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Vulnerability of Juvenile Clams to Predation by Shore Crabs

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18 **Abstract**

19 Predation, especially by crabs, is a common source of mortality for natural and farmed
20 populations of intertidal clams. Consumption of juvenile “seed clams” forces aquaculturists to
21 try to exclude predators and/or raise juveniles in hatcheries until they can reach a size refuge.
22 We ran a variety of lab experiments assessing vulnerabilities of juvenile clams to small,
23 common shore crabs (*Hemigrapsus* spp.). Crabs <1 cm width can consume hardshell Manila
24 clams larger than those normally used for “seed”, and can readily crush even larger softshell
25 *Mya* clams. We suggest that using netting to prevent consumption by shore crabs is not
26 practical given that smaller individuals can fit through mesh openings. Raising seed in
27 hatcheries until they are 10-15 mm will provide a size refuge from shore crabs, but not larger
28 cancrid crabs. Farming on beaches with little habitat (e.g., cobbles) for shore crabs can likely
29 reduce juvenile clam mortality. A better understanding of predation threats to commercially
30 important clams is critical, especially as the invasion of the green crab *Carcinus* to Washington
31 shorelines further threatens survival of juvenile clams.

32

33 **1. Introduction**

34 Aquaculture is an increasingly important contributor to food production and the global
35 economy, with the worldwide farming of shellfish increasing by 650% in the past 30 years
36 (Saurel, Ferreira, Cheney, Suhrbier, Dewey, Davis, Cordell, 2014). While some aspects of
37 shellfish farms raise ecological and aesthetic concerns (Bendell, 2015; Munroe, Kraeuter, Beal,
38 Chew, Luckenbach, Peterson, 2015), culturing bivalves (oysters, mussels, and clams) can
39 provide ecosystem services as well as a valuable protein source. These services include reducing
40 water turbidity and excess nitrogen (Higgins, Stephenson, Brown, 2010), sequestering carbon in
41 shells, and even reducing wave energy that erodes shorelines (Peterson, Grabowski, Powers,
42 2003).

43 A substantial challenge to the success of both farmed and natural populations of
44 shellfish is reducing loss to predators. Diverse consumers such as seastars, carnivorous snails
45 (whelks and moonsnails), crabs, birds (shorebirds and diving ducks), and fishes (bony fishes and
46 rays) can all reduce densities of adult clams (Beal, 2006; Bendell, 2015; Beukema, Dekker,
47 Philippart, 2010; Munroe, McKinley, 2007; Myers, Baum, Shepherd, Powers, Peterson, 2007).
48 Recently settled (<1 mm) clams of various species are also vulnerable to mortality from a range
49 of predators including crangonid shrimp, juvenile crabs including hermit crabs, grapsids, and
50 portunids, nereid polychaetes, and perhaps even nematodes (Beukema, Dekker, 2005; 2014;
51 Hunt, Scheibling, 1997; Olafsson, 1989; Walton, MacKinnon, Rodriguez, Proctor, Ruiz, 2002;
52 Whitton, Jenkins, Richardson, Hiddink, 2012; Williams, 1980). Slightly larger clams (2-5 mm) can
53 be eaten by other predators including nemertean worms, numerous crab species, and

54 mummichog and other fishes (Beal, Vencile, 2001; Hunt, Mullineaux, 2002; Peterson,
55 Summerson, Huber, 1995; Walton, MacKinnon, Rodriguez, Proctor, Ruiz, 2002).

56 Large losses of clams at shellfish farms to predators, especially crabs, leads to expensive
57 mitigation efforts to increase clam survival (Peterson, Summerson, Huber, 1995). “Seed clams”
58 (usually 1-15 mm) have higher survival following outplanting when they are protected from
59 predators by plastic nets (reviewed by Munroe, Kraeuter, Beal, Chew, Luckenbach, Peterson,
60 2015) or by coarse substrate such as gravel added to the sediment surface (Glaspie, Seitz,
61 Ogburn, Dungan, Hines, 2018; Peterson, Summerson, Huber, 1995; Ruesink, Freshley, Herrold,
62 Trimble, Patten, 2014). Coarser substrates may give clams surfaces to attach to for stability
63 (Becker, Barringer, Marelli, 2008) or make it harder for predators to dig (Arnold, 1984; Liu,
64 Wang, Lu, Hu, Su, Liu, Zhu, 2019). Ironically, in some cases adding coarser substrate may
65 encourage residence of small crabs, which can consume seed clams (Smith, Langdon, 1998).
66 However, netting and sediment amendment will not increase survival if a key mortality source
67 is small predators that are undeterred by the large mesh of most anti-predator netting.

