Species–specific crab predation on the hydrozoan clinging jellyfish *Gonionemus* sp. (Cnidaria, Hydrozoa), subsequent crab mortality, and possible ecological consequences

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Here we report a unique trophic interaction between the cryptogenic and sometimes highly toxic hydrozoan clinging jellyfish *Gonionemus* sp. and the spider crab *Libinia dubia*. We assessed species – specific predation on the *Gonionemus* medusae by crabs found in eelgrass meadows in Massachusetts, USA. The native spider crab species *L. dubia* consumed *Gonionemus* medusae, often enthusiastically, but the invasive green crab *Carcinus maenus* avoided consumption in all trials. One out of two blue crabs (*Callinectes sapidus*) also consumed *Gonionemus*, but this species was too rare in our study system to evaluate further. *Libinia* crabs could consume up to 30 jellyfish, which was the maximum jellyfish density treatment in our experiments, over a 24-hour period. *Gonionemus* consumption was associated with *Libinia* mortality. Spider crab mortality increased with *Gonionemus* consumption, and 100% of spider crabs tested died within 24 hours of consuming jellyfish in our maximum jellyfish density containers. As the numbers of *Gonionemus* medusae used in our experiments likely underestimate the number of medusae that could be encountered by spider crabs over a 24-hour period in the field, we expect that *Gonionemus* may be having a negative effect on natural *Libinia* populations. Furthermore, given that *Libinia* overlaps in habitat and resource use with *Carcinus*, which avoids *Gonionemus* consumption, *Carcinus* populations could be indirectly benefiting from this unusual crab – jellyfish trophic relationship.

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17 **Abstract**

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20 assessed species – specific predation on the *Gonionemus* medusae by crabs found in eelgrass

21 meadows in Massachusetts, USA. The native spider crab species *L. dubia* consumed

22 *Gonionemus* medusae, often enthusiastically, but the invasive green crab *Carcinus maenus*

23 avoided consumption in all trials. One out of two blue crabs (*Callinectes sapidus*) also consumed

24 *Gonionemus*, but this species was too rare in our study system to evaluate further. *Libinia* crabs

25 could consume up to 30 jellyfish, which was the maximum jellyfish density treatment in our

26 experiments, over a 24-hour period. *Gonionemus* consumption was associated with *Libinia*

27 mortality. Spider crab mortality increased with *Gonionemus* consumption, and 100% of spider

28 crabs tested died within 24 hours of consuming jellyfish in our maximum jellyfish density

29 containers. As the numbers of *Gonionemus* medusae used in our experiments likely

30 underestimate the number of medusae that could be encountered by spider crabs over a 24-hour

31 period in the field, we expect that *Gonionemus* may be having a negative effect on natural

32 *Libinia* populations. Furthermore, given that *Libinia* overlaps in habitat and resource use with

33 *Carcinus*, which avoids *Gonionemus* consumption, *Carcinus* populations could be indirectly

34 benefiting from this unusual crab – jellyfish trophic relationship.

36 **Introduction**

37   Gelatinous zooplankton are important and often conspicuous members of many marine

38 communities, but blooms are often problematic as they may interfere with fisheries and

39 aquaculture, clog power plant intake pipes, and present sting risks to humans (Purcell, Uye & Lo

40 2007; Graham & Bayha, 2010). Anthropogenic activities have contributed to the spread of

41 jellyfish outside their native range (Purcell, Uye & Lo 2007; Graham & Bayha, 2010), where

42 they can also have negative consequences to the ecosystem (Manzari et al. 2015). A likely

43 potential impact of invasive jellyfish is through alteration of native food webs, often thought to

44 manifest through predation and competition (Pauly et al. 2009; Graham & Bayha 2010).

45 Jellyfish are less often thought of as prey (Arai & Jacobs 1980; Arai 2005; Ates 2017) and are

46 sometimes assumed to be trophic dead-ends (Sommer et al. 2002; Lynam et al. 2006; Yamamato

47 et al. 2008; Condon et al. 2011), but this paradigm is changing (Cardona et al. 2012; Diaz-Briz et

48 al. 2017; McInnis et al. 2017).

49   "Gelata" is a general term that refers to phylogenetically diverse gelatinous zooplankton,

50 including members of the phylum Cnidaria belonging to the Scyphozoa, Cubozoa, and Hydrozoa

51 (collectively known as the Medusozoa), the phylum Ctenophora (ctenophores), and the phylum

52 Chordata (salps, doliolids, and pyrosomes) (Haddock 2004). Of these groups, most research has

53 focused on a relatively small number of conspicuous scyphozoans (Purcell, Uye & Lo 2007).

54 Despite the relative lack of attention, the Hydrozoa is by far the most speciose and diverse group

55 with around 842 valid medusa (i.e., jellyfish) - producing species (Bouillon & Boero, 2000a).

56 The Hydrozoa is phylogenetically well-supported (Collins et al. 2006; Kayal et al. 2013; Zapata

57 et al. 2015) and is sometimes referred to as a superclass (Bouillon & Boero 2000b; Xu et al.

58 2014).

59   The clinging jellyfish *Gonionemus* sp. (Cnidaria, Hydrozoa, Limnomedusae; Fig. 1) is an

60   increasingly conspicuous member of Northwest Atlantic eelgrass communities, and populations

61   may be comprised of native and invasive lineages (Govindarajan et al. 2017). Like many

62   cryptogenic species, insufficient taxonomy complicates our understanding of its biogeography

63   (Govindarajan et al. 2017). Clinging jellyfish described as *Gonionemus murbachii* Mayer, 1901

64   (but later synonymized with *Gonionemus vertens* Agassiz, 1862) were first noted in

65   Massachusetts and Connecticut in 1894, but nearly disappeared in the 1930s when its eelgrass

66   habitat was decimated by a wasting disease (Govindarajan & Carman 2016). In recent years,

67   clinging jellyfish have made a comeback in these areas (Govindarajan & Carman 2016).

