

Case Study: Is Laying Roe Friend or Foe? Investigating the relationship between *Phyllaplysia taylori* and *Zostera marina* in False Bay, San Juan Islands, WA

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Abstract

Estuarine ecosystems, similar to that of False Bay in the San Juan Islands of WA, are indispensable and therefore high priority in conservation efforts due to their highly specialized and endemic inhabitants. Anthropogenic influences on estuarine ecosystems (dredging, trawling, coastal development, eutrophication, compound effects of climate change) damage subtidal and intertidal estuaries. The eelgrass species, *Zostera marina*, is prevalent in both East and West Coast estuaries. Eelgrasses require approximately 24% more photosynthetic light than other angiosperms, making them more vulnerable to environmental change, such as rising sea surface temperatures (Orth et. al. 2006). This study examines the relationship between facilitative sea hare grazers, *Phyllaplysia taylori*, and their respective substrate of choice, *Zostera marina*. We investigated the abundance of *P. taylori* in False Bay and found a linear relationship between surface and subsurface egg mass abundance. In the field, data was collected on the characteristics of where egg masses were laid. The analyses revealed that height location on the blade was a significant factor for egg mass laying, but the epiphyte coverage surrounding the egg mass was not. Additionally, we ran a series of manipulative experiments to get a better understanding of the multivariable relationship between *P. taylori* and *Z. marina*. While *P. taylori* keeps the eelgrass blades relatively clean as a grazer, their eggmasses can block up to 69% of light to the eelgrass plant. Here we offer a case study of False Bay to further understand the symbiosis between *Z. marina* and *P. taylori*, which can help to inform the ecological conditions needed to support shrinking *Z. marina* beds.

Introduction

Zostera marina eelgrass is a foundational species creating nearshore habitat in the Pacific Northwest, where dense submerged meadows provide nursery, foraging, and refugia for juvenile salmon, crabs, bivalves, seabirds, mollusks, and many other organisms (Short et. al. 2011). In addition to supporting biodiversity, eelgrass beds stabilize sediments, reduce erosion, improve water quality, and store essential molecules, like carbon, nitrogen, and phosphorus, making them important contributors to coastal ecosystem function and resilience (Ward M. & Beheshti K. 2023). Although seagrass habitats occupy only about 0.1% of the coastal ocean, their annual rate of carbon accumulation is roughly $83 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Kennedy et al. 2010). The local economy also benefits from healthy eelgrass, as the nurseries support local commercial fishing stocks. Eelgrass also serves as an important storm barrier by protecting shorelines and attenuating violent wave action (Short et. al. 2011).

Eelgrass ecosystems are also highly sensitive to environmental stressors, particularly nutrient enrichment (Balata et al. 2010). Coastal eutrophication is the runoff of excess nutrients from land into the ocean (Pelletier et al. 2024). An overabundance of nutrients can reduce seagrass productivity, directly and indirectly, by stimulating epiphyte and macroalgal growth that limits light availability to host plants (Balata et al. 2010). Since epiphytes often respond strongly to nutrient input, changes in nutrient loading can alter the balance between eelgrass growth and surface fouling, potentially affecting meadow persistence and function (Balata et al. 2010). In urban coastal regions, runoff may further intensify these pressures and contribute to long term habitat decline and lack of species resilience.

This case study examines interactions between the charismatic zebra green sea hare, *Phyllaplysia taylori*, and eelgrass beds at False Bay, San Juan Island, WA. *P. taylori* relies on the availability of balanced eelgrass habitat in the Pacific Northwest, as it is endemic to the region. This particular sea hare is perfectly adapted to blend in with blades of eelgrass, grazes on encrusting epiphytes, and deposits its eggs on the same substrate, linking its life history closely to eelgrass habitat (Tanner 2018). By removing abundant epiphytes that can interfere with photosynthesis, this grazer plays an important role in maintaining eelgrass condition and meadow health (Tanner 2018). Historically, there was one paper in the literature authored by Cecilia B. Bridges in 1975 that describes the larval development of *P. taylori*, but the rest of the literature is limited to Dr. Richelle Tanner's work. This results in numerous gaps in the understanding of the ecological importance of this endemic sea hare.

False Bay is a dynamic mudflat with extreme tidal fluctuations and is surrounded by residential development and agricultural land despite its marine protected area designation. Over the past decade and a half, the ecosystem composition has shifted as eelgrass, sand dollars, and other species experienced a decline (J. Allen, personal communication). Instead, opportunistic species such as *Ulva* green algae and the bubble snail *Haminoea vesicula* dominate the dynamic mudflats (Mackenzie 2005). Through our team's field observations, we decided to explore the density of *H. vesicula* egg masses, as well as their grazing behavior when compared to *P. taylori*. A massive *Ulva* bloom was observed in False Bay during field work, indicating a disturbance in the ecosystem and making False Bay an ideal candidate for this case study.

