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1   **Title:** Interactive effects of shell hash and predator exclusion on 0-year class recruits of two

2   infaunal intertidal bivalve species in Maine, USA.

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Abstract

24

25   Biotic and abiotic factors affecting survival and growth of recently settled infaunal bivalves not

26   only determine the strength of 0-year class populations, but the structure and function of benthic

27   soft-bottom communities. At mudflats across north-central Casco Bay, a 517 km^2 embayment in

28   the western Gulf of Maine, USA, intertidal sediments are generally acidic (pore water pH range

29   = 7.09-7.85), which can negatively affect settlement and subsequent recruitment success of

30   infaunal bivalves due directly or indirectly to shell dissolution. In addition, predation on bivalves

31   by invasive green crabs, *Carcinus maenas*, and native consumers is intense in this region. Two

32   commercially important infaunal bivalve species occupy these sediments (softshell clams, *Mya*

33   *arenaria*; hard clams, *Mercenaria mercenaria*). Fisheries managers, legislators, and others have

34   suggested that adding crushed shells of *M. arenaria* to the surface of mudflats can ameliorate

35   negative effects of acidic sediment pore water through chemical buffering. We investigated the

36   interactive effects of modifying surface sediments using crushed and weathered shells of *Mya*

37   and predator exclusion on abundance and size of 0-year class individuals of these two bivalve

38   species in large-scale plots (9.3 m^2) and small-scale experimental units (EU; 182.4 cm^2). Field

39   experiments were conducted over three years (170-204 days yr^{-1}; each initiated prior to spawning

40   and continuing well after settlement had ceased). Shell hash in large-scale plots (mean particle

41   size = 19.3 mm) varied across three levels (0, 0.63, and 1.27 kg m^{-2}), and between 0 and 1.27 kg

42   m^{-2} in EU where shell size varied from 1.9-19.3 mm. Small-scale experiments also used granite

43   chips that, like crushed shells, increased habitat heterogeneity but did not buffer sediments.

44   Density and size of both bivalve species at the end of most field trials were significantly greater

45   in predator-exclusion treatments vs. controls independent of shell treatment. In all trials, neither

46   *Mya* nor *Mercenaria* responded positively to the presence of shell additions. Fisheries managers

47   should focus attention on mitigating effects due to predators instead of spreading shell hash to

48   buffer intertidal sediments.

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52   **KEYWORDS:** *Mya arenaria*; *Mercenaria mercenaria*; sediment buffering; shell hash;

53   predator exclusion; bivalve recruits

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70 **Highlights**

71 Field experiments in the soft-bottom intertidal focused on bivalve recruitment

72 Interactive effects of shell hash to buffer acidic sediments and predator exclusion

73 Crushed shell did not enhance abundance of 0-year class bivalves

74 Predation plays a disproportionate role in post-settlement survival of bivalves

75 Mitigation efforts should focus on limiting predator access to bivalve recruits

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1. Introduction

Populations of infaunal marine bivalves are regulated by a variety of interacting biotic (Glaspsie et al., 2018; Seitz and Lipcius, 2001; Vincent et al., 1994) and abiotic (Clements and Hunt, 2018; Genelt-Yanovskiy et al., 2018; Kim et al., 2017; Weinberg, 1985) factors that operate directly or indirectly (sensu Maire et al., 2010; Tomiyama, 2018), and affect spatial and temporal fluctuations in distribution and abundance, especially during the early life-history phase. For example, post-settlement mortality due to predation plays a disproportionate role in reducing densities of some infaunal bivalve populations by >95% during the first year (Commito, 1982; Gosselin and Qian, 1997; Tezuka et al., 2012). Similarly, sediment carbonate chemistry has been shown to modify pH of pore water and control recruitment success (Green et al., 1998, 2013; Meseck et al., 2018).

In Maine, USA, landings of the commercially important infaunal bivalve, *Mya arenaria* L., have declined by over 55% during the past two decades (ME DMR, 2019). Fishery-independent data suggest that high rates of predation on 0-year class individuals (0.5-38 mm SL, shell length) is largely responsible for the decline rather than variable fishing effort (Beal et al., 2016, 2018). This aligns with what others have observed for commercially-important bivalves in the northeast U.S. over the same period (MacKenzie and Tarnowski, 2018).

The decline in *Mya* stocks also has occurred during a time when sea surface temperatures in the Gulf of Maine have warmed at a faster rate than 99% of the global ocean (Pershing et al., 2015), and when sea surface pH in that region has dropped by 0.03 units (Salisbury and Jönsson, 2018). It is not unusual for intertidal sediments to be more acidic than overlying seawater (Jansen et al.,

116 2009), suggesting that some benthic organisms are adapted to some level of acidity and

117 corrosiveness (Mevenkamp et al., 2018). Early, post-settlement bivalves that burrow into these

118 corrosive sediments are most vulnerable to dissolution pressure and resulting mortality agents

119 (Clements and Hunt 2017; Parker et al., 2013; Peng et al., 2017).

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121 The Casco Bay Estuary, located in central southern Maine, is a 517 km^2 embayment in the

122 western Gulf of Maine with depths ranging from 3-50 m that encompasses 14 coastal

123 communities, including two of Maine's largest cities, Portland and South Portland. More than

124 925 km of shoreline and 785 islands occur within the bay (Casco Bay Estuary Project, 2019).

125 The major tidal constituent is the semi-diurnal lunar tide (M_2) with current amplitudes as high as

126 0.6 m s^{-1}, and a tidal sea-level range of approximately 3 m near Portland (Janzen et al., 2005).

127 Casco Bay contains ~ 60,000 ha of marine habitat, including over 4,000 ha of tidal flats

128 (Whitlow and Grabowski, 2012). Recent surveys of carbonate chemistry from the pore water of

129 intertidal surface sediments (top few mm) in this estuary (Bohlen, 2013; Green et al., 2009,

130 2013; Miller et al., 2016) indicate highly variable pH (range = 6.48-8.75) as well as

131 undersaturation with respect to aragonite in sediment pore water (i.e., $\Omega_{aragonite} < 1.0$).

132

133 It may be possible to ameliorate negative effects of corrosive sediments (e.g., raising local pore

134 water pH and $\Omega_{aragonite}$) on populations of calcified benthic macrofauna by adding crushed

135 bivalve shells to the surface of mudflats (Rodil et al., 2013). Localized increases of $CaCO_3$

136 provide a buffering agent that may act to balance or mitigate the corrosive sedimentary

137 conditions, and is one strategy that may help preserve commercially and ecologically important

138 populations of infaunal bivalves in coastal areas (Clements and Chopin, 2017; Green et al.,

139   2009). Several field trials in Casco Bay, Maine (Green et al., 2009, 2013) and elsewhere

140   (Greiner et al., 2018; Ruesink et al., 2014) have examined effects of adding crushed shell (hash)

141   to surface sediments on the fate of 0-year class bivalve recruits or cultured juveniles with mixed

142   results (Table 1). Nonetheless, bivalve fishery managers have been encouraged to spread shell

143   hash in the intertidal to mitigate coastal acidification effects on populations of commercially-

144   important shellfish (Bentley and Schneider, 2015; Billé et al., 2013; Cooley et al., 2015;

145   Kapsenberg and Cyronak, 2019; WABRPOA, 2012).

146

147   The addition of shell hash to mudflat environments not only has the capacity to buffer acidic

148   sediments, and therefore improve conditions for settling bivalves, but it may attract predators

149   such as crabs that respond to localized enhancement of their preferred prey (e.g., juvenile

150   bivalves; Iribarne et al., 1995; Seitz et al., 2001) or provide a heterogeneous habitat that

151   enhances settlement and survival for crabs (Fernandez et al., 1993; Palacios et al., 2000;

152   Moksnes, 2002). Conversely, increasing structural complexity in soft-bottom marine habitats

153   generally results in decreasing predation rates with concomitant increases in prey refugia and

154   diversity (Irlandi and Peterson, 1991; Grabowski 2004).

155

156   We conducted a series of short-term (~6 mo) manipulative field experiments over three

157   consecutive years at two spatial scales near the mid intertidal at four soft-bottom flats within a 5

158   km radius of each other in Casco Bay, Maine to examine effects of introducing shell hash in

159   predator-deterrent and control plots on sediment pore water pH, as well as abundance and size

160   distribution of 0-year class individuals of two species of commercially-important bivalves.

161   Specifically, we addressed two primary questions across three separate large-scale experiments

162 related to the three variables: 1) What is the relative importance of shell hash presence vs.

163 predator deterrence? and 2) Is a threshold amount (mass/unit area) of shell hash required to elicit

164 a biologically meaningful (positive) response in abundance and/or size of 0-year class bivalves?

165 Two additional questions were examined across five small-scale experiments: 1) Is juvenile

166 bivalve abundance more strongly associated with buffering (crushed shells - a habitat with some

167 buffering capacity) or increased habitat complexity (granite chips - a habitat without buffering

168 capacity)? and, 2) How do different sizes of crushed shell affect abundance or size of 0-year

169 class bivalves?

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171 **2. Methods and Materials**

172 *2.1. Study Sites*

173 Field trials (2014-2016) were conducted seasonally beginning in April/May (prior to annual

174 reproduction of the softshell clam, *Mya arenaria* [Ropes and Stickney, 1965; B. Beal, pers. obs.],

175 and hard clam, *Mercenaria mercenaria* [Stanley and DeWitt, 1983; B. Beal, pers. obs.]), and

176 ending in October/November (after settlement and subsequent survival of juveniles to a size

177 retained by a 1 mm mesh [ca. 1.4 mm in shell width] [Beal et al., 2016, 2018]) in the soft-bottom

178 mid-intertidal at four locations in the town of Freeport, Maine (Fig. 1; Table 2). Sediment grain

179 size at each site varied between 1-3.5 ϕ units (medium to very fine sand; sensu Folk, 1980).

180 Occasionally, mudflat surface irregularities were associated with dead, and mostly disarticulated,

181 valves of *M. arenaria*, Baltic clam, *Limecola balthica*, hard clam, *M. mercenaria*, American

182 oyster, *Crassostrea virginica*, and blue mussel, *Mytilus edulis* that may have been accumulating

183 for > 2 yr (C. Coffin, pers. obs.). Two species of mobile epibenthic gastropods were observed

184 regularly at the sites: common periwinkle, *Littorina littorea*, and eastern mud snail, *Tritia*

185 *obsoleta*. To permit the greatest degree of sediment buffering using crushed shells of *M.*

186 *arenaria*, sites were chosen to reflect intertidal flats with relatively low pH based on *in situ*

187 samples taken near the beginning of a field trail at 5-7 mid-intertidal locations. Locations also

188 were chosen to reflect flats that were once productive, where softshell clam harvesting occurred

189 historically, but where little to no commercial activity had occurred for several years (C.

190 Goodenow, Jr., pers. obs). pH was measured (top 2 mm of sediments) during ebb tide, when

191 intertidal flats had been exposed for approximately 30 minutes, using a Fisher Accumet AB 115

192 pH meter with Accumet 13-620 AP50A combination electrode, which was cleaned using

193 deionized water and re-calibrated to three points at pH 7.01, pH 4.0 and pH 10.0 after five

194 consecutive measurements were taken. For example, Staples Cove (SC) was chosen as a study

195 site in 2014 (Table 2) because median pH was the lowest recorded among five sites sampled at

196 that time (Fig. 2). Similarly, during spring 2015 and 2016, Little River (LR) and either Winslow

197 Park (WP) or Recompence (RC) had the two lowest median pH estimates from seven intertidal

198 sites sampled.

199

200 *2.2. Large-Scale Experiments at Staples Cove-2014; Little River & Winslow Park-2015*

201 A large-scale experiment was conducted at SC (2014) and at WP and LR (2015) (Table 2) to

202 examine short-term, interactive effects of adding crushed, weathered shells of *Mya arenaria* to

203 buffer sediments and predator-exclusion on sediment pore water pH as well as on density and

204 size-frequency of 0-year class individuals (recruits) of softshell and hard clams. A 5 x 6 matrix

205 was established by creating thirty 9.29 m^2 plots. Plots in adjacent rows and columns were

206 separated by 5 m. To establish initial densities and size ranges of the two bivalves (Table 2), a

207 single benthic core (area = 0.018 m^2 to a depth of 15 cm; in these sediments, cores sample *M.*

208 *mercenaria* to 100 mm SL and *M. arenaria* to 80 mm SL, B. Beal, pers. obs.) was taken from

209 within each of the thirty plots prior to adding shell or netting (see below). Six treatments (n = 5),

210 reflecting two orthogonal factors (mass of large, crushed shells of *M. arenaria* per plot, Table 3,

211 a = 3 – 0.00, 0.63, and 1.27 kg m^{-2}; predator exclusion netting [4.2 mm aperture],

212 https://www.industrialnetting.com/ov7100-168-polypropylene-netting.html, b = 2 – present vs.

