**AN EXPERIMENTAL TEST OF BIOTIC AND ABIOTIC DRIVERS OF SPATIAL VARIATION IN ABUNDANCE OF EPIPHYTE *SMITHORA NAIADUM* ON SEAGRASS *ZOSTERA MARINA***

Gwendolyn Griffiths1, Rhea Sanders-Smith2, Margot Hessing-Lewis2, Angeleen Olson, Laura Wegener Parfrey1, Mary I. O’Connor1

1. Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4
2. Hakai Institute...

Manuscript in preparation for a Research Paper in [Aquatic Botany](https://www.elsevier.com/journals/aquatic-botany/0304-3770/guide-for-authors)

Corresponding Author:

Mary I. O’Connor, Department of Zoology, 6270 University Boulevard, University of British Columbia, Vancouver, BC, Canada V6T 1Z4

oconnor@zoology.ubc.ca

Keywords: red algae, microbial ecology, grazers, experiment, community

[ABSTRACT, < 250 words] Ecological communities vary in space at a variety of scales. In marine communities, dramatic changes in species composition can occur across a small spatial distance, resulting in communities that vary across seascapes. Through an experimental manipulation of seagrass (*Zostera marina*), we examined the processes that drive the abundance and distribution of *Smithora naiadum*, an epiphytic red alga, in *Zostera marina* meadows on the central coast of British Columbia. At, the shoot level, we hypothesized that *Smithora* could be controlled by invertebrate grazing or bacterial facilitation. Whereas, at the site level, we hypothesized that Smithora could be controlled by environmental factors leading to the recruitment and persistence of the epiphyte on seagrass shoots. We used a reciprocal transplant to investigate whether *Smithora* load was affected by shoot level characteristic, location (and associated environmental characteristics) or an interaction between them. We found that uncolonized blades were colonized when placed in a high *Smithora* environment, while colonized blades did not lose their existing *Smithora* when moved to a *Smithora* free environment. Using illumina sequencing of bacterial DNA isolated from surface swabs of seagrass transplants, we found a significant difference between bacterial communities on shoots with and without *Smithora*. Further, we found that shoots with *Smithora* had a higher invertebrate abundance, indicating that *Smithora* is likely not grazer controlled. Our results suggest that seagrass associated bacterial and invertebrate communities could be altered by the colonization of epiphytic *Smithora,* or could be subject to the same spatial processes as *Smithora*. This research suggests potential drivers of epiphytic community composition in seagrass meadows.

**Highlights**

**Graphical Abstract (anyone?)**

1. **Introduction**

[***spatial variation in host - epiphyte relative abundance***]

Understanding patterns in species abundance and distribution across spatial scales continues to puzzle ecologists (Boström et al., 2006, A. Driscoll, 2008; Levins, 1969). In communities strongly influenced by foundation species and abiotic factors, variation in the presence and abundance of resident species may reflect spatial patterns in the host species or in the environment (Wahl 2008). When these patterns emerge at small spatial scales we are presented with an opportunity to investigate at fine detail potential drivers for differences in community structure. *What about adding microbial communities as a possible driver to this opening paragraph?*

[***seagrass host - epiphyte system***]

Seagrasses are foundation species that host diverse animal and algal communities. Algal epiphytes living on seagrass blades support secondary productivity (Fry 1984) (Figure 1), yet also compete with seagrasses for light and nutrients (Mcroy and Goering 1974), (Sand-Jensen 1977), (Penhale 1977), (Harlin 1973a) (Coleman and Burkholder 1994) (Lin et al. 1996) (Morgan and Kitting 1984). Thus the foundation species and the biodiversity it hosts exist in a complex network of positive and negative interactions (Connolly 1994) (Boström and Bonsdorff 1997) (Sheridan 1997) (Webster, Rowden, and Attrill 1998) (Heck and Orth 1980; Heck Jr and Orth 1980) (Attrill, Strong, and Rowden 2000) (Tolan, Holt, and Onuf 1997) (Harlin 1975) (Fong, Lee, and Wu 2000).