68   *Gonionemus* lineages vary in their toxicity (Naumov 1960), and some Sea of Japan

69   populations are associated with stings that can cause severe pain, respiratory difficulty, paralysis,

70   and other neurological symptoms, while populations in other parts of the world are harmless to

71   humans (Naumov 1960; Otsuru et al. 1974; Yakovlev & Vaskovsky 1993). Nineteenth and early

72   20th century Northwest Atlantic *G. murbachii* populations were not associated with stings.

73   However, painful stings similar to those associated with Sea of Japan populations began

74   occurring in Massachusetts, USA, in 1990, suggesting an invasion of a new and highly toxic

75   lineage (Govindarajan & Carman 2016). Since then, clinging jellyfish blooms have been

76   occurring regularly in Massachusetts, and the jellyfish appear to be expanding their range both

77   inside and outside of Massachusetts (Govindarajan & Carman 2016; Gaynor et al. 2016;

78   Govindarajan et al. 2017).

79   Govindarajan et al. (2017) suggested that based on mitochondrial COI sequences and

80   subtle morphological features that the Northwest Atlantic and Pacific forms (including highly

81   toxic populations) were similar to each other, and different from *G. vertens* from the Northeast

82 Pacific. It seems likely that the Northwest Atlantic/Northwest Pacific form is *G. murbachii*

83 Mayer, 1901. However, a definitive link between past and contemporary populations is still

84 lacking (Govindarajan & Carman 2016; Govindarajan et al. 2017). Thus, we refer here to this

85 form, which is our focal taxon in this study, as *Gonionemus* sp. (or simply "*Gonionemus*").

86   Clinging jellyfish are found primarily in eelgrass meadows, where they "cling" to

87 eelgrass blades using the adhesive structures on their tentacles (Naumov 1960; Fig. 1). Adult

88 medusae typically range in size from 1 – 2.5 cm (Govindarajan et al. 2017) and feed on a variety

89 of small zooplankton such as amphipods and isopods (Yakovlev & Vaskovsky 1993). They are

90 not known to have any predators, although molluscs may feed on the minute polyp life cycle

91 stage (Yakovlev & Vaskovsky 1993). The highly toxic nature of some *Gonionemus* lineages

92 might act as a deterrent to potential predators, but it is also possible that predation on clinging

93 jellyfish has been overlooked.

94   Northwest Atlantic eelgrass meadows are also home to predatory native and invasive crab

95 species (Able et al. 2002; Garbary et al. 2014; Neckles 2015; Matheson et al. 2016). We

96 investigated the possibility that crabs can prey on *Gonionemus*, and the potential impact of

97 *Gonionemus* prey on crab predators. The Massachusetts, USA eelgrass beds where *Gonionemus*

98 medusae are found are home to native spider crabs (*Libinia dubia* Milne Edwards, 1834) and,

99 occasionally, blue crabs (*Callinectes sapidus* Rathbun, 1896), and the invasive green crab

100 (*Carcinus maenus* Linnaeus, 1758). Green crabs in particular are highly destructive to eelgrass

101 ecosystems as they uproot eelgrass shoots while foraging and may graze directly on the eelgrass

102 shoots (Malyshev & Quijón, 2011; Garbary et al. 2014). All three crab species feed on a wide

103 variety of invertebrates (Aldrich 1974; Grosholz & Ruiz 1996; Harding 2003; Baeta et al. 2006).

104 While predation on jellyfish is often not considered (Arai 2005), *Carcinus maenus* (Lauckner

105   1980)*, Callinectes sapidus* (Farr 1980), and *Libinia dubia* (Phillips, Burke & Keener 1969) have

106   been reported to feed on scyphozoan medusae.

107   Our results demonstrated a new trophic interaction between crabs and a highly toxic

108   hydrozoan jellyfish with consequences for invasive species impacts in ecologically sensitive

109   eelgrass meadows. We found that the native spider and blue crabs consumed *Gonionemus*, but

110   that the invasive green crabs did not. We further found that *Gonionemus* ingestion resulted in

111   crab death when large numbers of jellyfish were consumed; however, blue crabs were too rare at

112   our site to be assessed at higher jellyfish densities. Thus, we hypothesize that *Gonionemus* may

113   potentially impact native ecosystems via differential predation by a native species (spider crabs)

114   that may lead to a decline of that species, while avoidance of *Gonionemus* by a notoriously

115   destructive invasive species (green crabs) may facilitate its dominance.

