

Meiofaunal Diversity on Invasive *Sargassum muticum* Versus Native Seaweeds

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ABSTRACT

The meiofaunal assemblage on the invasive brown alga, *Sargassum muticum*, was compared to that on three native algal species. I predicted that differences in the meiofaunal diversity, abundance, and community composition would be influenced by the morphological complexity and palatability of an alga. I found that the algal structural palatability, rather than chemical palatability, was a factor in the preferences of one genus of meiofauna (*Lacuna sp.*). The results also suggest that the level of structural complexity of an alga determines its relative abundance of meiofauna, while the type of structural complexity determines its meiofaunal community composition. Even though *Sargassum* did not support a lower diversity of meiofauna compared to each individual native species, a monoculture of *Sargassum* would support a less diverse community of meiofauna compared to a diverse community of native seaweeds.

INTRODUCTION

An invasive species is an introduced species that threatens native diversity. An invasive species negatively impacts a community by dominating space, altering habitat structure, and/or changing biodiversity (Schaffelke and Hewitt 2007). The brown alga *Sargassum muticum* is considered one of the most invasive seaweeds in temperate ecosystems (Wiencke and Bischof 2012). It colonized eastern Pacific coastlines via oysters transported from Japan for the aquaculture industry; *S. muticum*'s high growth and reproductive rates and high tolerance for environmental stress facilitated its invasion into shallow subtidal waters from southern Alaska to northern Mexico (Lamb and Hanby 2005, Wiencke and Bischof 2012). Britton-Simmons (2004) found that *S. muticum*

negatively affects the community structure and reduces growth of native algae in the San Juan archipelago.

Seaweeds are an important source of food and shelter for many marine organisms, from microfauna to macrofauna. Intermediate are the meiofauna, which are mobile animals distinguished by size rather than taxonomy or morphology. Meiofauna are important for ecosystem function, as high meiofaunal diversity supports a greater diversity of higher trophic levels (Piot et al. 2014). Harpacticoid copepods, for example, are an important prey item of juvenile fishes such as salmon (Levings et al. 1983, Coull 1990, Burd et al. 2008).

High meiofaunal diversity is influenced by high algal diversity and structural complexity. Since diverse seaweed communities support more species of herbivores than monocultures (Best et al. 2014), there should be effects on the diversity of meiofauna and subsequently on higher trophic levels if an invasive seaweed such as *Sargassum* were to take over an area and become a monoculture. Morphological complexity of algae also plays a role in meiofaunal diversity. Finely structured seaweeds support more meiofauna (Taylor and Cole 1994, Christie et al. 2009), and some turf-forming algae support a higher density and diversity of meiofauna because their high surface areas provide more space to feed upon and better shelter (Frame et al. 2007, Smith et al. 2014). In addition, some meiofauna prefer a seaweed host with greater structural complexity because it can better trap nutrients from the water, which these meiofauna eat rather than the seaweed itself (Best et al. 2014).

In addition to morphology, algal chemical composition can influence meiofaunal preference of species for both habitat and food. While some taxa of meiofauna avoid

eating a species of seaweed because it has chemical defenses (Steinberg 1985), many other meiofauna have been found to prefer seaweeds that are chemically defended and thus less palatable to larger grazers like sea urchins (Taylor and Steinberg 2005). Feeding by these larger herbivores selects for the production of chemical defenses in seaweeds, while meiofauna that live and feed on the algae are often resistant (Hay et al. 1988). Some species of Amphipoda, for example, have become specialized for a seaweed species with chemical defenses that provides protection from predators, just as insects can become specialized to feed on chemically-defended terrestrial plants (Hay et al. 1987, Hay et al. 1990). In some cases, the relationship between the chemically-defended seaweed and the protected meiofauna is considered whole-community mutualism (Bracken et al. 2007, Amsler et al. 2014). *S. muticum* is chemically defended, with varying concentrations of phenolic content depending on the season (Plouguerne et al. 2006) and latitude (Tanniou et al. 2014). There is little research in chemical defenses of *S. muticum* in the Pacific Northwest, however. Cronin and Hay (1996) found that *Sargassum filipendula* produces chemical defenses as well, but plants with varying phenolic content did not differ in palatability to amphipod grazing.