68 The Manila clam, *Ruditapes philippinarum* (Adams & Reeve, 1850) (also known as
69 *Venerupis philippinarum*, *Venerupis japonica* and *Tapes japonica*), is an important fisheries
70 species in the Caribbean, Mediterranean, North Atlantic Ocean and North Pacific Ocean. In
71 2014, global production was 4,000,000 tons (Cultured Aquatic Species Information Programme
72 2005: http://www.fao.org/fishery/culturedspecies/Ruditapes_philippinarum/en). Manilas were
73 introduced to the US west coast in the late 1930s and are now an important farmed species in
74 Washington State (Smith, Langdon, 1998). Another introduced species that is less broadly
75 farmed in Washington is the softshell clam *Mya arenaria* Linnaeus, 1758, which is an

76 economically critical shellfish species in the northeast US (Glaspie, Seitz, Ogburn, Dungan,
77 Hines, 2018). For Manilas, as many as 100,000 larvae per m² may settle into natural sediment
78 (Tezuka, Kamimura, Hamaguchi, Saito, Iwano, Egashira, Fukuda, Tawaratsumida, Nagamoto,
79 Nakagawa, 2012) but <1% survive to harvestable size (40 mm in length; e.g., Williams, 1980).
80 This very high post-settlement mortality could stem from abiotic factors such as salinity or
81 temperature variation, or biotic factors such as predation and competition for resources
82 (Dethier, Ruesink, Berry, Sprenger, 2012; Hunt, Scheibling, 1997; Williams, 1980).

83 As part of a larger study on sources of mortality to juvenile clams on Washington shorelines,
84 we investigated the vulnerability of juvenile clams to crab predation, and how this is affected by
85 clam size and species. Here we focus on the potential role of shore crabs, *Hemigrapsus nudus*
86 (Dana, 1851) and *H. oregonensis* (Dana, 1851). These small (< 4 cm width) crabs are abundant
87 on shorelines from Alaska to the Gulf of California, inhabiting numerous habitat types (mud to
88 bedrock) but especially soft-sediment shorelines where cobbles or debris give them protection
89 at low tide (Harger, 1972; Kozloff, 1993; Low, 1970). The two species are largely sympatric
90 although *H. oregonensis* tends to prefer somewhat more wave-protected shores (Harger,
91 1972). Unlike other decapods such as cancrid crabs or invasive green crabs (*Carcinus maenas*)
92 that are known consumers of shellfish, Quayle (1988) dismissed *Hemigrapsus* as important
93 predators on shellfish; he noted that these species are commonly found under clusters of
94 oysters but that “they are scavengers and do no harm to oysters” (p. 93). Other authors have
95 considered them to be herbivorous or omnivorous (Knudsen, 1964; Yamada, Boulding, 1998).

96 While *Hemigrapsus* spp. are not usually considered to be significant intertidal predators, we
97 hypothesized that they could contribute to high field mortality of newly settled clam spat and

98 juveniles. We were particularly interested in when clams reach size refuges from these
99 predators. If small crabs that are not excluded by shellfish farm netting can consume seed
100 clams, then seed clam sizes may need to be increased to reduce field mortality.

101 2. Methods

102 2.1 Field data on predator densities

103 Work reported elsewhere (Dethier, Kobelt, Yiu, Wentzel, Ruesink, 2019) at study
104 beaches around Washington State quantified abundances of large (> 5 cm) cancrid crabs, but
105 mesh size of the Fukui traps used was too large (12 mm) to retain smaller predators such as
106 shore crabs. We counted shore crabs in quadrats along 50 m horizontal transects in the mid-
107 shore (+1 m above Mean Lower Low Water (MLLW)), but found that this method also did not
108 effectively quantify these mobile predators; at low tide they tend to cluster under cobbles or
109 debris (e.g. logs, netting) that were not necessarily found along the transect. We thus present
110 data from other studies showing the ranges of abundances of shore crabs on Washington
111 beaches. These data (Dethier, Schoch, 2005) come from monitoring surveys of over 30 sites and
112 up to 15 years. In each case, site-date values are counts of crabs averaged over ten 0.25 m²
113 quadrats along horizontal transects at either MLLW or +1 m MLLW.

114 2.2 Lab experiments with crabs consuming clams

115 Experiments were conducted in indoor sea tables with running seawater (at 10.5-12.3°C) at
116 the Friday Harbor Laboratories (FHL), Washington (48° 32' 45" N 123° 00' 45" W) during 2017.
117 We worked with juvenile clams of two commercially important species: *Ruditapes*
118 *philippinarum* (Manila clams) that were obtained from Taylor Shellfish at 1 or 2 mm shell length

119 or field-collected at larger size; and softshell clams *Mya arenaria* that were collected at various
120 field sites. All clams were kept in sea tables while being fed Shellfish Diet 1800 (Instant Algae®).
121 Shore crabs *Hemigrapsus nudus* and *H. oregonensis* were collected from under intertidal
122 cobbles on the FHL beach. For all individuals used in experiments we measured both carapace
123 width and dactyl length (inner surface) of the larger claw. Yamada and Boulding (1998) show
124 that female crabs have smaller claws; we did not track sex as we assumed that the key
125 parameter in ability to consume clams was claw size regardless of sex. Crabs were fed ulvoid
126 algae if kept in lab for more than several days, but were always starved for 24 hours before
127 experiments. Each individual crab was only used in one experiment.