213 absent; Fig. 3a), were assigned randomly to positions within the matrix. Shells of dead,

214 disarticulated softshell clams (50-90 mm SL – greatest anterior-posterior distance) that had been

215 processed commercially (i.e., meats shucked; A.C. Inc., Beals, ME, USA; 44° 30' 21.6792"N,

216 67° 36' 2.2572"W), and had weathered outdoors in a pile in a terrestrial environment for over a

217 year, were collected and crushed manually. Netting was secured around one-half of the plots at

218 each location by spreading a piece (11.24 m^2) on the surface of each plot, and then walking along

219 the net periphery so that it was forced (anchored) into the soft sediments approximately 20-25

220 cm below the mudflat surface (sensu Beal et al., 2018). A single Styrofoam float (10 cm

221 diameter x 7.6 cm thick) was affixed to the underside middle of each of the fifteen netted plots so

222 that during periods of tidal inundation, nets would lift 5-10 cm off the bottom to decrease

223 potential direct interference with clam feeding, settlement and post-settlement movement, and

224 other processes. After 170 days (2014) and 183 days (2015), two pH measurements were taken

225 of sediment pore water to a depth of 2 mm at two random locations within each plot. In addition,

226 five benthic cores (0.018 m^2 to a depth of 15 cm) were taken from each of the thirty plots in 2014

227 (N = 150 samples), and two cores were taken from each plot in 2015 (N = 60 samples) to

228 measure density and size-frequency of the two bivalves. The contents of each sample were

229 washed through a 1 mm sieve, and the number and SL (measured with digital calipers to the

230 nearest 0.01 mm) of all live individuals of *M. arenaria* and *M. mercenaria* recorded. (0-year

231   class individuals of *M. arenaria* attain shell lengths between 1.8 mm and 38.8 mm in this region

232   between spring and fall [Beal et al., 2018] whereas recruits of *M. mercenaria* rarely exceed 10

233   mm SL during their first fall [B. Beal, pers. obs.].) Seawater temperatures (°C), recorded using

234   Onset HOBO water temperature Pro v2 data loggers placed at each study site on the mudflat

235   surface from the beginning to end of each trial (Table 2), varied between 9.8°-26.8° in 2014 and

236   4.3°-24.6° in 2015.

237

238   *2.3. Small-Scale Experiments during 2014 - 2016*

239   Adding crushed shell on top of ambient sediments may not only buffer sediments and create a

240   chemical refuge for recently-settled bivalves and other fauna (Greiner et al., 2018), but provide

241   other ecosystem services (Morris et al., 2019), including potential microhabitats for settlers (both

242   predators and prey) of planktonic larvae. In an attempt to separate potential buffering effects

243   from potential habitat effects on number/size of recruits of *Mya arenaria* and *Mercenaria*

244   *mercenaria*, a series of small-scale experiments was conducted at the same sites where the large-

245   scale experiments occurred in 2014 and 2015, and at LR and RC in 2016 (Table 2). Treatments

246   included crushed shell that could potentially act to buffer sediments as well as provide

247   microhabitats for settling bivalves and their predators, and material (granite chips) of similar size

248   as large, crushed shells that could potentially act as a microhabitat, but without any buffering

249   capacity.

250

251   *2.3.1. Staples Cove – 2014; Little River & Winslow Park – 2015*

252   An 8 x 10 matrix was established adjacent to the large-scale experiment at each site in the spring

253 (Table 2) with 1 m distances between rows and columns. Plastic horticultural pots (15.2 cm

254 diameter x 15.2 cm deep; 0.018 m^2) filled to within 1 cm of the top with ambient sediments were

255 used as experimental units (EU). The experiment (Fig. 3b) was a completely random design

256 with two orthogonal factors: A = Material (added to the surface substrate; a = 4: ambient

257 sediment, large crushed shells of *M. arenaria* [25 g EU^{-1} ~ 1.27 kg m^{-2}], marble chips [65 g EU^{-1}

258 ^{1}], and granite chips [150 g EU^{-1}]; Table 3), and B = Netting (4.2 mm flexible netting, as

259 described above; b = 2: present or absent). Crushed shells and marble chips acted as potential

260 buffering agents as well as provided potential habitat for bivalves and their predators, while the

261 granite chips provided no buffering capacity, but potentially increased habitat heterogeneity. EU

262 were dug into the flat to a depth of 15 cm. A piece of flexible netting (18 cm x 18 cm; aperture =

263 4.2 mm) was affixed to half of the EU with a rubber band, similar to that described in Beal

264 (2006). EU remained in the// flats until early fall (Table 2), when the contents of each was

265 washed through a 1 mm sieve. All recruits of softshell clams and hard clams were enumerated,

266 and the SL of each live individual measured to the nearest 0.01 mm using digital calipers.

267

268 *2.3.2. Little River & Recompence – 2016*

269 A study similar to that described for LR and WP (2015) was established at both sites during early

270 spring (Table 2). To establish ambient densities of softshell clams and hard clams, 25 core

271 samples were taken (as described above) at the beginning of the experiment in the area of the

272 experimental matrix prior to establishing any EU. Similarly, 25 core samples were taken at the

273 end of the experiment within the experimental matrix but not within 0.5 m of any EU. Two

274 orthogonal factors were used to examine interactive effects of crushed shell and other material (a

275 = 6), and predator exclusion netting (b = 2). Six of the twelve treatments were identical to those

276 used in 2015 (control, large crushed shell, and granite, with and without predator deterrent

277 netting). An additional six treatments used similar masses of two smaller sizes of crushed

278 softshell clam shells and one size of crushed oyster (*Ostrea lurida*) shell (25 g EU^{-1}; Table 3) in

279 both protected and control EU (Fig. 3c). Smaller pieces of shell were used to test whether the

280 fragments might increase the rate of dissolution; hence, help neutralize sediment pore water pH

281 faster, and create a more habitable environment for settling bivalves. EU (as described above)

282 were filled with ambient sediment to which material was added to surface substrate, and then

283 forced into the sediments to a depth of 15 cm within a 10 x 12 matrix (row and column spacing

284 as described above). EU remained in the flat at both sites until early fall (Table 2) when all were

285 removed, and the contents of each washed separately through a 1 mm sieve. Counts of recruits

286 and SL of individuals of *M. arenaria* and *M. mercenaria* were recorded. To examine spatial and

287 temporal variability in sediment pore water pH, measurements (as described above) were made

288 on ten occasions at both LR and RC beginning 17 May and continuing approximately every

289 other week until 6 October. On each sampling date, two sediment pore water pH samples were

290 taken from each of five 0.5 m^2 quadrats tossed haphazardly (distance between quadrats = 2-3 m)

291 that were adjacent (within 5 m) to the experimental matrix. In late October (10-24: LR; 10-25:

292 RC), three pH measurements were made from two and three randomly chosen replicate EU from

293 the 12 treatments at LR and RC, respectively. Seawater temperatures at the mudflat surface

294 within the experimental matrix were collected using HOBO recorders (as described above), and

295 ranged from 5.4°-23.2°C at LR and 5.4°-23.9°C at RC.

296

297 *2.4. Statistics*

298 *2.4.1. Large-scale experiments*

299   Analysis of variance (ANOVA), log-linear regression analyses, and permutational multivariate

300   analysis of variance (PERMANOVA) were conducted to test main and interactive effects of shell

301   mass and predator exclusion on sediment buffering (measured as final mean pH of sediment pore

302   water), mean recruit density and mean SL for both bivalve species. ANOVA and the other

303   analyses were used to investigate specific hypotheses concerning effects on mean pH and SL.

304   The crushed shell and predator exclusion factors (Table 2; Fig. 3a) were both fixed and

305   orthogonal to each other, while plot was considered a random factor, and was nested within the

306   interaction of shell and exclusion.

307

308   Two a priori, single degree-of-freedom, orthogonal contrasts were used to investigate specific

309   hypotheses concerning the effects of shell mass treatments. The first was No Shell vs. Shell.

310   This contrast examines whether the addition of shell to intertidal plots provides significant

311   sediment buffering measured as mean pH, or enhances mean number or SL of two bivalve

312   species compared to control plots without additional shell. The second was Low vs. High Mass

313   of Shell (0.63 kg m^{-2} vs. 1.27 kg m^{-2}). This contrast examines whether the measured variables

314   respond to a doubling in mass of large shell material.

315

316   Underwood (1997) was consulted to determine appropriate mean square estimates for each

317   source of variation. When violations of the assumptions of normality (Shapiro-Wilks test) and/or

318   variance homogeneity (Levene's test) occurred, a $\log_e$ (mean SL) transformation was used (Sokal

319   and Rohlf, 1995).

320

321   The bivalve density data was highly skewed due to an overabundance of zeros in the benthic

322   cores, and could not be transformed to meet ANOVA assumptions of normality and variance

323   homogeneity. Therefore, two independent analyses were performed using a generalized linear

324   model that extends the traditional linear model, and that do not assume data are normally

325   distributed or variances are similar across treatments. The first was regression analysis (log-

326   linear model; Proc GENMOD - SAS 9.4 TS Level 1M5) that frequently is used to model count

327   data (Vincenzi et al., 2006; de Fouw et al., 2020). Akaike information criterion (AIC) was used

328   to selct the most appropriate model (Poisson or negative binomial), which was then compared

329   with the original count data to determine the adequacy of the model using a χ^2 log-likelihood

330   goodness-of-fit test. For each analysis, the selected model resulted in a reasonable fit to the

331   theoretical distribution ($P > 0.33$). The second was permutational multivariate analysis of

332   variance (PERMANOVA) on the univariate count data based on Euclidean distance resemblance

333   matrices. Tests were performed using type III sums of squares (partial) with unrestricted

334   permutations of raw data, and 9999 permutations (Primer v 6.1.12 & PERMANOVA+ v 1.02;

335   Anderson, 2001), and yield classical univariate F-statistics (Anderson, 2017). The two analyses

336   are meant to complement one another with the PERMANOVA providing a non-parametric

337   alternative to the log-linear regression model that was not 100% successful in attaining the

338   appropriate model. In addition, G-tests of independence or Fisher's exact tests were used to

339   examine treatment effects on the size-frequency distribution of recruits of *M. arenaria* and *M.*

340   *mercenaria*. Typically 4-5 bins were used for the sizes (I: < 3 mm; II: 3-3.99 mm; III: 4-4.99

341   mm; IV: 5-5.99 mm; V: $\geq$ 6 mm).

342

343   *2.4.2. Small-scale experiments*

344   *2.4.2.1 2014 & 2015*

345   ANOVA was used to test site-specific treatment effects on mean SL for both bivalves. Neither

346   raw nor transformed count data (bivalve density) met assumptions of ANOVA; therefore, recruit

347   density data was analyzed using regression analysis and PERMANOVA (as described in section

348   2.4.1.).

349

350   The two main factors (experimental material and predator exclusion; Table 2, Fig. 3b,c) were

351   both fixed and crossed. Three single degree-of-freedom, orthogonal, a priori contrasts were used

352   to examine specific hypotheses concerning effects of the experimental material added to the EU

353   on the mean of each measurement variables. The first was Control (no experimental material) vs.

354   Experimental Material (Shell, Marble, Granite). This contrast compares whether the mean from

355   the three experimental material treatments is similar to that of the control EU with no added

356   material. The second was Shell & Marble vs. Granite. This contrast compares the mean of the

357   two $CaCO_3$ treatments (potential sediment buffering and habitat effects) to that of the non-

358   buffering treatment (potential habitat effects). The third was Shell vs. Marble. This contrast

359   compares means of the two $CaCO_3$ treatments – one with a relatively short (shell) vs. relatively

360   long (marble chips) dissolution horizon.

361

362   *2.4.2.2 2016*

363   ANOVA was used to test site-specific main and interactive effects of the two orthogonal factors

364   (Material,   a = 6; Netting, b = 2; Table 3) on mean pH, mean SL, and the square root-

365   transformed mean number of softshell clams EU^{-1} (abundance data was not zero-inflated). Hard

366   clam abundance data was highly skewed due to an abundance of zeros in a majority of EU;

367   hence, regression analysis and PERMANOVA were used to test main and interactive effects (as

368   described above). Five orthogonal, single-degree-of-freedom, a priori contrasts were conducted

369   to examine specific hypotheses involving the material added to the EU. They were as follows: 1)

370   Control (no material) vs. Material (large, medium, and small crushed shells of *Mya*, oyster shell,

371   and granite) – compares whether the mean of the variables measured from the five experimental

372   material treatments is similar to that of the control EU with no added material; 2) Shell vs.