In order to assess the impacts of the invasive *Sargassum* on meiofaunal assemblages, I investigated the differences in meiofaunal diversity, abundance, and community composition between *Sargassum* and native seaweeds. I compared the meiofaunal assemblages associated with *Sargassum muticum*, *Costaria costata*, *Egregia menziesii*, and *Saccharina bongardiana* (the latter three all native brown algae). I hypothesized that the taxon richness and diversity, species composition, and relative abundance of meiofauna would differ among the algal species. I predicted that these

differences would be due to the differing morphological complexities of the algae, as well as their chemical and structural palatability. I also performed feeding trials (using the gastropod *Lacuna sp.* as it was the most abundant and naturally found on all algal species used) to test feeding preferences for fresh native versus invasive algae. I hypothesized that the *Lacuna* would prefer what appeared to be the most structurally and chemically palatable alga, *Costaria*, to other species of seaweed offered.

METHODS

Algal and meiofaunal collection

We collected *Costaria* (n = 4), *Saccharina* (n = 4), *Egregia* (n = 7), and *Sargassum* (n = 7) from the shallow subtidal via either snorkeling or SCUBA. We captured meiofauna by bagging the entire alga *in situ* using a bag made of fine plankton net mesh (180 microns). Bags were cinched-off just above the holdfasts and then the algae were ripped off their substrate so that each mesh bag contained a single algal thallus and associated meiofauna; bagging was executed quickly and with minimal handling to avoid scaring or losing meiofauna.

Calculation of meiofaunal abundance and diversity

I separated the meiofauna from each alga via shaking and rinsing the alga (while still inside the bag) with freshwater, using the mesh bag as a sieve to collect meiofauna. I then transferred the meiofauna from each alga into separate containers and preserved them with 70% isopropyl. I dried the algae with paper towels and then measured the wet weight (g) and the volume (mL) by water displacement. The mass and volume measurements did not accurately capture the differences in morphological complexity

among the four algal species, but the qualitative descriptions were as follows: *Costaria*, a singular blade and highly rippled in structure; *Saccharina*, a singular blade often split at the senescent end that was mostly smooth (with a few ripples) and produced a thin layer of mucus on its surface; *Egregia*, just as the common name “feather boa kelp” implies, had a thick, heavy midrib with small blades attached laterally; and *Sargassum* had whorled branching with small bladelettes and bladders.

Meiofauna were counted using a dissection microscope and identified to the lowest possible taxonomic unit. For Copepoda, I split the Harpacticoida into five easily recognizable morphotypes and estimated the abundances by tens. For Malacostraca, I identified Decapoda to the taxonomic unit family or lower (e.g. Majidae) and Amphipoda to suborder or lower (e.g. Gammaridea). Within the classes Gastropoda and Polychaeta, I identified the individuals to genus. I calculated meiofaunal diversity values using the Shannon-Wiener index. One-Way Analyses of Variance (ANOVA) were done to test whether the differences in meiofaunal abundance and diversity values among the algal species were significant ($p < 0.05$).

Feeding preference trials

For feeding preference trials, I used *Sargassum*, *Egregia*, *Costaria*, *Saccharina*, and *Agarum fibriatum*. I included *Agarum* as a comparison to *Sargassum* because both are chemically defended but *Agarum* is native. I removed the meiofauna from the algae using the rinsing method described above. I selected Gastropoda to test feeding preference because they eat more and are easier to observe than the other classes of meiofauna; within Gastropoda, I chose *Lacuna sp.* because it was the only gastropod found on all five of the algal species. I starved the *Lacuna* for 3-4 days before running

the experiment. After placing 20 *Lacuna* in each of the 10 identical containers, I put 10 grams (wet weight, initial) of each alga of each pairing in the appropriate containers. I then placed the containers (which had fine mesh on two sides to allow for water flow) in a seatable. After 48 hours, I removed the algae and blotted them dry before determining the mass (wet weight, final). These trials were repeated twice more, the second trial with 20 new *Lacuna* and the third trial with 40 new *Lacuna* in each container. For each pairing of seaweeds, I calculated the average amount of each alga consumed per *Lacuna*. I used Mann-Whitney U tests and paired t-tests to determine whether one algal species was preferred over another for each combination ($p \leq 0.05$).

RESULTS

Meiofaunal abundance and diversity

There were 13 meiofaunal taxa exclusive to the native species of algae, and there were exclusive taxa on each algal species: *Costaria*, 6; *Saccharina*, 1; *Egregia*, 3; and *Sargassum*, 3. The most abundant class on *Costaria* and *Saccharina* was Copepoda, while the most abundant class on *Sargassum* and *Egregia* was Malacostraca (Fig. 5a). *Costaria* had an average of 9.2 ± 4.1 copepods g^{-1} wet weight (Fig. 9); this was the highest abundance of any taxon on any seaweed species.