False Bay eelgrass beds are vulnerable to nutrient enrichment and algal blooms from agricultural runoff and other stressors, with additional concerns from warming temperatures and eelgrass wasting disease. Therefore, understanding whether *P. taylori* contributes to eelgrass health and maintenance is an important step toward assessing coastal nearshore habitat resilience in this system (Balata et al. 2010; Aoki et al. 2025). We wanted to investigate the different behaviors of *P. taylori* and how they impact eelgrass health. We hypothesized that *P. taylori* increases eelgrass photosynthetic productivity by grazing on red algae epiphytes and increasing light attenuation to the blade. While *P. taylori* may graze light-blocking epiphytes off of eelgrass blades, we hypothesized that egg masses block light from reaching eelgrass blades, possibly impacting photosynthesis. Additionally, *P. taylori* presence should indicate a healthy eelgrass bed because they preferentially lay on clean, green blades. This analysis will further allow us to evaluate the health of the eelgrass beds of False Bay through a charismatic indicator species.

Methods

Field Study

Eelgrass beds in False Bay, San Juan Island, WA (48° 28' 56" N 123° 04' 16" W) were sampled for four consecutive days during mid-day low tide (-1.75 ft, -1.77 ft, -1.65 ft, -1.36 ft). Using a 0.25 m² quadrat, we haphazardly sampled by throwing the quadrat in the air. Using a Garmin GPS, we logged the coordinates where the quadrat landed, held the quadrat in place, and swept clear the *Ulva lactuca* coverage. For the first 14 replicates (data collected on 6/30 and 7/1), we counted the amount of *P. taylori* egg masses, *Haminoea vesicula* egg masses, and *P. taylori* adults from a surface level view. We then examined the first ten *Z. marina* blades found and noted the presence of any egg masses or *P. taylori* adults. If an egg mass was located, we noted its relative height on the blade (low, medium, high), as well as the surrounding epiphyte coverage (clean, moderate, dirty). After the ten blades, we sifted through the remaining blades within the quadrat and counted the total number of *P. taylori* egg masses and adults. On the last day of sampling (7/2), we haphazardly collected data on surface counts for 18 quadrats after confirming a linear relationship between *P. taylori* egg mass surface count and total count within a quadrat. The linear relationship was confirmed by a linear regression (Fig. 2). These quadrat counts were categorized into three distinct regions: the land edge (ledge), the middle, and the sea edge (sedge) of the bed.

Laboratory Experiments

Laying Preference



Figure 1. The constructed design for our laying experiment.

Using a 3 x 5 seedling container, we lined each compartment with 4 blades of eelgrass: 1 clean blade with a ~1.5 cm egg mass, 1 clean blade without an egg mass, 1 epiphyte-covered blade with a ~1.5 cm egg mass, and 1 epiphyte-covered blade without an egg mass. Each blade was measured to the same length to cover two sides and the bottom of a compartment. The order by which blades were placed within each compartment was determined by a random number generator. We obtained 30 *P. taylori* individuals from our sea tables that had been collected from False Bay in the weeks prior. We randomly generated numbers 1-15 for where to place

the individuals until each compartment had two *P. taylori*. We sealed the container with a mesh lining using rubber bands and tied strings. The container was secured in an upright position in the sea table with constant flowing sea water and left for 5 days. After 5 days, we unwrapped the mesh and counted the number of egg masses laid and noted additional observations such as mortalities and detached egg masses suspended in the water column.

Epiphyte Grazing

Epiphyte-covered eelgrass blades were cut into 10cm pieces. The blades were photographed on both sides, with an “L” carved into the base of each eelgrass blade to differentiate the two sides in photos. We selected four visibly smaller *P. taylori* from the sea table, collected from False Bay, and weighed them. Their masses were 1.6g, 1.6g, 1.8g, and 1.8g. We then weighed *H. vesicula* in groups until their total mass equaled that of the *P. taylori* counterpart. These groups of animals were isolated into eight mesh lined containers, and a 10 cm blade of epiphyte-covered eelgrass was added to each container. The animals remained in these containers for 5 days. Each day, we rotated the location of paired containers to standardize the amount of water flow each replicate received. We also pipetted out the fecal waste that built up at the bottom of the containers. At the end of the experiment, the blades were removed and photographed again in order to analyze them for a difference in epiphytes before and after. Using side by side images of each side of each blade, we classified “grazed” or “not grazed” based on visual differences.

