3-2014

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Recommended Citation  
Guidone, Michele; Newton, Christine; and Thornber, Carol S., "Utilization of the Invasive Alga Gracilaria Vermiculophylla (Ohmi) Papenfuss by the Native Mud Snail Ilyanassa Obsoleta (Say)" (2014). *Biology Faculty Publications*. 57.  
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Utilization of the invasive alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss by the native mud snail *Ilyanassa obsoleta* (Say)

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Abstract

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

Key words: *Gracilaria vermiculophylla, Ilyanassa obsoleta*, invasive macroalga, mudflat, Narragansett Bay, substrate preference
1. Introduction

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

One recent macrophyte invader in Atlantic and Eastern Pacific soft sediment habitats is the red alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Bellorin et al., 2004; Freshwater et al., 2006; Nettleton et al., 2013; Saunders, 2009; Thomsen et al., 2005). Originally from eastern Asia, *G. vermiculophylla* forms dense beds in the intertidal and shallow subtidal where its superior stress tolerance (Martínez-Lüscher and Holmer, 2010; Rueness, 2005; Thomsen, 2007), ability to recruit to a wide variety of hard substrates (Thomsen, 2005), and association with the
polychaete *Diopatra cuprea* (where they co-occur; Thomsen and McGlathery, 2005; Thomsen et al., 2009) helps it to dominate unvegetated flats and outcompete native macrophytes. However, several studies have also found a positive correlation between *G. vermiculophylla* and epiphyte and invertebrate biodiversity (Thomsen, 2010; Thomsen et al., 2006, 2009). Additionally, there is mounting evidence that *G. vermiculophylla* can serve as a nursery habitat for juvenile blue crabs, an economically important species that has suffered massive declines in the Chesapeake Bay, USA, due to seagrass habitat loss (Falls, 2008; Thomsen et al., 2009).

In this study, we explored the interaction between *G. vermiculophylla* and the native mud snail *Ilyanassa obsoleta* (Say). *I. obsoleta* is one of the most abundant invertebrates in sheltered soft sediment communities in eastern North America (Curtis and Hurd, 1981); it co-occurs with *G. vermiculophylla* throughout the alga’s invaded range. *I. obsoleta* reproduces by depositing egg capsules on hard substrates located within the lower intertidal and shallow subtidal, directly linking *I. obsoleta*’s reproductive success to the availability of appropriate substrate, which can be sparse in soft sediment habitats (Brenchley, 1981; Pechenik, 1978). Previous work has shown that these snails deposit their capsules on macroalgae as well as seagrasses, shells, and wood, but that they avoid deposition on rocks (Brenchley, 1982). Given that *G. vermiculophylla* has largely invaded soft sediment habitats where usable substrates for *I. obsoleta* capsule deposition are scarce, we hypothesized that *G. vermiculophylla* may provide a novel, suitable surface for *I. obsoleta* egg capsule deposition. To examine this hypothesis, we quantified the average abundance of *I. obsoleta* egg capsules on *G. vermiculophylla* as well as other common estuarine macroalgae. In addition, we conducted mesocosm experiments to determine if *I. obsoleta* prefers to deposit egg capsules on native substrates or *G. vermiculophylla*. Following our observation that *I. obsoleta* lays thick layers of egg capsules on *G. vermiculophylla* and a second red alga,
Ceramium virgatum Roth, we assessed snail usage of these thalli by quantifying where on the thallus egg capsules were laid. We also examined whether the presence of egg capsules had a negative impact on the growth of these two algal species. We discuss our results within the context of how this new interaction may directly impact I. obsoleta populations, with cascading impacts for the entire soft sediment community.