For each algal species, there was a strong correlation between mass and volume (Fig. 1; $R^2 = 0.80$ to 1.00), suggesting that either of these measurements could be used to standardize the meiofaunal counts. The total meiofaunal abundance is highly correlated with mass for *Saccharina* (Fig. 2; $R^2 = 0.93$), somewhat correlated for *Egregia* ($R^2 =$

0.54), poorly correlated for *Sargassum* ($R^2 = 0.26$), and not at all correlated for *Costaria* ($R^2 = 0.00$).

Mean meiofaunal abundance was significantly different among the algae ($p < 0.001$), with *Costaria* and *Sargassum* having many more meiofauna than *Saccharina* and *Egrefia* (Fig. 3). The Shannon-Wiener diversity index of taxa was significantly different among the algae ($p = 0.039$; Fig. 4), while the mean meiofaunal taxon richness was not significantly different among the algae ($p = 0.356$). Since the diversity index takes both richness and evenness into account, the differences in diversity were caused by the differing evenness of taxa among the algae. The meiofaunal diversity was greatest for *Saccharina*, because its meiofaunal evenness was highest. *Costaria* had the lowest diversity, due to its low taxon evenness caused by the abundance of meiofauna from the taxa Harpacticoida Type 1 and Harpacticoida Type 2.

The class evenness was also very different among the algae (Fig. 5a); as a result, the average diversity of meiofaunal classes significantly differed ($p < 0.001$; Fig. 5b). *Sargassum* had the highest class evenness, and thus the highest diversity; *Costaria* had the lowest evenness due to the abundance of meiofauna in the class Copepoda, and thus the lowest diversity. Within the class Malacostraca, the average diversity of orders (Fig. 6) significantly differed with the algae ($p = 0.001$). *Costaria* and *Saccharina* had the highest diversity, while *Sargassum* and *Egrefia* were dominated by the order Amphipoda, and thus had the lowest diversity.

Within the class Gastropoda, a total of 12 genera were found on the algae. Ten of the 12 genera were found on *Costaria*, while 5 were found on *Saccharina*, 3 on *Egrefia*, and 7 on *Sargassum*. The average diversity by genus was not significantly different

among the algae ($p = 0.132$; Fig. 7a). This could be predicted by the very low species evenness in every alga (Fig. 7b). The variation was driven by the large and irregular abundance of *Lacuna* on all the algae, as well as that of *Alia* on *Sargassum*.

Every alga had a very uneven distribution of the six Copepoda taxa, particularly *Costaria* (Fig. 8a), so the diversity values of this class were consistently low. There was a significant difference in the diversity among the species of algae, however ($p = 0.024$; Fig. 8b). *Egrefia* had the highest diversity of meiofauna within the class Copepoda, while *Costaria* had the lowest diversity. When considering the abundance of Copepoda per gram of each species of seaweed, there were very significant differences among the algae ($p < 0.001$; Fig. 9). *Costaria* had a much higher relative abundance of Copepoda than the others; *Sargassum* had a significantly lower value than *Costaria*, but higher than that of *Saccharina* and *Egrefia*.

Feeding preference trials

Based on the average amounts of alga consumed in each pairing, the *Lacuna* order of preference is *Costaria* > *Agarum* > *Saccharina* > *Egrefia* > *Sargassum* (Fig. 10). Using the Mann-Whitney U test ($p = 0.05$), *Costaria* was significantly preferred over *Egrefia* and *Saccharina*, *Agarum* was significantly preferred over *Sargassum* and *Saccharina*, and *Saccharina* was preferred over *Egrefia* and *Sargassum*. With the paired t-test, the mass consumed of *Agarum* was greater than that of *Saccharina* ($p = 0.017$). The differences in the average mass of seaweed consumed in the other pairings are not significant because of the low number of replications ($n = 3$) and relatively large variation.

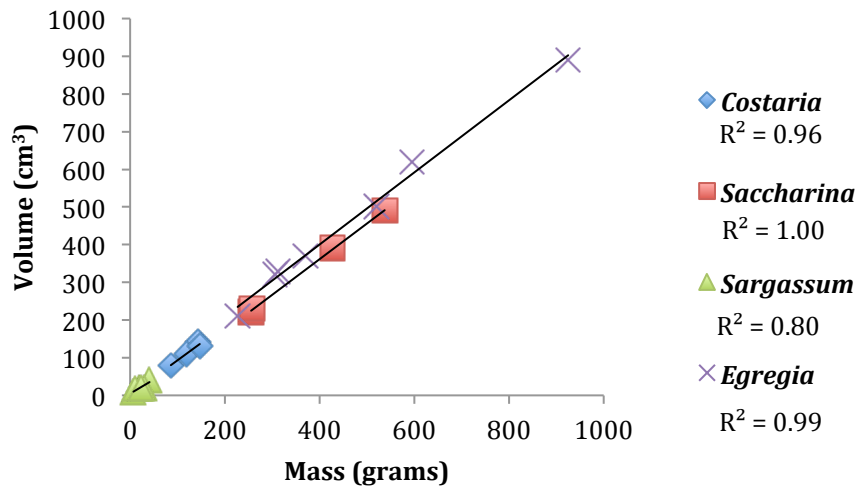


Fig. 1. Correlation between mass and volume for each algal species.

