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1 Utilization of the invasive alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss by the native mud
2 snail *Ilyanassa obsoleta* (Say)

3

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12

13 **Abstract**

14 The recent invasions of the red alga, *Gracilaria vermiculophylla*, to the Atlantic and Eastern
15 Pacific Oceans have the potential to significantly alter intertidal and subtidal soft sediment
16 communities. In particular, *G. vermiculophylla* increases habitat complexity and provides a novel
17 hard substrate in an otherwise two dimensional habitat. Following our observations that the
18 native omnivorous mud snail *Ilyanassa obsoleta* utilizes *G. vermiculophylla* for egg capsule
19 deposition, our field surveys demonstrated that the *in situ* abundance of egg capsules on *G.*
20 *vermiculophylla* matched abundances on a native alga *Ceramium virgatum* and were at least 11-
21 50 times greater than on all other co-occurring macrophytes. Additionally, through mesocosm
22 experiments, we showed that *I. obsoleta* preferentially deposits eggs on the invasive *G.*
23 *vermiculophylla* over native substrates. However, despite the thick layer of egg capsules found
24 on *G. vermiculophylla*, no detrimental effects were seen on thalli growth. In contrast, growth of
25 the native red alga *Ceramium virgatum* was significantly reduced when egg capsules were
26 present, suggesting *G. vermiculophylla* can out-compete native macrophytes in areas of *I.*
27 *obsoleta* abundance, while facilitating reproduction of the native mud snail. This novel
28 interaction has the potential to significantly alter biological interactions in soft sediment
29 communities through a variety of different mechanisms, including the alteration of trophic
30 cascades via the increase in mud snail abundance. Furthermore, facilitation of the reproductive
31 success of *I. obsoleta* may lead to increases in the occurrence of cercarial dermatitis, as *I.*
32 *obsoleta* is a known intermediate host organism.

33

34 Key words: *Gracilaria vermiculophylla*, *Ilyanassa obsoleta*, invasive macroalga, mudflat,
35 Narragansett Bay, substrate preference

36 1. Introduction

37 In soft sediment estuarine habitats, the establishment of an invasive macrophyte can have
38 an enormous impact on the structure of the habitat and, subsequently, its inhabitants. Invasive
39 macrophytes physically and chemically alter soft sediment flats (Crooks, 2002; Wallentinus and
40 Nyberg, 2007), shifting them from relatively two-dimensional surfaces to complex three-
41 dimensional landscapes with reduced water flow and sediment grain size (Posey, 1988),
42 increased sedimentation rates and detritus biomass (Allen, 1998; Ruesink et al., 2006; Shi et al.,
43 2000), and modified sediment and water column chemistry (Larned, 2003). In addition, invasive
44 macrophytes create a novel hard substrate that can be utilized by epiphytic algae and sessile
45 invertebrates (Jones and Thornber, 2010; Prado and Thibaut, 2008). Increased habitat complexity
46 and substrate creation can positively impact some mudflat inhabitants and recruit species from
47 neighboring vegetated areas, leading to an overall increase in biodiversity (Crooks, 2002; Posey,
48 1988). However, habitat alterations due to dense macrophyte beds can also result in the loss of
49 species, particularly larger mobile animals that cannot effectively forage in dense vegetation
50 (Levi and Francour, 2004; Posey, 1988). Additionally, when macrophytes invade vegetated
51 areas, they often outcompete the natives, altering the macrophyte canopy (Hacker and Dethier,
52 2006; Meyerson et al., 2000).

53 One recent macrophyte invader in Atlantic and Eastern Pacific soft sediment habitats is
54 the red alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Bellorin et al., 2004; Freshwater et
55 al., 2006; Nettleton et al., 2013; Saunders, 2009; Thomsen et al., 2005). Originally from eastern
56 Asia, *G. vermiculophylla* forms dense beds in the intertidal and shallow subtidal where its
57 superior stress tolerance (Martínez-Lüscher and Holmer, 2010; Rueness, 2005; Thomsen, 2007),
58 ability to recruit to a wide variety of hard substrates (Thomsen, 2005), and association with the

59 polychaete *Diopatra cuprea* (where they co-occur; Thomsen and McGlathery, 2005; Thomsen et
60 al., 2009) helps it to dominate unvegetated flats and outcompete native macrophytes. However,
61 several studies have also found a positive correlation between *G. vermiculophylla* and epiphyte
62 and invertebrate biodiversity (Thomsen, 2010; Thomsen et al., 2006, 2009). Additionally, there
63 is mounting evidence that *G. vermiculophylla* can serve as a nursery habitat for juvenile blue
64 crabs, an economically important species that has suffered massive declines in the Chesapeake
65 Bay, USA, due to seagrass habitat loss (Falls, 2008; Thomsen et al., 2009).