128 We tested the abilities and preferences of *Hemigrapsus* spp. of different sizes to consume
129 clams of different sizes. Feeding trials were run by placing individual crabs in small (ca.
130 10x10x10 cm) lidded plastic containers with mesh sides to allow water flow. Pilot studies
131 quantifying predation rates with or without sediment in the containers showed no consistent
132 differences, so experiments were run without sediment to improve the consistency of data
133 collected. To determine how large a clam could be consumed by crabs, a single measured
134 (length) clam was placed in a container with a crab. After 24 hours, the clam was recorded as
135 intact or crushed and consumed, and the crab was measured and released. Most experiments
136 were run with small Manila clams, but some parallel trials were run with juvenile *Mya arenaria*.

137 To determine relative predation rates, individual crabs were given 10-20 small measured
138 Manila clams, either all one size (to quantify consumption rates) or of a range of sizes (to
139 quantify preferences). Numbers and sizes consumed were quantified after 24 hours.

140

141 **3. Results**

142 3.1 Predator densities at field sites

143 In quadrats at eight sand-pebble beach sites (Dethier, Kobelt, Yiu, Wentzel, Ruesink,
144 2019), *Hemigrapsus* spp. were sparse (overall average of less than one per 0.1 m² quadrat) and
145 tended to be very small (average size of 5 mm) individuals that could hide effectively along the
146 transect in clam holes or under pebbles. More and larger (up to 3 cm) individuals were seen
147 when cobbles or debris were overturned at almost any intertidal elevation. Other beaches in
148 the state (see Methods) had densities of *H. oregonensis* ranging from 4-40/m² in the mid shore
149 (at ~+1 m, N = 82 site-date combinations) and 0.4 to 20 in the low shore (MLLW, N = 186 site-
150 dates). Highest densities were found where cobbles provided shelter on sand or gravel beaches.
151 *H. nudus* is more common higher on the shore than at either of these transect elevations
152 (Dethier, pers. obs.) and tends to be more abundant at higher-energy sites (Harger, 1972;
153 Kozloff, 1993). Yamada and Boulding (1996) reported densities of *Hemigrapsus* spp. up to
154 300/m² on optimal gravel-cobble beaches. Low (1970) found that densities of both species
155 were very low (ca. 0.1/m²) on bedrock shores and on plain sand and mud beaches with little 3D
156 structure, but as high as 500/m² on beaches with loose rocks on the surface. The amount of
157 cover, especially from cobbles, was the best predictor of abundance of both crab species.
158 Diverse vertebrates prey on them, including raccoons, gulls, a variety of fishes, and many diving
159 ducks, so significant populations are only found where they have refuges during both low and
160 high tides (Low 1970).

161

162

163 3.2 Lab experiments with crabs

164 Our feeding observations showed minimal differences in predation rates or preferences
165 between *Hemigrapsus nudus* and *H. oregonensis*, so we pooled results from these two taxa.
166 Both crab species ranged in sizes of carapace width from approx. 5 to 25 mm and dactyl length
167 from 0.5 to 7.7 mm. The tight correlation ($r^2 = 0.88$, $N = 66$) between carapace and dactyl sizes
168 suggests that at least in our sampled mixed-gender and mixed-species population, there was
169 not a substantial difference among sexes or species in relative claw sizes (Suppl. Fig. 1). Here we
170 report results by dactyl length, assumed as the more relevant parameter for ability to break a
171 clam shell.

172 Both shore crab species showed high individual variance in behavior in terms of how many
173 small (2 mm) clams they ate in a given 24 hour period. Crabs of every size tested ate from 0 to
174 10 (all) clams per day, with no discernable pattern to these differences ($N = 126$ trials; Suppl.
175 Fig. 2). We thus focus our analyses on how big a clam *could* be eaten by a particular size crab,
176 and on relative rates of predation as crab and clam sizes were varied. We found that even the
177 smallest *Hemigrapsus* tested (~1 cm carapace width, with ~1 mm dactyls) could crush 2 mm
178 Manila clams. When offered the thinner-shelled *Mya* clams, small crabs could crush a much
179 larger individual compared to Manila clams (Figure 1); a 12 mm (carapace width) crab with a 2.5
180 mm dactyl could crush a *Mya* almost its size (11 mm shell length). Larger Manila individuals (ca.
181 10 mm) could only be crushed by the larger (~25 mm carapace) shore crabs.

182 Because we had few juvenile *Mya* available for experiments, predation rate experiments
183 with shore crabs were run only with Manila clams. Small crabs (dactyl < 4 mm) readily ate small
184 (<5 mm) clams, sometimes consuming all 10 offered within 24 hours (Fig. 2). The data from

185 medium-sized crabs (dactyl 4-6 mm; carapace 15-20 mm) show a pattern of the crabs eating
186 fewer large clams than medium or small ones in the same period of time. Large crabs readily
187 ate all sizes of clams including the larger individuals (Fig. 2).

188 When medium to large (mean dactyl length 6.8 mm: carapace width ~20mm) shore
189 crabs were offered a choice of 5 individuals of each of the 3 size classes of clams, they showed
190 no preferential consumption for any size (Suppl. Fig. 3), eating ca. half of all the clams
191 regardless of size.