373   Granite – compares the mean of the four $CaCO_3$ treatments (potential sediment buffering and

374   habitat effects) to that of the non-buffering treatment (potential habitat effects); 3) Crushed shells

375   of *M. arenaria* vs. *O. lurida* – compares the mean from all three crushed shell treatments of *Mya*

376   (comprised mostly of aragonite [White et al., 1977]) to that of the crushed shells of *Ostrea*

377   (comprised mostly of calcite [Stenzel, 1963]) that tests potential species-specific differences in

378   buffering and habitat suitability for 0-year class *Mya* and *Mercenaria*; 4) Large crushed *Mya*

379   shells vs. Small & Medium crushed *Mya* shells - compares the mean from the large crushed shell

380   treatment to the mean of the two other crushed shell treatments that tests the effect of potentially

381   different shell dissolution rates on bivalve recruit dynamics; and, 5) Small crushed *Mya* shells vs.

382   Medium crushed *Mya* shells – compares means from among the two smallest crushed *Mya* shell

383   treatments.

384

385   Unless otherwise stated, untransformed means are presented with their 95% confidence interval.

386

387 **3. Results**

388 *3.1   Large-Scale Experiments*

389 *3.1.1 Staples Cove - 2014*

390   No significant difference was observed in mean pH of sediment pore water among treatments (F

391   = 2.0, df = 5, 24, P = 0.115) in November. Mean pH pooled across all treatments in November

392   was 7.72 ± 0.07 (n = 30), which was significantly higher (two-sample t-test) than the mean pH at

393   SC in May (Table 2; T = 7.79, df = 38, P < 0.001).

394

395   0-year class individuals of the softshell clam occurred in 20 of the 150 cores (13.3%), with

396   approximately 4x more recruits (SL range = 2.07-7.02 mm; Fig. 4a) occurring in core samples

397   from netted vs. control plots (1.3 ± 0.9 ind., vs. 0.3 ± 0.3 ind., respectively; n = 15) (χ^2_{obs} = 9.64,

398   df = 1, P = 0.002; F = 4.74, df = 1, 24, P = 0.033; Table 4). Mean SL of softshell clams was

399   significantly smaller by nearly 30% in protected (3.4 ± 0.6 mm, n = 15) vs. control (4.4 ± 2.1

400   mm, n = 5) plots; however, a 6 x 4 Fisher's exact test (6 treatments x 4 sizes [$\leq$ 2.99 mm; 3-3.99

401   mm; 4-4.99 mm; and, > 5.0 mm] indicated no significant effect of treatment on size-frequency

402   distribution (P = 0.688).

403

404   Recruits of *Mercenaria mercenaria* occurred in 29 of the 150 cores (19.3%). Approximately 40x

405   more hard clam recruits occurred in netted vs. control plots (2.9 ± 1.3 vs. 0.07 ± 0.1 ind. core^{-1}, n

406   = 15; Fig. 5). Likelihood ratio statistics generated from Poisson regression analysis demonstrated

407   that the only significant source of variation was netting (Table 4). Hard clam recruits ranged in

408   size from 1.9-5.6 mm (mean SL = 3.9 ± 0.3 mm, n = 29; Fig. 4b). There was no significant

409   effect of any source of variation on mean SL (P > 0.60), or on size-frequency distribution (4 x 4

410   Fisher's exact test; P = 0.352).

411

412   *3.1.2   Little River - 2015*

413   Due to inclement weather during the fall sampling date (Table 2), no pH measurements were

414   taken at this location. *Mya* recruits occurred in 31 of 60 core samples (~52%); however, no

415   recruits of *Mercenaria* occurred in any samples. Likelihood ratio statistics from negative

416   binomial regression analysis and results of PERMANOVA demonstrated a significant effect due

417   to netting (Table 4). Approximately 22x more recruits of *Mya* were found in samples taken from

418   netted vs. unnetted plots (10.5 ± 5.2 ind. core^{-1} vs. 0.47 ± 0.35 ind. core^{-1}, n = 15; Fig. 6). *Mya*

419   recruits (N = 165) ranged in SL between 2.0-29.1 mm (mean SL = 5.77 ± 0.69 mm; 95% of

420   recruits were < 15 mm SL). No significant treatment effects on mean SL were detected (P >

421   0.05), and size-frequency distribution was similar between treatments (6 x 5 G-test: P = 0.587).

422

423   *3.1.3 Winslow Park - 2015*

424   Mean pH of sediment pore water on 30 October varied significantly with netting (P < 0.0001),

425   but not with shell (P = 0.681) or shell x netting (P = 0.6028). In netted plots, mean pH (7.27 ±

426   0.05, n = 15) was approximately 2.5x more acidic [H^+ ion concentration] than in unnetted plots

427   (7.69 ± 0.12, n = 15), regardless of level of shell material in each. Recruits of *Mya* were found in

428   15 of 60 core samples (25%), with 70x more occurring in netted vs. unnetted plots (14.0 ± 18.5

429   ind. core^{-1} vs. 0.2 ± 0.2 ind. core^{-1}, n = 15; Fig. 6). Extreme variability in recruit number

430   between samples, especially from netted plots (coefficient of variation = 238.6%), likely

431   contributed to ambiguity in results between regression analysis and PERMANOVA (Table 4).

432   Regression analysis demonstrated that the effect due to netting was significant (P < 0.001), while

433   PERMANOVA yielded a P-value of 0.079 (Table 4). *Mya* recruits (N = 213) ranged in SL

434   between 1.42-7.47 mm (mean SL = 2.84 ± 0.15 mm). No significant treatment effects on mean

435   SL were detected (P > 0.50), and size-frequency distribution was similar between treatments (6 x

436 4 Fisher's exact test: P = 0.393). Only four individuals of *M. mercenaria* were found in 3 of the

437 60 core samples, each taken from a netted plot (4.82 mm – Shell [0.63 kg m^{-2}]; 4.38 mm and

438 3.84 mm – Shell [1.27 kg m^{-2}]; 2.5 mm – Control).

439

440 *3.2   Small-scale Experiments*

441 *3.2.1 Staples Cove - 2014*

442 *Mya* recruits occurred in 45 of 80 EU (~56%), and varied significantly across netting treatments

443 (χ^2 = 9.48, df = 1, P = 0.002; F = 6.72, df = 1, 72, P = 0.005). Samples from netted EU,

444 independent of type of material used, contained significantly more (2.3 x) recruits than EU

445 without predator exclusion netting (1.3 ± 0.51 vs. 0.57 ± 0.25 ind. EU^{-1}, n = 40; P < 0.015). No

446 other sources of variation, including contrasts, were statistically significant. *Mya* recruits ranged

447 in size from 1.79-19.6 mm (mean SL = 6.77 ± 1.16 mm, n = 64), and no significant effects on

448 size occurred due to any sources of variation (P > 0.05). Size-frequency distribution of *Mya*

449 recruits did not vary significantly with treatment (8 x 5 Fisher's exact test, P = 0.114).

450 *Mercenaria* recruits occurred in 16 of the 80 EU (~23%). Poisson regression analysis and

451 PERMANOVA on the count data yielded similar results (P > 0.1) for each source of variation as

452 well as contrasts. *Mercenaria* recruits ranged in size from 2.01 mm to 7.23 mm (mean SL = 3.72

453 ± 0.72 mm, n = 17). Mean SL did not vary significantly with any of the main or interaction

454 sources of variation (P > 0.35); however, size-frequency distribution varied significantly across

455 treatments (7 x 4 Fisher's exact test: P = 0.011), as more hard clams smaller than 4 mm occurred

456 in control EU (regardless whether netting was present) than in any other treatments.

457

458 *3.2.2 Little River - 2015*

459   Recruits of *Mya* (mean SL = 9.06 ± 0.99 mm, n = 112; min = 2.79 mm, max = 27.88 mm) were

460   found in 46 of 80 EU (~58%), whereas no individuals of *Mercenaria* were encountered in any

461   EU. Count data of *Mya* recruits were adequately modeled by a negative binomial distribution (P

462   = 0.248). No significant treatment effects on counts of recruits occurred with either regression

463   analysis or PERMANOVA (P > 0.33), and no contrasts associated with the experimental

464   materials were significant (P > 0.39). Mean SL of *Mya* recruits did not vary significantly with

465   any source of variation (P > 0.10), and size-frequency distribution did not vary significantly

466   across treatments (3 x 8 G-test: P = 0.111).

467

468   *3.2.3 Winslow Park - 2015*

469   *Mya* recruits occurred in 57 of 80 EU (~71%), and ranged in SL from 2.12-35.24 mm (mean =

470   12.24 ± 0.95 mm, n = 268). No individuals of *M. mercenaria* were collected. Count data

471   followed a negative binomial distribution (P = 0.199), and both regression analysis and

472   PERMANOVA yielded similar results showing a significant effect due to the presence of the

473   predator deterrent netting (χ^2 = 22.84, df = 1, P < 0.001; F = 10.64, df = 1, 72, P < 0.001). No

474   contrasts examining effects due to experimental material were significant (P > 0.11).

475   Approximately 4x more recruits of *Mya* occurred in EU protected from predators with flexible

476   plastic netting than in control EU (5.35 ± 2.37 vs. 1.35 ± 0.67 ind. EU^{-1}, n = 40). Softshell clam

477   recruits in netted EU were nearly 80% larger than conspecifics in control EU (12.54 ± 2.35 mm,

478   n = 33 vs. 7.03 ± 2.63 mm, n = 24; P = 0.004). Size-frequency distributions followed a similar

479   pattern with relatively more recruits > 10 mm SL in protected vs. open EU (G-test: P < 0.001).

480

481   *3.2.4 Little River - 2016*

482   Mean pH in sediment pore water adjacent to the experimental matrix varied both spatially (i.e.,

483   quadrat-to-quadrat in the vicinity of the experimental matrix; P = 0.025) and temporally (P <

484   0.001) from a high of 8.0 on 14 June to a low of 6.89 on 26 August (Fig. 7). Mean pH at LR

485   pooled across the ten sampling dates was 7.39 ± 0.08 (n = 106). In late October, measurements

486   taken from EU revealed no significant difference in mean pH (7.65 ± 0.09, n = 24) for either

487   main effects (netting, P = 0.184; material, P = 0.219), or their interaction (P = 0.969).

488

489   Live recruits of *Mya* occurred in 103 of the 120 EU (~86%) in October. ANOVA on the square

490   root-transformed count data demonstrated no significant effect due to netting, experimental

491   material, or interaction (Table 5; P > 0.05; Fig. 8a); however, one of the four contrasts for

492   experimental material (Large vs. Medium & Small crushed shell) was statistically significant (P

493   = 0.009, Table 5). Approximately 2.5x as many recruits of *Mya* occurred in treatments with

494   small and medium crushed *Mya* shell (8.58 ± 3.24 ind. EU^{-1}, n = 40) compared to treatments

495   with large crushed *Mya* shell (3.5 ± 1.93 ind. EU^{-1}, n = 20). This pattern occurred equally among

496   both protected and unprotected treatments (P = 0.451; Table 5). Clam recruits pooled across all

497   treatments ranged in SL from 2.3-37.8 mm (mean SL = 13.5 ± 0.69 mm, n = 782). Mean SL of

498   recruits in netted EU were approximately 55% larger than conspecifics in control EU (13.7 ±

499   2.12 mm, n = 52 vs. 8.8 ± 1.83 mm, n = 51; P = 0.001). No other sources of variation were

500   statistically significant (P > 0.49). A 5 x 12 G-test of independence (size [< 5 mm; 5-9.99 mm;

501   10-14.99 mm; 15-19.99 mm, > 20 mm] x treatment) was highly significant (df = 44, G = 302.81,

502   P < 0.001). Relatively more recruits < 15 mm SL occurred in open EU while relatively more

503   recruits > 15 mm SL occurred in protected EU.

504

505   *M. mercenaria* recruits were found in 36 of 120 EU (30%), and ranged in SL from 2.4-8.5 mm.

506   Regression analysis (Poisson distribution; P = 0.548) and PERMANOVA on the count data

507   indicated a significant effect due to the presence of netting (P < 0.001 and 0.004, respectively),

508   but no other main or interactive effects were statistically significant (P > 0.36). Similar results

509   were obtained using PERMANOVA (Netting, P = 0.004). Approximately 2.7x as many hard

510   clam recruits occurred in control vs. netted plots (0.60 ± 0.21 vs. 0.22 ± 0.14 ind. core^{-1}, n = 60).

511   No significant treatment effects on mean SL or on size-frequency distribution were detected (P >

512   0.20).