116   **Material & Methods**

117   *Study area*

118   The experimental animals in our study were obtained from Farm Pond (41.44756, -

119   70.55694) and Lagoon Pond (41.44816, -70.59022), which are semi-enclosed coastal ponds that

120   harbor eelgrass beds on the northeastern side of the island of Martha's Vineyard in

121   Massachusetts, USA (Fig. 2). Lagoon Pond covers 544 acres with a mean depth of 3 m, and

122   Farm Pond covers 33 acres, is tidally restricted, and has a mean depth of 1.5 m. Both ponds have

123   a tidal range of < 1 m. The ponds are located in the town of Oak Bluffs, separated by about 4 km

124   of land, and are the sites of ongoing research on invasive species (Carman, Grunden & Ewart

125   2014; Carman et al. 2016; Colarusso et al. 2016). *Gonionemus* was first observed in Farm Pond

126   in 2007 (Govindarajan & Carman, 2016) and has not been observed in Lagoon Pond. Permission

to collect animals at our field sight was obtained through D. Grunden (Oak Bluffs, Massachusetts

128 Shellfish Constable; in accordance with Massachusetts General Laws Chapter 130 Section 98).

129 *Identification of predatory crab species*

130 We conducted 4 trials during June and July 2016 to identify which, if any, local crab

131 species prey on *Gonionemus*. Crabs were trapped in Farm and Lagoon Ponds the week prior to

132 each experiment using crab traps. The crabs were then kept in the cages for one week in a

133 relatively barren area of Farm Pond that lacks *Gonionemus* habitat.

134 At the start of each experiment, individual crabs were transported in tubs of seawater to

135 the laboratory at the Town of Oak Bluffs Shellfish Department in Massachusetts (Fig. 2). Crab

136 size (carapace width) was recorded. At the same time as the crabs were removed from the crab

137 traps, *Gonionemus* specimens were also collected from the eelgrass meadow in Farm Pond using

138 hand held nets while wading and snorkeling, and transported along with the crabs to the

139 laboratory.

140 Experiments were conducted in closed tubs (42 cm x 33 cm x 17 cm) of seawater. Five

141 adult jellyfish (15-20 mm bell width) were placed in a tub with a single crab. Between 2 and 6

142 replicate tubs per crab species were set up on each sampling date, depending on the number of

143 crabs that were caught (Table 1). Additionally, control tubs consisting of crabs only (with no

144 jellyfish) and jellyfish only (with no crabs) were also set up for each experiment (Table 1). The

145 number of jellyfish remaining and crab condition (dead or alive) were recorded at three time

146 points (5 minutes, 3 hours, and 24 hours). We verified our assumption that jellyfish

147 disappearances were due to predation by the crabs by: 1) direct observation of crabs consuming

148 jellyfish, which we recorded by taking representative photographs and video; and 2) running

149 jellyfish-only controls with each trial to assess jellyfish mortality independent of the crabs.

150   *Impact of jellyfish consumption on spider crabs*

151   As a follow-up to our first set of trials which documented predation on jellyfish by

152   *Libinia* (as well as the relatively rare *Callinectes sapidus*) and a possible association between

153   jellyfish consumption and mortality, we assessed *Libinia* predation at higher jellyfish densities.

154   We ran similar predation experiments on two dates in July 2017 at four additional jellyfish

155   densities: 10, 15, 20, and 30 jellyfish per crab. The experiments were carried out in the

156   laboratory at the Martha's Vineyard Shellfish Group, Inc.'s John T. Hughes Hatchery and

157   Research Facility (leased from the Massachusetts Division of Marine Fisheries) in Oak Bluffs

158   (Fig. 2). As with the 2016 experiments, crabs were trapped during the week before the

159   experiment and held in Farm Pond without supplemental food. Also as in the 2016 trials,

160   jellyfish were obtained from Farm Pond immediately prior to the start of the experiments. Crabs

161   were placed in tubs with a given number of jellyfish (10, 15, 20, or 30 adult jellyfish); with 6

162   replicates per jellyfish density. Control tubs with crabs only and jellyfish only were also set up

163   on each experiment date. The number of jellyfish remaining and crab condition (dead or alive)

164   after 15 minutes and 24 hours were recorded.

165   To confirm that the *Gonionemus* densities we used in our predation trials were realistic

166   compared to what the crabs encounter in nature, jellyfish densities were recorded on three dates

167   in 2017 by counting the number of jellyfish in representative 3 m x 3 m areas in the part of Farm

168   Pond where the jellyfish are found. The jellyfish were collected by net scoops and counted. This

169   method likely underestimates the true *Gonionemus* abundance, and so is a conservative

170   depiction.

171   **Results**

172   *Identification of predatory crab species*

173   Several spider crabs (*Libinia dubia*) and green crabs (*Carcinus maenas*) were collected in

174   our crab traps, as well as 2 blue crabs (*Callinectes sapidus*). Mean carapace width was 62 mm ±

175   9 S.D. in *Libinia* (n = 30), 62 mm ± 6 S.D. in *Carcinus* (n = 30), and 63 mm and 78 mm in the

176   two *Callinectes* individuals.

177   Twenty-one out of 22 spider crabs and one out of the 2 blue crabs obtained consumed

178   *Gonionemus* (Fig. 3, 4A), but none of the green crabs did. We observed *Libinia* predation on the

179   jellyfish almost immediately at the start of our trials (Fig. 3). Often, spider crabs consumed 100%

180   of the jellyfish, and most jellyfish consumption occurred within the first 3 hours (Fig. 4A).

181   At the end of the 24-hour periods, *Libinia* mortality (27.3%) was higher than in the

182   corresponding no – jellyfish controls (12.5%), and *Carcinus* trials with (5%) and without

183   (12.5%) jellyfish. To assess the role of crab size on mortality, the 22 *Libinia* that received the

184   jellyfish were sorted into 3 size (carapace width) categories: 50 – 58 mm, 60 – 69 mm, and 70 –

185   82 mm. The percent mortality increased with size category (Fig. 5). Each size category contained

186   individuals used on all 4 of the trial dates (suppl. data). For all trials, 100% of the jellyfish in the

187   jellyfish-only control tubs were alive at the end of the 24-hour periods.