2. Methods

2.1 Study Site and Species

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

Ilyanassa obsoleta is a deposit feeder that mainly consumes motile benthic diatoms, although it also opportunistically consumes macroalgae and carrion (Connor et al., 1982; Curtis and Hurd, 1981; Guidone et al., 2010; Scheltema, 1964). Natural densities of I. obsoleta (180-1400 snails m⁻²; Pace, 1979; Guidone and Thornber, unpublished data) have a profound impact on mudflat communities, severely reducing benthic microalgal biomass and annelid abundance.
through their grazing activities (Connor et al., 1982; Kelaher et al., 2003; Pace et al., 1979). In Narragansett Bay, *I. obsoleta* reproduction peaks in May-June (Brenchley, 1981; Guidone, personal observation). *I. obsoleta* has separate sexes; however, they are difficult to distinguish without dissection. Therefore, all experiments examining egg capsule deposition used a high number of snails to ensure that multiple females were present.

### 2.2 Survey

We conducted egg capsule-algal surveys at two sites within Narragansett Bay where *I. obsoleta* and *G. vermiculophylla* co-occur: Oakland Beach (41°41.216'N, 71°24.143’W) and Warwick City Park (41°41.263’N, 71°24.381’W), Warwick, RI. These sites were specifically selected to represent the different algal communities in which *G. vermiculophylla* and *I. obsoleta* coexist; thalli at Oakland Beach were primarily attached to shells and small pebbles, while thalli at Warwick City Park were typically found drifting in shallow subtidal algal mats. We conducted surveys in May and June 2011. A single 30 m subtidal transect was laid out perpendicular to the shoreline during low tide at Warwick City Park; two replicate 30 m transects placed 125 m apart were used at Oakland Beach. Algae were sampled at 3 m intervals along each transect using a net (40 cm width, 6 mm mesh) that was dragged across the substrate for 0.5 m. This method ensured our collection of all attached and drifting algal individuals in a standard 0.2 m² area. All algae were returned to the laboratory where they were identified to genus or species level, spun in a salad spinner to remove excess water, weighed, and the number of egg capsules per species recorded. Algal wet mass was adjusted to account for egg capsule mass using an average egg capsule wet mass of 0.0019 g (calculated from 20 individually weighed eggs). To determine temporal and spatial patterns in egg capsule abundance, we analyzed the number of egg capsules per g of algae per sample using a two-way fixed factor ANOVA for differences among sites and
months (JMP version 8, SAS Institute Inc., North Carolina, USA). Due to the uneven distribution
of the individual algal species among the sites and between samples within a site, differences in
egg capsule abundance among algal species were analyzed separately using a one-way ANOVA;
species that were observed in fewer than 5 samples were excluded from this analysis.

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

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

Additionally, we estimated the surface area of all collected thalli in order to compare
results for egg capsule densities per gram of algal tissue to densities per cm$^2$ of algal thallus. Due
to the presence of egg capsules, we could not accurately calculate surface area via image analysis
or other direct tests on the thalli of interest. Therefore, surface area was first estimated for thalli
collected without egg capsules using the acetone-detergent assay (Hicks, 1980). These data were
used to create a regression relationship with thallus wet mass, which allowed us to accurately
estimate the surface area of thalli with egg capsules once we had adjusted their wet masses to
account for egg capsule mass (see Results).
2.4 Substrate Preference

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

Twenty *I. obsoleta* were placed into each mesocosm containing a selection of substrate choices. The assortment of substrates consisted of materials commonly found within Narragansett Bay soft sediment habitats. Ten mesocosms contained *G. vermiculophylla, C. virgatum, Scytosiphon lomentaria,* and wrack of *Spartina alterniflora,* all of which have a generally cylindrical morphology. A second nine mesocosms contained *Ulva* spp. (blade with intact holdfast), *Punctaria* spp., and a shell of the ribbed mussel *Geukensia demissa,* all of which have a non-cylindrical morphology. Substrates were divided based on their overall morphology of “generally cylindrical” or “non-cylindrical” due to inadequate space for all seven substrates within a single mesocosm unit. All substrates were cut to a length of 4 cm; due to logistical challenges, we did not standardize the width or overall surface area of the substrates placed in the mesocosms. As egg capsules were absent from all substrate choices at the start of the experiment, substrate surface area was estimated using Image J (version 1.43, http://rsbweb.nih.gov/ij/). Snails were given one week to lay their egg capsules, after which the substrates were removed and the number of eggs on each substrate, as well as deposited on the mesocosm container itself, were recorded. Results of each substrate experiment were analyzed.
for egg deposition preferences using the multivariate preference index (Lockwood, 1998) with Mathematica (v8.0.4).