513

514   *3.2.5   Recompence - 2016*

515   Mean pH of sediment pore water varied significantly both spatially (P = 0.004) and temporally

516   (P < 0.001) in the area adjacent to the experimental matrix from a high of 8.15 on 14 June to a

517   low of 7.09 on 9 September (Fig. 7). During the 154-day period, mean pH was 7.60 ± 0.08 (n =

518   109). Mean pH varied significantly across the netted treatments (P = 0.019), with sediments in

519   netted plots (7.63 ± 0.12, n = 18) approximately 1.6x more acidic than in EU without netting

520   (7.86 ± 0.15, n = 18). No significant difference in mean sediment pH occurred across the

521   material treatments (P = 0.361), and the effect of netting was similar across the material

522   treatments (netting x material: P = 0.562).

523

524   Live 0-year class individuals of *M. arenaria* occurred in 82 of 120 EU (~68%). ANOVA on the

525   square root-transformed count data demonstrated a significant effect due to netting (P < 0.001;

526   Table 5) with approximately 10x more recruits in netted vs. unprotected EU (9.6 ± 3.2 vs. 0.9 ±

527   0.3 ind., n = 60; Fig. 8b), but effects due to experimental material and netting x material were not

528   statistically significant (P > 0.68). Of 567 recruits of *Mya*, 517 (91.2%) were recovered from

529   netted EU. Mean SL (21.3 ± 0.8 mm; min: 4.3 mm, max: 36.7 mm) of recruits was not affected

530   significantly by either main or interaction sources of variation (P > 0.092). A 5 x 12 G-test of

531   independence was highly significant (P < 0.001), and showed that 58% of recruits in netted EU

532   were > 20 mm, whereas in EU without netting only 42% of recruits were > 20 mm.

533

534   *Mercenaria* occurred in 57 of 120 EU (~48%), and ranged in SL from 2.4-9.9 mm (mean SL =

535   4.7 ± 0.5 mm, n = 95). Counts of individuals fit a negative binomial distribution (P = 0.379).

536   Approximately 1.7x more recruits of *Mercenaria* occurred in netted vs. unnetted EU (1.00 ± 0.41

537   vs. 0.58 ± 0.19 ind. EU^{-1}, n = 60), and this difference was statistically significant (P = 0.033).

538   PERMANOVA yield similar results (P = 0.044). No significant differences on counts of

539   *Mercenaria* were observed for the other main factor (material) or the interaction term (netting x

540   material) (P > 0.42) for both analyses. No significant treatment effects on mean SL or on size-

541   frequency distribution were detected (P > 0.35).

542

543   **4. Discussion**

544   The addition of crushed, weathered shells of adults of *Mya arenaria* (mean particle size range:

545   1.9-19.3mm) or *Ostrea lurida* (mean size = 2.5 mm) did not result in an enhancement of 0-year

546   class individuals of either *M. arenaria* or *Mercenaria mercenaria* compared to controls without

547   shell hash either in large- or small-scale field experiments. Conversely, the presence of predator-

548   deterrent netting resulted in significant enhancement of both bivalves 75% of the time (Table 6).

549

550   *4.1 Attempts to mitigate effects of corrosive sediments*

551   Pore water in surface sediments at each site was acidic, ranging from 7.09-7.53 units at the

552   beginning of trials (April-May) to 7.46-7.85 units at the end of trials (Oct-Nov; Table 2). Similar

553   ranges in sediment pore water were observed at other intertidal sites within Casco Bay by Green

554   et al. (2009, 2013) who added biogenic $CaCO_3$ (*M. arenaria* shell; mean particle size ranged

555   from 1-5 mm, See Table 1) to sediments that resulted in raising mean pH and mean Ω_{arg} by ~0.3

556   units and ~2x, respectively. In those studies, softshell clam recruitment increased by 2- to 3.5x

557   compared to controls, presumably due to the buffering effect from the shell hash. In the

558   laboratory, increasing pH and Ω_{arg} resulted in a higher proportion of burrowing in juveniles of *M.*

559   *mercenaria* compared to control sediments (Green et al.,2013). Similar results were obtained

560   with small juveniles of *Mya* in the laboratory using intertidal sediments in the Bay of Fundy

561   (Canada). When pH varied between 6.84 and 7.13, less than 50% of clams burrowed, but when

562   pH was increased to levels between 7.13 and 7.50, burial rates increased to 80-100% (Clements

563   et al., 2016). These data support the hypothesis that sediment geochemistry influences

564   burrowing rates and settlement cues for both bivalve species, yet no similar buffering was

565   detected in the present study as a result of adding shell hash to ambient sediments either in the

566   large- or small-scale experiments. In fact, on two occasions, sediments were more acidic (Large-

567   scale: WP-2015 [2.5x]; Small-scale: RC-2016 [1.6x]) in netted vs. unnetted plots and EU

568   independent of shell hash treatment; yet, samples from these protected sediments contained 10-

569   70x more *Mya* recruits and nearly twice as many *Mercenaria* recruits than in samples from

570   unnetted controls.

571

572   *4.2 Buffering and alternative hypotheses*

573   In addition to buffering acidic pore water in intertidal sediments, several alternative hypotheses

574   exist relating to the mechanism by which shell hash can provide a more suitable environment for

575   settling and/or pre-existing bivalve juveniles. Crushed shell may act to discourage predators

576   from preying on clams because increasing habitat heterogeneity in an otherwise homogeneous

577   environment may result in increased search and/or handling times much like the belowground

578   complexity of seagrasses protects a variety of benthic infauna by reducing foraging rates of

579   epibenthic predators (Goshima and Peterson, 2012; Wong, 2013). Shell and stone substrata have

580   been used on relatively large scales to increase yields of cultured juveniles of *M. mercenaria*

581   (Castagna and Kraeuter, 1977; Kraeuter and Castagna, 1980; Kraeuter et al., 2003). In

582   Chesapeake Bay, USA, densities of *M. arenaria* were higher in complex (seagrass and shell) vs.

583   more homogeneous (mud, sand, gravel) benthic habitats in Chesapeake Bay, USA (Glaspie et al.,

584   2018). Further, hard clam juveniles in eastern North Carolina, USA demonstrated higher survival

585   rates in bottom habitats with oyster shell hash vs. unvegetated sand and mud sediments (Peterson

586   et al., 1995). Similar refuges that increase habitat heterogeneity and afford other prey protection

587   from predators are common in the literature (Byers et al., 2017; Hill and Weissburg, 2013; Loher

588   and Armstrong, 2000; van der Heide et al., 2014). The addition of crushed shell in the intertidal

589   may affect tidal and wind-driven currents to create localized low-flow zones (micro-habitats)

590   where bivalves settle and remain through complex bedload transport dynamics (Hunt et al.,

591   2007; Morse and Hunt, 2013). Shell hash or other materials added to intertidal sediments can

592   influence bottom roughness and alter predation intensity through the modification of odor

593   exchange between predators and prey (Ferner et al., 2009).

594

595   In this study, recruitment of juveniles of both bivalve species generally was higher in plots and

596   EU that were covered or protected with predator-deterrent netting, regardless whether or not

597   shell hash was present. The design of the large-scale trials did not permit an assessment of

598   whether buffering capacity and/or physical presence of shell hash contributed to an enhancement

599   of bivalve recruits because no controls (i.e., material that increased habitat heterogeneity but was

600   not composed of $CaCO_3$) accompanied the biogenic $CaCO_3$ treatments. Results demonstrated,

601   however, that shell hash did not enhance abundance of either bivalve species in shelled vs.

602   control plots regardless of netting treatment. On the other hand, each of the small-scale trials

603   used both crushed shells (with a capacity to buffer and increase habitat heterogeneity) as well as

604   granite chips that increase habitat heterogeneity without the capacity to buffer. None of the

605   regression analyses (SC, 2014 or LR & WP, 2015) or orthogonal contrasts comparing mean

606   abundance in EU with shell hash vs. granite chips (2016) demonstrated a significant effect on 0-

607   year class *Mya* or *Mercenaria*. Rather, the results suggest that deterring predators from foraging

608   on recently-settled bivalves is a more effective tool to enhance young-of-the-year clams than

609   returning crushed shells to intertidal sediments. In addition, because no significant difference

610   was detected in abundance of 0-year class bivalves in large-scale experiments between control

611   (no shell) vs. the two shell treatments, it is likely that there is no threshold amount of shell hash

612   (within the range of 0-1.27 kg m^{-2}) that would yield higher bivalve recruit abundances. Future

613   studies should increase the density of crushed shell to levels > 1.27 kg m^{-2} to determine a

614   threshold.

615

616   The shell hash used in the three large-scale trials (2014-2015) may have been too large (mean

617   particle size = 19.3 mm; Table 3) to effectively buffer sediments, although Greiner et al. (2018)

618   used a mixture of oyster and clam shells (up to 50 mm chips) that that resulted in higher

619   carbonate chemistry parameters (pH and Ω_{arg}) compared to controls over 55 days. Smaller sizes

620   of crushed shells of *M. arenaria* (mean = 1.9-9.3 mm) were used in the 2016 small-scale

621   experiments at LR and RC; however, no concomitant increases in pH in those treatments were

622   observed.

623

624   *4.3 Relative importance of predation vs. shell hash in regulating bivalve density and size*

625   In the present study, excluding predators had dramatic results on abundance of both species of

626   bivalves in both large- and small-scale field experiments. For example, combining probabilities

627   from the three large-scale and five small-scale tests of significance relating to the effect of

628   predator-exclusion netting on recruit density of the most abundant bivalve, *Mya arenaria*,

629   demonstrated a significant, positive response (χ^2 = 116.097, df = 16, P < 0.001; Sokal and Rohlf,

630   1995). In addition, no significant netting x shell (large-scale trials) or netting x experimental

631   material (small-scale trials) interaction were present in any test (Table 6), suggesting that shell

632   hash played little to no role in the enhancement effect of bivalve recruits associated with predator

633   exclusion. It is unclear whether predators were important in regulating densities of early post-

634   settled individuals of *Mya* in previous studies conducted in Casco Bay (Green et al., 2009, 2013),

635   but field experiments in eastern Maine prior to those dates (Beal, 2006; Beal and Kraus, 2002;),

636   and, subsequently, in Casco Bay (2014-2015; Beal et al., 2018; Munroe et al., 2015) underscore

637   the importance of predators in regulating populations of 0-year class individuals of *M. arenaria*.

638   Since no controls for the presence of biogenic $CaCO_3$ were used by Green et al. (2009, 2013), it

639   is unclear whether the observed 2- to 3-fold enhancement of recruits of *Mya* was a result of

640   buffering of the sediment pore water, a modification of habitat that was conducive for bivalve

641 settlement (Gutiérrez et al., 2003), a spatial refuge from predation (sensu Glaspie and Seitz,

642 2017), or combination of these or other factors.

643

644 Analysis of shell length measurements suggests that predation is an important mechanism

645 regulating 0-year class populations of both bivalve species. When differences in mean SL or

646 size-frequency distribution were detected for a given experiment, 75% of the time *M. arenaria*

647 recruits were significantly larger in netted vs. control plots and EU. While it is possible that

648 differences in sizes of clams between protected vs. unprotected treatments can be explained by

649 differential settlement times across treatments, deterrent netting reduces foraging/physical

650 contact with the predator, and can positively affect clam growth rates, especially juveniles (Beal

651 et al., 2001; Nakaoka, 2000). In addition, *Mya* can detect chemical cues from predators that

652 induce morphological responses that can divert energy from shell to siphon growth (Whitlow,

653 2010); however, acidified sediments may change clam behavior. For example, Glaspie et al.

654 (2017) used a probe to simulate a predator moving through sediments, and discovered that

655 juveniles of *M. arenaria* (mean SL = 28.5 mm) grown in ambient conditions (pH = 7.8) reacted

656 by ceasing their pumping behavior when the probe was ~ 30 cm away compared to juveniles that

657 had spent four weeks in CO_2-acidified water (pH = 7.2) that did not react until the probe was ~

658 11 cm away.