188   *Impact of jellyfish consumption on spider crabs*

189   Thirty - six *Libinia* were obtained to assess the effects of increased *Gonionemus* density

190   on crab predation and mortality. Mean carapace width was 73 mm ± 9 S.D. Crab size differed

191   between treatments (ANOVA, $P = 0.039$, $F = 3.36$, df = 3) and crabs in the 20 *Gonionemus*

192   treatment were significantly smaller than in the 15 *Gonionemus* treatment (Tukey's HSD test, P

193   < 0.05), but none of the other pairwise comparisons of *Gonionemus* density treatments differed

194   significantly. As in the 2016 trials, jellyfish consumption began in the first few minutes, and was

195   at or near 100% after 24 hours for many crabs in all *Gonionemus* density treatments (Fig. 4;

196 suppl. video https://figshare.com/s/e866fe9860a2eaf7304e , suppl. data) We also found that

197 *Libinia* mortality increased as *Gonionemus* density increased, and 100% of the crabs died at the

198 highest *Gonionemus* density treatment (Fig. 6). None of the crabs in the crab-only controls died,

199 and none of the *Gonionemus* in the jellyfish-only controls died.

200 *Gonionemus* abundance was estimated on July 19, 2017, August 7, 2017, and August 11,

201 2017 and was 310 (after 60 minutes of netting), 39 (after 45 minutes of netting), and 19 (after 45

202 minutes of netting) medusae per 3 m x 3 m search area, respectively. These values do not

203 represent absolute numbers of *Gonionemus* in the search areas and are based on different

204 amounts of search efforts. Rather these values should be considered catch per unit effort

205 estimates and represent a minimum quantity (i.e., there were likely more *Gonionemus* in the

206 search areas, but not less). As *Gonionemus* is primarily sedentary we do not expect that there was

207 influx into the search area from outside the search area over our search periods.

208 **Discussion**

209 We documented a novel trophic interaction between native crabs and a cryptogenic

210 hydrozoan jellyfish, that may indirectly facilitate dominance of a highly destructive invasive crab

211 in ecologically sensitive eelgrass meadows. Our results are the first example that we are aware of

212 that demonstrates predation on hydrozoan medusae by crabs. As well, the toxic effects of the

213 jellyfish on the native crabs, coupled with lack of jellyfish consumption (and accompanying

214 toxic effects) by the invasive crabs, provides a mechanism for an indirect, but potentially

215 significant ecological impact on eelgrass communities. The native *Libinia* and invasive *Carcinus*

216 co-exist in eelgrass meadows; however, *Carcinus* can be very destructive to eelgrass shoots

217 (Garbary et al. 2014; Neckles 2015; Matheson et al. 2016). Both *Libinia* and *Carcinus* have

218 similar diets – both are generalists that prey on a wide variety of organisms (Aldrich 1974;

219   Grosholz & Ruiz,1996). *Gonionemus* thus has the potential to promote *Carcinus* populations by

220   inducing mortality in a native competitor.

221   While our study was based on laboratory observations, it is very likely that *Libinia* is

222   preying on *Gonionemus* in the field. *Libinia* and *Gonionemus* occupy the same eelgrass

223   microhabitat. In contrast to most jellyfish which are found in the water column, *Gonionemus*

224   medusae spend most of their time attached to eelgrass, in particular near the bottom of the

225   eelgrass where they would be most susceptible to crab predation. Even if the medusae were to

226   cling to the middle or upper part of the eelgrass blades, *Libinia* has the ability to climb (D.

227   Grunden & M. Carman pers. obs.). While our field *Gonionemus* density counts do not reflect

228   absolute densities, they do document a minimum baseline that establishes that our laboratory

229   treatments were realistic. It is very likely that *Libinia* encounters far more than 30 *Gonionemus*

230   individuals (as in our maximum *Gonionemus* density treatment, which resulted in 100%

231   mortality) in a 24-hour period, especially at the height of the *Gonionemus* season in July.

232   It is possible that in the field, given a variety of prey options, that *Libinia* would be less

233   likely to consume large numbers of *Gonionemus* that would have toxic effects. However, our

234   observations showed the crabs had no reluctance in consuming the jellyfish once they were

235   encountered (link to supplemental video https://figshare.com/s/e866fe9860a2eaf7304e), and

236   consumption of large numbers of jellyfish may not be necessary to elicit a fatal or even a

237   debilitating sublethal effect, as seen by the elevated mortality rate in our lower density trials.

238   Our results suggest conflicting observations that crab size might be a factor in

239   *Gonionemus* – related crab mortality. In our 2016 trials where 5 *Gonionemus* were offered to

240   each crab, crab mortality was inversely related to crab size category. We did not evaluate

241   possible trial date effects, but note that crabs collected at all 2016 trial dates were represented in

242 each size category. In our 2017 *Gonionemus* density trials, we found that crabs in the 20

243 *Gonionemus* density treatment were significantly smaller than in the 15 *Gonionemus* density

244 treatment, but this group suffered twice the mortality rate (66.7%) than the 15 *Gonionemus*

245 density treatment (33.3%). However, any potentially beneficial size effects were likely over-

246 ridden by the increase in jellyfish consumption. Thus, the possible relationship between crab size

247 and *Gonionemus* – induced mortality needs further evaluation.