[***shoot-level or abiotic drivers: possibilities and examples. (shoot-level: microbes, other?; location: abiotic, or grazers…)***]

Spatial variation in the types and abundance of epiphytes on a single foundation species can reflect local environmental conditions, such as nutrient concentration or flow rates (Lavery and Vanderklift 2002) (Milchakova 2000) (Alcoverro, Duarte, and Romero 1997) (Kendrick and Burt 1997; Cebrian et al. 1999) (Reyes and Sansón 1997; Johnson et al. 2005). For example, large changes in epifaunal communities can be associated with seagrass meadow edges (Bowden, Rowden, and Attrill 2001; Bell et al. 2001, Tanner 2005, Prado et al. 2007)[*find a better example*]. In general, edge effects affect communities due to changes in physical structure, abiotic conditions or grazing pressure (Soule 1986) (Renhorn et al. 1996; Fagan, Cantrell, and Cosner 1999). Abundances of invertebrates can vary significantly both between and within meadows due to predation by fish (Amundrud, Srivastava, and O’Connor 2015) (Boström and Mattila 1999) (Tanner 2005). Understanding the drivers of this spatial variation helps to understand the dynamics of the eelgrass-based community, supporting better understanding of temporal variation and events such as algal blooms.

Another possible driver of variation in algal epiphytes is variation in the host plant’s structure or chemistry. *Z. marina* plants could be changing their blade surface chemistry to discourage epiphyte colonization (Bell, Lang, and Mitchell 1974) (Mejia et al. 2016). Colonization of *Zostera marina* by spores of epifaunal organisms is accomplished through the establishment of a suitable bacterial community before the spores attach (Sieburth and Thomas 1973). Unique bacterial groups are associated with a specific blade surface chemistry (Bagwell et al. 2002) (Crump and Koch 2008) (Hamisi et al. 2009) (Weidner et al. 2000) (Duarte, Holmer, and Marba 2005), and the growth of unique bacterial communities can discourage the attachment of spores on marine macrophytes.

One way to begin to distinguish among multiple possible explanations is through reciprocal transplant experiments. Seagrass reciprocal transplants done to investigate epiphytic algal abundance have mainly focused on grazer control as the mechanism for biomass variation of microalage (Reynold et al. 2015). Other reciprocal transplants in eelgrass (*Zostera marina*) have found that…looked at changes in seagrass leaf morphology following a reciprocal transplant but did not measured any epifaunal communities (Backman 1991) (Kenworthy and Fonseca 1977). Studies have compared microbial communities between the edge and interior of patches (Ettinger et al. 2017) and while microbial, invertebrate, and algal consistently vary significantly between the edge and interior of seagrass patches; the mechanisms for this variation and any correlations between microbial communities and other levels of community structure remain uninvestigated.

[***our objectives***]

Our main objective was to investigate potential drivers of changes in abundance of a dominant epiphyte, the red algae *Smithora naiadum,* on the eelgrass *Zostera marina*. We performed a reciprocal transplant experiment of seagrass shoots between zones of high and low *Smithora* within a single, large *Zostera* meadow. We tested the hypotheses that *Smithora* abundance on eelgrass is determined by characteristics of the host plant rather than by the local environment. We investigated the host-plant microbial community as a possible host attribute that could influence settlement of *Smithora*. Our experiment therefore allowed us to test whether epiphyte abundance is clearly determined by the environment or the host plant and its associates

*Can we addone more sentence linking this to host plant health without epiphytes?*

2. Materials and Methods

2.1 Study System

*Zostera marina* is a meadow forming eelgrass common along coastlines in the northern hemisphere (*find an old ref for this statement, this is the kind of thing you want the first paper for, not just a recent paper.*). As a foundation species, *Z. marina* provides habitat for hundreds of invertebrate and fish species that in turn provide food for fish and other large consumers. Thus, eelgrass meadows are highly productive environments, and much of this secondary productivity is derived from epiphytic algae – mostly diatamos and other benthic micro-algae - growing on the seagrass blades rather than the seagrass itself (Valentine and Heck, Edgar and Shaw 1995, Taylor 1998).

*Smithora* *naiadum,* is thought to specialize on *Z. marina. Smithora* abundance and distribution varies widely along the Pacific Northwest coast (Harlin 1975). After colonizing as a microscopic spore, it forms tough basal cushions and then grows into lobed blades (Hansen 1986, Harlin 1973b, Hawkes 1988). *Smithora*’s successful colonization depends on the survival of spores as well as the microenvironment of the *Z. marina* blade. Due to *Smithora*’s large variation over a small distance, *Smithora* on *Zostera marina* is an interesting system in which to investigate the drivers of changes in epiphyte abundance in *Zostera marina* meadows (Kitting, Fry, and Morgan 1984).

