Discussion notes:

Notes from composition plots:

smithora dominated by: Flavobacteraia,Thiotrichaceae,unknown,rhodobacteria,Hyphomonadacea

* signals of decay on smithora, from microbial perspective they were dying (rhizomes not attached). There were also signals of zostera colonization. Be clear about this, and what we can infer from it, and what are the limitations; shoots grouped together post transplant, and separately from the healthy shoots.

Saprosporacea methylophalacae are probably indicators of healthy shoots, and higher in smithora covered shoots.

- marcus can remake the figures.

ambient obs: ambient shoots from august dominated by: Saprospiracea, one edge dominated by Shewanellaceae,rickettsiacea (3 but not edge 2), Methylophilaceae, Rhodobacteria, Unknown, vibrio also in other edge one

July Edge controls; Saprospiraceae, Methylophilaceae, Flavobacteriacea, Thiotrichacea, Unknown

July Interior controls; More even in appearance: Saprospiracea, Rhodobacteria, Shewanelliacea, Unknown, Verrucomicrobiacea, Cryomorphaceae.

After shows no real difference between either: Thiotrichaceae common, vibrio became present on inner shoot

July edge: Sapro,Methy only consistent ones that edge share

July interior: Flavo, Sapro,Rhodo,Thio,unknown, Rickett

August experiments: colonized by everything

Based on observations of data: all communities increased in diversity following transplant accept for interior shoots which decreased. Maybe smithora discouraged diatom colonization?

No idea why there is such huge variation in diversity on smithora blades. Could be because they are dominated by one family. High diversity is usually correlated with community health, but all diversity increased indicating that seagrass plants potentially maintain their own bacterial diversity.

Models that just used transplant to explain differences in diversity were the most effective in describing the data.

Discussion outline:

**There appears to be high abundance of smithora at the edge of the seagrass meadow versus the interior.**

-AIC model comparison showed that location was the most imporatnt factor dictating smithora abundance in candidate models.

-On the map we can see that areas with a large amount of smithora are generally at the edge of the meadow.

-High abundances of algae at the edges could be due to a variety of factors: habitat filtering…

-Previous studies have shown that abundances do not vary significantly throughout the meadow and so this effect could be due to a unique characteristic of smithora.

**At the wolf beach study site we found higher biomass at the edge, and a higher density of shoots at the edge.**

**-**At our study site seagrass quadrats at the edge had a higher density of shoots.

-It could be that a certain density of shoots is required to capture smithora spores. Slowing down of the particles through microturbulence between the blades (the same method that allows sediment settlement.

**Smithora did not disappear from plants that were moved to the interior of the meadow.**

-Smithora was capable of surviving in the interior of the meadow for a month

-Smithora looked healthy while seagrass shoots were quite close to dead

-This shows that smithora is capable of surving in the iterior of the meadow. However smithora biomass was lower on these transplanted shoots compared to control edge shoots that were not transplanted.

**Smithora colonized plants that had previously no smithora were colonized when moved to the edge of the meadow.**

**-**Smithora was capable of colonizing shoots that had previously had no smithora.

-This could because smithora was incapable of dispersing to the location.

-Could also be because we essentially killed the plant and so any bacterial/chemical defenses it had were compromised.

**Control shoots at both locations did not change in smithora abundance following detachment.**

**-**Control shoots in the interior were not colonized by smithora even though their health was compromised after detachment

-Likely not shoot health that is the only factor dictating whether shoots are colonized.

-one author showed that time was important in dictating smithora growth. Not because older shoots stop producing phenols but our transplanted shoots had similar biomass levels compared to controls even though they were only exposed to smithora for one month.

**Bacterial composotion plots show unique bacterial communities at the family level for blades of smithora.**

**-**Makes sense algae and seagrass have different properties

-Smithora also had lower diversity at the family level and species level.

-A large proportion of bacterial families on smithora were unknown. It has a very unique community.

**Shoots with and without smithora differed in composition.**

-Composition plots show that before transplant, shoots with and without smithora look very different.

-However following transplant these differences become less striking

-Shoots with smithora were still more similiar to other seagrass shoots compared to smithora blades.

**Shoots before and after transplant differed in composition**

-The increase in diversity after transplant can be seen in the composition graphs

-all shoots communities changed following transplant and 1 month

-There is much less differences between shoots with and without smithora after transplant, indicating that the effect of smithora on seagrass community is stronger when the plant is alive.

**Bacterial diversity is best explained by transplant alone.**

**-**This could be because of the effect of time on bacterial community. Additionally smithoar increased on all shoots following transplant regardless of smithora presence. However control shoots from the interior decreased in diversity following transplant. The only difference between these shoots and others is these shoots were never colnized by smithora. It could be that diversity was higher for these shoots because they weren’t in contact with smithora and when their health was conpromised there were no macroalgae communities to rescue the bacterial surface of the blade.

**Overall, transplant, smithora, and thier interaction had a signifiacnt effect on bacterial community.**

-From the NMDS you can see that shoots clusters based on before/after and smithora

-The most strking effect on community is the effect of transplant. It is important to note that this transplant was left in the new environment for 1 month. Changes we see with transplant are also confounded with time.

