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Research Article

A preliminary assessment of crab predation on epifaunal fouling organisms attached to eelgrass at Martha's Vineyard, Massachusetts, USA

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Abstract

Eelgrass (*Zostera marina*) is an ecologically valuable seagrass which is exposed to a wide range of stressors and has declined worldwide. The proliferation of epifaunal fouling organisms such as the sponge *Halichondria panicea*, colonial tunicate *Botryllus schlosseri*, and solitary tunicate *Molgula manhattensis* represents additional stress for eelgrass. Predation of this epifauna that would otherwise cause harm to eelgrass, will likely reduce their impact. On Martha's Vineyard, an island in the Northwest Atlantic off southern Massachusetts, USA, green crabs *Carcinus maenas* and spider crabs *Libinia dubia* were examined as potential predators of sponges and tunicates attached to eelgrass. Crabs were somewhat starved for one week and then, in the lab, put in enclosures with three eelgrass shoots and tunicate/sponge epifauna. Consumption of prey items and crab survival were measured at one and 24 hours. After one hour, *C. meanas* did not consume any prey, while predation by *L. dubia* did occur. After 24 hours, *C. meanas* had still not consumed any tunicates or sponges, while *L. dubia* consumed eelgrass with *H. panicea* (100%); *B. schlosseri* (40% completely, 40% partially, and 20% unconsumed); and *M. manhattensis* (60% completely, 20% partially, and 20% unconsumed). High densities of *M. manhattensis* often occurs on eelgrass at Martha's Vineyard (up to 6,700 per m^2), thus we sought to determine a *M. manhattensis* consumption rate for *L. dubia* in the lab. A single *L. dubia* can consume at least 30 *M. manhattensis* in a 24-hour period. Because of the recent declines in eelgrass acreage, understanding the ecological mechanisms that minimize impacts to eelgrass can be advantageous to both the individual pant and the meadow. Natural predation by *L. dubia* in eelgrass meadows heavily fouled by tunicates and sponges is an important ecosystem function that may contribute to controlling the epifauna, and thus maintaining healthy eelgrass and eelgrass habitat. However, the extent to which crabs control eelgrass epifauna in the field is unknown. Our results were determined in a laboratory setting and further work should be done to confirm that similar results will be found in the field.

Key words: *Botryllus schlosseri*, *Carcinus maenas*, *Halichondria panicea*, *Libinia dubia*, *Molgula manhattensis*, Northwest Atlantic, *Zostera marina*

Introduction

Eelgrass

Eelgrass (*Zostera marina* Linnaeus, 1758) has been widely recognized as an ecologically important nearshore seagrass that serves as habitat for a wide range of fish and invertebrates (Thayer et al. 1984). Eelgrass provides many important ecologic functions including sediment stabilization, coastal protection, and sequestration of blue carbon (Roman and Able 1988; Barbier et al. 2011; Röhr et al. 2018).

Seagrasses are exposed to a wide range of anthropogenic and natural stressors (Short and Wyllie-Echeverria 1996). Global distributions of seagrasses have been declining and the rate of that decline has recently accelerated (Short et al. 2007; Waycott et al. 2009). For example, in Massachusetts, eelgrass, the dominant seagrass species, has experienced extensive declines in acreage. Since the 1990’s, some of the highest annual rates of decline have been in the coastal ponds of Martha’s Vineyard, where declines in areal distribution were approximately 7–9% per year (Costello and Kenworthy 2011).

Eelgrass has been widely used as an indicator species, due to its sensitivity to changes in water quality (Dennison et al. 1993; Trowbridge 2009). Reductions in water clarity can trigger substantial declines in vitality of individual eelgrass shoots (Dennison and Alberte 1982; Dawes 1998; Ochieng et al. 2010) and areal coverage of existing meadows (Moore et al. 1997).

Epifauna on eelgrass: sponges and tunicates

Organisms such as sponges (Demospongiae) and tunicates (Ascidiacea) that colonize eelgrass block sunlight from reaching the blade, disrupting photosynthesis and decreasing growth rates (Wong and Vercaemer 2012; Long and Grosholz 2015; Colarusso et al. 2016; Carman et al. 2016). Sponge and tunicate smothering overgrowth can similarly impact other natural substrates such as coral (Mclean et al. 2015) and red algae (Barthel 1988).