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

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

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

3.1 Survey

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

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

We found a strong relationship between surface area:wet mass for both *G. vermiculophylla* (surface area = 3.40 + 16.36* wet mass; $R^2 = 0.90, p < 0.0001$) and *C. virgatum* (surface area = 5.06 + 28.68* wet mass; $R^2 = 0.95, p < 0.0001$), allowing us to accurately estimate the surface area of specimens based on wet mass alone. When comparing egg capsule densities by surface area, capsules were found to be almost twice as abundant on *G. vermiculophylla* than they were on *C. virgatum*, although this difference was not statistically significant (mean *G. vermiculophylla* = 7.75 capsules/cm$^2$; *C. virgatum* 4.17 = capsules/cm$^2$; $t_{16.58} = 0.47, p = 0.65$). Similarly, when egg capsule densities were evaluated per gram of algae, capsules densities were 2.7 times greater on *G. vermiculophylla*, though, in contrast, this was a
significant difference (mean *G. vermiculophylla* 205.87 capsules/g; *C. virgatum* 76.00 capsules/g; $t_{14.58} = 3.49, p = 0.0034$).

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

### 3.3 Egg Capsule Substrate Preference

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

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

Thallus growth did not differ between snail and control treatments for either species, despite the presence of egg capsules (*G. vermiculophylla* $t_8 = 0.11, p = 0.92$; *C. virgatum* $t_9 = 1.43, p = 0.19$; Fig. 3). When snails were removed to examine the impact of egg capsules alone,
G. vermiculophylla grew equally well with capsules present and absent ($t_8 = 1.29, p = 0.23$). In contrast, C. virgatum with egg capsules lost twice as much mass as thalli without egg capsules ($t_8 = 4.091, p = 0.0035$; Fig. 3).

4. Discussion

Invasive species that create three dimensional structures in otherwise two dimensional habitats can have large impacts on their new environments (Crooks, 2002; Wallentinus and Nyberg, 2007). Here, we demonstrated that the invasive macroalga *Gracilaria vermiculophylla* creates a novel substrate in soft sediment communities that is preferentially utilized by the native mud snail *Ilyanassa obsoleta* for egg capsule deposition. While our surveys showed that *G. vermiculophylla* was not preferred more than the native *Ceramium virgatum*, *C. virgatum* at our study sites is often found as an epiphyte on *G. vermiculophylla*, directly linking its abundance to *G. vermiculophylla*’s and potentially amplifying the link between *G. vermiculophylla* and *I. obsoleta* egg capsule deposition. Only one other species, the native *G. tikvahiae*, was found to have a large number of egg capsules present at the field sites. However, within our study system *G. tikvahiae* does not grow attached within the *I. obsoleta* egg capsule deposition zone, indicating it may only be utilized when it opportunistically drifts into shallow subtidal areas containing *I. obsoleta*, as it commonly does at our drift algae site (Warwick City Park). Indeed, given the greater number of egg capsules found at our drift algae site, we can also surmise that *I. obsoleta* either prefers drift algae to attached algae as a deposition substrate, or *I. obsoleta* capsules increase the drag on attached algae, thus causing them to have a higher incidence of holdfast failure and a greater presence in drift mats.
In our surveys, we utilized algal wet mass to calculate egg capsule density per species due to a need for a rapid estimate before algal tissues degraded. Our subsequent analyses of egg capsule densities specifically on *G. vermiculophylla* and *C. virgatum* indicated that egg capsule density based on algal wet mass and algal surface area yield similar values. Therefore, while egg capsule densities are more likely a function of the algal surface area that is available for capsule deposition, algal wet mass offers a quick and accurate way of estimating density across numerous species.