659

660 *4.4 Survival and shell production in acidic sediments*

661 In the present study, both bivalve species apparently settled, survived, and grew (produced shell)

662 in corrosive sediments (mean pH ranged from 7.09 to 7.85). In general, sediments protected from

663 predators enjoy a higher diversity and density than those where predator foraging or grazing

664　from mobile gastropods occurs unabated (Danovara et al., 2007; Petrowski et al., 2016). It is

665　likely that differential organic enrichment and benthic respiration rates across treatments resulted

666　in the formation of organic and inorganic acids that cause pore water pH to decline (Sunda and

667　Cai, 2012; Prezoisi et al., 2019).

668

669　Results from other studies suggest that early survival and shell accretion occur in acidic

670　sediments (i.e., Ω_{arg} < 1). For example, Green et al. (2009) increased mean sediment saturation

671　state in the field from Ω_{arg} = 0.25 to only 0.53, and still saw a concomitant 3-fold increase in *Mya*

672　recruits compared to controls over two weeks.　provides new evidence of how marine bivalves

673　respond to high $p\text{CO}_2$ levels *in situ*.　In a mesocosm study, juveniles of *Mya* (5-10 mm SL) in

674　sediments were exposed to overlying seawater for three months with one of four $p\text{CO}2$ regimes

675　(900, 1500, 2,900, and 6,600 µatm, corresponding to pH of 7.8, 7.7, 7.4, and 7.0, respectively;

676　Zhao et al., 2018). No mortality occurred in any treatment, but shell growth varied as a function

677　of treatment, with fastest growth occurring in the control (mean = 4.75µ day^{-1} @ 900 µatm),

678　slowest at the highest regime (mean = 1. 75µ day^{-1}), and intermediate growth occurring at the

679　two middle regimes (mean = 3.0µ day^{-1}).　This suggests that *M. arenaria* may be able to mitigate

680　partially the corrosive effects of low pH pore water by modifying the calcifying fluid chemistry

681　and maintaining pH homeostasis.　Specifically, at $p\text{CO}2$ levels ≤ 2,900 µatm, animals most likely

682　concentrated HCO_3^- in the calcifying fluid through an exchange of $\text{HCO}_3^-/\text{Cl}^-$ while maintaining

683　pH homeostasis through active removal of protons during CaCO_3 precipitation (Marin et al.,

684　2012).　Glaspie et al. (2017) observed shell growth of large juveniles (~ 28 mm) under acidified

685　conditions (pH = 7.2); however, mean shell mass was significantly less than similar size clams

686　held under control conditions (pH = 7.8).

687 *4.5 Management considerations*

688 Seawater temperature has both direct and indirect effects on the strength of 0-yr classes of

689 infaunal bivalves such as *Mya* and *Mercenaria* (Philippart et al., 2003; Glaspie et al., 2018).

690 Mean seawater temperatures in the Gulf of Maine are expected to increase by 3-4°C by 2050

691 (Saba et al., 2016). The thermal tolerance of both *Mya* (-15° to 34°C; Kennedy and Mihursky,

692 1971; Bourget, 1983) and *Mercenaria* (-1° to 34°C; Pernet et al., 2006; Bricelj et al., 2017)

693 throughout its geographic range suggests that their populations, at least within the Gulf of Maine,

694 are not yet threatened, and would be physiologically competent to withstand increases in

695 seawater temperatures predicted by 2050. In this study, seawater temperatures observed at SC,

696 LR, and WP (2014-2015 trials) and at LR and RC in 2016 (Fig. 7) fell well within the thermal

697 tolerance range of both species. Populations of the invasive *Carcinus maenas*, the major

698 predator of these bivalves in this region (Whitlow, 2010; Beal et al., 2018), increase their

699 numbers and foraging rates with increasing seawater temperatures (Welch, 1968; Freitas et al.,

700 2007). For example, in Wales, predation rates on the cockle *Cerastoderma edule* by *C. maenas*

701 rose steeply with increasing temperature (Sanchez-Salazar et al., 1987), and on tidal flats in the

702 Wadden Sea, green crabs are more abundant after mild vs. cold winters (Beukema, 1991;

703 Beukema and Dekker, 2014). With rising ocean temperatures in the Gulf of Maine, a rational

704 hypothesis would predict higher predation rates by green crabs, and other poikilotherm predators,

705 on *Mya* and *Mercenaria* in future that could have severe effects on the fishery of these species.

706 For example, softshell clam landings in Maine vary negatively with average winter seawater

707 temperatures (Beal et al., 2016) that have been warming gradually since the 1980s (Fig. 9), and

708 reflect seawater temperature trends throughout the Gulf of Maine (Pershing et al., 2015;

709 Salisbury and Jönsson, 2018).

710   Climate change also has focused attention on coastal acidification and its negative effects on

711   bivalve larvae and early juveniles (Salisbury et al., 2008; Waldbusser et al., 2015; Clements and

712   Chopin, 2017; Lesser et al., 2019). Mitigating effects of acidic pore water on the fate of bivalve

713   settlers to the benthos by applying shell hash to these corrosive sediments has been touted as a

714   possible management strategy to decrease dissolution mortality of early post-settled bivalves

715   (Green et al., 2009). Using those results, coastal communities in Maine, USA have been

716   encouraged by fisheries managers and others to use shell hash as a buffering agent for the

717   purposes of "restoring recruitment of softshell clams" (Bentley and Schneider, 2015). In

718   Washington, USA, a blue-ribbon panel recommended that "spreading shell material in shallow

719   waters can increase survival of newly settled bivalve larvae, both native and cultured, by

720   buffering corrosive conditions" (WABRPOA, 2012). Predation, especially by *C. maenas* (Beal

721   et al., 2001, 2018; Young and Elliot, 2020), and other consumers, likely masks any long-term

722   beneficial effects of shell hash additions; however, managers may wish to repeat these large-

723   scale experiments to determine if additional time beyond 5-6 months (Ruesink et al., 2014)

724   and/or increasing the areal density of shell hash (i.e., > 1.27 kg m^{-2}) that could address the lack of

725   a threshold detected in this study will yield different results.

726

727   While predator-exclusion netting can be used to protect cultured clam juveniles (Beal and Kraus,

728   2002; Cigarría and Fernández, 2000), or naturally-established wild clams (Beal et al., 2016), it

729   does not attract bivalve settlers or early juveniles, and its use is limited by logistics to relatively

730   small areas (< 1-2 hectares) that are managed by coastal communities (McClenachan et al., 2015)

731   or individual fishers. Instead, new regional and coastwide policies (sensu Bidegain et al., 2013;

732 Brousseau, 1978; Joaquim et al., 2008) should be evaluated by state fisheries managers with the

733 goal of reversing the nearly 50-year trend of decreasing commercial softshell clam landings.

734

735 **Declaration of Interests**

736 The authors declare that they have no known competing financial interests or personal

737 relationships that could have appeared to influence the work reported in this paper.

738

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747

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Table 1. Results from recent intertidal experiments where crushed shell was used experimentally to modify substrate or to mitigate effects of low pH and/or $\Omega_{aragonite}$ on bivalve recruitment or survival and growth of cultured juvenile bivalves.

Author(s)	Crushed Shell Species	Particle Size (mm)	Location	Date	Results
Dethier et al. (2019)	*Crassostrea gigas*	<10 mm	Salish Sea, Washington, USA	Jul-Sept 2017 (64-75 days)	Neither survival nor growth of 3-6 mm cultured individuals of *Ruditapes philippinarum* differed between units with pebble-sand v. crushed shell.
Green et al. (2009)	*M. arenaria*	5 mm	West Bath, Maine, USA	Jul 2007 (16 days)	Ω_{arg} increased from 0.25 in control plots to 0.53 in buffered plots. Recruits of *M. arenaria* increased 3.5x in buffered v. control plots.
Green et al. (2013)	*M. arenaria*	1 mm	Portland, Maine, USA	Jun-Jul 2009 (35 days)	Ω_{arg} increased from 0.68 in control cores to 1.3 in buffered cores. Recruits of *M. arenaria* increased by 2x in buffered v. control cores.
Greiner et al. (2018)	70% *C. gigas*; 30% mixed species clam shell	<50 mm	Fidalgo Bay; Skokomish Delta, Washington, USA	Jul-Aug 2016 (55 days)	pH and Ω_{arg} increased significantly in crushed shell treatment. Recruitment of *R. philippinarum* did not respond to crushed shell additions.
Ruesink et al. (2014)	*M. arenaria* *R. philippinarum* *C. gigas*	10-20 mm	Willapa Bay, Washington, USA	Jul-Aug 2014 (49 days)	Settlement of *R. philippinarum* and *M. arenaria* was insensitive to substrate modification.

1186 **Table 2.** Intertidal study sites (SC = Staples Cove; LR = Little River; WP = Winslow Park; RC = Recompence), latitude/longitude,

1187 scale of experiment[1], initiation and completion dates, mean pH (± 1 SE), and sample size. Sampling occurred near the mid-intertidal

1188 on each date using a Fisher Accumet AP 115 pH meter with Accumet pH electrode that was inserted into the intertidal sediments to a

1189 depth of 2 mm. Initial mean density (± 1 SE) of *Mya arenaria* per core (0.018 m^2). '***n***' refers to sample size. '**nd**' refers to no data.

1190

Year	Site	Lat. ºN	Long. ºW	Scale of Experiment	Initial Date	Initial mean pH	n	Final Date	Final mean pH[2]	n	Initial Density	n	Initial Size Range (mm)
2014	SC	43.807	-70.110	Lg & Sm	18 May	7.09(0.10)	10	4 Nov	7.59(0.04)	5	0.07(0.05)	30	8.2-10.7
2015	LR	43.823	-70.087	Lg & Sm	29 Apr	7.35(0.09)	10	29 Oct	nd		7.15(3.03)	30	2.7-10.4
	WP	43.801	-70.121	Lg & Sm	30 Apr	7.37(0.11)	10	30 Oct	7.61(0.10)	5	0.00(0.00)	30	
2016[3]	LR	43.823	-70.087	Sm	8 Apr	7.19(0.04)	5	29 Oct	7.46(0.07)	2	6.30(1.07)	25	2.6-19.2
	RC	43.825	-70.071	Sm	9 Apr	7.53(0.04)	5	28 Oct	7.85(0.08)	3	0.20(0.08)	25	3.4-11.6

[1] Lg refers to large-scale plots (9.3m^2). Sm refers to small-scale experimental units (= EU; 0.018 m^2).
[2] 2014 & 2015 pH samples were taken from large-scale control plots without shell or netting.
[3] Initial pH samples were taken from ambient sediments within the experimental matrix prior to deploying EU. Final pH samples
  were taken from control (no material/no netting) EU at both sites.

1208 **Table 3.** Material (and mean size ± 1 SE) used in large- (LG) and small- (SM) scale sediment

1209 buffering experiments (2014-2016). ANOVA indicated that mean size of the material varied

1210 significantly (P < 0.0001), and the a posteriori Student-Newman-Keuls (SNK) test showed that

1211 only the small crushed shells of *Mya* and *Ostrea* were similar in mean size. n = 25

1212

Year	Material	Size (mm)	min (mm)	max (mm)	Experiment[1]
2014-2016	Large crushed shells of *Mya arenaria*	19.3 (0.77)	13.8	27.1	LG & SM
2014-2015	Marble chips[2]	15.4 (0.57)	9.9	20.6	SM
2014-2016	Granite chips	22.0 (1.22)	14.3	31.4	SM
2016	Medium crushed shells of *Mya arenaria*	9.3 (0.46)	6.6	14.1	SM
	Small crushed shells of *Mya arenaria*	1.9 (0.15)	0.9	3.9	SM
	Crushed shells of *Ostrea lurida*[3]	2.5 (0.17)	1.1	3.8	SM

1231 [1] See footnote #1 from Table 2.

1232 [2] Vigoro® Mini Marble Chips (see: https://www.homedepot.com/p/Vigoro-0-5-cu-ft-Mini-
1233 Marble-Chips-54142V/202257775)
1234

1235 [3] Product purchased as Pacific Pearl Oyster Shell Flour (see:
1236 https://www.lindmarine.com/services-products/oyster-shell-calcium-for-poultry/)
1237
1238

Table 4. Results of Poisson and negative binomial regression (χ^2 likelihood ratio statistics) and univariate PERMANOVAs for large-scale experiments 2014-2015. None of the two single degree-of-freedom contrasts associated with the crushed shell source of variation were significant (P > 0.092). _**Syn**_ = Synthesis of the two analyses: ns = P > 0.05, * = P ≤ 0.05 (Sokal and Rohlf, 1995). Dependent variable = number of recruits per core sample. SC = Staples Cove; LR = Little River; WP = Winslow Park (Fig. 1). Significant P-values are given in bold-face.

		Mya **recruits**					_Mercenaria_ **recruits**				
SC-2014[1]											
Source	DF	χ^2	P	F	P	_**Syn**_	χ^2	P	F	P	_**Syn**_
Crushed Shell	2	1.09	0.578	0.27	0.775	ns	5.72	0.057	1.78	0.191	ns
Netting	1	9.64	**0.002**	4.74	**0.033**	*	52.79	**<0.001**	25.50	**<0.001**	*
Shell x Netting	2	3.92	0.141	1.20	0.326	ns	3.31	0.191	2.33	0.112	ns
Plot(Shell, Netting)	24	39.33	**0.025**	1.82	**0.022**	*	5.22	0.516	1.33	0.154	ns
LR-2015[2]											
Crushed Shell	2	0.51	0.776	0.04	0.957	ns					
Netting	1	38.28	**<0.001**	14.92	**<0.001**	*		No _Mercenaria_ observed			
Shell x Netting	2	1.16	0.559	0.02	0.985	ns					
Plot(Shell, Netting)	24	43.54	**0.009**	1.30	0.171	*					
WP-2015[2]											
Crushed Shell	2	1.55	0.460	0.44	0.885	ns					
Netting	1	14.34	**<0.001**	2.36	0.079	*		Four _Mercenaria_ observed			
Shell x Netting	2	0.94	0.626	0.44	0.886	ns					
Plot(Shell, Netting)	24	52.82	**<0.001**	3.36	**0.017**	*					

[1] Poisson regression analysis for both species

[2] Negative binomial regression analysis

1272 **Table 5.** Analysis of variance on the square root-transformed mean count data for recruits of
1273 *Mya arenaria* from the 2016 small-scale field experiment at LR and RC, Freeport, Maine (Fig.
1274 1). Materials and Netting are described in Table 3. Orthogonal contrasts associated with
1275 material and netting x material are indented and occur directly beneath each source of variation.
1276 Significant P-values are given in bold-face. n = 10.