66 In this study, we explored the interaction between *G. vermiculophylla* and the native mud
67 snail *Ilyanassa obsoleta* (Say). *I. obsoleta* is one of the most abundant invertebrates in sheltered
68 soft sediment communities in eastern North America (Curtis and Hurd, 1981); it co-occurs with
69 *G. vermiculophylla* throughout the alga's invaded range. *I. obsoleta* reproduces by depositing
70 egg capsules on hard substrates located within the lower intertidal and shallow subtidal, directly
71 linking *I. obsoleta*'s reproductive success to the availability of appropriate substrate, which can
72 be sparse in soft sediment habitats (Brenchley, 1981; Pechenik, 1978). Previous work has shown
73 that these snails deposit their capsules on macroalgae as well as seagrasses, shells, and wood, but
74 that they avoid deposition on rocks (Brenchley, 1982). Given that *G. vermiculophylla* has largely
75 invaded soft sediment habitats where usable substrates for *I. obsoleta* capsule deposition are
76 scarce, we hypothesized that *G. vermiculophylla* may provide a novel, suitable surface for *I.*
77 *obsoleta* egg capsule deposition. To examine this hypothesis, we quantified the average
78 abundance of *I. obsoleta* egg capsules on *G. vermiculophylla* as well as other common estuarine
79 macroalgae. In addition, we conducted mesocosm experiments to determine if *I. obsoleta* prefers
80 to deposit egg capsules on native substrates or *G. vermiculophylla*. Following our observation
81 that *I. obsoleta* lays thick layers of egg capsules on *G. vermiculophylla* and a second red alga,

82 *Ceramium virgatum* Roth, we assessed snail usage of these thalli by quantifying where on the
83 thallus egg capsules were laid. We also examined whether the presence of egg capsules had a
84 negative impact on the growth of these two algal species. We discuss our results within the
85 context of how this new interaction may directly impact *I. obsoleta* populations, with cascading
86 impacts for the entire soft sediment community.

87

88 **2. Methods**

89 **2.1 Study Site and Species**

90 Narragansett Bay, RI, USA, is a well-mixed temperate estuary of approximately 370 km²,
91 with a mean depth of 8.6 m. *Gracilaria vermiculophylla* is found throughout Narragansett Bay in
92 soft sediment intertidal and shallow subtidal habitats. Originally confused with the native *G.*
93 *tikvahiae*, its invasion was confirmed in 2008 via molecular sequencing (Saunders, 2009).
94 However, given the extent of its invasion throughout the bay, it was likely present in this area
95 long before 2008. We have found *G. vermiculophylla* attached to a variety of substrate types
96 including rocks, shells, debris, and tubes of the polychaete *Spirochaetopterus oculatus* (Guidone,
97 personal observation); it is also frequently found drifting subtidally and washed up onshore.
98 Epiphytes are rarely observed on *G. vermiculophylla* thalli, with the exception of *Ceramium*
99 *virgatum*, which is common in late spring (Guidone and Newton, personal observation).

100 *Ilyanassa obsoleta* is a deposit feeder that mainly consumes motile benthic diatoms,
101 although it also opportunistically consumes macroalgae and carrion (Connor et al., 1982; Curtis
102 and Hurd, 1981; Guidone et al., 2010; Scheltema, 1964). Natural densities of *I. obsoleta* (180-
103 1400 snails m⁻²; Pace, 1979; Guidone and Thornber, unpublished data) have a profound impact
104 on mudflat communities, severely reducing benthic microalgal biomass and annelid abundance

105 through their grazing activities (Connor et al., 1982; Kelaher et al., 2003; Pace et al., 1979). In
106 Narragansett Bay, *I. obsoleta* reproduction peaks in May-June (Brenchley, 1981; Guidone,
107 personal observation). *I. obsoleta* has separate sexes; however, they are difficult to distinguish
108 without dissection. Therefore, all experiments examining egg capsule deposition used a high
109 number of snails to ensure that multiple females were present.