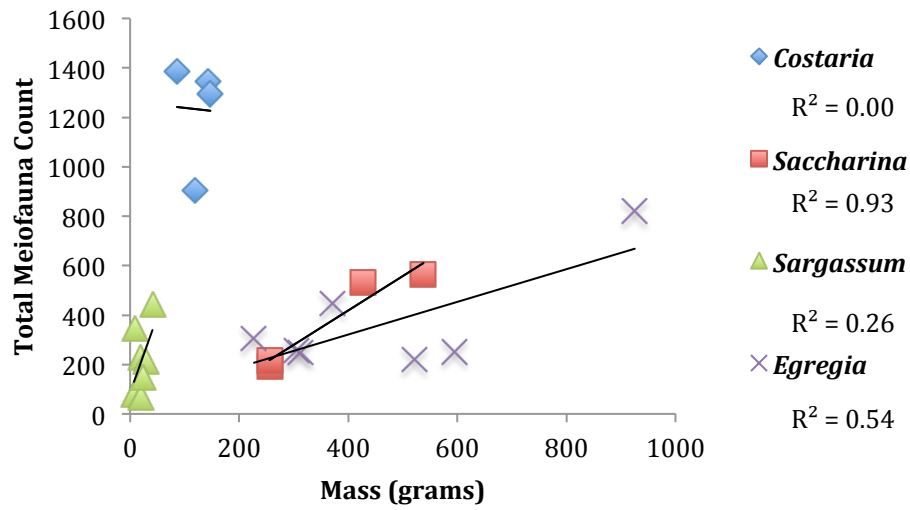


Fig. 2. The correlation between the total number of meiofauna and the mass of each alga.

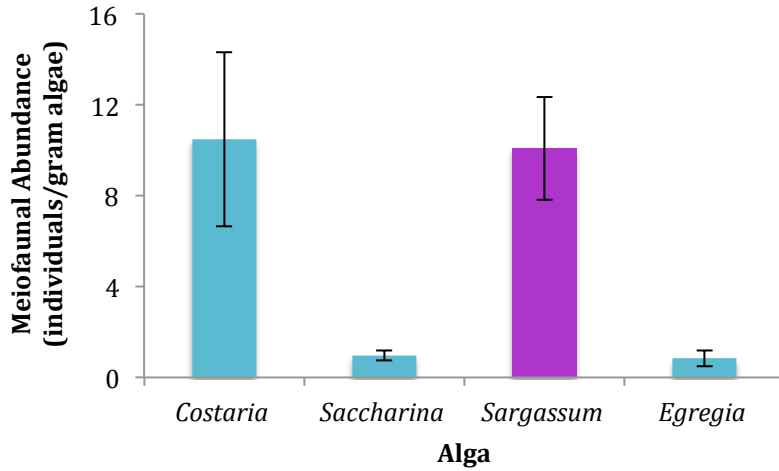


Fig. 3. The abundance of meiofauna per gram was significantly higher on *Costaria* and *Sargassum* than on *Saccharina* and *Egregia*. The error bars are ± 1 standard deviation.