Northwest Atlantic eelgrass meadows, including at Martha’s Vineyard, are commonly home to native and non-native epifaunal species that grow on eelgrass leaves including the sponge *Halichondria panicea* (Pallas, 1766), the colonial tunicates *Botryllus schlosseri* (Pallas, 1766) and *Botrylloides violaceus* Oka, 1927, and solitary tunicate *Molgula manhattensis* (DeKay, 1843) (Wong and Vercaemer 2012; Carman et al. 2016). An abundance of epifaunal invertebrates, especially sponges and tunicates, has a negative effect on seagrasses (Williams 2007; Carman and Grunden 2010; Wong and Vercaemer 2012; Carman et al. 2016; Colarusso et al. 2016). The full impact of epifaunal tunicates and sponges on seagrasses (Williams 2007) is poorly understood and has rarely been quantified. Even a minimal amount of tunicate or sponge fouling can substantially reduce the quantity of light reaching seagrass leaves (Wong and Vercaemer 2012). Reduction in light lowers photosynthesis in plants (Williams and McRoy 1982; Dennison and Alberte 1982; Dennison 1987; Ochieng et al. 2010), which in turn can reduce the number of leaves per shoot, shoot growth rate, and shoot density (Short et al. 1995). Colarusso measured a 75% reduction in light transmission due to the presence of 5 different species of invasive tunicates that occur on Martha's Vineyard (P. Colarusso *pers. comm.*). Epifaunal sponges and tunicates have the potential to exert a major influence on overall ecosystem functioning and when in great abundance, their influence can be detrimental (Bell 2008; Colarusso et al. 2016). Therefore, natural predators are necessary for their contribution toward balancing the ecosystem by keeping the sponge and tunicate populations on eelgrass minimal.

Potential predators of epifauna on eelgrass

Epiphytic and epifaunal growth on seagrasses is generally kept in check by two separate processes. First, during the growing season, leaf production occurs rapidly and older leaves are cast off. Rapid leaf turnover rates can prevent the accumulation of epiphytic biomass (Peterson et al. 2007). Grazing by small organisms, primarily gastropods, isopods, and amphipods, is a second process that can dramatically reduce the biomass and abundance of epiphytes (Neckles et al. 1994; Nelson 1997). Small predaceous neogastropods also graze on tunicate recruits but not on adult tunicates (Whitlatch and Osman 2009). Northwest Atlantic eelgrass meadows are home to predatory decapod crabs including the green crab *Carcinus maenas* (Linnaeus, 1758) and spider crab *Libinia dubia* H. Milne Edwards, 1834. Larger grazers such as these decapod crabs may also be able to reduce the biomass of epifaunal sponges and tunicates on eelgrass.

Predation by crabs such as *C. maenas,* has been identified as a serious threat to commercial bivalve resources. Many studies have concentrated on the green crab, *C. maenas*, because of its abundance, extensive distribution in the coastal zone of northeastern United States and Canada and Europe, predation on bivalves (Ropes 1989), and destruction of eelgrass (Neckles 2015; Matheson et al. 2016).

Crabs often have diets that include macroalgae (McRoy and Helfferich 1980; Ropes 1989; Poore et al. 2017). Ropes (1989) examined the stomach contents of five crab species: green crab *C. maenas*; blue crab *Callinectes sapidus* Rathbun, 1896; lady crab *Ovalipes ocellatus* (Herbst, 1799); mud crab *Neopanopeus texana* (*Dyspanopeus texanus* (Stimpson, 1859)); and spider crab *L. emarginata* in nearby Rhode Island, and found that *C. meanas* tended to be carnivorous and *L. dubia* tended to be herbivorous. Eighteen percent of the stomach contents of *C. meanas* contained plant foods, whereas 75% of the stomach contents of *L. dubia* contained plant foods (Ropes 1989). *Carcinus maenas* tended to prey on small snails (Osman and Whitlatch 2004). *Libinia dubia* consumed *Ulva, Gracilaria, Chondria, Padina, Hypnea* (Stachowicz and Hay 1999) and other members of eelgrass ecosystems, including the stinging jellyfish *Gonionemus* sp. (Carman et al. 2017), and may also consume other invertebrates such as tunicates and sponges.