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

Our mesocosm experiments did support our observations from our field surveys. *I. obsoleta* deposited more egg capsules on *G. vermiculophylla* than on the other cylindrically shaped substrates in 8 out of 10 replicates. Although not statistically significant, this was a mean of 4.5 times more capsules laid on *G. vermiculophylla* than on *C. virgatum* and nearly 28 times more capsules than were laid on *S. alterniflora*. Indeed, this experiment was statistically hampered by two factors: a high number of substrate choices (5) compared to only 10 replicates, and in one of these replicates, *C. virgatum* was the only substrate chosen. When given a choice
of non-cylindrical substrates, *I. obsoleta* utilized the mesocosm container as often as it used the other substrate choices, showing no overall preference for any of the substrates presented.

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

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

By creating an abundant substrate utilized by *I. obsoleta* for egg deposition, *G. vermiculophylla* has the potential to extensively impact soft sediment communities (Fig. 4). Primarily, this interaction may directly lead to an increase in *I. obsoleta* reproductive success,
and higher *I. obsoleta* densities. This population increase could negatively impact *I. obsoleta* prey densities, such as motile benthic diatoms (Connor et al., 1982; Pace et al., 1979), thus increasing competition between *I. obsoleta* and other deposit feeders, such as *Diopatra cuprea* (Magnum et al., 1968). In contrast, *I. obsoleta* predators including the invasive green crab *Carcinus maenas*, the moon snails *Polinices duplicatus* and *Lunatia heros*, and migratory birds (Brenchley, 1982) may benefit. Under these assumptions, *G. vermiculophylla* would have an indirect negative effect on *I. obsoleta* prey and an indirect positive impact on *I. obsoleta* predators (Fig. 4). However, these cascading impacts may be dampened if egg capsule predators, including native hermit crabs, the snail *Littorina littorea*, and the crab *C. maenas* (Brenchley, 1982), are able to limit *I. obsoleta* population growth.

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

5. Acknowledgements

We would like to thank J. Bonamusa, B. Konkle, S. Rinehart, R. Sacks, and T. Schollmeier for their help with collecting and processing samples. We would also like to thank
E. Baker for his help at the URI Center for Marine Life Science. This material is based upon work conducted at the Rhode Island EPSCoR supported Center for Marine Life Science, which is supported by the National Science Foundation under EPSCoR Grant #1004057.

6. Citations


Fig. 1 Field survey results for *Gracilaria vermiculophylla* (■), *G. tikvahiae* (□), *Ceramium virgatum* (■), *Polysiphonia* spp. (□), *Punctaria* spp. (□), *Ulva* blades (□), and *Ulva* tubes (□). Algal taxa that were present in the field but did not contain any egg capsules (*Chondria* spp., *Scytosiphon lomentaria*, and *Spermothamnion repens*), or contained fewer than 5 egg capsules (*Cladophora* spp.), are not shown.
Fig. 2 Substrate preference for *Ilyanassa obsoleta* egg deposition. Potential substrates were separated into two trials according to morphology. All data are means ± 1 SE. Different letters indicate significant differences among substrates (Multivariate preference index pairwise post-hoc analysis, p < 0.05)
Fig. 3 *Gracilaria vermiculophylla* and *Ceramium virgatum* growth in mesocosms with snails present and absent. All data are means ± 1 SE. * indicates a significant difference between treatments.
Fig. 4 Hypothesized ecological consequences of *Gracilaria vermiculophylla* facilitation. Solid lines show direct interactions, dashed lines show indirect interactions.