110 **2.2 Survey**

111 We conducted egg capsule-algal surveys at two sites within Narragansett Bay where *I.*
112 *obsoleta* and *G. vermiculophylla* co-occur: Oakland Beach (41°41.216'N, 71°24.143'W) and
113 Warwick City Park (41°41.263'N, 71°24.381'W), Warwick, RI. These sites were specifically
114 selected to represent the different algal communities in which *G. vermiculophylla* and *I. obsoleta*
115 coexist; thalli at Oakland Beach were primarily attached to shells and small pebbles, while thalli
116 at Warwick City Park were typically found drifting in shallow subtidal algal mats. We conducted
117 surveys in May and June 2011. A single 30 m subtidal transect was laid out perpendicular to the
118 shoreline during low tide at Warwick City Park; two replicate 30 m transects placed 125 m apart
119 were used at Oakland Beach. Algae were sampled at 3 m intervals along each transect using a net
120 (40 cm width, 6 mm mesh) that was dragged across the substrate for 0.5 m. This method ensured
121 our collection of all attached and drifting algal individuals in a standard 0.2 m² area. All algae
122 were returned to the laboratory where they were identified to genus or species level, spun in a
123 salad spinner to remove excess water, weighed, and the number of egg capsules per species
124 recorded. Algal wet mass was adjusted to account for egg capsule mass using an average egg
125 capsule wet mass of 0.0019 g (calculated from 20 individually weighed eggs). To determine
126 temporal and spatial patterns in egg capsule abundance, we analyzed the number of egg capsules
127 per g of algae per sample using a two-way fixed factor ANOVA for differences among sites and

128 months (JMP version 8, SAS Institute Inc., North Carolina, USA). Due to the uneven distribution
129 of the individual algal species among the sites and between samples within a site, differences in
130 egg capsule abundance among algal species were analyzed separately using a one-way ANOVA;
131 species that were observed in fewer than 5 samples were excluded from this analysis.

132 **2.3 Capsule Location on *G. vermiculophylla* and *C. virgatum***

133 Our initial field observations suggested that *I. obsoleta* preferred *G. vermiculophylla* and
134 *C. virgatum* for egg deposition more than all other available substrates. In order to assess
135 whether entire thalli or only particular portions (i.e. main axis or base) of a thallus are suitable
136 for *I. obsoleta* egg capsule deposition, we haphazardly collected ten thalli of *G. vermiculophylla*
137 and *C. virgatum* from the shallow subtidal area of Oakland Beach on May 11, 2011. For both
138 species, we recorded the wet mass and total length of each thallus. For *G. vermiculophylla*, we
139 recorded the number of egg capsules on the thallus as well as each capsule's location (main,
140 secondary, or tertiary branch). For *C. virgatum*, which has no central axis due to its
141 dichotomously branched morphology, we instead recorded the number of capsules within 1 cm
142 linear intervals along the thallus.

143 Additionally, we estimated the surface area of all collected thalli in order to compare
144 results for egg capsule densities per gram of algal tissue to densities per cm² of algal thallus. Due
145 to the presence of egg capsules, we could not accurately calculate surface area via image analysis
146 or other direct tests on the thalli of interest. Therefore, surface area was first estimated for thalli
147 collected without egg capsules using the acetone-detergent assay (Hicks, 1980). These data were
148 used to create a regression relationship with thallus wet mass, which allowed us to accurately
149 estimate the surface area of thalli with egg capsules once we had adjusted their wet masses to
150 account for egg capsule mass (see Results).

151 **2.4 Substrate Preference**

152 All mesocosm experiments were conducted at the University of Rhode Island's
153 Narragansett Bay Marine Life Sciences Facility in outdoor, flow-through seawater tables.
154 Mesocosms were constructed from 5 L plastic containers; eight mesh-covered holes around the
155 circumference of each container provided adequate flow of filtered, ambient temperature
156 seawater from Narragansett Bay, RI. For all experiments, snails and substrates were continuously
157 submerged, as previous work indicated that egg capsule deposition only occurs under submerged
158 conditions (Pechenik, 1978).