Carcinus maenas in northern New England and Maritime Canada have wreaked havoc on eelgrass meadows in some areas. For example, *C. meanas*

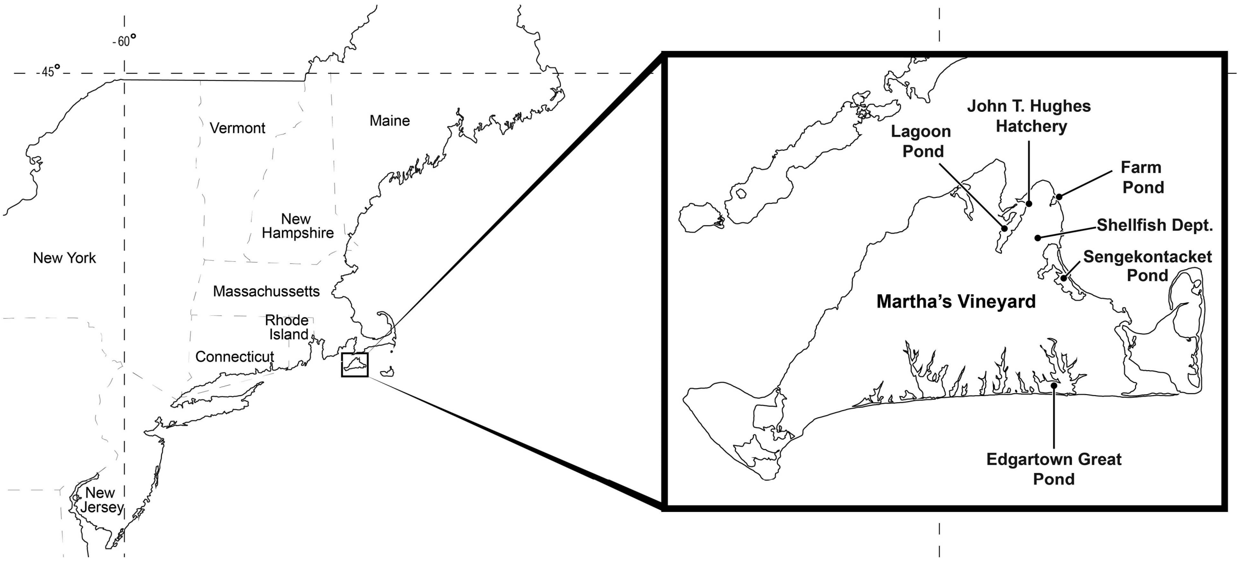

Figure 1. Map of Study Site.

did not consume eelgrass shoots in New Hampshire but destroyed naturally occurring eelgrass and transplanted eelgrass while foraging for clams (Davis et al. 1998). *Carcinus maenas* reduced eelgrass biomass by damaging eelgrass rhizomes and shoots when burying for shelter and digging for prey (Matheson et al. 2016), including cutting basal meristems (Neckles 2015). *Carcinus maenas*, in particular juveniles, may graze directly on eelgrass shoots (Malyshev and Quijon 2011; Garbary et al. 2014), but is probably not a preferred food.

There is little known about crab predation on sponges. *Libinia dubia* decorates itself with unpalatable sponges to protect against fish predation (Stachowicz and Hay 2000). Perhaps *L. dubia* also consumes sponges. *Halichondria* contain siliceous spicules that are not a deterrent to predation, instead chemical defenses or secondary metabolites deter predation (Waddell and Pawlik 2000a, b). Yet, snails, nudibranchs, fish, turtles, sea urchins, and sea stars will consume *H. panicea* (Knowlton and Highsmith 2000; Waddell and Pawlik 2000b; McClintock et al. 2005).

We investigated the possibility that decapod crabs may prey on epifaunal tunicates and sponge species growing on eelgrass.