Source of Variation	df	Little River			Recompence		
		MS	F	Pr > F	MS	F	Pr> F
Netting	1	0.476	0.23	0.632	90.157	50.78	**<0.001**
Material	5	4.572	2.22	0.057	0.796	0.45	0.814
Control v. Rest	1	2.963	1.44	0.233	1.576	0.89	0.348
Shell v. Granite	1	0.642	0.31	0.578	1.525	0.86	0.356
Mya v. *Ostrea*	1	4.179	2.03	0.157	0.234	0.13	0.719
Lg v. Sm & Med shell	1	14.661	7.12	**0.009**	0.151	0.09	0.771
Sm vs. Med shell	1	0.416	0.20	0.654	0.493	0.28	0.599
Netting x Material	5	1.524	0.74	0.595	1.099	0.89	0.686
Netting x Cont. v. Rest	1	0.003	0.00	0.970	3.479	1.96	0.164
Netting x Shell v. Granite	1	1.415	0.69	0.409	0.537	0.30	0.584
Netting x *Mya* v. *Ostrea*	1	3.168	1.54	0.218	0.688	0.39	0.535
Netting x Lg. v. Sm/Med	1	1.181	0.57	0.451	0.015	0.01	0.926
Netting x Sm v. Med	1	1.856	0.90	0.345	0.773	0.44	0.511
Error	108	2.058			1.776		
Total	119	2.128			2.449		

1312 **Table 6.** Results from three large-scale (2014-2015; n = 5) and five small-scale (2014-2016; n = 10 or 12) intertidal field experiments in north-
1313 central Casco Bay, Maine that examined the interactive effects of sediment buffering using crushed and weathered bivalve shells (*Mya arenaria*;
1314 *Ostrea lurida*; Tables 2 & 3) and predation exclusion on abundance of 0-year class individuals (recruits) of *M. arenaria* and *Mercenaria mercenaria*.
1315 X = P ≤ 0.05; O = P > 0.05; The X below the contrast labeled Lg v. Small & Med Shell was associated with a greater mean abundance of *Mya*
1316 recruits in the two smaller shell hash sizes vs. larger shell size. See Table 3 for description of shell size.
1317
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				Main & Interactive Effects			Contrasts								
Year	Scale	Site	Species	Shell	Netting	Shell x Netting	Control v. Shell	0.63 v. 1.27 kg m^{-2}	Control v. Material	Shell & Marble v. Granite	Shell v. Marble	Shell v. Granite	*Mya* v. *Ostrea*	Lg v. Small & Med Shell	Small v. Med
2014	Large	SC	*Mya*	O	X	O	O	O							
			Mercenaria	O	X	O	O	O							
2015	Large	LR	*Mya*	O	X	O	O	O							
		WP	*Mya*	O	X	O	O	O							
2014	Small	SC	*Mya*	O	X	O			O	O	O				
			Mercenaria	O	O	O			O	O	O				
2015	Small	LR	*Mya*	O	O	O			O	O	O				
		WP	*Mya*	O	X	O			O	O	O				
2016	Small	LR	*Mya*	O	O	O			O			O	O	X	O
			Mercenaria	O	X	O			O			O	O	O	O
		RC	*Mya*	O	X	O			O			O	O	O	O
			Mercenaria	O	X	O			O			O	O	O	O

1347 **Figure Legends**

1348

1349 **Figure 1.** Map of the four intertidal study sites (red dots) in Freeport, Maine (see Table 2 for

1350 additional information). Numbers under the scale bar refer to distances in kilometers.

1351

1352 **Figure 2.** Box-and-whisker plots (five-number summaries) of pH on 8 May 2014 (see Fig. 1 for

1353 site locations). Closed circles represent outliers. Median pH at Staples Cove was approximately

1354 8% lower than overall median pH of other sites. n = 10.

1355

1356 **Figure 3.** Schematic of the design for: a) large-scale (n = 5), and b) small-scale (n = 10) field

1357 experiments at Staples Cove (2014) and Little River and Winslow Park (2015). c) small-scale (n

1358 = 10) field experiments at Little River and Recompence (2016).

1359

1360 **Figure 4.** Size-frequency distribution of recruits of **a)** *Mya arenaria* (n = 24), and **b)**

1361 *Mercenaria mercenaria* (n = 44) in large-scale plots at Staples Cove (4 November 2014).

1362

1363 **Figure 5.** Box-and-whisker plots (five-number summaries) of number of hard clam, *Mercenaria*

1364 *mercenaria*, recruits sampled in benthic cores (A = 0.018 m^2) in large-scale plots at Staples Cove

1365 (n = 5, pooled across five plots per treatment; N = 25 per treatment). Experiment was initiated

1366 on 18 May and ended on 4 November 2014. "Shells +" and "Shells ++" refers to treatments in

1367 which bottom plots received 0.63 kg m^{-2} or 1.27 kg m^{-2} of large, crushed shells of *M. arenaria,*

1368 respectively. Plastic netting (4.2 mm aperture) was applied to 9.29 m^2 plots to deter predators.

1369   Black dots refer to outliers. (See Table 4 for results from regression analysis and

1370   PERMANOVA).

1371

1372   **Figure 6.** Box-and-whisker plots (five-number summaries) of number of *Mya* recruits from core

1373   samples (area = 0.01824 m^2) taken from large-scale plots from Little River and Winslow Park (n

1374   = 2 cores $plot^{-1}$ x 5 plots per treatment, N = 10 cores per treatment; Fig. 1; Table 2) in October

1375   2015. "Shells +" and "Shells ++" refers to treatments in which bottom plots received 0.63 kg m^{-2}

1376   or 1.27 kg m^{-2} of large, crushed shells of *M. arenaria,* respectively. Black dots refer to outliers.

1377   (See Table 4 for results from regression analysis and PERMANOVA).

1378

1379   **Figure 7.** Mean pH and temperature (± SE) of sediment pore water in small-scale experiments

1380   from ambient sediments at Little River and Recompence on ten dates from 5-17 to 10-24 2016 (n

1381   = 3). Measurements taken on 10-24 were from control EU (without shells or net) (n = 6).

1382   Numbers beneath x-axis label refer to specific sampling dates (e.g., 5-17 = 17 May 2016).

1383   Pearson correlation coefficient (r): Little River (-0.37, P = 0.26), Recompence (-0.34, P = 0.302).

1384

1385   **Figure 8.** Untransformed mean (+ 95% CI) number of 0-year class individuals of *Mya arenaria*

1386   from EU during 2016 small-scale experiments at: **a**) Little River, and **b**) Recompence. Black

1387   bars = EU without predator-deterrent netting, Meshed bars = EU with predator-deterrent netting

1388   (4.2 mm aperture). See Table 5 for ANOVA results. n = 10.

1389

1390   **Figure 9.** Mean sea surface temperatures (black dots) recorded daily at West Boothbay Harbor,

1391   Maine (approximately 36 km west of Freeport, ME) from 1 January to 31 March (1945-2018),

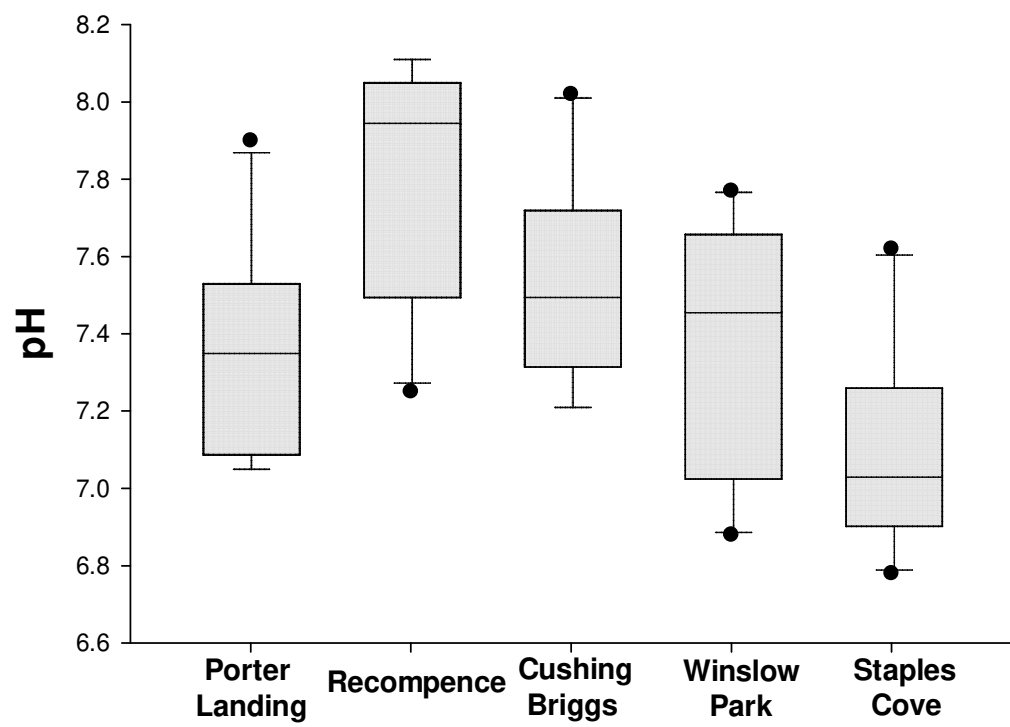1392   and decadal (red triangles) means for the same period of time. Data acquired from

1393   https://www.maine.gov/dmr/science-research/weather-tides/bbhenv.html.

1394 **Figure 1.**

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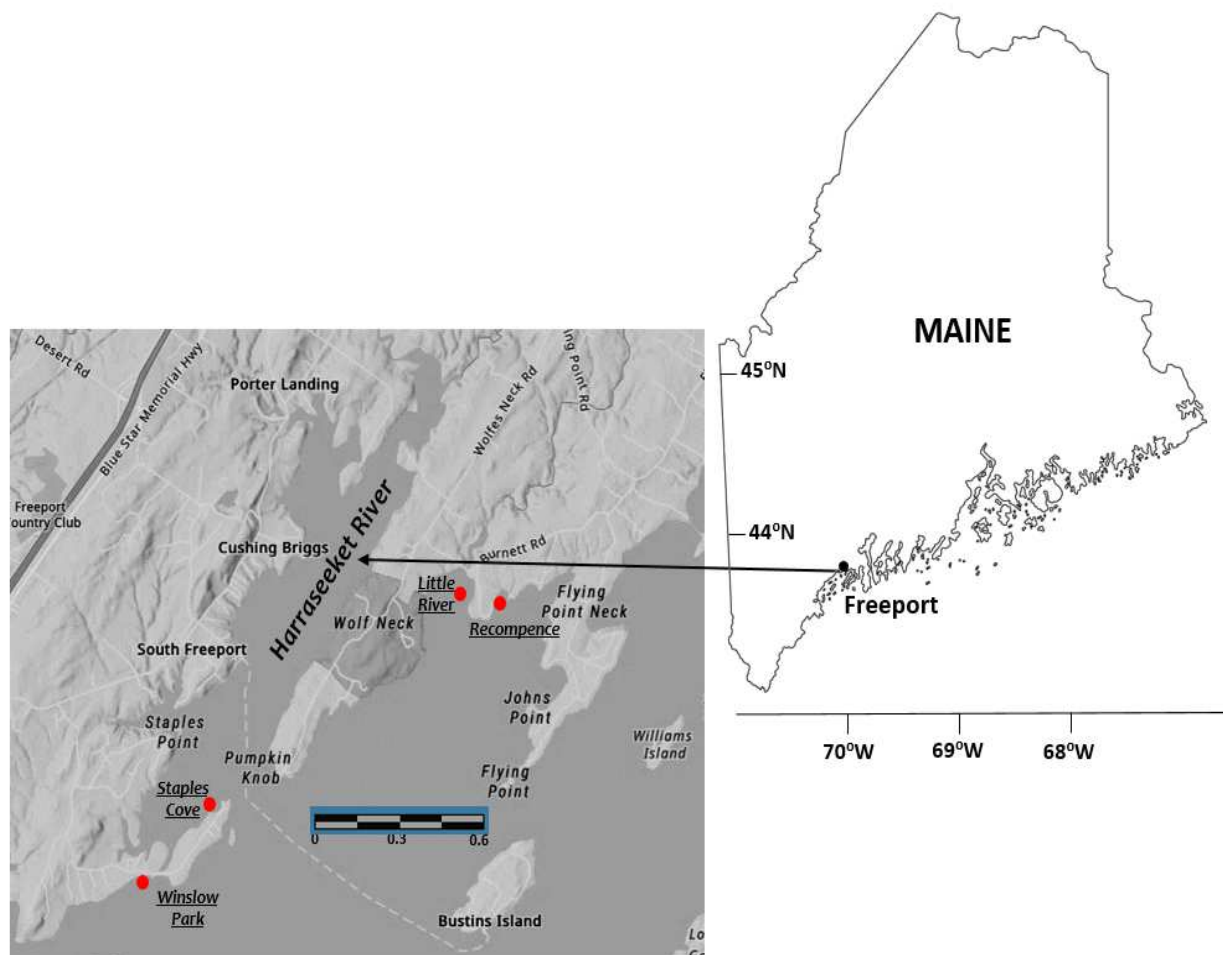
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1399   **Figure 2.**