159 Twenty *I. obsoleta* were placed into each mesocosm containing a selection of substrate
160 choices. The assortment of substrates consisted of materials commonly found within
161 Narragansett Bay soft sediment habitats. Ten mesocosms contained *G. vermiculophylla*, *C.*
162 *virgatum*, *Scytosiphon lomentaria*, and wrack of *Spartina alterniflora*, all of which have a
163 generally cylindrical morphology. A second nine mesocosms contained *Ulva* spp. (blade with
164 intact holdfast), *Punctaria* spp., and a shell of the ribbed mussel *Geukensia demissa*, all of which
165 have a non-cylindrical morphology. Substrates were divided based on their overall morphology
166 of “generally cylindrical” or “non-cylindrical” due to inadequate space for all seven substrates
167 within a single mesocosm unit. All substrates were cut to a length of 4 cm; due to logistical
168 challenges, we did not standardize the width or overall surface area of the substrates placed in
169 the mesocosms. As egg capsules were absent from all substrate choices at the start of the
170 experiment, substrate surface area was estimated using Image J (version 1.43,
171 <http://rsbweb.nih.gov/ij/>). Snails were given one week to lay their egg capsules, after which the
172 substrates were removed and the number of eggs on each substrate, as well as deposited on the
173 mesocosm container itself, were recorded. Results of each substrate experiment were analyzed

174 for egg deposition preferences using the multivariate preference index (Lockwood, 1998) with
175 Mathematica (v8.0.4).

176 **2.5 Egg Capsule Impacts on *G. vermiculophylla* and *C. virgatum* Growth**

177 We placed a known wet mass of either *G. vermiculophylla* or *C. virgatum* in a mesocosm
178 with twenty adult snails; an equal number of non-snail controls were run concurrently (n=10 for
179 each treatment). To control for individual variation among thalli, snail treatment and control
180 pieces were taken from the same algal thallus in a paired design. Snails were allowed ten days to
181 deposit their eggs on the thalli, after which the algae were reweighed, and the number of eggs per
182 thallus counted. Changes in each species wet mass were analyzed using paired t-tests.

183 At the conclusion of this experiment, we observed that thalli in the snail treatment were a
184 darker color than their control counterparts, indicating a potential positive impact from *I.*
185 *obsoleta* nitrogenous wastes (Tyler and McGlathery, 2006). Therefore, to examine the impact of
186 *I. obsoleta* egg capsules on algal growth in the absence of further snail nitrogen inputs, we
187 conducted a follow up experiment. *G. vermiculophylla* thalli from the snail treatments were
188 divided in half. On one half, the egg capsules were left intact, on the second half the capsules
189 were gently removed; both halves were retained within the same mesocosm. Capsule removal
190 was not possible for *C. virgatum* without causing considerable thallus damage, therefore the
191 thalli pieces from the snail and control treatments were combined into one mesocosm. All algae
192 were weighed at the start of this follow-up experiment and again after one week; data were
193 analyzed as above.

194

195 **3. Results**

196 **3.1 Survey**

197 *Ilyanassa obsoleta* egg capsules were present on eight of the eleven macroalgal taxa at
 198 our two field sites. Egg capsule density per gram of algae differed significantly among these taxa
 199 ($F_{5,207} = 17.45$, $p < 0.0001$; Fig. 1), with 11-50 times more capsules on *Gracilaria*
 200 *vermiculophylla* and *Ceramium virgatum* than the other taxa (Tukey post-hoc test $p < 0.05$; due
 201 to their rarity, *Chondria* spp., *G. tikvahiae*, *Polysiphonia* spp., *Scytosiphon lomentaria*, and
 202 *Spermothamnion repens* were excluded from this analysis). Egg capsules were found at both
 203 survey sites during May and June. Capsules per gram of algae were approximately twice as
 204 abundant at Warwick City Park in May and seven times more abundant in June than they were at
 205 Oakland Beach (Site: $F_{1,54} = 16.45$ $p = 0.0002$; Month: $F_{1,54} = 0.59$, $p = 0.45$; Fig. 1), resulting in
 206 a significant month-site interaction ($F_{1,54} = 4.37$, $p = 0.04$; Fig. 1)..