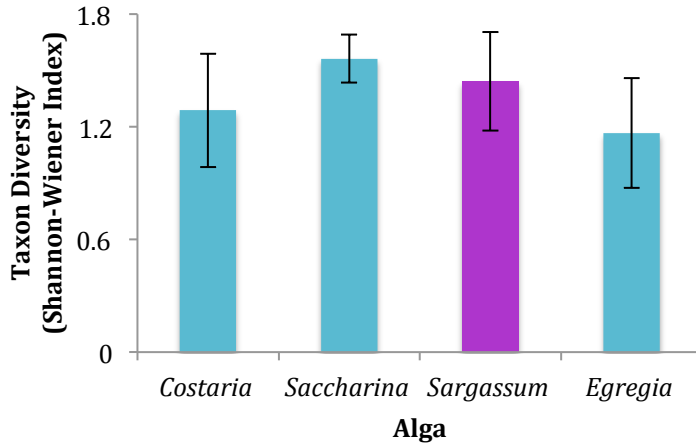
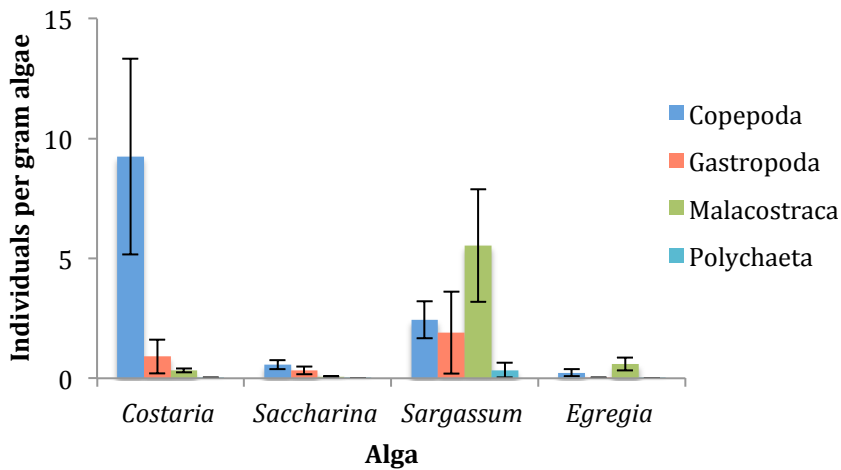
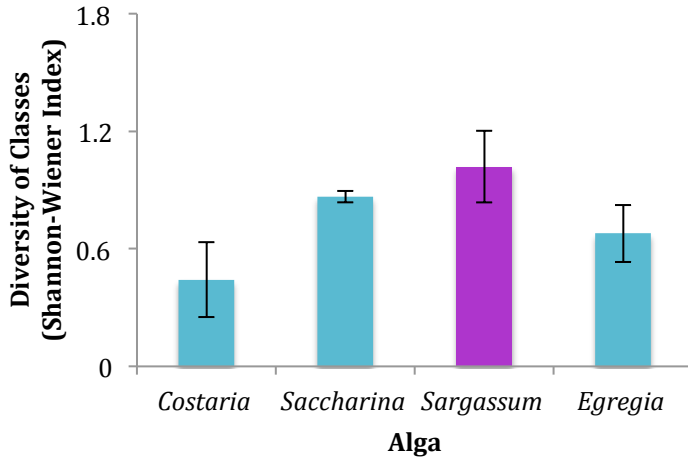


Fig. 4. The average diversity of taxa (± 1 standard deviation) was significantly different among the algae.



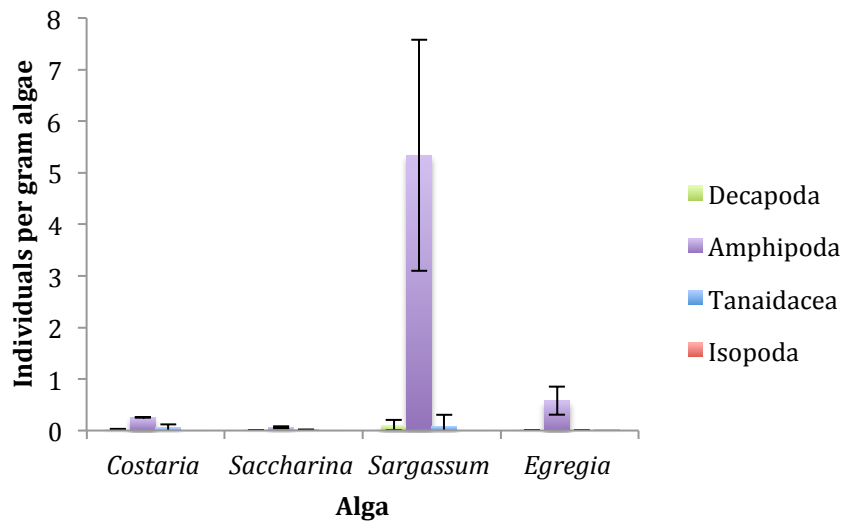
(a)



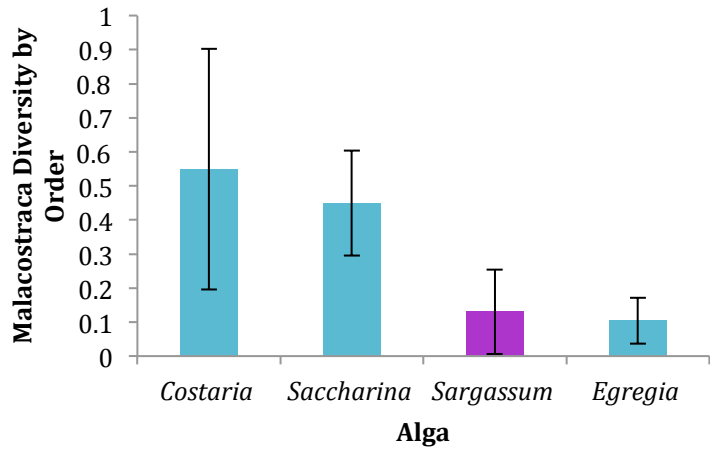
(b)

Fig. 5. (a) The average abundance of each class of meiofauna per gram of each alga (± 1 standard deviation). A fifth class, Polyplacophora, is not shown on the graph; the count for this class was one on *Costaria* only.