Light Attenuation

To determine the influence of various materials on the photosynthetic productivity of eelgrass, we used an Apogee MA-510 Full-Spectrum Quantum light sensor placed flat on a deck. Light measurements were collected in terms of Photosynthetically Active Radiation (PAR, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), which refers to the range of light from 400 to 700 nanometers that is absorbed in photosynthesis. For each trial, we measured control ambient light by recording the light meter reading every 5 seconds for a total of three values to obtain an average reading and account for cloud coverage variation. We then covered the light probe with a layer of our substrate of interest: *H. vesicula* egg mass, light *P. taylori* egg mass, dark *P. taylori* egg mass, clean *Z. marina* blade(s), dirty *Z. marina* blade, *Ulva lactuca* layer(s), and *Ulva intestinalis*. Each of these treatments were repeated for a total of three trials. We divided the average of each treatment trial reading by the average control in order to determine the proportion of light penetration.

Data Analysis

We created linear regressions to compare surface and total egg mass counts for both *P. taylori* and *H. vesicula* to determine a correlation between apparent surface and subsurface egg mass abundance. Kruskal-Wallis tests were conducted to determine if there was a difference in the number of *P. taylori* and *H. vesicula* egg masses visible from the surface in three different regions of the eelgrass bed (land edge, middle, and sea edge). T-tests were used to compare *P. taylori* and *H. vesicula* surface egg masses within each region. To ensure that our two factors, height on blade and epiphyte coverage, were independent of one another and had no compounding effects, a Chi-squared test of independence was run. Repeated-measures one-way ANOVA tests were conducted to detect differences in the heights of egg masses on the eelgrass blade and the level of

epiphytic cover around them for each of the focal species. Tukey post-hoc tests were then used to compare the different blade elevations and epiphyte levels to each other. Finally, one-way ANOVAs were conducted to detect differences in the average PAR ratios under different natural materials found in the eelgrass bed.

Results

Surface-Total Regression

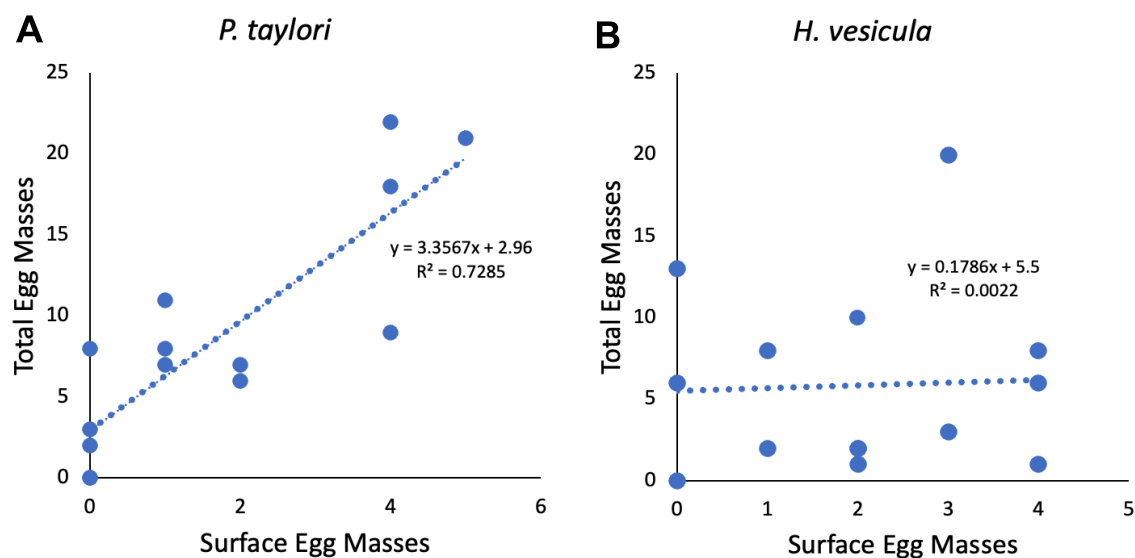


Figure 2. Linear regressions of surface egg masses to total egg masses for (A) *P. taylori* and (B) *H. vesicula*. R^2 values 0.7285 and 0.00222 respectively.

There is a linear relationship between *P. taylori* egg masses at the surface area of the quadrat and the total volume of the quadrat with an R^2 value of 0.7285. There is no notable relationship between the *H. vesicula* egg masses at the surface area of the quadrat and the total volume of the quadrat (R^2 value generated 0.0022). For quadrats 15-32, we measured only surface counts and used the equation $y = 3.3567x + 2.96$ to estimate the total *P. taylori* egg masses within a given quadrat.

