than the other species x density combinations, driving

360   a significant species x density interaction (Supp. Table 5). However, relatively long search times

361   for medium densities of *Mya* only occurred in certain habitats (sand, oyster shell, and seagrass),

362   resulting in a three-way interaction (Supp. Table 6).

363   Encounter rate was significantly lower in low-density trials than in medium-density trials

364   (Fig 4e, f; Table 2). The two treatments with the highest mean encounter rates were *Mya* at

365   medium density in sand (4.08 ind. h^{-1}) and *Mya* at medium density in seagrass (3.23 ind. h^{-1}).

366   The overall mean encounter rates for *Mercenaria* at low and medium densities were 0.79 ind. h^{-1}

367   and 1.80 ind. h^{-1}, respectively. The overall mean encounter rates for *Mya* at low and medium

368   densities were 0.81 ind. h^{-1} and 2.85 ind. h^{-1}, respectively.

369

370   **DISCUSSION**

371

372   Blue crabs were the main predators of *Mya* in all habitats we examined, with no

373   significant difference between stockades and uncaged plots and high incidence of crushed shells,

374   which is evidence of crab predation rather than another source of mortality [3]. This was in line

375   with our hypothesis that crab predation would be important. Despite evidence in the literature

18

376   that schooling rays can result in mass mortality of bivalves [38], and evidence from gut content

377   analysis that cownose rays consume *Mya* [28], we did not observe evidence that cownose rays

378   increased predation in uncaged plots relative to stockade plots during the time frame of our field

379   experiment (May). These results were contrary to our hypothesis and indicate that over the time

380   and spatial scale of this study, rays were not a major source of mortality for *Mya*.

381   Predation-related mortality was high for juvenile *Mya* that were not protected by a cage.

382   Over a period of five days, exposure to predators decreased survival of juvenile *Mya* by 76.3% as

383   compared to caged individuals. Clam survival was habitat dependent, and both sand and seagrass

384   provided more refuge from predation than mud. *Mya arenaria* has previously been shown to

385   achieve a low-density refuge in sand [14,21]; however, the results from the field caging

386   experiment went against our hypothesis that the added complexity afforded by seagrass habitats

387   provides an extended refuge for juvenile *Mya*. In the laboratory study, there was an effect of

388   habitat on predator-related mortality only for *Mya*, which had lower survival in sand and

389   seagrass than in shell hash or oyster shell habitats. However, in the case of a prey species that

390   relies on achieving a low-density refuge for persistence, proportional survival may not be the

391   best measure of success. Shell hash, oyster shell, and seagrass habitats had higher occurrence of

392   trials with at least one clam remaining, which may be biologically meaningful. Habitat that

393   allows survival of one or a few clams may maintain the low-density refuge for *Mya*.

394   Seagrass did not provide a refuge from predation for *Mya* in the field or in the laboratory

395   experiment. However, seagrass in both studies was patchy; mesocosms were small, and caging

396   sites were chosen so that the three habitat types (mud, sand, and seagrass) were in close

397   proximity. Fragmented seagrass may not be able to provide much protection from generalist

398   predators such as blue crabs, especially if they feed efficiently at patch edges [39]. Despite little

399   evidence for patchy seagrass as a refuge from predation from this study, *Mya* are more likely to

400   be found in seagrass than all other habitat types in the lower Chesapeake Bay [24]. This indicates

401   that dense, contiguous seagrass stands may still provide a refuge from predation for *Mya*. Future

402   research examining the effect of seagrass density or patch size on the survival of juvenile *Mya* is

403   warranted.

404   Predators on *Mercenaria* (thick-shelled infaunal) and *Mya* (thin-shelled infaunal) had

405   significantly different functional responses. Predators on *Mya* had a type III sigmoidal functional

406   response, with a negative relationship between density and proportional survival, as has been

407   seen in previous studies [14]. Predators on *Mercenaria* had a type II hyperbolic functional

408   response, as has been seen previously [16], exhibiting either a positive relationship between

409   density and proportional mortality or no density dependence, depending on the habitat. This

410   difference is relevant to population dynamics and persistence of these two bivalve species

411   because a type II functional response is unstable and can lead to local extinction of prey if they

412   are driven to low densities, but a type III functional response may lead to prey persistence at low

413   density [7,40]. The type II functional response of predators feeding on *Mercenaria* means this

414   bivalve species must remain at relatively high densities to achieve population stability.

415   Conversely, the type III functional response of predators feeding on *Mya* allows the species to

416   persist, even at very low density.