Materials and methods

Study area

The experimental invertebrate animals in our study were obtained from Farm Pond (41.44756; −70.55694), Lagoon Pond (41.44816; −70.59022), Sengekontacket Pond (41.41713; −70.56956), and Great Pond (41.3580; −70.48845) which are semi-enclosed coastal ponds that harbor eelgrass beds on the eastern side of the island of Martha's Vineyard in Massachusetts, USA (Figure 1). Farm Pond covers 33 acres with a mean depth of 1.5 m; Lagoon Pond covers 544 acres with a mean depth of 3 m;

Sengekontacket Pond covers 726 acres with a mean depth of 1 m; and Great Pond covers 4,850 acres with a mean depth of 1.1 m. All four ponds have a tidal range of < 1 m. Farm and Lagoon Ponds are located in the town of Oak Bluffs, separated by about 4 km of land; Sengekontacket Pond is located in the towns of Oak Bluffs and Edgartown; Great Pond is located in the town of Edgartown. These ponds are the sites of ongoing research (Carman et al. 2014, 2016, 2017, 2019; Colarusso et al. 2016). We have recently observed *Halichondria panicea, Botryllus schlosseri,* and *Molgula manhattensis* attached to eelgrass, and larger crabs in all four ponds. Permission to collect invertebrates at these field sites was obtained through Masssachusetts state licensure to D. Grunden (Oak Bluffs, Massachusetts Shellfish Constable).

Trial #1: Identification of predatory crab species

Experimental lab trials were conducted during August 2016, to identify which, if any, larger, local crab species may prey on *H. panicea, B. schlosseri,* or *M. manhattensis* attached to eelgrass. Crabs were trapped in Farm and Lagoon Ponds the week before the experiment using crab traps. The crabs were kept in cages for one week on the seafloor in a relatively barren area of Farm Pond, making them at least somewhat starved. No cannibalism occurred. At the start of the experiment, crabs were retrieved from the pond and transported in tubs of seawater to the laboratory at the Oak Bluffs Shellfish Department on Martha's Vineyard. Crab size was measured (carapace width). The same day crabs were removed from the crab cages, *H. panicea, B. schlosseri,* and *M. manhattensis* attached to eelgrass were collected from the eelgrass meadow in Sengekontacket Pond by snorkeling. Crabs and eelgrass were transported separately to the lab.

Experiments were conducted in enclosed tubs (42 cm × 33 cm × 17 cm) of seawater. Flow through seawater was not used because of the large number of tubs and to limit the introduction of any unwanted organisms. Three similar lengths of eelgrass with *B. schlosseri*, *H. panicea*, or two adult *M. manhattensis* of approximately the same size were placed in a tub with a single crab. Five replicate tubs for each crab species were prepared (Supplementary material Table S1). Control tubs consisting of crabs only (with no tunicates or sponge) and tunicates and sponge only (with no crabs) were also set up (Table S1). Consumption was divided into three categories: partially consumed (any amount of consumption), completely consumed (completely consumed including the eelgrass), or unconsumed. *Halichondria panicea*, *B. schlosseri, M. manhattensis,* and crab condition (dead or alive) were recorded at two time-points (one hour and 24 hours). We verified our assumption that tunicate and sponge disappearances were due to predation by the crabs by 1) direct observation of crabs consuming the tunicates and sponge, and taking representative photographs of the consumption, and 2) running tunicate and sponge only controls with the experimental trial to assess tunicate and sponge mortality independent of the crabs.

Trial #2: Crab predation on density of Molgula manhattensis

As a follow-up to our first trial which documented predation on *H. panicea, B. schlosseri,* and *M. manhattensis* by *L. dubia*, we assessed *L. dubia* predation at higher *M. manhattensis* densities. We ran a predation experiment in the lab, similar to Trial #1, in August 2017, at three additional *M. manhattensis* densities: 10, 20, and 30 *M. manhattensis* of approximately the same size. The experiment was carried out at the Massachusetts Division of Marine Fisheries John T. Hughes Hatchery and Research Facility in Oak Bluffs (Figure 1). As with the 2016 experiment, crabs were trapped during the week before the experiment and held in Farm Pond without supplemental food. Specimens of *M. manhattensis* were collected by snorkeling in the eelgrass meadow in Edgartown Great Pond (EGP) the day before the experiment, transported in buckets of seawater to the lab, and placed in a large flow through seawater wet table. As in the 2016 trial, *L. dubia* were obtained from the crab cage in Farm Pond immediately prior to the start of the experiment. Crab size was measured (carapace width) and the sex determined. Crabs were placed in tubs with a given number of tunicates (10, 20, or 30 adult *M. manhattensis* removed from eelgrass); with 6 replicates per tunicate density. An equal number of control tubs with crabs only and tunicates only were also prepared. The number of tunicates consumed (partially, completely, or unconsumed) and crab condition (dead or alive) after one hour and 24 hours were recorded.