207 **3.2 Capsule Location on *G. vermiculophylla* and *C. virgatum***

208 We found a strong relationship between surface area:wet mass for both *G.*
 209 *vermiculophylla* (surface area = $3.40 + 16.36 \cdot \text{wet mass}$; $R^2 = 0.90$, $p < 0.0001$) and *C. virgatum*
 210 (surface area = $5.06 + 28.68 \cdot \text{wet mass}$; $R^2 = 0.95$, $p < 0.0001$), allowing us to accurately
 211 estimate the surface area of specimens based on wet mass alone. When comparing egg capsule
 212 densities by surface area, capsules were found to be almost twice as abundant on *G.*
 213 *vermiculophylla* than they were on *C. virgatum*, although this difference was not statistically
 214 significant (mean *G. vermiculophylla* = 7.75 capsules/cm²; *C. virgatum* $4.17 =$ capsules/cm²; $t_{16,58}$
 215 = 0.47 , $p = 0.65$). Similarly, when egg capsule densities were evaluated per gram of algae,
 216 capsules densities were 2.7 times greater on *G. vermiculophylla*, though, in contrast, this was a

217 significant difference (mean *G. vermiculophylla* 205.87 capsules/g; *C. virgatum* 76.00
 218 capsules/g; $t_{14,58} = 3.49$, $p = 0.0034$).

219 On *G. vermiculophylla*, capsules were approximately four times more abundant on the
 220 main branches (mean 5.48 capsules/cm) than the secondary branches (mean 1.29 capsules/cm)
 221 and only a few egg capsules were found on the smaller tertiary branches ($F_{2,361} = 111.01$, $p <$
 222 0.0001). On *C. virgatum*, capsules were two to five times more abundant within the first 5 cm of
 223 the thallus base (mean 45.5 capsules) than they were in the second 5 cm (mean 10.3 capsules)
 224 from the thallus base ($t = -4.01$, $p = 0.0009$); thalli larger than 10 cm had no capsules present
 225 beyond 10 cm from the algal holdfast.

226 3.3 Egg Capsule Substrate Preference

227 In mesocosm experiments, *I. obsoleta* preference varied significantly among cylindrical
 228 substrates (critical $F_{4,5} = 33.22$, Hotelling's $T^2 = 19390$, $p < 0.0001$), with a strong preference for
 229 depositing egg capsules on *G. vermiculophylla*: more than 4.5 times as many capsules were
 230 found on *G. vermiculophylla* (mean = 22.3 eggs/cm²) than on the second most preferred substrate
 231 *C. virgatum*. However, capsule deposition on *G. vermiculophylla* was only significantly greater
 232 than on *S. lomentaria* and the mesocosm bucket itself (multivariate pairwise analysis, Fig. 2, $p <$
 233 0.05). Egg capsule deposition also varied significantly among the non-cylindrical substrates
 234 (critical $F_{4,4} = 44.73$, Hotelling's $T^2 = 1099.49$, $p < 0.0001$); however, no significant ($p < 0.05$)
 235 pairwise differences were found (Fig. 2).

236 3.4 Egg Capsule Impacts on *G. vermiculophylla* and *C. virgatum* Growth

237 Thallus growth did not differ between snail and control treatments for either species,
 238 despite the presence of egg capsules (*G. vermiculophylla* $t_8 = 0.11$, $p = 0.92$; *C. virgatum* $t_9 =$
 239 1.43 , $p = 0.19$; Fig. 3). When snails were removed to examine the impact of egg capsules alone,

240 *G. vermiculophylla* grew equally well with capsules present and absent ($t_8 = 1.29$, $p = 0.23$). In
241 contrast, *C. virgatum* with egg capsules lost twice as much mass as thalli without egg capsules (t_8
242 = 4.091, $p = 0.0035$; Fig. 3).

243

244 **4. Discussion**

245 Invasive species that create three dimensional structures in otherwise two dimensional
246 habitats can have large impacts on their new environments (Crooks, 2002; Wallentinus and
247 Nyberg, 2007). Here, we demonstrated that the invasive macroalga *Gracilaria vermiculophylla*
248 creates a novel substrate in soft sediment communities that is preferentially utilized by the native
249 mud snail *Ilyanassa obsoleta* for egg capsule deposition. While our surveys showed that *G.*
250 *vermiculophylla* was not preferred more than the native *Ceramium virgatum*, *C. virgatum* at our
251 study sites is often found as an epiphyte on *G. vermiculophylla*, directly linking its abundance to
252 *G. vermiculophylla*'s and potentially amplifying the link between *G. vermiculophylla* and *I.*
253 *obsoleta* egg capsule deposition. Only one other species, the native *G. tikvahiae*, was found to
254 have a large number of egg capsules present at the field sites. However, within our study system
255 *G. tikvahiae* does not grow attached within the *I. obsoleta* egg capsule deposition zone,
256 indicating it may only be utilized when it opportunistically drifts into shallow subtidal areas
257 containing *I. obsoleta*, as it commonly does at our drift algae site (Warwick City Park). Indeed,
258 given the greater number of egg capsules found at our drift algae site, we can also surmise that *I.*
259 *obsoleta* either prefers drift algae to attached algae as a deposition substrate, or *I. obsoleta*
260 capsules increase the drag on attached algae, thus causing them to have a higher incidence of
261 holdfast failure and a greater presence in drift mats.