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1404   **Fig. 3**

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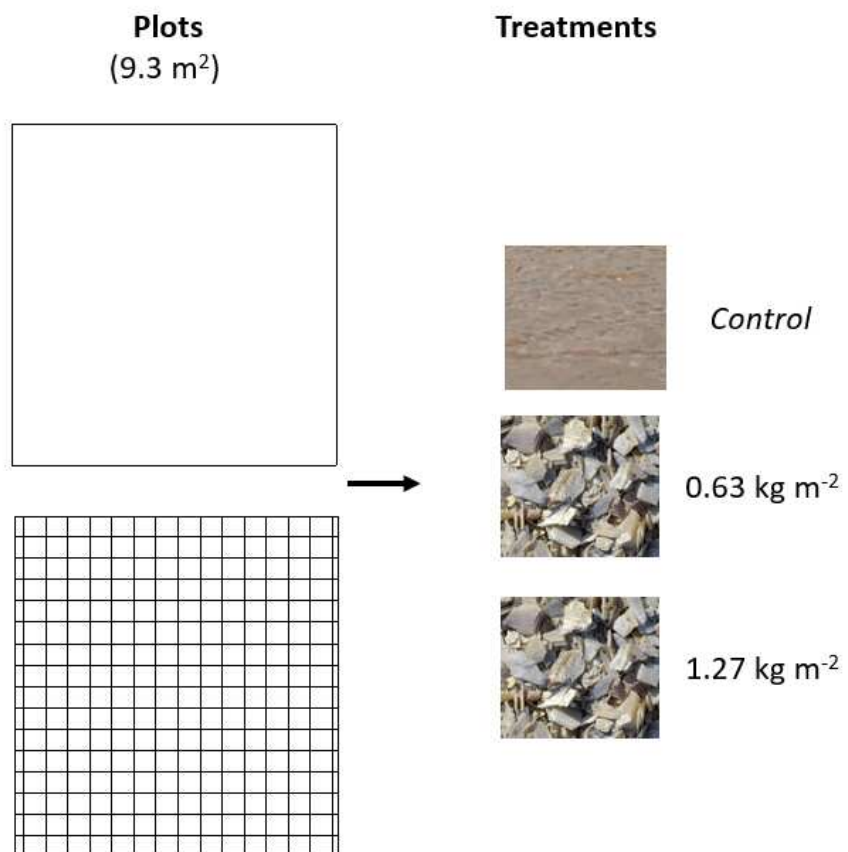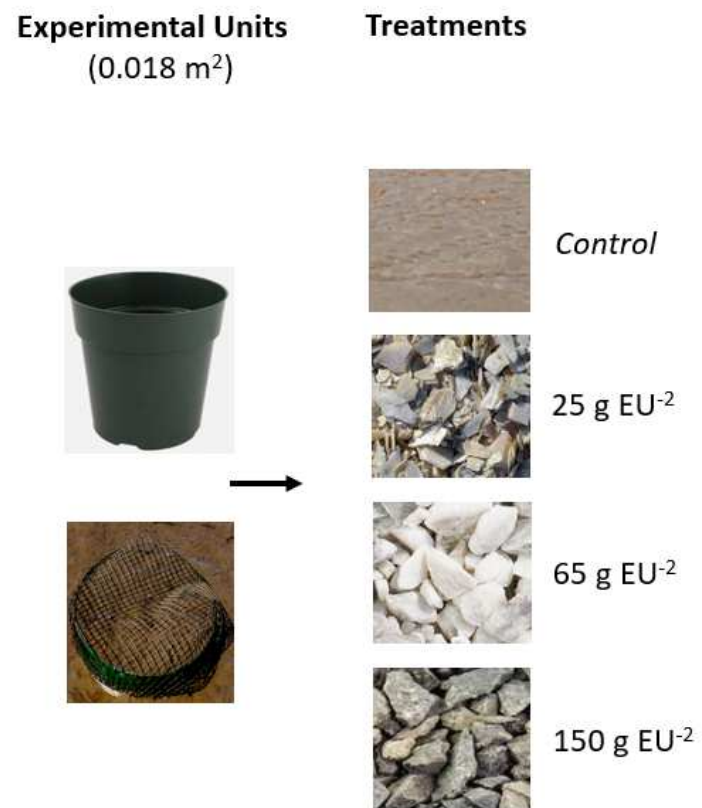
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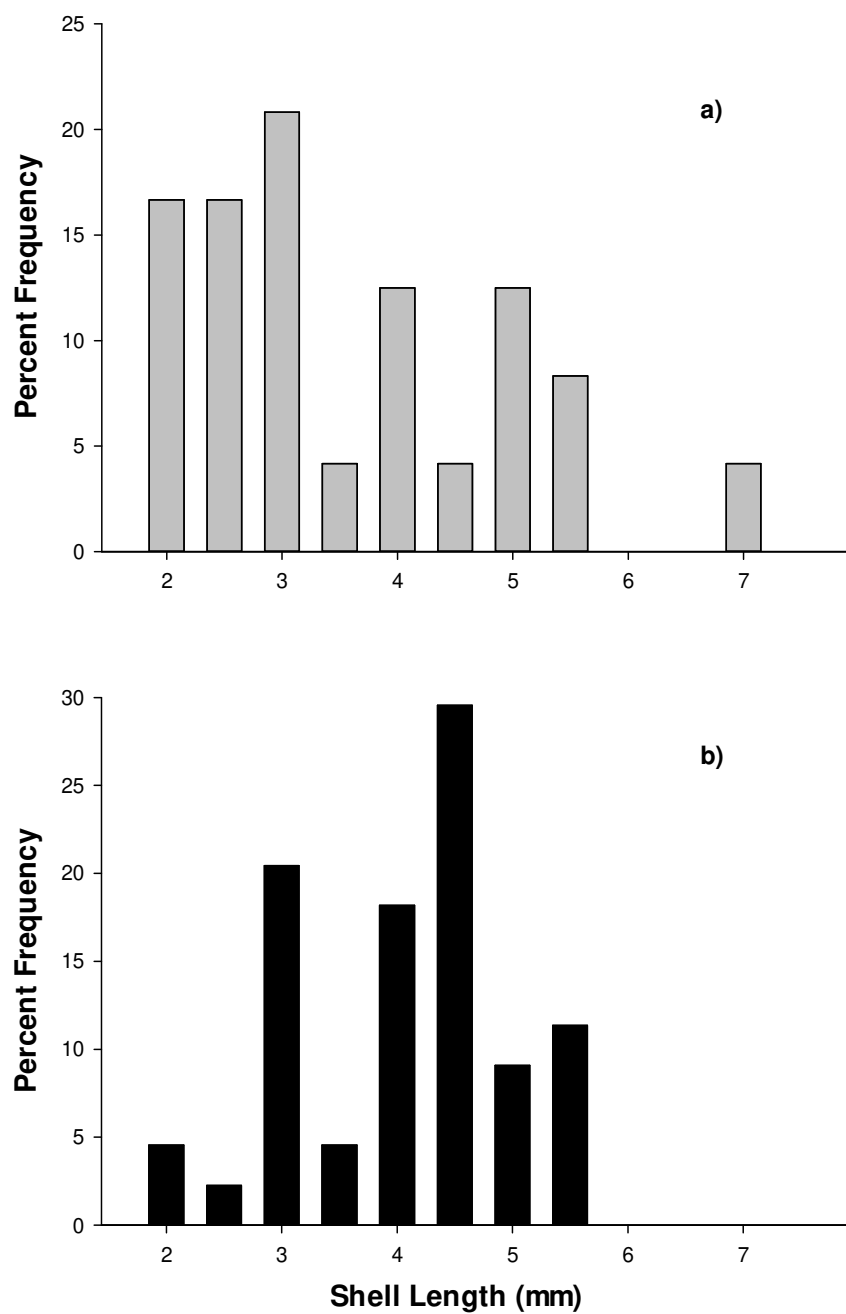
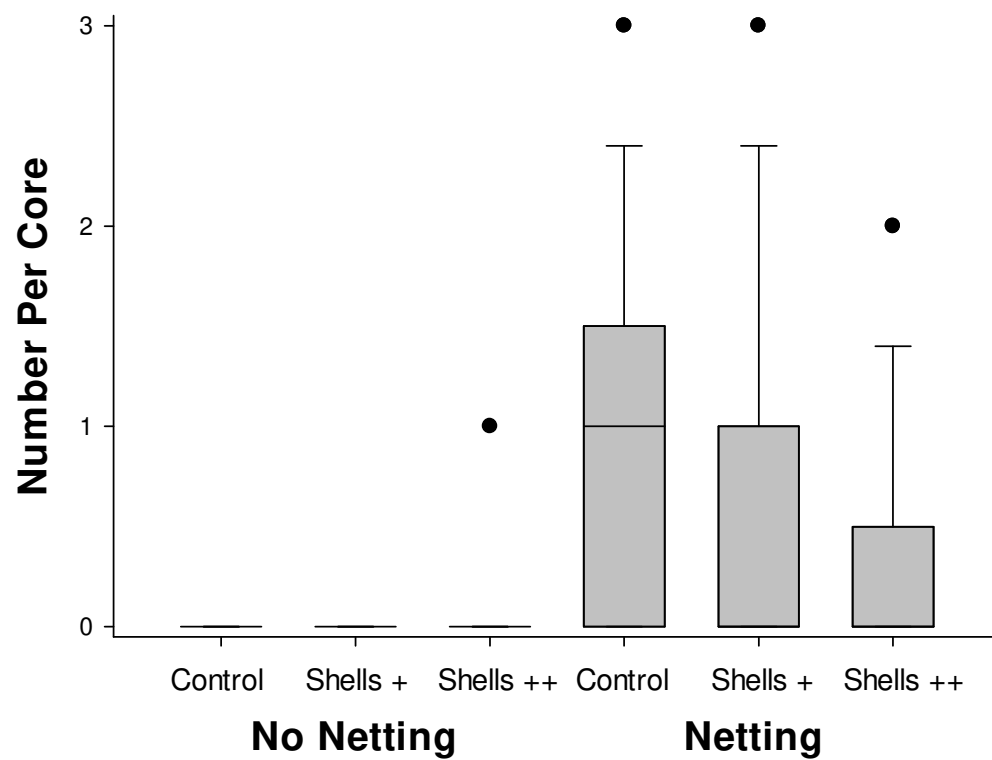1408 **Figure 3. (cont.)**