Edge Effects

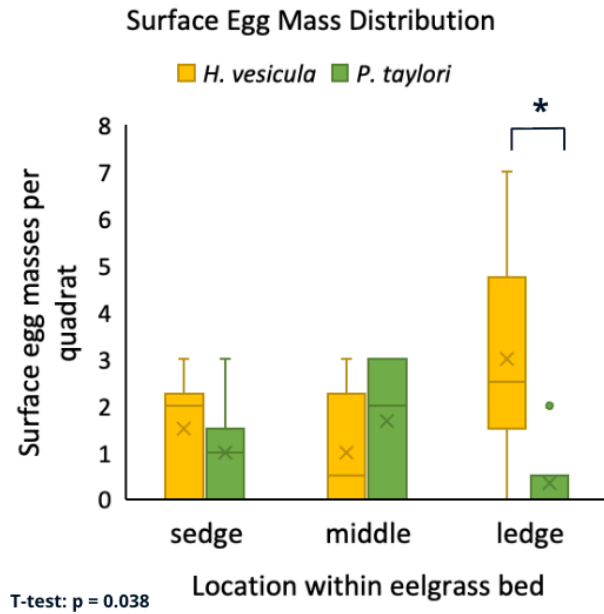


Figure 4. Surface egg mass distributions in relation to the location within an eelgrass bed.

Location in the eelgrass bed (land edge, middle, or sea edge) does not have a significant effect on the number of egg masses visible from the surface for *H. vesicula* or *P. taylori*. (Kruskal-Wallis $p = 0.1512$, $p = 0.1962$). There are significantly more *H. vesicula* eggmasses than *P. taylori* visible at the surface in the land-side edge of the eelgrass bed (t-test $p = 0.038$). There is no significant difference between the number of eggmasses of each species at the sea edge and middle areas (t-test $p = 0.415$, $p = 0.5549$).

Egg Mass Height and Epiphyte Coverage

There is no statistically significant relationship between epiphyte coverage and height on the blade of where eggmasses were found for either *P. taylori* or *H. vesicula*. The independence of these factors allows us to run separate ANOVAs for each variable (*P. taylori*: $p = 0.24$, *H. vesicula*: $p = 0.33$).

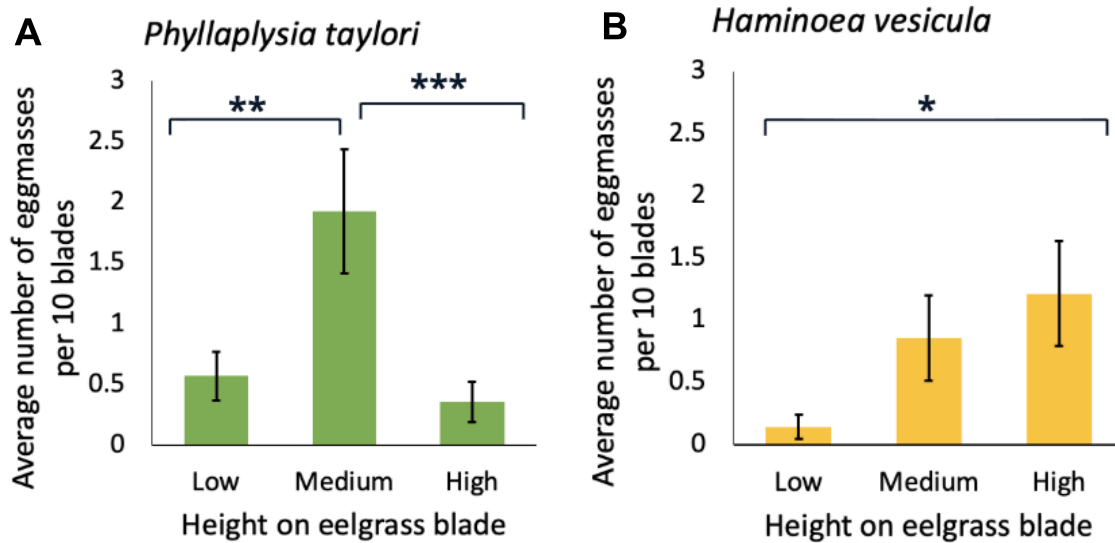


Figure 5. Egg mass relationship of average count and relative height found per 10 eelgrass blades for (A) *P. taylori* and (B) *H. vesicula*. Error bars represent $\pm$ SEM.

There is a significant difference between the average number of (A) *P. taylori* egg masses per 10 blades at different heights on the blade (ANOVA, $F_{13} = 3.18$, $p = 0.006$). There are significantly more *P. taylori* egg masses, on average, at a medium height than at low and high positions on the eelgrass blade (Tukey HSD, $p = 0.002$, $p < 0.001$). There is no significant difference between the average number of egg masses at low and high levels on the blade (Tukey HSD, $p = 0.820$).

There is also a significant difference between the number of (B) *H. vesicula* egg masses per 10 blades at different heights on the blade (ANOVA, $F_{13} = 3.15$, $p = 0.006$). The average number of *H. vesicula* egg masses is significantly higher at the high tip of the eelgrass blade than the low region (Tukey HSD, $p = 0.012$). There is no significant difference between the average number of egg masses when comparing low and medium heights and medium and high heights on the eelgrass blade (Tukey HSD, $p = 0.116$, $p = 0.562$).