262 In our surveys, we utilized algal wet mass to calculate egg capsule density per species
263 due to a need for a rapid estimate before algal tissues degraded. Our subsequent analyses of egg
264 capsule densities specifically on *G. vermiculophylla* and *C. virgatum* indicated that egg capsule
265 density based on algal wet mass and algal surface area yield similar values. Therefore, while egg
266 capsule densities are more likely a function of the algal surface area that is available for capsule
267 deposition, algal wet mass offers a quick and accurate way of estimating density across
268 numerous species.

269 In examining specific deposition sites on *G. vermiculophylla* and *C. virgatum*, we found
270 *I. obsoleta* preferentially deposited egg capsules on the main branches of *G. vermiculophylla* and
271 at the base of *C. virgatum*. This suggests that these portions present a more stable and easily
272 handled substrate, possibly owing to their branch diameter (in the case of *G. vermiculophylla*) or
273 their proximity to the holdfast (*C. virgatum*). If branch diameter is the key factor in *I. obsoleta*'s
274 choice, this may help to explain the snails' general preference for *G. vermiculophylla*, which has
275 a thicker thallus than *C. virgatum*. However, these species also differ in texture, branching
276 patterns, and likely chemical composition, warranting further investigations.

277 Our mesocosm experiments did support our observations from our field surveys. *I.*
278 *obsoleta* deposited more egg capsules on *G. vermiculophylla* than on the other cylindrically
279 shaped substrates in 8 out of 10 replicates. Although not statistically significant, this was a mean
280 of 4.5 times more capsules laid on *G. vermiculophylla* than on *C. virgatum* and nearly 28 times
281 more capsules than were laid on *S. alterniflora*. Indeed, this experiment was statistically
282 hampered by two factors: a high number of substrate choices (5) compared to only 10 replicates,
283 and in one of these replicates, *C. virgatum* was the only substrate chosen. When given a choice

284 of non-cylindrical substrates, *I. obsoleta* utilized the mesocosm container as often as it used the
285 other substrate choices, showing no overall preference for any of the substrates presented.

286 *Ilyanassa obsoleta*'s utilization of macroalgae as an egg deposition substrate has the
287 potential to negatively impact macroalgal growth by interfering with nutrient absorption and/or
288 light reception. While we found no evidence for a negative impact of *I. obsoleta* egg capsules on
289 the growth of *G. vermiculophylla*, *C. virgatum* growth was significantly reduced when snail
290 capsules were present and the facilitative impacts of *I. obsoleta* nitrogenous waste inputs were
291 removed. While this observed impact may have been an artifact of our experimental design, it
292 merits further investigation as *I. obsoleta* egg deposition may further facilitate *G.*
293 *vermiculophylla* invasion by hindering the growth of its native competitors.

294 Previous studies have demonstrated that invasive macrophytes can facilitate epiphytic
295 algae and sessile invertebrates through substrate creation (e.g. Jones and Thornber, 2010; Prado
296 and Thibaut, 2008). This study, to our knowledge, is the first to demonstrate a facilitative
297 relationship between an invasive macrophyte and a mobile animal that preferentially selects the
298 invasive species as an egg capsule deposition site. Indeed, studies in egg depositing fish have
299 found the opposite relationship. The Atlantic silverside (*Menidia menidia*) almost exclusively
300 deposited its eggs among tubular *Ulva* spp. associated with the native *Spartina alterniflora*,
301 avoiding areas dominated by the invasive *Phragmites australis* (Balouskus and Targett, 2012). In
302 a second study, the fountain darter (*Etheostoma fonticola*) preferentially chose a range of native
303 substrates over the invasive *Hydrilla verticillata* (Phillips et al., 2011).