417   The differences in functional response of predators feeding on *Mya* and *Mercenaria* were

418   likely due to differences in predator behavior. Predators had shorter search time and encounter

419   rate when prey were in low densities as compared to high densities, in agreement with our

420   hypotheses, as predators appeared to give up foraging. At low densities, encounter rate did not

421   differ between the two bivalve species, indicating blue crabs had less trouble finding deep-

20

422   burrowing clams than we hypothesized. There was no evidence that blue crabs spent less time

423   foraging in complex habitats or when exposed to deep-burrowing prey; on the contrary, blue

424   crabs spent more time searching for *Mya* at medium densities than they did searching for

425   *Mercenaria* at medium densities, indicating crabs may have a preference for *Mya* as prey. This

426   tendency of blue crabs to pass up *Mercenaria* as prey may explain why handling times for

427   *Mercenaria* were not significantly greater than handling times for *Mya*; while some crabs spent

428   the extra time opening up the thick-shelled clams (*Mercenaria*), many predators also gave up

429   without investing much time into the encounter.

430   Declines in complex habitat will likely lead to declines in thin-shelled species such as

431   *Mya.* Oyster shell and shell hash provided juvenile *Mya* some protection from predation in

432   mesocosm trials; however, in Chesapeake Bay, hard-bottom substrate, such as shell, is relatively

433   uncommon [41]. Loss of many bivalves in the Bay, including oysters [42,43] and large-bodied

434   clams [24,44,45], will make hard-bottom shell-hash habitat even more rare in the future.

435   Seagrass has also experienced declines in the Chesapeake Bay [46], resulting in a decrease of

436   many potential sources of highly complex benthic habitat in the Bay and a subsequent decrease

437   in refuge for thin-shelled clams. *Mya* may retain a low-density refuge from predation even with

438   the loss of structurally complex habitats, though a loss of habitat-mediated refuge may eventually

439   result in clam densities that are not sustainable.

440   Loss of complex habitat in the Chesapeake Bay may have little impact on thick-shelled,

441   infaunal bivalves such as *Mercenaria, Rangia cuneata,* and ark clams (*Noetia ponderosa* and

442   *Anadara* spp.). We did not see an effect of habitat on *Mercenaria* survival in the current study,

443   yet in previous research, *Mercenaria* had higher survival in crushed oyster shell habitats than in

444   sand or mud [33]. This inconsistency is likely due to the use of larger clams in the current study

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445   (~30 mm shell length) as compared to the previous study, which used clams 5-10 mm shell

446   length [33]. Ontogenetic shifts in functional response may drive spatial distributions of hard-

447   shelled bivalves in Chesapeake Bay, which are most dense in oyster shell habitats [47].

448   However, the effect of habitat on survival of recruits does not appear to impact population

449   dynamics of large *Mercenaria*, which were present in multiple size classes throughout the year in

450   lower Chesapeake Bay. Future research should examine whether complex habitat reduces blue

451   crab encounter rates with small (< 10 mm) *Mercenaria* to determine the relationship between this

452   species and complex habitat over its entire ontogeny.

453

454   **Relevance for conservation**

455

456   Understanding the mechanism underlying bivalve refuges from predation is important in

457   a changing world. Loss of structured habitat such as seagrass, mangroves, coral reefs, and oysters

458   is occurring world-wide [48]. There is a current research need for models that can be used to

459   forecast the impacts of global change, such as habitat loss, on predator-prey interactions [49].

460   We demonstrated that understanding the effect of habitat loss on predator-prey interactions is

461   improved by understanding the mechanisms prey use to defend themselves against predators and

462   the effects of prey density.

463   Nonlinear predator-prey dynamics can result in catastrophic changes and regime shifts

464   [50,51]. An examination of the functional response is key in predicting the result of predator-

465   prey interactions over time, and determining if a population crash can be expected in a food web,

466   potentially leading to a regime shift. For instance, functional responses will be a major factor in

467   determining whether a species driven to low abundance is likely to become locally extinct, or if

22

468   it is likely to persist [19]. Documenting the functional response of bivalve species with a variety

469   of different physical characteristics can help ecosystem managers decide on which species to

470   focus conservation efforts, since species with a type II functional response are at higher risk of

471   local extinction [52,53], and populations exhibiting a type III functional response are generally

472   more stable over time [21,54,55].

473   A better understanding of density-dependent predator-prey interactions can be used to

474   inform a variety of ecosystem management decisions. For example, functional responses can be

475   used to determine a threshold density for reintroduction of endangered or depleted species [56],

476   stock enhancement, [12,13], and pest control [57,58]. Effective bivalve seeding efforts that take

477   into account predation may help restore marine bivalves, many of which have experienced severe

478   declines in the recent past [42,43,59,60]. A better understanding of density-dependent predator-

479   prey interactions will assist in the effort to maintain the integrity of marine trophic interactions

480   and the viability of marine resources.

481

482   **ACKNOWLEDGMENTS**

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653   **SUPPORTING INFORMATION**

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655   **S1 Table. Summary of Tukey HSD results for the caging study interaction term between**

656   **habitat and cage type.** For each pairwise comparison, 95% confidence intervals (CI) and

657   adjusted p values are presented. Data were Box-Cox transformed ($\lambda = 0.51$) prior to analysis and

658   are not back-transformed. Only interactions with significant p values at $\alpha = 0.20$ are shown.