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1412 **Fig. 4.**

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1416 **Figure 5.**

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1420   **Figure 6.**

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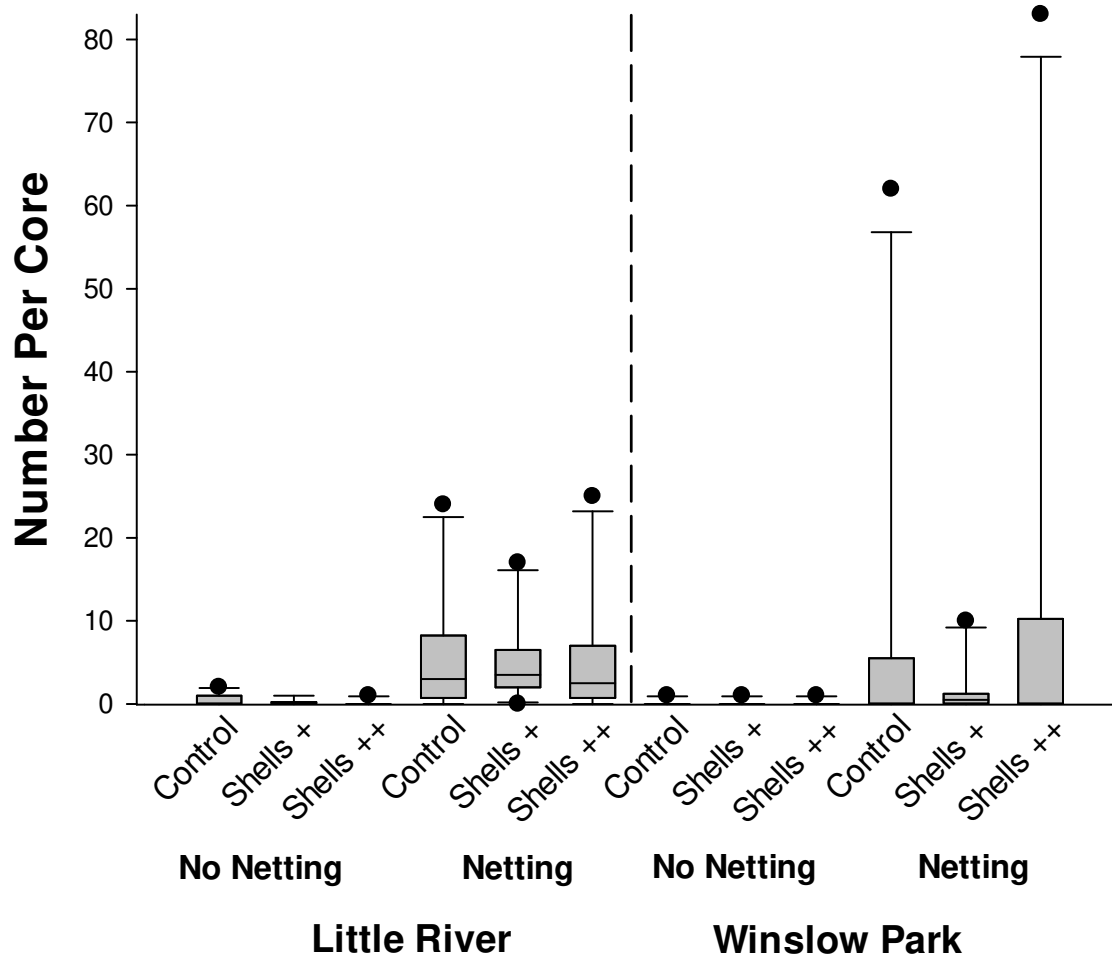
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1425 **Figure 7.**

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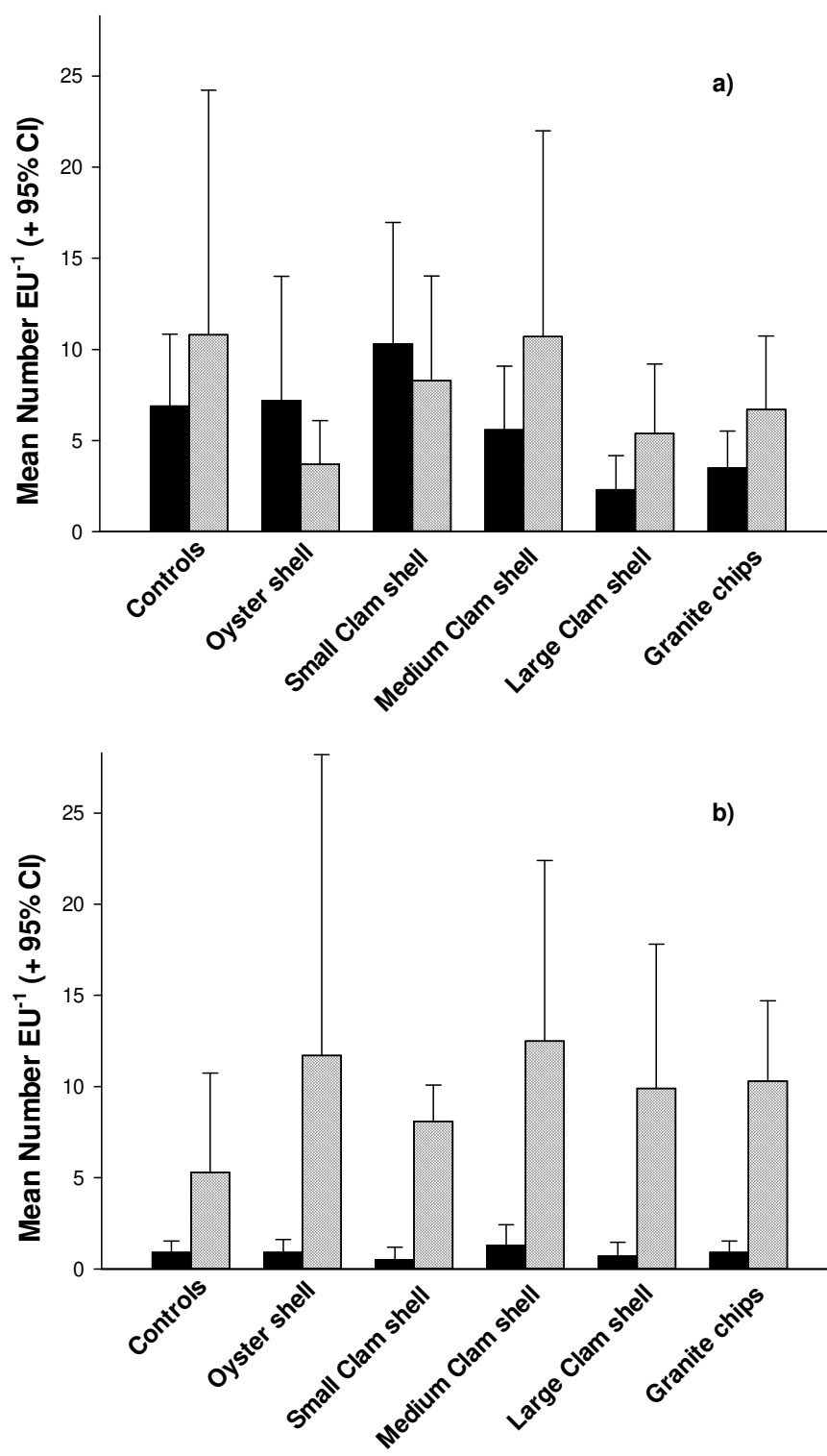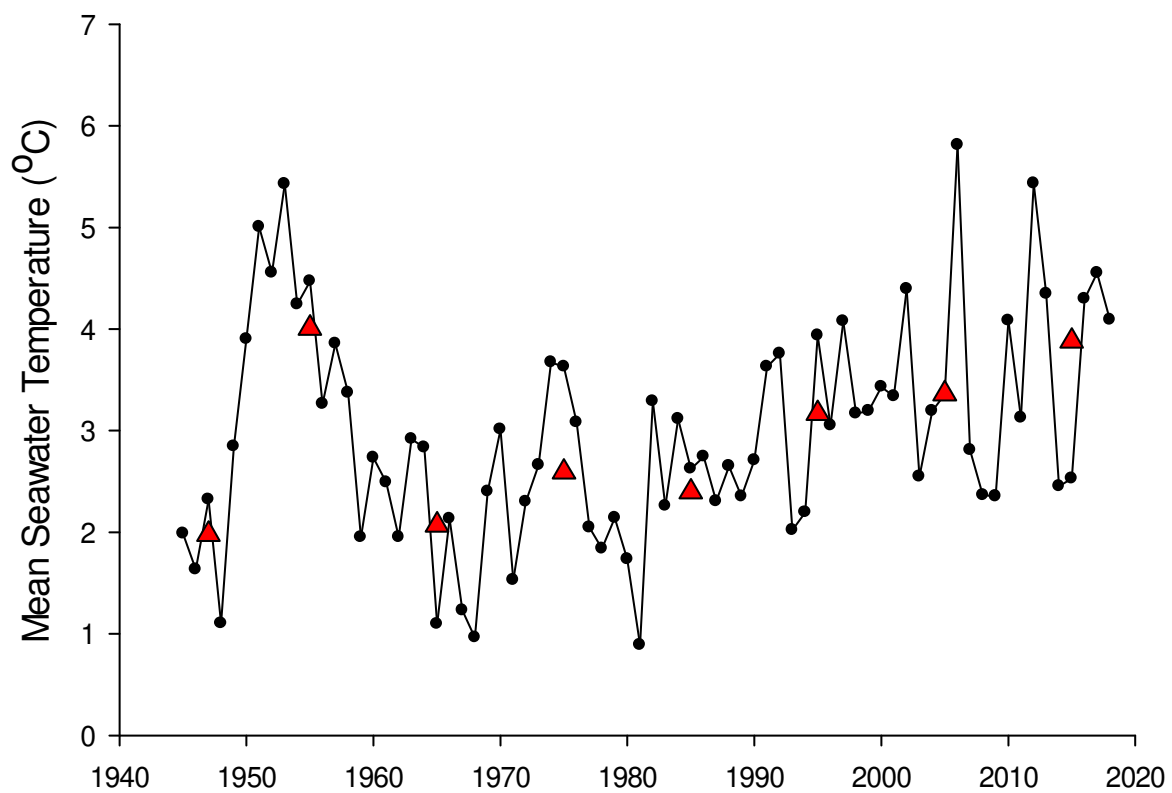1427   05-17   06-14   08-09   09-22   10-24
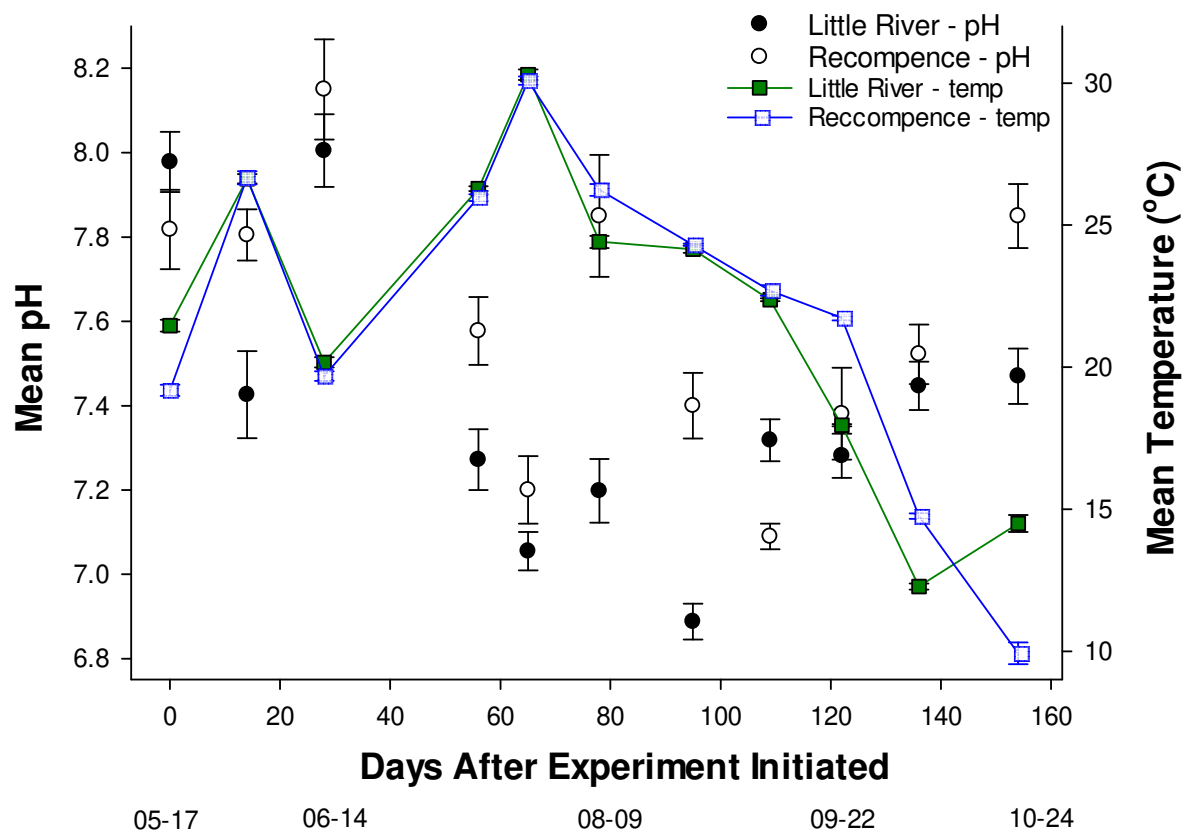
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1429

1430   **Figure 8.**

1431

1432   **Figure 9.**

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