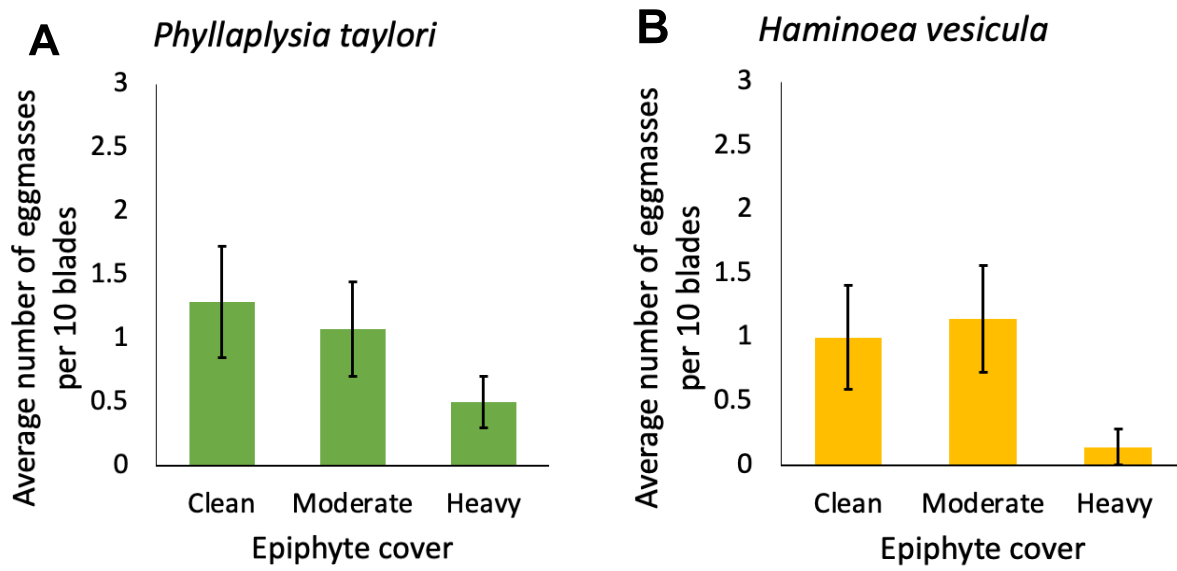


Figure 6. Average count and relative epiphyte coverage surrounding egg masses found per 10 eelgrass blades for (A) *P. taylori* and (B) *H. vesicula* egg masses. Error bars represent $\pm$ SEM.

According to repeated measures one-way ANOVA tests, there is a significant difference in the average number of egg masses per 10 blades for *P. taylori* and *H. vesicula* ($F_{13} = 2.381$, $p = 0.029$, $F_{13} = 2.294$, $p = 0.035$). However, when Tukey HSD post-hoc tests were run, no significant difference between the treatments were detected. Due to the nature of this count data and the high frequency of zero values, the data is likely not normal. An assumption of the one-way ANOVA is that the data is normal, so it is not the ideal test for this data. In the future, a non-parametric test such as Kruskal-Wallis could be a better way to analyze this data. When looking at the SEM error bars, it appears that the average number of *P. taylori* egg masses is significantly higher on clean blades than those heavily covered in epiphytes. It also appears that the average number of *H. vesicula* egg masses is higher on clean and moderately covered blades than heavily epiphyte-covered blades.

Preferential Laying

No statistically significant results were found from this experiment, as none of our 30 individuals laid any egg masses within the 5 days of containment. We observed that quantities of red algae and egg masses were found suspended in the water for the majority of our compartments.