(b) The average diversity by class (± 1 standard deviation) significantly differed among the algae.



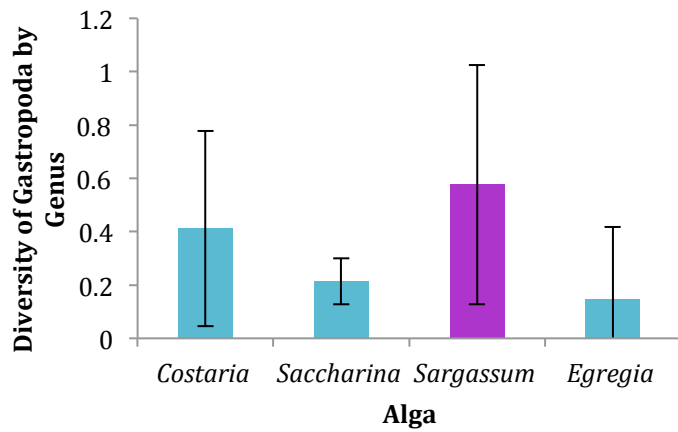
(a)



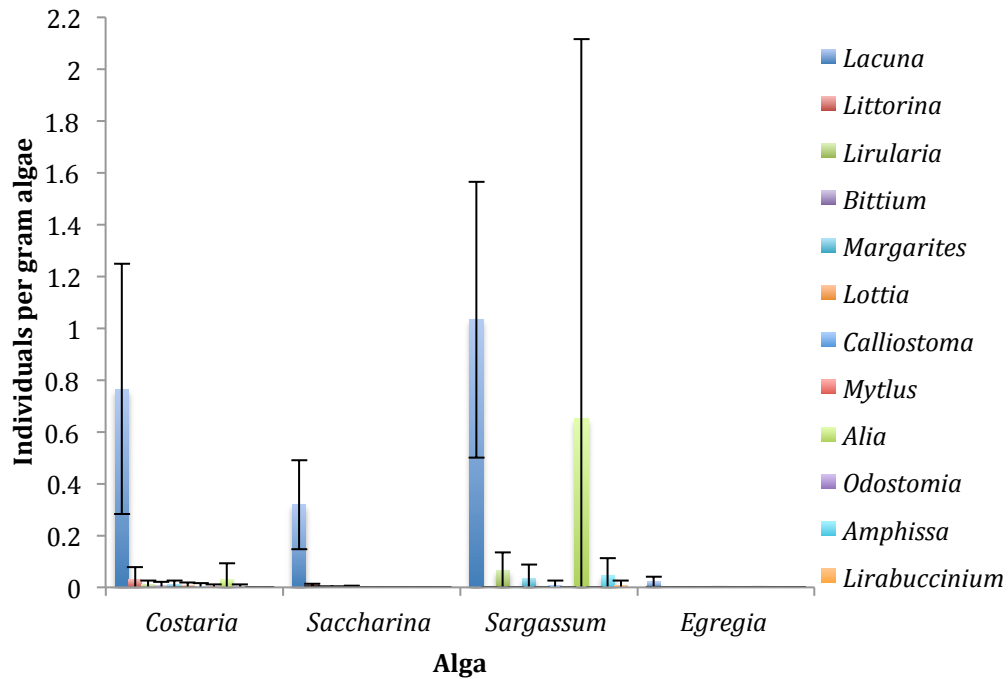
(b)

Fig. 6. (a) The average abundance of each order within the class Malacostraca (± 1 standard deviation). The high relative abundance of Amphipoda on *Sargassum* is responsible for the high number of Malacostraca shown in Fig. 4(a).

(b) The average diversity by order within the class Malacostraca (± 1 standard deviation) significantly differs with the algae.