192 **4. Discussion**

193 Crabs inhabiting the intertidal zone on Washington state shorelines (e.g., *Hemigrapsus*
194 spp.) or foraging there at high tide (cancerids; also majids, *Telmessus*: pers. obs.) likely constitute
195 significant sources of mortality for clams, as has been shown in numerous other systems (see
196 Introduction, also Boulding, 1984). Unfortunately, it is difficult to precisely quantify abundances
197 of such mobile predators. Other investigators have tried to quantify densities via snorkeling at
198 high tide (Grosholz, Ruiz, Dean, Shirley, Maron, Connors, 2000) or benthic trawling (Glaspie,
199 Seitz, Ogburn, Dungan, Hines, 2018). Crab abundances can be very patchy, e.g. due to local
200 hypoxia (Altieri, 2008), or the presence of refuges from their predators, e.g. from gulls (Beal,
201 2006). The *Hemigrapsus* shore crabs we worked with are broadly present on Washington
202 shorelines except at the most wave-exposed beaches, and can be present in hundreds per m² in
203 areas where cobbles or debris provide low-tide refuges (Low, 1970). Thus, their predatory
204 impact on juvenile clams could be substantial.

205 We found that in the lab, even very small *Hemigrapsus* spp. can crush and consume not
206 only juvenile softshell clams (*Mya*) but hardshell Manilas. Clams <5 mm were consumed by
207 even the smallest shore crabs tested (carapace width 5-10 mm). Adult shore crabs (carapace
208 >20 mm) readily ate 8 mm clams, even hardshell Manilas. Some crabs tended to eat fewer large
209 clams than smaller ones in the same period of time; this could result either from longer
210 handling times (not measured), or satiation when eating the larger prey. Crabs were very
211 individualistic in terms of feeding rates; under identical conditions (starved, then offered clams
212 for 24 hours in lab), some ate nothing while others consumed all the clams available.

213 As in other studies, consumption by crabs clearly varies not only with clam size but with
214 shell morphology (see also Boulding 1984), with the thinner-shelled *Mya* more vulnerable to
215 crushing. When clam shells are weakened by acidified porewater conditions, (Glaspie,
216 Longmire, Seitz, 2017; Green, Waldbusser, Reilly, Emerson, O'Donnell, 2009), this vulnerability
217 to shell-crushing predators increases. Some experiments have also shown that crab feeding
218 behavior can be directly affected by pH (Glaspie, Longmire, Seitz, 2017), complicating our ability
219 to predict the effects of this increasingly relevant abiotic stressor.

220 Our data thus contribute to the literature on the ability of clams to reach size refuges
221 from their predators. In our system, Manila clams, despite their hard shells, do not reach a size
222 refuge from the very common intertidal shore crabs until they are >12 mm. Although we did
223 not run experiments with adult clams, it is likely that there is no size refuge for Manilas from
224 the cancrid crabs that were present at most of our sites (Boulding, 1984; Boulding, LaBarbera,
225 1986; Dethier, Kobelt, Yiu, Wentzel, Ruesink, 2019; Yamada, Boulding, 1996; 1998). Small (20
226 mm) *Cancer oregonensis*, for example, can consume oysters over 30 mm length (Yamada,

227 Metcalf, Baldwin, 1993). Survival of farmed Manila clams to harvestable size thus must rely on
228 netting to exclude large crabs, except in the few places where crabs are naturally rare.
229 Eliminating predation on seed clams by shore crabs is likely impossible using netting, since
230 mesh size would have to be <1 cm to keep out the small crabs that are capable of consuming 2
231 mm clam seed. A viable alternative may be raising seed in hatcheries until they at least 10-15
232 mm, achieving a size refuge from shore crabs. This relatively large 'safe' size may be adequate
233 for various thick-shelled clams (Walton, MacKinnon, Rodriguez, Proctor, Ruiz, 2002) but may
234 need to be larger (>20 mm) when dense blue crabs are present (Peterson, Summerson, Huber,
235 1995). 'Safe' seed size for softshell clams is hard to calculate because they are so readily
236 crushed, or even peeled through their siphonal gape (Boulding, 1984). For shore crabs, farming
237 on beaches lacking the cobble or debris that provide crab habitat may help reduce juvenile clam
238 mortality.

239 Predation by crabs thus is a multifaceted problem for the valuable shellfish aquaculture
240 industry, especially when the crabs are diverse in their sizes and behaviors, as is true on the tide
241 flats in Washington. The continued invasion of the green crab *Carcinus maenas* into the inside
242 waters of Washington (Grason, McDonald, Adams, Litle, Apple, Pleus, 2018; Yamada, Thomson,
243 Gillespie, Norgard, 2017) will further exacerbate the challenge of clam losses to crab predators.
244