Grazing

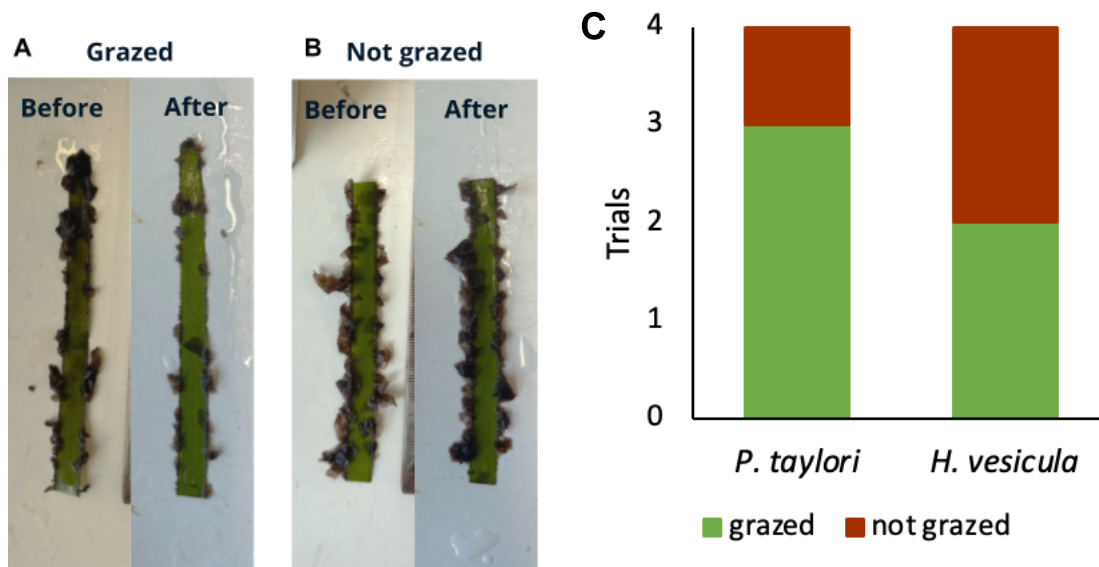


Figure 7. Examples of eelgrass blades categorized as (A) grazed and (B) not grazed by *P. taylori* and *H. vesicula* adults. (C) Proportion of trials that were determined as grazed or not grazed across the two species.

In the *P. taylori* trials, 3/4 individuals appeared to have grazed the epiphytes on the blade. In the *H. vesicula* trials, half of the individuals appeared to have grazed epiphytes.