248   Toxicity may vary between jellyfish individuals and individual crab reactions to the

249 jellyfish toxins may also vary (as they do in humans; Otsuru et al. 1974; Yakovlev & Vaskovsky

250 1993). Given that in some human cases, a sting caused by a single medusa is sufficient to cause

251 extreme pain (Otsuru et al. 1974; M. Carman and D. Grunden, pers. obs.) it seems possible that

252 similarly, consumption of even a single medusa by a crab could have a significant negative

253 effect. In humans, symptoms, which are non-lethal, can persist for a few days (Yakovlev &

254 Vaskovsky 1993); however, human studies may not be directly applicable to crabs. Determining

255 the type, duration, and impact of sublethal effects of *Gonionemus* consumption on crabs would

256 be an interesting future direction. Actual predation rates on *Gonionemus* in the field are hard to

257 assess as the jellyfish lack resistant parts that could be identified in crab gut content analyses

258 (Arai 2005). Molecular probes, however, have great potential to identify prey items in guts that

259 are not otherwise observable (e.g., McInnis et al. 2017), and should be considered in future work.

260   Cnidarian jellyfish predators include sea turtles, fish, molluscs, chaetognaths,

261 ctenophores, and other cnidarians (Arai 2005; Ates 2017). Most of these examples involve

262 predation on scyphozoan jellyfish, but predators of hydrozoan jellyfish (inclusive of

263 siphonophores and *Velella* hydroids) include fish (e.g., Brodeur, Lorz & Pearcy 1987); birds

264 (McInnis et al. 2017); hyperiid amphipods (e.g., Scheader & Evans 1975; Williams & Robins

265   1981); shrimp (Hefferman & Hopkins 1981; Roe 1984; Nishida, Pearcy & Nemoto 1988; Moore,

266   Rainbow & Larson 1993); barnacles (Bieri 1966); spiny lobster phyllosoma larvae (Wakabayashi

267   et al. 2012); nudibranchs and heteropods (Sentz-Braconnot & Carre 1966; Seapy 1980);

268   scyphozoan jellyfish (Purcell 1991a; Purcell, 1997; Båmstedt, Ishii & Martlnussen 1997; Arai &

269   Jacobs 1980); and even other hydrozoans (Arai and Jacobs 1980; Purcell 1981; Purcell 1991b).

270   The only example of crab predation on a hydrozoan that we could find, however, is the

271   Dungeness crab *Cancer magister* Dana 1852; who, as planktonic larvae, feed on the planktonic

272   hydroids of *Velella* (Wickham 1979).

273   A small number of jellyfish – crab interactions have been reported for scyphozoan

274   jellyfish (reviewed in Moyano et al. 2012 and Ates 2017) and ctenophores (Esser, Greve &

275   Boersma 2004). Most of these relationships are symbiotic, where the crabs are associated with

276   scyphomedusae and may benefit from dispersal. Intriguingly, many of the crabs involved in

277   these associations belong to the genus *Libinia*. A small subset of these crab-jellyfish associations

278   involves predation or partial predation on the jellyfish, as opposed to a symbiotic relationship.

279   These include: *Libinia dubia* feeding on the sea nettle *Chrysoara quinqecirrha* Desor 1848

280   (Phillips, Burke & Keener 1969), the cannonball jellyfish *Stomolophus meleagris* Agassiz 1862

281   (Shanks & Graham 1988; Tunberg & Reed 2004), and the moon jellyfish *Aurelia aurita*

282   Linnaeus 1758 (Jachowski 1963); and the graceful crab *Cancer gracilis* Dana 1852 feeding on

283   the moon jellyfish *Aurelia labiata* Chamisso & Eysenhardt 1821 (Towanda & Thuesen 2006).

284   Also, *Carcinus maenus* consumes at least some gelatinous zooplankton in its native European

285   range. Esser, Greve & Boersma (2004) describe *C. maenus* predation on the ctenophore

286   *Pleurobrachia pileus* Müller 1776 in the North Sea, particularly when the ctenophores approach

287   the seafloor, and Lauckner (1980) reported observations of *Carcinus maenus* consuming tissue

288   of the moon jelly *Aurelia aurita* in the Baltic Sea. Sweetman et al. (2014) reported that deep sea

289   galatheid crabs could consume dead scyphomedusan carcasses that originated in shallower water

290   (i.e., "jelly falls").

291   In addition to being unusual, the relationship between *Libinia* and *Gonionemus* may be

292   shaped by the presence of especially toxic *Gonionemus* lineages (Govindarajan & Carman 2016;

293   Govindarajan et al. 2017). We observed *Gonionemus*-induced mortality in *Libinia* at

294   *Gonionemus* numbers lower than what we expect the crabs encounter in the field. The hard shells

295   of the crabs probably provided protection from *Gonionemus* stings upon initial contact with the

296   jellyfish. However, the soft interior tissues are more likely to be vulnerable. It is interesting to

297   note that inadvertent human consumption of jellyfish on edible seaweed likely also results in

298   toxic effects similar to external stings (Otsuru et al. 1974); although again, the mechanisms

299   underlying the toxic effects may differ between crabs and humans.

300   The readiness of *Libinia* to unhesitatingly consume jellyfish which may result in their

301   death is consistent with the hypothesis of a recent introduction of a highly toxic strain

302   (Govindarajan & Carman 2016). It seems likely that consumption of toxic jellyfish would exert a

303   strong selection pressure on the consumers, that over time would result in the evolution of

304   jellyfish avoidance or toxin tolerance mechanisms, or the disappearance of crabs from jellyfish

305   habitats. Toxin tolerance mechanisms are possibly present in other crustacean predators of

306   jellyfish. Wakabayashi et al. (2012) observed that spiny lobster phyllosoma larvae consumed

307   both highly venomous jellyfish species (the Portuguese man-of-war *Physalia physalis* Linnaeus,

308   1758, the box jellyfish *Carybdea rastonii* Haacke, 1886, and the Japanese sea nettle *Chrysaora*

309   *pacifica* Goette, 1886) as well as less toxic species, with no ill effects described in any cases.