-Ambient shoots collected in august (while still alive and healthy) were more cimilar to dying transplanted shoots collected in august. This indicates that temporal effects are stronger than the seagrass health effects on bacterial community.

-Smithora was also swabbed a week before the initial shoots were swabbed. The extreme difference in community we see in Smithora could also be due to time rather than smithora differences.

**Grazer communities were also significantly different between the edge and interior.**

-High abundance of invertebrates at the edge compared to interior

-Most of this difference was in gammaridian amphipods

-High crustaceans at the edge has been shown before but it could be because of smithora offering food and habitat for these invertebrates.

**There is likely not grazer control of smithora on the location scale.**

-Grazers eat the smithora but its more likely that other factors are dictating it.

-If grazers were controlling the abundance of smithora you would expect to see less smithora where invertebrate abundances are higher.

**Community measurements between the shoot level and location level indicate that neither are sufficient to explain smithora zonation.**

**-**The sexual stage of smithora is unknown

-I think its likely that is dispersing from outside the meadow and then colonizing the first blades it contacts and not continuing further.

-More research into the spatial processes dictating algal spores would be helpful in determing what is driving these patterns in smithora abundance.

**Summary of results for reciprocal transplant**

Since there was no significant loss of *Smithora* when shoots were moved to a *Smithora* free zone I can infer that *Smithora*’s absence in the interior of the meadow is likely not due to grazing pressures by the invertebrates I identified. Shoots did not lose their *Smithora* after one month of being in a *Smithora* free environment. This indicates strongly that there is no change in an environmental variable between the edge and interior that prevents *Smithora* recruitment and settlement. Conditions may or may not be better at the edge for *Smithora*, but it can survive in the interior even though it is not present at that location. The ability of *Smithora* to grow in new locations when it is manually transplanted indicates that it could be experiencing dispersal limitation in Choked Pass.

When shoots were moved to the edge from the interior they were colonized with *Smithora*. This is likely due to *Smithora*’s continual release of spores (Hawkes, 1988b). The blades grow from a basal cushion and produce haploid spores from monostromatic tissue (Hawkes, 1988b). *Smithora* is known as a prolific colonizer and its high growth and colonization in a three-week time frame is not surprising. The fact that clean transplants were colonized indicates that shoots were *Smithora* free because of a lack of spores rather than a shoot level characteristic-and this could mean that *Smithora* is experiencing dispersal limitation.

Many models exist for explaining how currents and wave motions drive dispersal of algal spores (Gaylord et al., 2002). However in general these models show that there is huge variation in dispersal distances of species, and they are difficult to predict (Gaylord et al., 2002). Choked pass is a high current area, it could be that the current is so strong that spores drift at an angle, and are just swept off the meadow entirely. The speed of spreading is also related to the generation time of the species, as species can disperse small distances, grow and then release spores again (Norton 1992). *Smithora* individuals might take a while to develop before they can release spores, and the blades from which the spores release die back in the summer, limiting the dispersal of *Smithora* deeper into the meadow. A combination of life history and wave action could be limiting *Smithora* spread in Choked Pass.

The sexual stage of *Smithora* is unknown. However there is evidence for its existence (Hawkes, 1988b). The *Zostera marina* meadow is adjacent to a rocky intertidal habitat at the Wolf Beach site. *Smithora* is often found in the intertidal on *Phyllospadix spp*. and this plant has drifted into samples with *Smithora* attached. We also found *Smithora* on artificial seagrass units that were placed along the edge of the site. *Smithora* individuals are coming from somewhere, and it could be other haploid individuals or the diploid stage of the algae. Whether *Smithora* is dispersing as spores from a diploid crust or from blades already growing, limited dispersal from the rocky shore could be occurring. This suggests that dispersal could be highly important in dictating epiphyte community structure. Due to *Smithora*’s presence being influenced strongly by a change in location, it seems likely that we do not have *Smithora* communities in the interior of the meadow simply because the spores haven’t made it there yet, and this could be further tested by mapping seasonal spreading distribution.

**Bacterial Community Analysis**

The significant effect of transplant on bacterial diversity hints at a complex relationship between seagrass health, *Smithora* colonization, and temporal changes. *Zostera marina* possesses the ability to produce phenols that act as antioxidants and chemically defends against epiphytic colonizers (Harder, 2008). In response to shading *Zostera marina* has been shown to increase phenol content to deal with oxidative stress (Silva et al., 2013). Bacterial community is then affected by this change in phenol content (Holmström et al., 2002b). Removing a seagrass shoot from its root system is a stressful event for the plant. Moving a shoot could compromise its ability to produce protective phenols and allow for more species of bacteria to colonize the shoot. The fact that bacterial communities changed on each shoot that was transplanted with and without Smithora hints at some interesting links between seagrass health and bacterial community.