304 By creating an abundant substrate utilized by *I. obsoleta* for egg deposition, *G.*
305 *vermiculophylla* has the potential to extensively impact soft sediment communities (Fig. 4).
306 Primarily, this interaction may directly lead to an increase in *I. obsoleta* reproductive success,

307 and higher *I. obsoleta* densities. This population increase could negatively impact *I. obsoleta*
308 prey densities, such as motile benthic diatoms (Connor et al., 1982; Pace et al., 1979), thus
309 increasing competition between *I. obsoleta* and other deposit feeders, such as *Diopatra cuprea*
310 (Magnum et al., 1968). In contrast, *I. obsoleta* predators including the invasive green crab
311 *Carcinus maenas*, the moon snails *Polinices duplicatus* and *Lunatia heros*, and migratory birds
312 (Brenchley, 1982) may benefit. Under these assumptions, *G. vermiculophylla* would have an
313 indirect negative effect on *I. obsoleta* prey and an indirect positive impact on *I. obsoleta*
314 predators (Fig. 4). However, these cascading impacts may be dampened if egg capsule predators,
315 including native hermit crabs, the snail *Littorina littorea*, and the crab *C. maenas* (Brenchley,
316 1982), are able to limit *I. obsoleta* population growth.

317 In addition to the potential impacts on soft sediment communities, a *G. vermiculophylla*
318 mediated increase in *I. obsoleta* populations also raises human health and economic concerns. *I.*
319 *obsoleta* is the intermediate host organism for cercarial dermatitis (swimmer's itch) causing
320 avian schistosome *Austrobilharzia variglandis* (Barber and Caira, 1995; Sindermann, 1960),
321 therefore an increase in *I. obsoleta* populations may also lead to an increased incidence of
322 cercarial dermatitis. Although cercarial dermatitis is typically mild, it can lead to severe itching
323 and discomfort, and has been found to discourage recreational swimmers from returning to
324 locations where they contracted the disease, presumably resulting in economic losses for local
325 businesses and municipalities (Chamot et al., 1998).