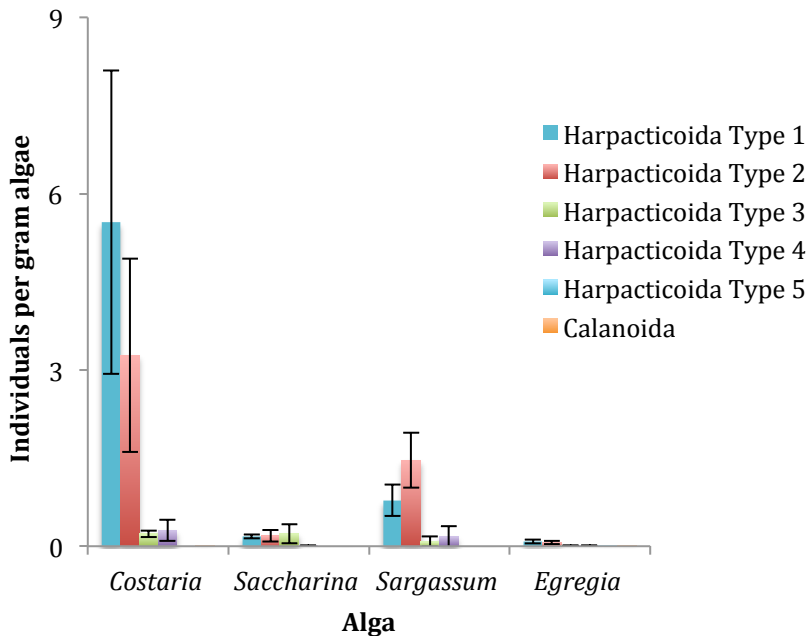


(a)

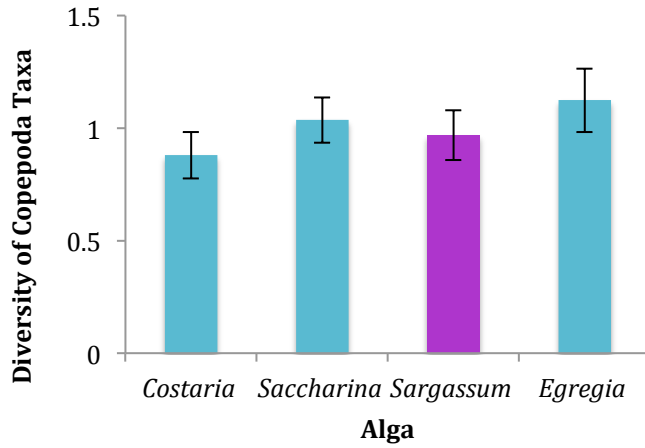


(b)

Fig. 7. (a) The diversity of Gastropoda by genus does not significantly differ among the algae. The variance within each group is very large, as evidenced by the large standard deviations on the graph. (b) The abundance of each genus of Gastropoda on each alga (± 1 standard deviation) is very uneven, causing low diversity values.



(a)



(b)

Fig. 8. (a) The relative abundance of each Copepoda taxon on the four algae (± 1 standard deviation). (b) The average diversity of taxa within the class Copepoda (± 1 standard deviation) is significantly different among the algae.

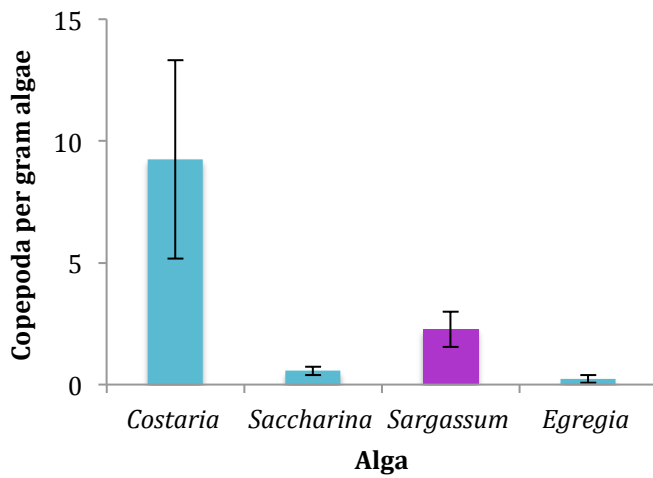


Fig. 9. The average number of Copepoda per gram of algae (± 1 standard deviation) is significantly different among the algae.