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256

257 **6. References**

- 258 Altieri, A.H., 2008. Dead zones enhance key fisheries species by providing predation refuge.
259 Ecol. 89, 2808-2818.
- 260 Arnold, W., 1984. The effects of prey size, predator size, and sediment composition on the rate
261 of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam,
262 *Mercenaria mercenaria* (Linne). J. Exp. Mar. Biol. Ecol. 80, 207-219.
- 263 Beal, B.F., 2006. Relative importance of predation and intraspecific competition in regulating
264 growth and survival of juveniles of the soft-shell clam, *Mya arenaria* L., at several spatial
265 scales. J. Exp. Mar. Biol. Ecol. 336, 1-17.
- 266 Beal, B.F., Vencile, K., 2001. Short-term effects of commercial clam (*Mya arenaria* L.) and worm
267 (*Glycera dibranchiata* Ehlers) harvesting on survival and growth of juveniles of the soft-
268 shell clam. J. Shellfish Res. 20, 1145-1157.
- 269 Becker, P., Barringer, C., Marelli, D., 2008. Thirty years of sea ranching Manila clams (*Venerupis*
270 *philippinarum*): successful techniques and lessons learned. Reviews in Fisheries Science.
271 16, 44-50.
- 272 Bendell, L.I., 2015. Favored use of anti-predator netting (APN) applied for the farming of clams
273 leads to little benefits to industry while increasing nearshore impacts and plastics
274 pollution. Mar. Pollut. Bull. 91, 22-28.
- 275 Beukema, J.J., Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in
276 the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries.
277 Mar. Ecol. Prog. Ser. 287, 149-167.
- 278 Beukema, J.J., Dekker, R., 2014. Variability in predator abundance links winter temperatures
279 and bivalve recruitment: correlative evidence from long-term data in a tidal flat. Mar.
280 Ecol. Prog. Ser. 513, 1-15.

281 Beukema, J.J., Dekker, R., Philippart, C.J.M., 2010. Long-term variability in bivalve recruitment,
 282 mortality, and growth and their contribution to fluctuations in food stocks of shellfish-
 283 eating birds. *Mar. Ecol. Prog. Ser.* 414, 117-130.

284 Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing
 285 vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.* 76, 201-223.

286 Boulding, E.G., LaBarbera, M., 1986. Fatigue damage: repeated loading enables crabs to open
 287 larger bivalves. *Biol. Bull.* 171, 538-547.

288 Dethier, M.N., Schoch, G.C., 2005. The consequences of scale: assessing the distribution of
 289 benthic populations in a complex estuarine fjord. *Est. Coastal Shelf Sci.* 62, 253-270.

290 Dethier, M.N., Ruesink, J.L., Berry, H., Sprenger, A.G., 2012. Decoupling of recruitment from
 291 adult clam assemblages along an estuarine shoreline. *J. Exp. Mar. Biol. Ecol.* 422, 48-54.

292 Dethier, M.N., Kobelt, J.N., Yiu, D., Wentzel, L., Ruesink, J.L., 2019. Context-dependence of
 293 abiotic and biotic factors influencing performance of juvenile clams. *Est. Coastal Shelf*
 294 *Sci.* 219, 201-209.

295 Glaspie, C., Longmire, K., Seitz, R.D., 2017. Acidification alters predator-prey interactions of blue
 296 crab *Callinectes sapidus* and soft-shell clam *Mya arenaria*. *J. Exp. Mar. Biol. Ecol.* 489,
 297 58-65.

298 Glaspie, C., Seitz, R.D., Ogburn, M., Dungan, C., Hines, A., 2018. Impacts of habitat, predators,
 299 recruitment, and disease on soft-shell clams *Mya arenaria* and stout razor clams *Tagelus*
 300 *plebeius* in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 603, 117-133.

301 Grason, E., McDonald, P.S., Adams, J., Litle, K., Apple, J.K., Pleus, A., 2018. Citizen science
 302 program detects range expansion of the globally invasive European green crab in
 303 Washington State (USA). *Management of Biological Invasions.* 9, 39-47.

304 Green, M.A., Waldbusser, G.G., Reilly, S.L., Emerson, K., O'Donnell, S., 2009. Death by
 305 dissolution: sediment saturation state as a mortality factor for juvenile bivalves. *Limnol.*
 306 *Oceanogr.* 54, 1037-1047.

307 Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L., Connors, P.G., 2000. The
 308 impacts of a nonindigenous marine predator in a California bay. *Ecol.* 81, 1206-1224.

309 Harger, J.R., 1972. Competitive coexistence among intertidal invertebrates. *Amer. Sci.* 60, 600-
 310 607.

311 Higgins, C., Stephenson, K., Brown, B., 2010. Nutrient bioassimilation capacity of aquacultured
 312 oysters: quantification of an ecosystem service. *Environmental Quality.* 40, 271-277.

313 Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of
 314 benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 155, 269-301.

315 Hunt, H.L., Mullineaux, L.S., 2002. The roles of predation and postlarval transport in recruitment
 316 of the soft shell clam (*Mya arenaria*). *Limnol. Oceanogr.* 47, 151-164.

317 Knudsen, J.W., 1964. Observations of the reproductive cycles and ecology of the common
 318 Brachyura and crablike Anomura of Puget Sound, Washington. *Pac. Sci.* 18, 3-33.

319 Kozloff, E.N., 1993. *Seashore Life of the Northern Pacific Coast.* University of Washington Press,
 320 Seattle.

321 Liu, D., Wang, F., Lu, Y., Hu, N., Su, X., Liu, J., Zhu, B., 2019. Behavioral mechanisms of swimming
 322 crab (*Portunus trituberculatus*) preying on Manila clams (*Ruditapes philippinarum*):
 323 effects of substrate and competition. *Mar. Biol.* 166.