310   They speculate that tolerance to jellyfish toxins may have evolved for open ocean predators,

311   where non-toxic prey items are relatively more scarce. However, their trials involved

312   consumption of single jellyfish, and it is possible that increasing consumption could lead to

313   mortality. In any case, *Libinia*'s eager consumption of *Gonionemus* coupled with its lack of

314   tolerance to its toxin suggests that this interaction is recent.

315   Records of *Gonionemus* sightings and stings also support the hypothesis that the *Libinia*

316   – toxic *Gonionemus* interaction may be new. Our study site, Farm Pond, is located close to

317   Sengekontacket Pond, where a less toxic *Gonionemus* population that was regularly accessed by

318   jellyfish collectors was known to exist for decades before the first stings were recorded

319   (Govindarajan & Carman 2016). However, debilitating stings have occurred only in the past few

320   years in Farm Pond (Govindarajan & Carman 2016; and directly to D. Grunden & M. Carman),

321   suggesting the arrival of a new, highly toxic form. While we did not quantify the toxicity of the

322   jellyfish used in our experiments, Govindarajan et al. (2017) found that Farm Pond primarily

323   contained a mitochondrial haplotype that is found in other Northwest Atlantic locations where

324   stings have occurred.

325   Our finding that in contrast to *Libinia*, *Carcinus* does not consume *Gonionemus* has

326   significant implications for eelgrass ecosystem health. *Carcinus* is native to Europe, where a less

327   toxic form of *Gonionemus* (*Gonionemus vertens* A. Agassiz, 1862) is thought to be introduced

328   (Edwards 1976; Bakker 1980). Thus, it may not have historically been exposed to selective

329   pressure by the more toxic form that would explain its avoidance of *Gonionemus* consumption.

330   Future experiments should test whether *Carcinus* consumes European *Gonionemus vertens*, or if

331   predation-induced *Libinia* mortality is determined by the lineage of its *Gonionemus* prey (as the

332   lineages vary in their toxicity to humans; Naumov 1960; Govindarajan & Carman 2016).

333   The difference we observed between *Carcinus* and *Libinia* might instead be due to a

334   stronger pre-existing preference of *Libinia* to consume jellyfish. While both *Carcinus* and

335   *Libinia* have broad and overlapping diets, preferences differ between the two species. *Carcinus*

336   tends to be more aggressively predatory (Ropes 1968; Griffen 2014), although it can shift

337   towards herbivory in response to competition (Griffen et al. 2008). Spider crabs, such as *Libinia*,

338   tend to be omnivorous scavengers, often feeding on carrion and algae (Wicksten 1980;

339   Stachowicz & Hay 1999). As noted earlier, *Libinia* is known to consume scyphozoan jellyfish

340   (that presumably lack the extreme toxic effects of *Gonionemus*) (Philips, Burke & Keener 1969).

341   We also observed *Gonionemus* predation by one out of the 2 blue crabs that we evaluated. While

342   blue crabs were too rare to evaluate further, it is interesting that like *Libinia*, they have been

343   reported to consume scyphozoan jellyfish (Farr 1980).

344   Our results also have implications for a broader understanding of invasive species

345   impacts. In addition to having direct effects on native species, for example through competition

346   or predation, invasive species can have indirect effects, but these are less explored (White,

347   Wilson & Clarke 2006). Indirect effects occur when one species affects another via a third

348   species (Wootton 1994), and include apparent competition, indirect mutualism/commensalism,

349   trophic cascades, and exploitative competition (White, Wilson & Clarke 2006). We have

350   identified a unique indirect mechanism by which a cryptogenic jellyfish can potentially increase

351   the abundance of an aggressive and highly destructive invasive species, *Carcinus*. Both *Carcinus*

352   and *Libinia*, overlap in habitat and as generalists, they are both known to feed on a broad array of

353   other species, and so they are likely competing for common prey resources. Thus *Gonionemus* –

354   induced mortality of *Libinia* could benefit *Carcinus* populations by increasing prey abundance.

355   Given the highly negative impact of *Carcinus* to sensitive eelgrass systems, it is important to

356 evaluate this hypothesis as well as identify other ecosystem effects of *Gonionemus* (e.g., its role

357 as a predator, as well as prey).

358

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366

367

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Experimental design and timeline of predation trials

Trial date	Treatment	Crabs tested and # replicates
June 30, 2016	5 jellyfish	Green crabs - 5 Spider crabs - 5 Blue crabs - 1
	0 jellyfish	Green crabs - 5 Spider crabs - 5
	5 jellyfish	No crabs – 2
June 30, 2016	5 jellyfish	Green crabs - 5 Spider crabs – 5 Blue crabs - 1
	0 jellyfish	Green crabs - 2 Spider crabs - 2
	5 jellyfish	No crabs – 2
July 21, 2016	5 jellyfish	Green crabs - 6 Spider crabs - 6
	0 jellyfish	Green crabs - 6 Spider crabs - 6
	5 jellyfish	No crabs – 2
July 28, 2016	5 jellyfish	Green crabs - 6 Spider crabs - 6
	0 jellyfish	Green crabs - 2 Spider crabs - 2
	5 jellyfish	No crabs – 2
July 7, 2017	10 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2
	15 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2
July 18, 2017	20 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2
	30 jellyfish	Spider crabs - 6
	0 jellyfish	No crabs – 2

Figure 1

The clinging jellyfish *Gonionemus* cf. *murbachii.*

The blue arrow points to the end of the tentacles where the adhesive structures are found.