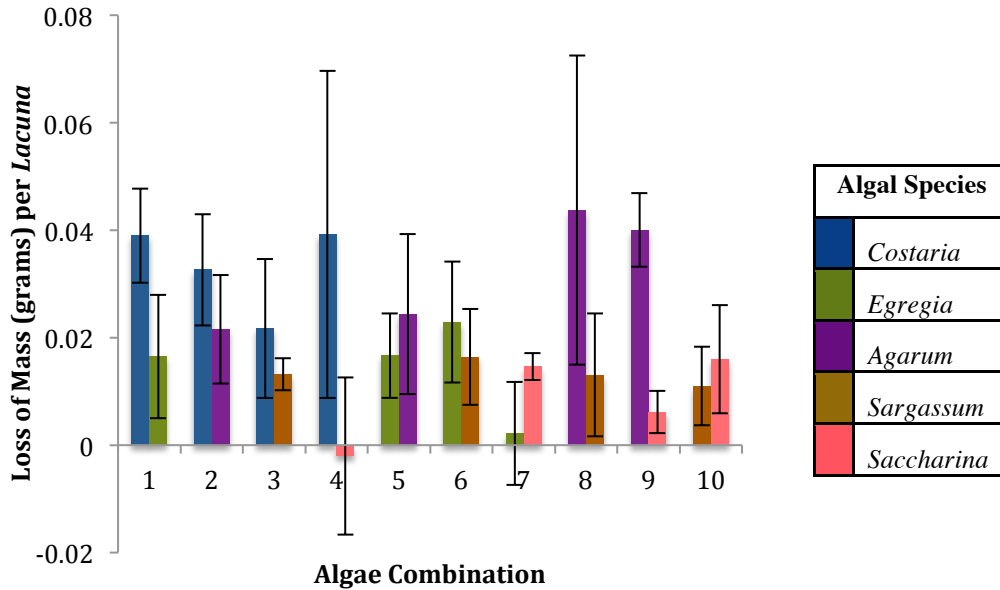


Fig. 10. Average loss of alga mass per *Lacuna* for each pair of algae (± 1 standard deviation). The corresponding algal species are shown in the table by color.

DISCUSSION

The meiofaunal diversity and abundance differed among the algal species, but there was no one alga with the highest values for every calculation (total taxa, classes, within each class). The four algal species each supported a unique community of meiofauna. My hypothesis of differences in meiofaunal diversity, species composition, and relative abundance among the algal species was partially supported. I predicted that these differences would be due to the varying algal morphology and palatability. For further study, it would be beneficial to quantify structural complexity, in order to make more accurate conclusions about the correlation between algal structure and meiofaunal composition. In recent research by Veiga et al. (2014), the algal complexity was quantified by fractal measurements. Also, this study could be improved by sampling the algae throughout the year, to determine whether there is seasonal variation in meiofaunal composition.

Chemical palatability seemed to be less important than structural palatability in determining the meiofaunal assemblages. *Sargassum* is chemically defended, but its diversity and abundance values were not consistently higher or lower than the others. In the preference feeding trials, *Sargassum* may have been least preferred by the *Lacuna* because of its chemical defenses; although *Agarum* is chemically defended as well, and it was the second most preferred algal species. The structural palatability of the algal species was the more important factor in the *Lacuna* preference. Even though the relative *Lacuna* abundances did not differ between *Costaria* and *Sargassum*, *Costaria* was most preferred and *Sargassum* was least preferred. Both algal species are likely suitable habitat for *Lacuna*, but *Costaria* is more palatable because of its thin, easily torn blades. A larger sampling of feeding trials, as well as trials with more types of meiofauna, would be beneficial to make further connections between algae as food and habitat.

The differences in structure among the algal species, though qualitatively observed rather than empirically quantified, likely explain the differences in meiofaunal composition, relative abundance, and diversity. *Costaria* was complex with highly rippled blades, while *Sargassum* was structurally complex with whorled branching. *Egregia* had branched blades but a thick, flat midrib, and *Saccharina* had thick, smooth blades. The strong correlation between the number of meiofauna and the mass of *Saccharina* was likely because it is the least structurally complex alga. Mass did not accurately predict the meiofaunal abundances of *Sargassum* and *Costaria*; their complex morphologies allowed for more habitat and surfaces to feed on, and therefore a greater density of meiofauna (Christie et al. 2009). Greater algal morphological complexity

supported a higher abundance of meiofauna, whereas the different types of structural complexity resulted in different communities of meiofauna.

Greater morphological diversity in a community of algae supports a more diverse community of meiofauna. The invasive *Sargassum* did not support a less diverse community of meiofauna compared to each native alga, but it supported a different community. The rippled structure of *Costaria* supported a huge abundance of Copepoda, while the thin, branched structure of *Sargassum* supported more Amphipoda. This means that a combination of differently structured algal species results in a greater diversity of meiofauna than a monoculture or algal species of the same structure; this supports previous research by Best et al. (2014). *Sargassum* is a threat to meiofaunal diversity because of its ability to take over a community and become a monoculture by reducing native algal growth (Britton-Simmons 2004). Diversity in the morphology of algae of a community is necessary to have a more diverse assemblage of meiofauna, which would support a more diverse group of higher trophic levels.

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