Light Attenuation

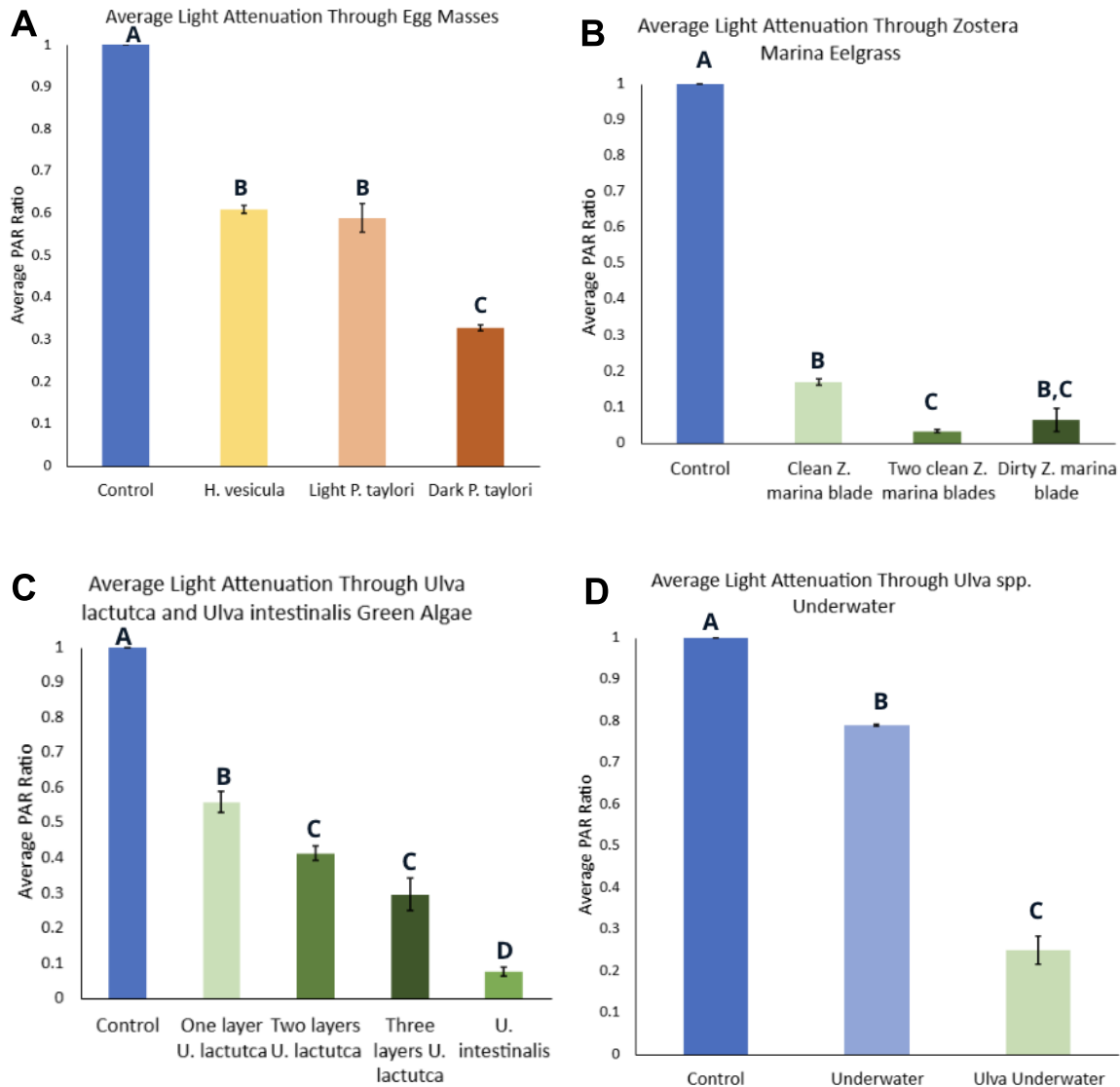


Figure 8. Light attenuation (average Photosynthetically Active Radiation) through (A) egg masses, (B) *Z. Marina* eelgrass, (C) *Ulva* spp. green algae, and (D) underwater treatments. Error bars represent $\pm$ SEM.

All egg mass, eelgrass, and green algae treatments exhibited significantly reduced Photosynthetically Active Radiation (PAR) when compared to control PAR values (Figure 8, one-way ANOVA, $p < 0.001$). *H. vesicula* and light *P. taylora* egg masses blocked a minimum of 36% of measured control PAR, with dark *P. taylora* egg masses blocking a maximum of 69% of PAR (Figure 8A). Dark *P. taylora* egg masses blocked significantly more light than *H. vesicula* and light *P. taylora* egg masses (Tukey HSD, $p < 0.001$). However, all eelgrass treatments blocked significantly more light than all eggmass types (Tukey HSD, $p < 0.001$). Eelgrass treatments blocked a range of 81%-100% of PAR, among which 2 layers of clean eelgrass obstructed significantly more light than one layer of clean eelgrass (Figure 8B, Tukey HSD, $p = 0.023$). “Dirty” blades coated with *Smithora*

spp. red algae epiphytes were not significantly different from treatments of one or two layers of clean blades (Tukey HSD, $p=0.98$ and $p=0.99$, respectively). One layer of *Ulva lactuca* blocked a minimum of 39% of PAR, while three layers of *U. lactuca* blocked a maximum of 79% of light (Figure 8C). Meanwhile, *Ulva intestinalis* reduced PAR light availability by up to 94%, blocking significantly more light than other *U. lactuca* layer treatments (Tukey HSD, $p<0.001$). The average amount of photosynthetically available light blocked by one layer of *U. lactuca* was 44% when placed above water, and significantly increased to 75% when placed under water (Figure 8D, Tukey HSD, $p<0.001$). The treatment of water itself also significantly reduced light penetration by an average of 21% (Tukey HSD, $p=0.012$).

Discussion

As climate change, urbanization, and runoff-related eutrophication contribute to the decline of eelgrass beds (Orth et al. 2006), building an understanding of what ecological factors and organisms impact eelgrass bed productivity is important to support future conservation and restoration efforts. Epiphyte coverage on eelgrass substantially decreases eelgrass bed health by causing physical damage to leaves, competition for nutrients, and lowering photosynthetic rates (Howard and Short 1986). Herbivorous grazers, such as *Phyllaplysia taylori*, reduce epiphytes, which in turn increases light availability to the eelgrass blade (Howard and Short 1986). As seen in Figure 8B, the clean *Zostera marina* blade (no epiphyte cover) let through almost 3 times as much photosynthetically available light as the dirty *Z. marina* blade (high epiphyte cover), indicating that epiphyte-free eelgrass has a greater photosynthetic capacity. Grazing organisms such as *P. taylori* and *Haminoea vesicula* clean epiphytes off of *Z. marina*, increasing its photosynthetic productivity and health. Our grazing experiment results found that 3 of 5 *P. taylori* and 2 of 4 *H. vesicula* grazed a visibly distinguishable quantity of red algae epiphytes within 5 days (Figure 7). Scaled for biomass, *P. taylori* grazing has a greater effect than *H. vesicula* on clearing the red alga photosynthetic inhibitor. In contrast, egg masses were found to block light availability for eelgrass, with dark *P. taylori* egg masses blocking significantly more light than *H. vesicula*'s bright yellow egg masses. However, *P. taylori*'s lifetime of grazing and laying on *Z. marina* may result in a net cleaning of eelgrass blades from light blockage. Since eelgrass is a light-limited foundational species, its availability to photosynthesize and the presence of epiphyte grazers dictate the status of the overall eelgrass bed community (Orth et al. 2006).