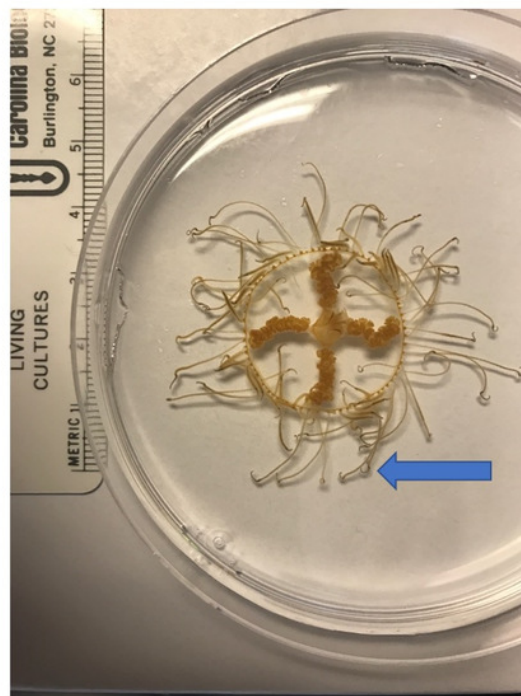



Figure 2

Study locations.

Animals were collected at Lagoon Pond and Farm Pond, and experiments were conducted at the Oak Bluffs Shellfish Department and John T. Hughes Hatchery.

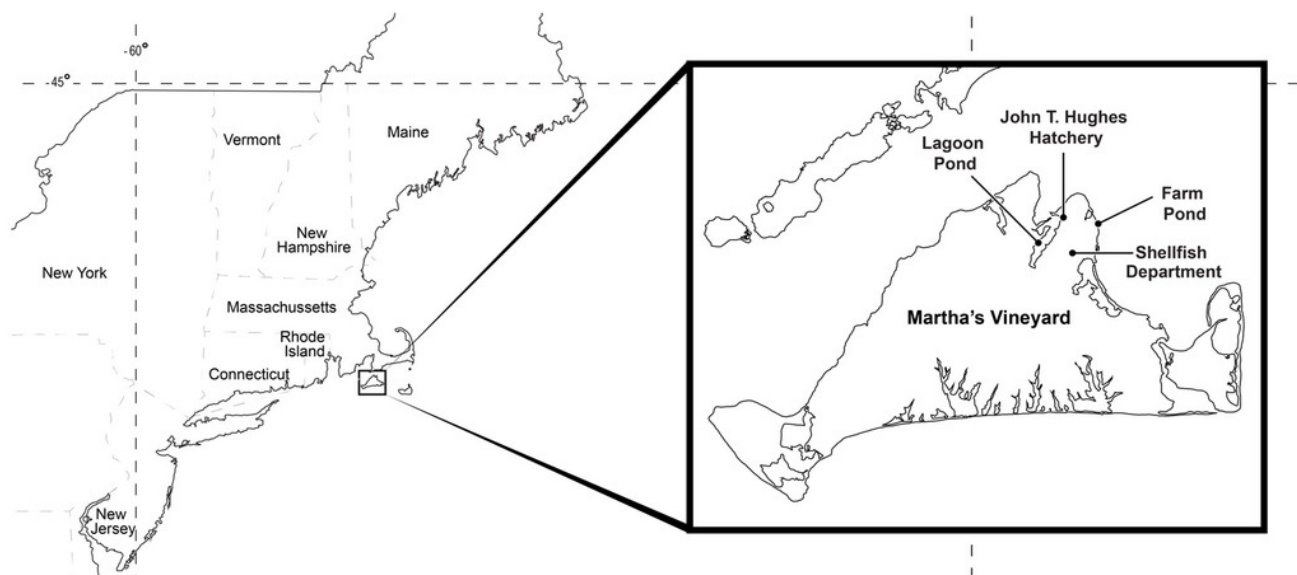
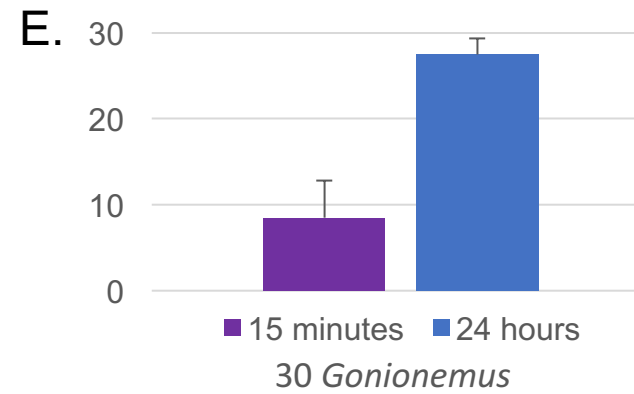
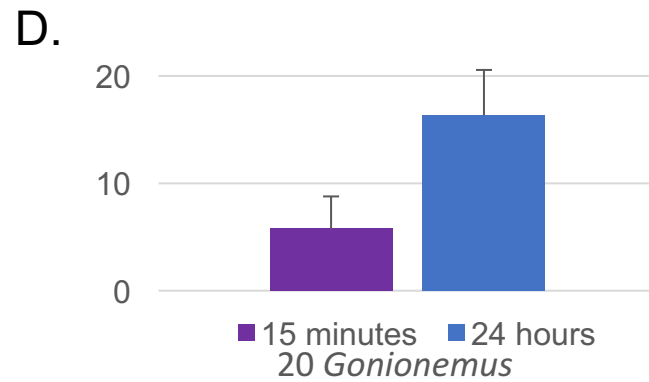
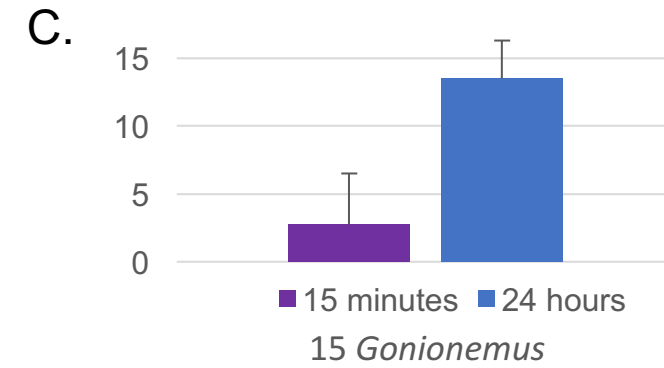
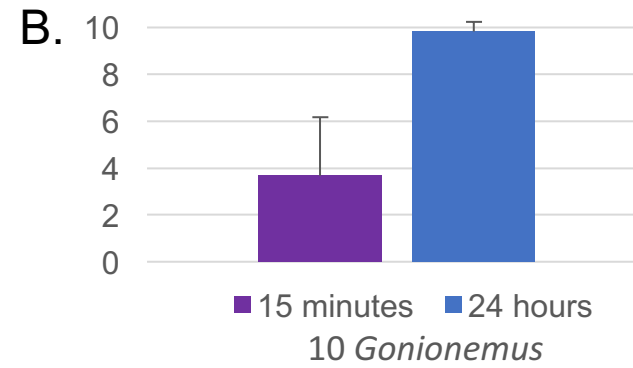
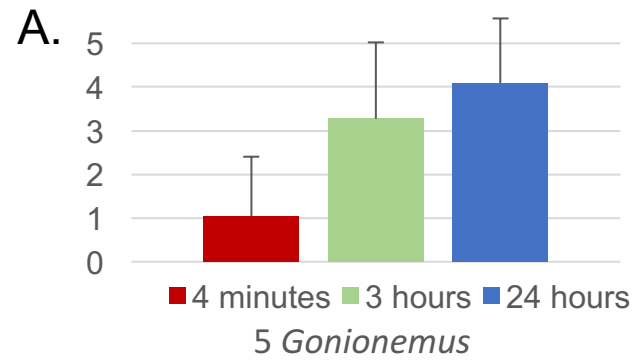