However, we also measured bacterial communities on shoots after a month had passed. If you look at the bacterial NMDS you can see that ambient healthy shoots collected in August are more smiliar to transplanted shoots swabbed at the same time than they are to healthy shoots from July. If phenols and seagrass health were the dominant forces shaping the bacterial communities then you would expect healthy shoots to be more similar to each other than transplanted shoots. Since shoots from the two time frames cluster together regardless of their algal presence or health it indicates that the time that the shoot is swabbed has a large effect on the bacterial community that is observed. In fact time has a similar effect on bacterial communities in a reciprocal transplant in sponges (Weigel and Erwin 2017). Abiotic factors proved to result in less bacterial community change compared to the simple passage of time (Weigel and Erwin 2017). However, healthy ambient shoots collected at the same time as damaged transplanted shoots had different bacterial species present on their surfaces, indicating that time alone is not sufficient to explain these community shifts.

A PERMANOVA and NMDS shows that there is still clustering of shoot level communities based on the presence of *Smithora*, Bacterial communities are very responsive to shoot level changes such as spore colonization. I believe that *Smithora* colonization itself could be altering the blade level community, rather than a specific bacterial community existing at the edge of the meadow that allows spores to colonize.

Furthermore, bacterial communities after transplant appear to cluster more closely than communities before transplant. In the before transplant group shoots with and without Smithora are distinctly different. Shoot communities after transplant appear to cluster much more tightly. Perhaps when the health of the shoot is compromised it loses its unique bacterial community and all unhealthy shoots become more similar regardless of algal colonization. From the NMDS It appears that healthy shoots with and without smithora are more different than unhealthy shoots with and without Smithora. Given the sensitivity of the shoot level communities to shoot health and time, it seems unlikely that a unique bacterial community exists on Z. marina that encourages Smithora colonization.

However, there is still a possibility that bacterial community could be promoting *Smithora* colonization. *Ulva* spores (a green algae species) have been shown to respond to chemical cues produced by a specific bacterial community (Joint et al., 2002). We see a significant correlation between *Smithora* presence and bacterial community composition, and we could be observing chemical communication between prokaryotes and eukaryotes. There is also the possibility that the detrimental impacts of shading caused by *Smithora* are changing the chemical environment of the blade and promoting a different bacterial community. Based on *Smithora*’s ability to colonize various substrates, and the colonization of clean blades that were moved to the high *Smithora* environment, I suggest that bacteria community does not determine *Smithora* colonization, rather *Smithora* colonization alters bacterial community.

*Smithora* colonization is correlated with community change at the bacterial level and this has implications for the larger seagrass community. Microbial communities in seagrass sediments have been connected to overall shoot health (Milbrandt et al. 2008), however this has yet to be shown conclusively with blade level microbial communities. Bacterial shifts on the surface of the blade could be linked to seagrass degradation, epiphytic colonization, or the presence of wasting disease.

**Grazer Community Analysis**

The increase in amphipod abundance correlated with *Smithora* presence suggests that *Smithora* is likely not grazer controlled. Invertebrate herbivores are widely known to eat macroalgae in seagrass meadows (Heck and Valentine, 2006). Amphipods have also been shown to consume a large amount of microalgae (Cruz-Rivera and Hay, 2000). The high fatty acid content makes *Smithora* very nutritious and epiphytic grazers turn red from eating it (Oregon university,Pers. Obs). I expected to Smithora abundance to be negatively correlated with grazer abundance, because of previous evidence for predator-grazer-epiphyte trophic cascades in *Zostera marina* meadows (Amundrud et al., 2015; Duffy et al., 2015)(Duffy et al., 2015)(Duffy et al., 2015).

Recent studies in the Choked Pass seagrass meadow have shown that juvenile rockfish use the meadow edge frequently as habitat, which is also where there is the highest abundance of Smithora (Olson 2017). Predation by rockfish could be reducing grazer abundance and allowing Smithora to grow at these edge habitats. However, a common food source of juvenile rockfish, gammaridian amphipods, had a dramatic increase in abundance where *Smithora* load was high (Cruz-Rivera and Hay, 2000). This suggests that top-down control is not what is causing the dramatic decline in *Smithora* from the edge to the interior of the seagrass meadow. *Smithora* could be providing a food source to amphipods and also sheltering them from predation, which would be influencing the community structure from the bottom up.

However there are many more epifaunal grazers than amphipods. It could be that grazer control of Smithora is occurring at the microscopic scale. Perhaps micrograzers such as copepods are consuming Smithora spores as they disperse before they have a chance to settle and grow. More information on how which grazing species are found in edge and interior habitats would be useful in determining the importance of consumer control in this system.

**5. Conclusion**

In conclusion three layers of the epifaunal community of *Zostera marina* were found to vary in space. *Smithora* varies in abundance from the edge to the interior of the seagrass meadow, possibly through dispersal limitation. Bacterial and invertebrate communities vary significantly on shoots with and without *Smithora*. Whether these variations in communities with *Smithora* are a result of species interactions or spatial processes remains unknown. Edge effects in seagrass meadows are likely playing a crucial role that needs to be further investigated.

Epibiotic communities on seagrass blades represent an intriguing system to use small scale processes to explain large scale patterns. Species interactions on a single blade when multiplied over every shoot in a meadow can have dramatic effects. Understanding the drivers of changes in seagrass epiphytic community structure will help predict large scale changes in the seagrass ecosystem.

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