Molgula manhattensis *field density determination*

To confirm that the *M. manhattensis* densities used in our predation trials were realistic compared to what the crabs encounter in the wild, tunicate densities were recorded in August 2017, by counting the number of *M. manhattensis* in representative quadrats (25 cm × 25 cm) in EGP. Quadrats were placed randomly along a 10 m transect line in eelgrass (after Carman et al. 2016). Tunicates were collected by snorkeling and counted. This method likely represents the true *M. manhattensis* abundance that can be found in EGP and other marine ponds of Martha's Vineyard and the number of *M. manhattensis* that a *L. dubia* could encounter in a 24-hour period.

Results

Trial #1: Identification of predatory crab species

Both male and female crabs were used in our study. Mean carapace width was 61 mm ± 10 S.D. in *Libinia dubia* (n = 10) and 65 mm ± 4 S.D. in *Carcinus maenas* (n = 10).

After the one hour and 24-hour experimental periods, only *L. dubia* showed any feeding activity on the tunicates and sponge attached to eelgrass (Figure 2); *C. maenas* did not display any predation nor did they kill

Figure 2. Spider crab eating *Molgula*. Photo by M. Carman.

the molgulids (*M. manhattensis*). We observed predation by *L. dubia* during the first hour of our trials (Table S1). After one hour, *L. dubia* consumed eelgrass with *B. schlosseri* (40% partially consumed and 60% unconsumed), *M. manhattensis* (40% partially consumed and 60% unconsumed), and *H. panicea* (20% completely consumed and 80% partially consumed). No crab death occurred in the first hour.

After 24 hours, *L. dubia* consumed eelgrass with *B. schlosseri* (40% completely consumed, 40% partially consumed, and 20% unconsumed), *M. manhattensis* (60% completely consumed, 20% partially consumed, and 20% unconsumed), and *H. panicea* (100% completely consumed) (Table S1). No crab death occurred during the 24-hour experiment period. Sometimes, spider crabs consumed the sponge by peeling it off of the eelgrass, eating the sponge and eelgrass separately, and at other times, they consumed the sponge and eelgrass without separating. Often small pieces or fragments of *B. schlosseri* and *H. panicea* remained (partially consumed) after the 24-hour experiment period. No mortality of crabs, sponges, or tunicates occurred in any of the treatments during the experiment.

Trial #2: Crab predation on density of Molgula manhattensis

Twenty-six *L. dubia* were collected from the crab traps to assess the maximum amount of *M. manhattensis* that a *L. dubia* could consume in a

Figure 3. *Molgula* with internal tissue (lower left), internal tissue with tunic removed (top), and tunic with internal tissue removed (lower right). Photo by M. Carman.

24-hour period. Mean carapace width was 76 mm ± 6 S.D. (n = 26). As in Trial #1, tunicate consumption began within the first hour (Table S2). After one hour, *M. manhattensis* was 6% completely consumed, 8% partially consumed, and 86% unconsumed. Interestingly, *L. dubia* commonly consumed *M. manhattensis* partially by only eating the internal tissue and leaving the tunic. Often a crab (*Libinia dubia*) would grasp a solitary tunicate (*Molgula manhattensis*) with its claws, puncture and tear open the tunic (exterior layer) using both claws, then treat the tunic like a feed sack, using one claw to hold the sack open and the other claw to select out internal tissue to eat, leaving the tunic unconsumed (Figures 2, 3). In some instances, the crabs ate the entire tunicate including the tunic and internal tissue (Figure 3). After 24 hours, *M. manhattensis* was 14% completely consumed, 66% partially consumed, and 20% unconsumed (Table S2). No crab death occurred. The greatest number of *M. manhattensis* consumed within 24 hours by a single *L. dubia* was 30 (partially + completely consumed). While 30 molgulids was the greatest density offered, they may be able to consume more than 30 in a 24-hour period. None of the experimental crabs, control crabs, or control tunicates died.