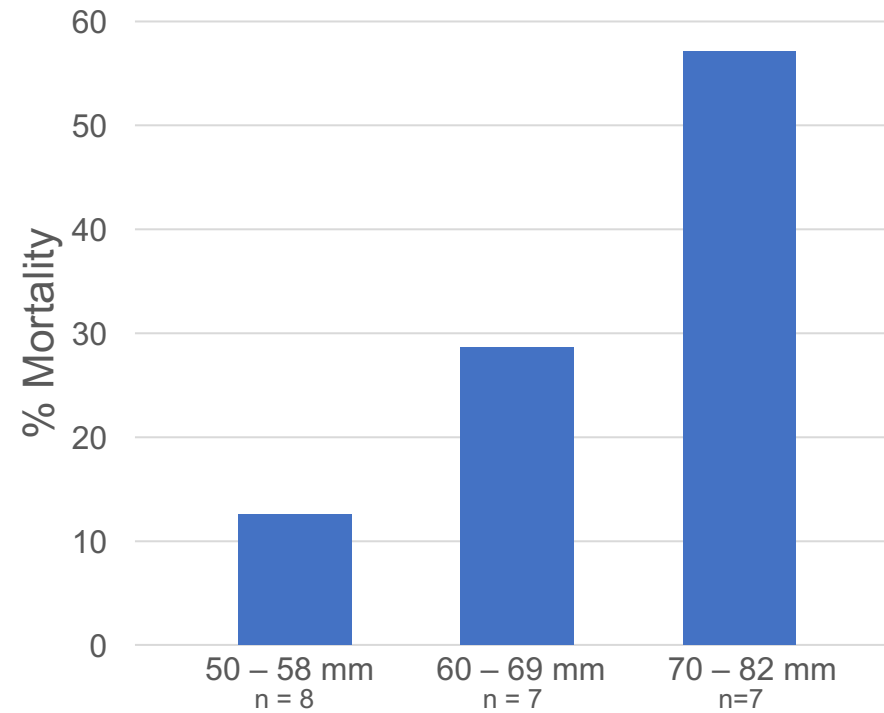
Figure 3

Predation on *Gonionemus*.

Spider crab using its claws to capture and consume a *Gonionemus* medusa (indicated by the blue arrow).

Mean number of *Gonionemus* consumed at different *Gonionemus* densities and exposure times.

Predation values are cumulative over the course of exposure. Error bars represent standard deviations. Note the differences in the y - axis scales for each graph. In each graph, the top gridline indicates the number of *Gonionemus* placed in each crab tub.

Libinia mortality in each size class

Data are from the *Libinia* used in the 5 - *Gonionemus* trials.

Spider crab mortality and different *Gonionemus* densities and consumption levels.

Mean *Libinia* mortality as a function of *Gonionemus* density (number of medusae initially placed in crab containers) and *Gonionemus* predation (number of medusae consumed after 24 hours).