324 Low, C.J., 1970. Factors affecting the distribution and abundance of two species of beach crab,
325 *Hemigrapsus oregonensis* and *Hemigrapsus nudus*, Zoology. University of British
326 Columbia, Vancouver, B.C.

327 Munroe, D., McKinley, R.S., 2007. Commercial Manila clam (*Tapes philippinarum*) culture in
328 British Columbia, Canada: the effects of predator netting on intertidal sediment
329 characteristics. Est. Coastal Shelf Sci. 72, 319-328.

330 Munroe, D., Kraeuter, J., Beal, B.F., Chew, K.K., Luckenbach, M., Peterson, C.P., 2015. Clam
331 predator protection is effective and necessary for food production. Mar. Pollut. Bull.
332 100, 47-52.

333 Myers, R., Baum, J., Shepherd, T., Powers, S.P., Peterson, C., 2007. Cascading effects of the loss
334 of apex predatory sharks from a coastal ocean. Science. 315, 1846-1850.

335 Olafsson, E.B., 1989. Contrasting influences of suspension-feeding and deposit-feeding
336 populations of *Macoma balthica* on infaunal recruitment. Mar. Ecol. Prog. Ser. 55, 171-
337 179.

338 Peterson, C., Summerson, H., Huber, J., 1995. Replenishment of hard clam stocks using hatchery
339 seed: combined importance of bottom type, seed size, planting season, and density. J.
340 Shellfish Res. 14, 293-300.

341 Peterson, C., Grabowski, J., Powers, S.P., 2003. Estimated enhancement of fish production
342 resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser.
343 264, 249-264.

344 Quayle, D.B., 1988. Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries and
345 Aquatic Sciences. 218, 1-241.

346 Ruesink, J.L., Freshley, N., Herrold, S., Trimble, A.C., Patten, K., 2014. Influence of substratum on
347 non-native clam recruitment in Willapa Bay, Washington, USA. J. Exp. Mar. Biol. Ecol.
348 459, 23-30.

349 Saurel, C., Ferreira, J., Cheney, D.P., Suhrbier, A.D., Dewey, B., Davis, J., Cordell, J.R., 2014.
350 Ecosystem goods and services from Manila clam culture in Puget Sound: a modelling
351 analysis. Aquaculture Environment Interactions. 5, 255-270.

352 Smith, M., Langdon, C., 1998. Manila clam aquaculture on shrimp-infested mudflats. J. Shellfish
353 Res. 17, 223-229.

354 Tezuka, N., Kamimura, S., Hamaguchi, M., Saito, H., Iwano, H., Egashira, J., Fukuda, Y.,
355 Tawaratsumida, T., Nagamoto, A., Nakagawa, K., 2012. Settlement, mortality and
356 growth of the asari clam (*Ruditapes philippinarum*) for a collapsed population on a tidal
357 flat in Nakatsu, Japan. J. Exp. Mar. Biol. Ecol. 439, 108-112.

358 Walton, W.C., MacKinnon, C., Rodriguez, L.F., Proctor, C., Ruiz, G.M., 2002. Effect of an invasive
359 crab upon a marine fishery: green crab, *Carcinus maenas*, predation upon a venerid
360 clam, *Katelysia scalarina*, in Tasmania (Australia). J. Exp. Mar. Biol. Ecol. 272, 171-189.

361 Whitton, T., Jenkins, S., Richardson, C., Hiddink, J., 2012. Aggregated prey and predation rates:
362 juvenile shore crabs (*Carcinus maenas*) foraging on post-larval cockles (*Cerastoderma*
363 *edule*). J. Exp. Mar. Biol. Ecol. 432, 29-36.

364 Williams, J.G., 1980. Growth and survival in newly settled spat of the Manila clam, *Tapes*
365 *japonica*. Fish. Bull. 77, 891-900.

366 Yamada, S.B., Boulding, E.G., 1996. The role of highly mobile crab predators in the intertidal
367 zonation of their gastropod prey. J. Exp. Mar. Biol. Ecol. 204, 59-83.

368 Yamada, S.B., Boulding, E.G., 1998. Claw morphology, prey size selection and foraging efficiency
369 in generalist and specialist shell-breaking crabs. *J. Exp. Mar. Biol. Ecol.* 220, 191-211.
370 Yamada, S.B., Metcalf, H., Baldwin, B.C., 1993. Predation by the crab, *Cancer oregonensis* Dana,
371 inside oyster trays. *J. Shellfish Res.* 12, 89-92.
372 Yamada, S.B., Thomson, R.E., Gillespie, G.E., Norgard, T.C., 2017. Lifting barriers to range
373 expansion: the European green crab *Carcinus maenas* (Linnaeus, 1758) enters the Salish
374 Sea. *J. Shellfish Res.* 36, 1-8.
375

FIGURE CAPTIONS

Figure 1. Relative sizes of crabs (*Hemigrapsus* spp.) and clams in trials where crabs were able to consume the clams offered. N = 33 trials with Manila clams, N = 20 trials with *Mya*. R² values of linear regression for each clam species: *Mya* 0.20, Manila 0.46.