Molgula manhattensis *field density determination*

Molgula manhattensis abundance was estimated in August 2017, using 20 quadrat collections in EGP. *Molgula manhattensis* abundance ranged from 8–420 *M. manhattensis* per quadrat (Figure 4), a density of up to 6,700 per m^2. These values are not absolute numbers of *M. manhattensis* in the search area,

Figure 4. Density of *Molgula* on eelgrass from Edgartown Great Pond. Photo by M. Carman.

but rather, these values should be considered as the probable representative quantity of *M. manhattensis* that may occur in eelgrass meadows in EGP and other marine ponds on Martha's Vineyard. *Molgula manhattensis* are sessile so there is no movement, while *L. dubia* are motile and they could potentially travel the distance equivalent of more than one quadrat (25 cm) within a 24-hour period and thus have access to more than 30 molgulids (the maximum amount offered and consumed by a single *L. dubia* in 24 hours).

Discussion

We documented the novel trophic interaction of *L. dubia* feeding on eelgrass, sponges, and tunicates. This interaction may directly and indirectly facilitate the health of eelgrass beds. Our results are the first example that we are aware of that demonstrate predation on eelgrass with *H. panicea,* *B. schlosseri,* and *M. manhattensis* by *L. dubia.* In contrast, we did not find any predation on these species by *C. maenas*. The removal of these epifaunal, fouling organisms from eelgrass by *L. dubia* may directly provide a significant ecological impact on eelgrass communities. A reduction in the number of leaves per shoot and canopy height represents a reduction in the complexity of the habitat for fish and other species that utilize it. Hughes et al. (2002) showed that fish community abundance and diversity is dependent on eelgrass meadow complexity. Thus, by reducing eelgrass meadow complexity, sponges and tunicates may be indirectly impacting fish abundance and diversity.

Extensive fouling of eelgrass can weigh down leaves and causes them to break off (Wong and Vercaemer 2012). This could lead to a benefit for these fouling organisms by providing a transport mechanism (rafting) allowing for colonization of new areas in the eelgrass meadow and in neighboring bays (Worcester 1994). Further, extensive fouling may be compromising some of the ecological functions that eelgrass provides. For example, juvenile bay scallops and blue mussels that attach to eelgrass leaves, derive benefit from being up in the water column. This elevated position serves as a refuge from benthic predators and allows greater access to food resources (Ambrose and Irlandi 1992). The elevated position is lost when eelgrass leaves, fouled by sponges or tunicates, become negatively buoyant and lay over on adjacent shoots on the seafloor.

Carcinus maenas does not appear to be contributing to the removal (consumption) of epifauna on eelgrass (Davis et al. 1998; Garbary et al. 2014; Neckles 2015; Matheson et al. 2016). Similarly, *C. maenas* did not prey on the solitary tunicate *Styela clava* Herdman, 1881, on oysters in aquaculture enclosures (http://www.exoticsguide.org/styela_clava), nor did they consume *Ciona intestinalis* (Linneaus, 1767) (Carver et al. 2003). However, *C. meanas* may have needed more time to acclimate to the lab setting in our experimental trial and trials of longer duration should be tried.

It is not known if predation by *L. dubia* would benefit or harm eelgrass or if it would depend on the predation method and how destructive *L. dubia* is while ripping epifauna off an eelgrass shoot. Removing only the section of leaf that has the epifauna would not likely harm the plant, but removing more living plant tissue may. Our study represented a single point in time. Additional experiments should be conducted to see if *L. dubia* displays a preference for consuming eelgrass with or without epifauna, including sponges and tunicates. Further, it is unknown if the feeding behavior of *L. dubia* would destroy (kill/uproot) eelgrass plants laden with an abundance of tunicates or if *L. dubia* would consume only the part of the eelgrass plant where tunicates tend to live (eelgrass leaves and not the basal area of the plants), and thus not destroy the plant. Unlike *L. dubia*, *C. maenas* did not display any feeding activity on the sponge and tunicate epifauna in our study. However, its foraging behavior can be destructive to eelgrass (Neckles 2015; Matheson et al. 2016).

Because of the recent declines in eelgrass acreage, finding ways to enable eelgrass growth can be advantageous to both the individual plant and the meadow. The natural removal of tunicates and sponges attached to eelgrass leaves without causing harm to the plant should reduce the impact of tunicate and sponge overgrowth. During summer eelgrass plants may be stressed from a heavy abundance of *M. manhattensis* fouling their leaves and may be further stressed by cropping of the plants, i.e. by predation and removal of eelgrass leaves with *M. manhattensis* by *L. dubia*. Large masses of easily accessible tunicates can be tempting to *L. dubia* as they have the capacity to consume large quantities of *M. manhattensis* in a relatively short period of time. *L. dubia* may also inadvertently consume eelgrass while it feeds on attached epifauna.