In the land edge area of the eelgrass bed, most of the blades appeared withered and brown. *P. taylori* were largely absent from the land edge, but *H. vesicula* and their egg masses were found in these conditions (Figure 4), with numerous egg masses floating in the degrading and uprooted blades. *P. taylori* adults and egg masses were primarily found on visually healthy eelgrass blades, which were in greater abundance in the middle and sea edge of the eelgrass bed. *P. taylori* can be an indicator of eelgrass health, as their presence correlates and may rely on healthy, green eelgrass blades to provide oxygen and camouflage. The majority of *P. taylori* and *H. vesicula* egg masses were found on eelgrass blades with low to moderate epiphyte coverage (Figure 6), indicating a possible preference for laying on healthy eelgrass blades that may result in higher hatching and juvenile success. In addition to epiphyte coverage, significantly more *P. taylori* egg masses were found on the middle region of eelgrass blades, and *H. vesicula* also appeared to have a significant preference for laying on the highest third of eelgrass blades over the lower region (Figure 5). In order to optimize their fitness, *P. taylori*

and *H. vesicula* egg masses must remain suspended in the middle of the water column throughout the tidal cycle in order to avoid benthic predation from predators such as crabs, providing a possible explanation for the reduced prevalence of egg masses on the lower portion of eelgrass blades. The sun-exposed top and middle regions of eelgrass blades are the most important areas of the blade for photosynthesis. Although *P. taylori* and *H. vesicula* graze light-blocking epiphytes from eelgrass blades as adults, their egg masses laid on the upper region of blades were found to be capable of blocking at least 36% of PAR, posing a possible danger to eelgrass photosynthetic production. However, egg masses were observed to be widely dispersed across the eelgrass bed in False Bay, mitigating their impact on light availability for individual eelgrass blades. *Z. marina* has been found to require at least 115 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ of PAR for 12 hours per day to achieve ideal growth during restoration (Eriander 2017). When light penetration through *P. taylori* egg masses was measured at peak sunlight, a range of 766 to 1389 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ of PAR was able to penetrate through the egg masses. However, the daily progression of light exposure during tidal cycles and the exact impact of egg mass presence on eelgrass production remains unknown.

Another contribution that hinders light availability for eelgrass beds is the abundance of *Ulva* green alga, which develop a canopy above the eelgrass and outcompete for light and nutrient reserves. Underwater, a single piece of *U. lactuca* blocked up to 82% of photosynthetic light from penetrating to $\sim\frac{1}{2}$ meter below the water surface (Figure 8d). *Ulva* is a disturbance indicator, and can periodically bloom due to eutrophication and pollutant runoff (Mackenzie 2005). At False Bay, we observed an abundance of *Ulva* algal blooms, which could harm the photosynthetic abilities of *Z. marina*, and in turn, the organisms the eelgrass ecosystem facilitates. As eutrophication and ocean warming related algae blooms become more common, it is important to further understand the threats runoff, sedimentation, and *Ulva* blooms pose to eelgrass bed productivity.

Conclusion/ Future directions:

As a foundational species, eelgrass beds are important to study due to their influence on the presence and health of a myriad of organisms. As *P. taylori* appear to benefit the health of *Z. marina*, investigating their behavior to a further extent allows us to better predict and understand factors that contribute to future eelgrass populations and conservation.

During the in-lab experiment to evaluate *P. taylori* laying surface preferences, we were unable to induce laying for *P. taylori* in a short time span within a confined space. In the future, this experiment could be repeated with more recently collected individuals in a less confined space in order to increase the likelihood of laying. While viewing the results of the attempted laying experiment, several of the glued *P. taylori* egg masses were missing from their previous location, and some individuals appeared notably larger. It would be interesting to determine if *P. taylori* will eat their own egg masses or the egg masses of other individuals when there is a shortage of resources. In addition to the laying experiment, the in-lab grazing experiment could also be modified to include a control in order to observe the natural decay of an epiphyte-covered eelgrass blade without the influence of grazing. When visually analyzing epiphyte coverage before and after grazing, a machine learning system could be used to more quantitatively ascertain the impact of grazing.

While collecting data at False Bay, a surprising abundance of *H. vesicula* adults and egg masses was observed in prominent locations both within and outside of eelgrass beds, raising questions of whether the species may have chemical defenses against predation that allow them to inhabit unsheltered areas. Spider crabs in the lab readily ate *P. taylori* adults and egg masses and *H. vesicula* egg masses, but it is unknown if they eat *H. vesicula* adults or if egg mass consumption time and diet preferences would differ in different species of crab or other predators.

Future field data on *P. taylori* and *H. vesicula* interactions with eelgrass should be expanded to include more eelgrass beds at both False Bay and additional sites in order to provide a broader representation of spatial variability. We would like to develop our spatial data with a more accurate and reliable GPS system. This would contextualize each sampling point within the eelgrass bed, allowing us to further explore edge effects. It would also be valuable to collect underwater light attenuation data in the field in order to better understand the photosynthetic light conditions that eelgrass experiences outside of a lab environment, which can help inform water quality policy and other conservation efforts.

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