Figure 2. Predation rates by crabs on Manila clams of varying sizes. Crab Dactyl sizes: Small \leq 4 mm; Medium = 4.1 to 6.0; Large = 6.1 to 8.0 mm. Bars are mean and one s.e. of N trials; replicate N's per bar (left to right) = 130, 0, 0, 41, 12, 8, 19, 14, 18. No trials were run (ND = no data) attempting to feed medium or large clam categories to small crabs.

Figure 1.

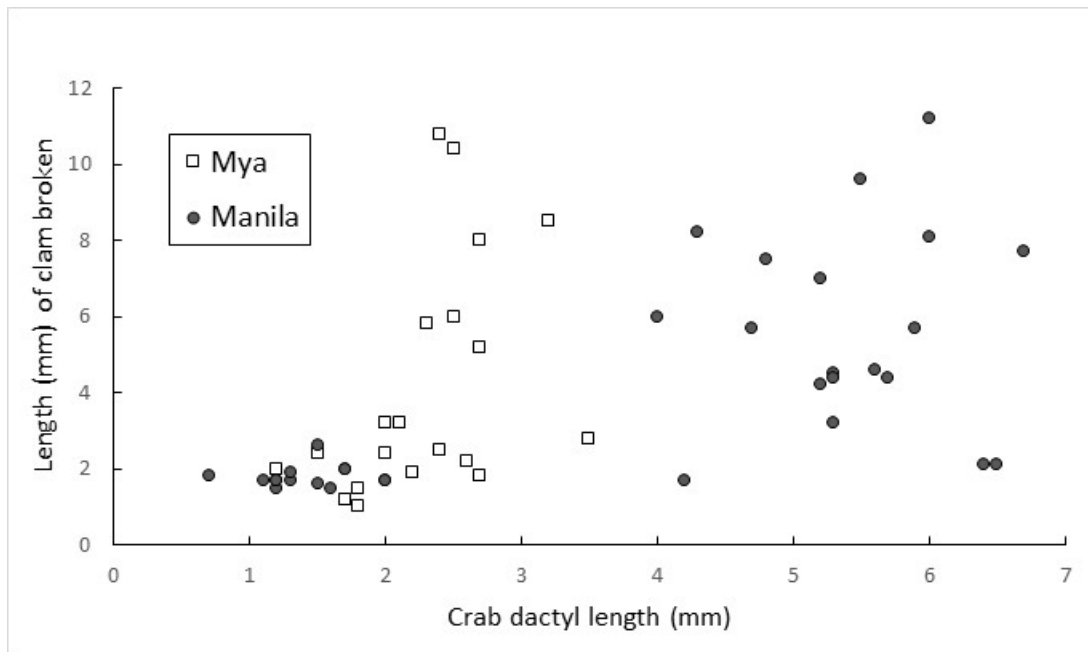
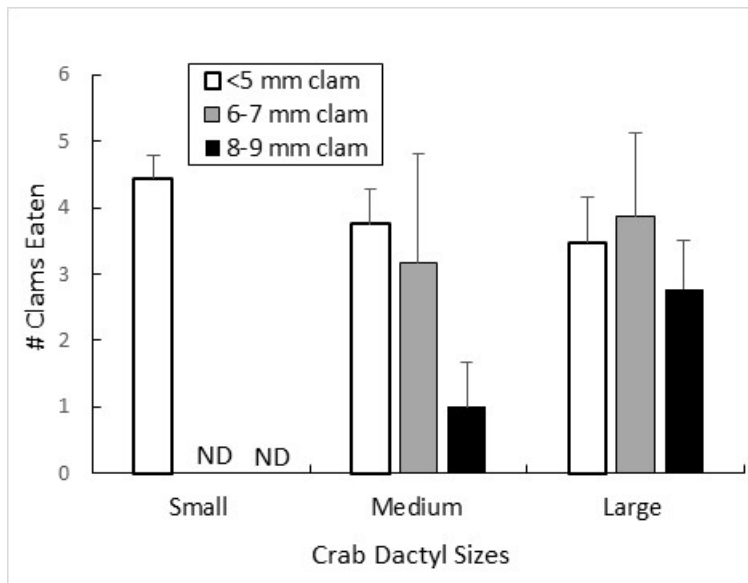
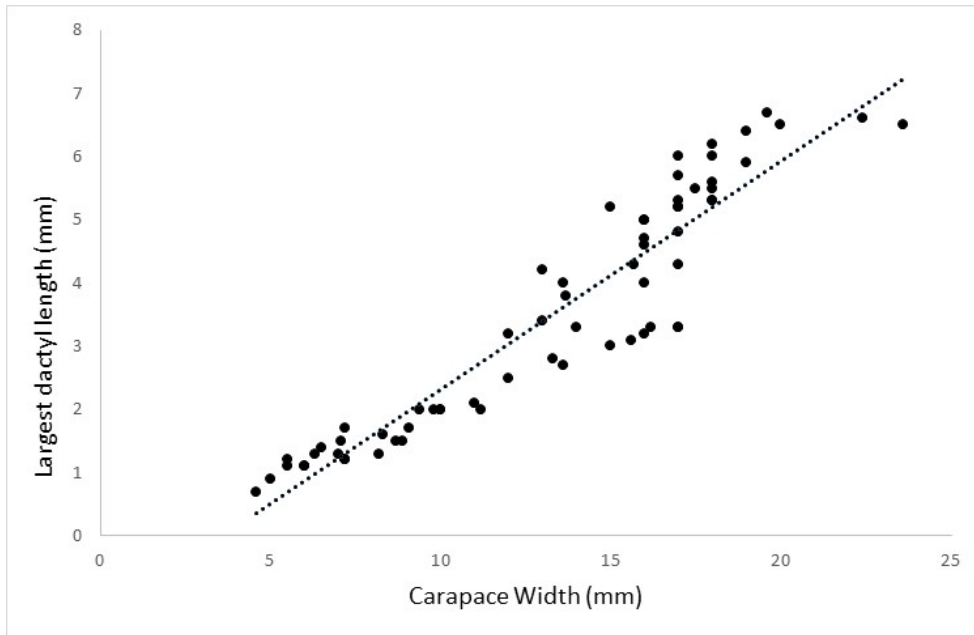