While our field *M. manhattensis* density counts in EGP do not reflect absolute densities, they are similar to other quadrat analyses on Martha's Vineyard (Carman et al. 2016; Colarusso et al. 2016). They also document a baseline that confirms our lab experiments were realistic. It is likely that *L. dubia* will encounter these species of tunicates and sponge in the eelgrass meadows of Martha's Vineyard and sometimes in high densities.

In our experimental trials, *L. dubia* consumed up to 30 adult *M. manhattensis* in a day (the maximum offered). They may be able to consume *M. manhattensis* at a greater rate. It is possible that in the wild, given a variety of prey options, *L. dubia* consumes fewer *M. manhattensis*. However, our observations showed that *L. dubia* had no reluctance in consuming the molgulids, and that consumption of larger numbers of molgulids had no negative effect on their survival. Further work should be done to determine if natural predator densities, and the timing of their abundance, coincide with high density fouling.

Both male and female crabs were used in our study. No noticeable difference in consumption between sexes was observed but a further study should be done to see if there is a difference in female and male consumption.

The extent that crab predation plays in bio-controlling tunicates and sponges in eelgrass beds, is not well understood. However, if native *L. dubia* can function as a bio-controller of fouling species, but non-native *C. maenas* does not, then this would have implications for a broader understanding of the impacts of *L. dubia* and *C. maenas* to native habitats. At the time of our experimental trials we did not have access to eelgrass fouled with invasive species of tunicates, but we recommend further studies to test crab consumption of invasive tunicates. The negative effect of additional, native and non-native fouling organisms on eelgrass may compound the epifaunal impact to eelgrass. It is unknown if *L. dubia* will graze on other epifaunal tunicates such as, *B. violaceus, Diplosoma listerianum* (Milne-Edwards, 1841), or *Didemnum vexillum* Kott, 2002. Freeman et al. (2016) found that

Hemigrapsus, another invasive crab in the Northeast, preferred native *Molgula* to other invasive tunicates. Although our study looked at *C. maenas*, the conclusion by Freeman et al. (2016) that invasive crabs prey on native tunicates disproportionally, allowing invasive tunicates room to expand is worth noting, particularly because that is not what we found with *C. maenas*. Carver et al. (2006), also found that *Carcinus* crabs were less interested in eating tunicates than were rock crabs.

Siliceous and calcareous spicules are present in *H. panicea* (Wong and Vercaemer 2012). There is conflicting evidence about the presence of spicules in some sponge functioning as a deterrent to predation (Waddell and Pawlik 2000b; McClintock et al. 2005). In our study, the spicules in *H. panicea* did not appear to deter predation by *L. dubia*, and *H. panicea* did not appear to have any overgrowth or attachment of other organisms. It is unknown if spicules inhibited *C. maenas* predation in our trials.

Fragments (from partially consumed samples) that were created by *L. dubia* during our feeding trials may have the ability to reattach and grow on other substrates. Fragments of sponges and colonial tunicates, including *Halichondria, Botryllus*, and *Didemnum* have the ability to reattach and grow through asexual reproduction (Hoffmann et al. 2003; McCarthy et al. 2007; Bullard et al. 2007; Carman et al. 2014). Re-established fragments can also be sexually reproductive and thus add larvae to the ecosystem (Stoner 1989; McCarthy et al. 2007; Reinhardt et al. 2012). Therefore, although consumption of tunicates and sponges may help eelgrass growth, it also might perpetuate growth of additional tunicates and sponges on eelgrass and this concern needs further investigation.

Our report adds to the knowledge that crab predation is likely occurring in eelgrass meadows on sponge and tunicate epifauna. The extent to which *L. dubia* controls eelgrass epifauna in the field is unknown. *Halichondria panicea, B. schlosseri, M. manhattensis, C. maenas,* and *L. dubia* live elsewhere in Northwest Atlantic eelgrass habitats and these ecosystems could be experiencing similar interactions. Our results were determined in the laboratory and further work should be done to confirm similar results in longer term studies and in the field.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Predation on tunicates and sponges attached to eelgrass experiment results (August 4, 2016).
Table S2. Predation on density of *Molgula* experiment results (August 23, 2017).

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