659

660   **S2 Table. Summary of Tukey HSD results for the mesocosm study proportional mortality**

661   **interaction term between species and density.** For each pairwise comparison, 95% confidence

662   intervals (CI) and adjusted p values are presented. Data were Box-Cox transformed ($\lambda = -0.14$)

663   prior to analysis and are not back-transformed. Only interactions with significant p values at $\alpha = $

664   0.20 are shown.

665

666   **S3 Table. Summary of Tukey HSD results for the mesocosm study bivalve proportional**

667   **mortality interaction term between species and habitat.** For each pairwise comparison, 95%

668   confidence intervals (CI) and adjusted p values are presented. Data were Box-Cox transformed

669   ($\lambda = -0.14$) prior to analysis and are not back-transformed. Only interactions with significant p

670   values at $\alpha = 0.20$ are shown.

671

672   **S4 Table. Summary of Tukey HSD results for the mesocosm study *Callinectes sapidus***

673   **handling time interaction term between species and habitat.** For each pairwise comparison,

674   95% confidence intervals (CI) and adjusted p values are presented. Data were fourth-root

31

675   transformed prior to analysis and are not back-transformed. Only interactions with significant p

676   values at α = 0.20 are shown.

677

678   **S5 Table. Summary of Tukey HSD results for the mesocosm study *Callinectes sapidus***

679   **search time interaction term between species and density.** For each pairwise comparison,

680   95% confidence intervals (CI) and adjusted p values are presented. Data were fourth-root

681   transformed prior to analysis and are not back-transformed. Only interactions with significant p

682   values at α = 0.20 are shown.

683

684   **S6 Table. Summary of Tukey HSD results for the mesocosm study *Callinectes sapidus***

685   **search time interaction term between species, density, and habitat.** For each pairwise
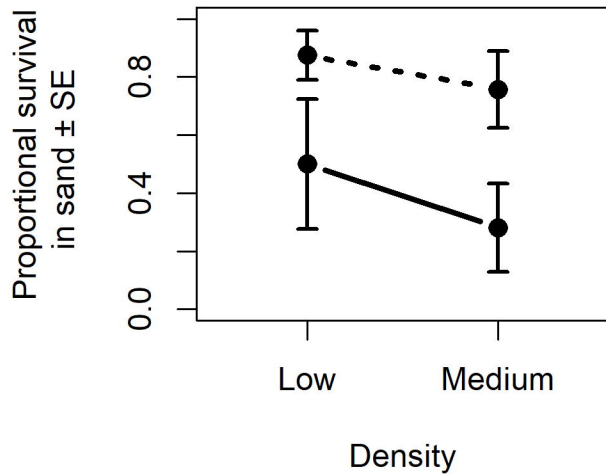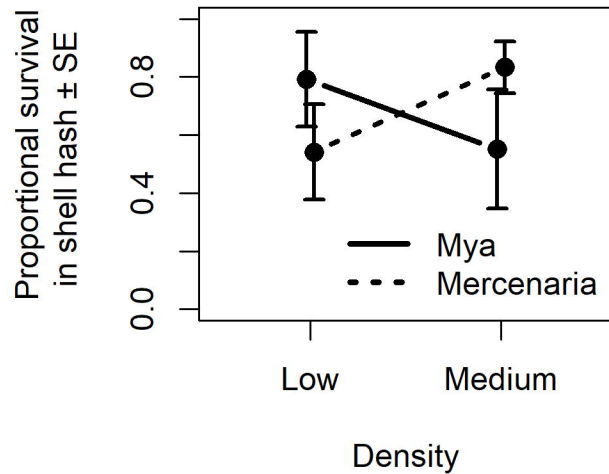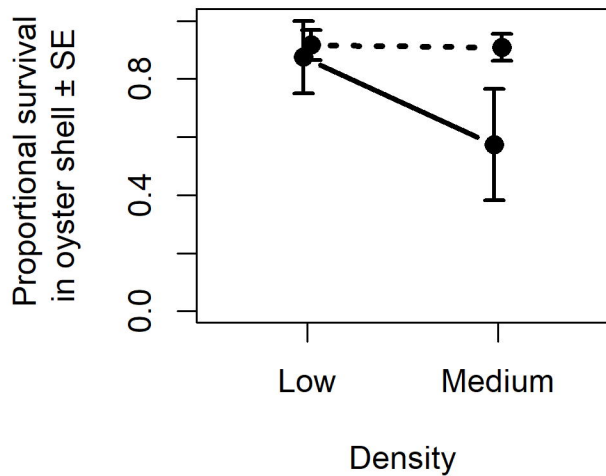
686   comparison, 95% confidence intervals (CI) and adjusted p values are presented. Data were

687   fourth-root transformed prior to analysis and are not back-transformed. Only interactions with

688   significant p values at α = 0.20 are shown.

689

a.

b.

Mya
Mercenaria

c.

d.