326

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334 **6. Citations**

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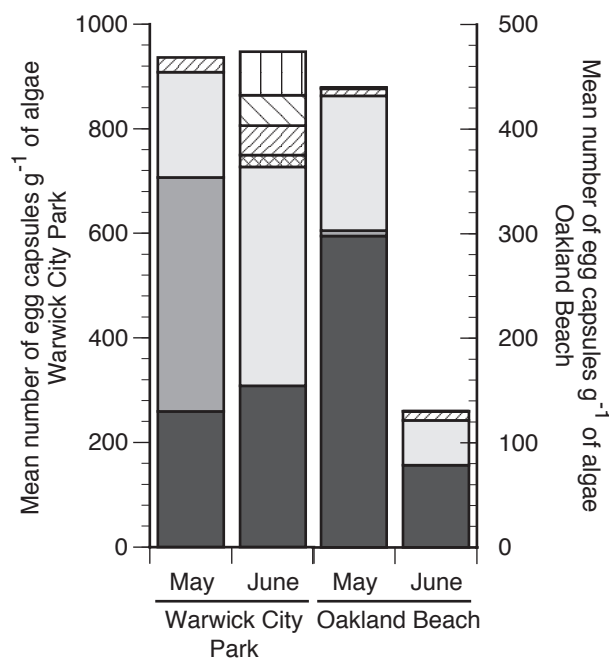
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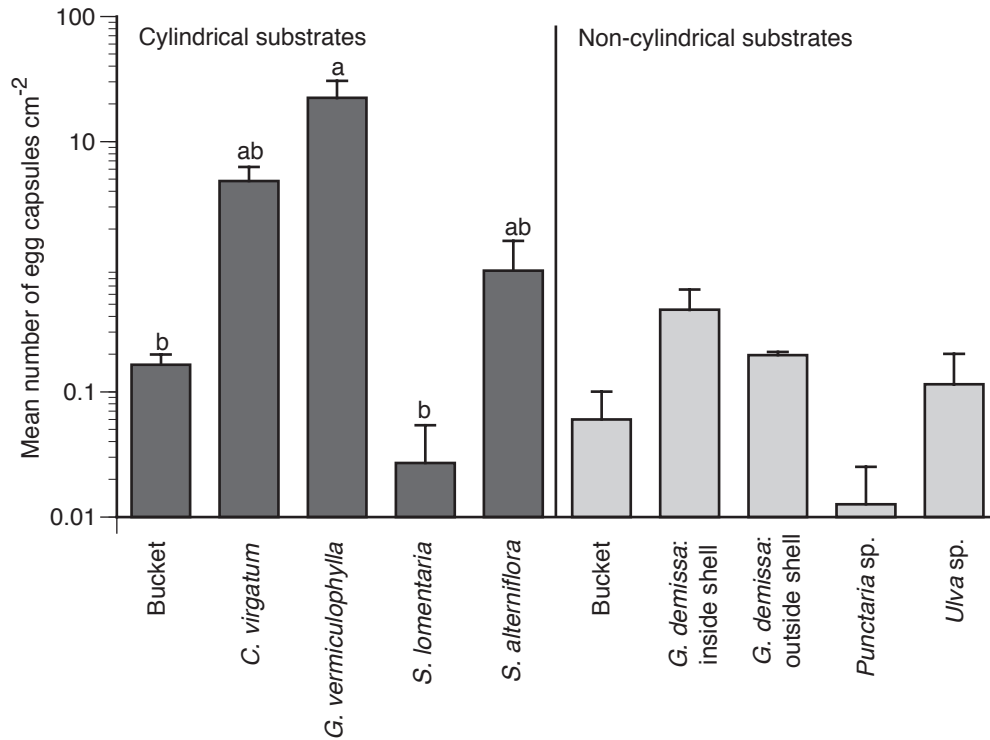
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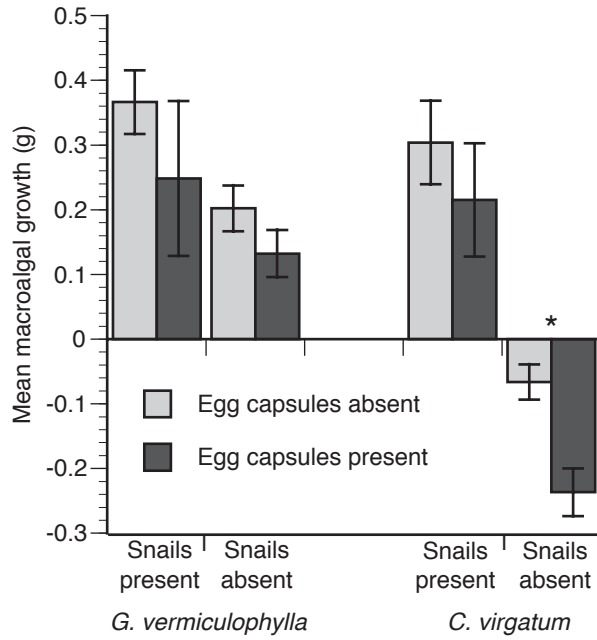
446 **Fig. 1** Field survey results for *Gracilaria vermiculophylla* (■), *G. tikvahiae* (▣), *Ceramium*
 447 *virgatum* (□), *Polysiphonia* spp. (▤), *Punctaria* spp. (▥), *Ulva* blades (▦), and *Ulva* tubes (▧).
 448 Algal taxa that were present in the field but did not contain any egg capsules (*Chondria* spp.,
 449 *Scytosiphon lomentaria*, and *Spermothamnion repens*), or contained fewer than 5 egg capsules
 450 (*Cladophora* spp.), are not shown



451

452 **Fig. 2** Substrate preference for *Ilyanassa obsoleta* egg deposition. Potential substrates were
 453 separated into two trials according to morphology. All data are means \pm 1 SE. Different letters
 454 indicate significant differences among substrates (Multivariate preference index pairwise post-
 455 hoc analysis, $p < 0.05$)

456

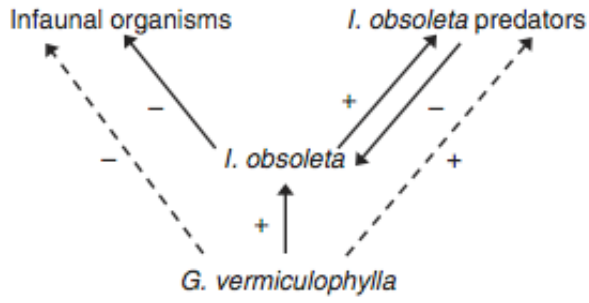


457

458 **Fig. 3** *Gracilaria vermiculophylla* and *Ceramium virgatum* growth in mesocosms with snails459 present and absent. All data are means \pm 1 SE. * indicates a significant difference between

460 treatments

461



462

463 **Fig. 4** Hypothesized ecological consequences of *Gracilaria vermiculophylla* facilitation. Solid

464 lines show direct interactions, dashed lines show indirect interactions

465

466