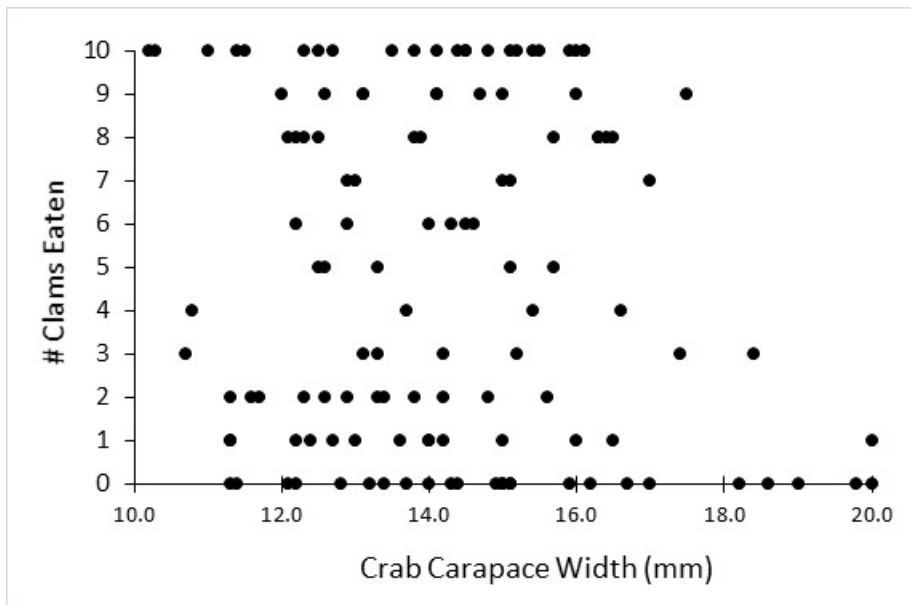
Figure 2.



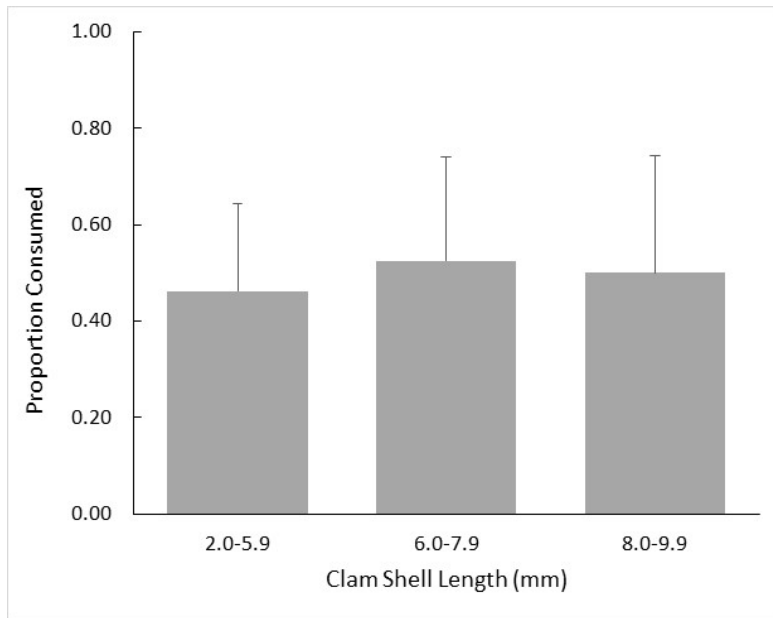
Dethier et al. SUPPLEMENTAL FIGURES



Supplemental Figure 1. Correlation between carapace size and dactyl length for *Hemigrapsus oregonensis*. N = 66 crabs, $r^2 = 0.88$



Supplemental Figure 2. Numbers of small (2 mm) clams eaten out of 10 offered to different sizes of *Hemigrapsus* spp. over 24 hours. N = 126 trials, each point is a separate individual crab.



Supplemental Figure 3. Mean (one s.d.) proportion of clams consumed by shore crabs when offered a choice of 5 clams of each size class. N=16 trials (separate crabs).