2.2 How do *Zostera, Smithora* and associated epifuanal and microbial species assemblages vary between meadow edge and interior?

We studied the interaction between *Smithora* and *Z. marina* on the central coast of British Columbia, Canada, in June-August 2015 in Choked Pass, Calvert Island (Figure 1). In a large continuous eelgrass meadow approximately 367,000 square meters in area (Hakai geospatial team), *Smithora* is prevalent on *Zostera* blades along the edges of the meadow, but not in the meadow interior. The site is primarily ocean influenced, with salinities of XX and temperatures between 6 and 10 degrees C in summertime (Rhea’s data).

Within the Choked Pass eelgrass meadow, we quantified spatial variation in *Smithora* abundance on eelgrass. We surveyed 8 40-m transects, four in the meadow interior (>200m from the closest edge) and four at the meadow edge (2m from bordering sand habitats) throughout the primary growing season, May to August (Olson 2017; Fig. 2). All transects were in permanently subtidal seagrass, and were separated by at least 100 m. Using SCUBA, we collected one shoot every 10m along each transect (n = 5 shoots per site visit) by covering shoots with a Ziplock bag and detaching at the rhizome. From each shoot, we measured *Z. marina* shoot dry weight and *Smithora* dry weight.

In a second survey, we quantified epifaunal grazer abundance and diversity on *Z. marina* shoots at the meadow edge and interior at two adjacent cites: WF and IA (Figure 1). *Z. marina* shoots were collected from 0.25m X 0.25m quandrats (n = 6) from the interior (IA) and edge (WF) in early June, 2015. Following standard processing protocol (Duffy et a 2015), all invertebrates were removed from shoots and preserved with 95% ethanol. Invertebrates > 500 um in diameter were visually classified to the lowest possible taxonomic group (Appendix 1), usually family but sometimes to species, using a stereo microscope, and invertebrates known to associate with *Zostera* and graze epiphytic algae were enumerated (Whippo et al in review, Duffy et al 2015).

2.3 Does location and abiotic environment explain variation in epiphyte and microbial communities living on Zostera? A reciprocal transplant experiment.

To test whether *Smithora* abundance on an eelgrass shoot reflects the shoot’s location (environmental conditions) or the shoot itself (defenses, microbiota, age, etc), we conducted a reciprocal transplant experiment. We identified two adjacent source sites within the Choked Pass meadow typical of the high *Smithora* zone (WF) at the meadow edge and the low *Smithora* zone (IA) at the meadow interior. These zones differed in *Smithora* abundance on shoots, from 0.37 + 0.39 *Smithora* / *Z. marina* (g/g dry wt) in the high *Smithora* zone at WF to 0.02 + 0.06 *Smithora* / *Z. marina* (g/g dry wt) in the low *Smithora* zone at IA. Depth and substrate (sandy) were consistent, and the two sites were 5 meters apart and connected by continuous eelgrass habitat.

From each zone, we collected twelve shoots and exposed them to one of two treatments (n = 6): transplant and control. Transplanted shoots were collected and moved to the other zone (WF shoots moved to IA zone, and IA shoots moved to WF zone). Control shoots were collected and replaced in their zone of origin to control for the effect of uprooting on *Smithora* abundance and bacterial community. Collection, initial sampling, and replanting procedures consisted of the following steps: Shoots were collected on SCUBA on July 9th. They were clipped in the field at the sediment surface, leaving the rhizomes. Shoots were placed in a ziploc bag in the field underwater, and transported to the lab immediately. In the lab, shoots were photographed for morphometric analysis and swabbed for bacterial community analysis. When not being processed they remained submerged in seawater. Each shoot was identified and labelled with flagging tape so that it could be re-sampled at the end of the experiment. Shoots were replaced in the field on July 10th by attaching them by the sheath with zipties to PVC submersible platforms. In the field, platforms were secured to the sediment surface to keep shoots on the sandy substrate and floating upright. On August 10th, all 24 treatment and control shoots were collected and processed and photographed in the lab. We also collected 2 ambient shoots next to each transplant platforms to compare transplanted shoots to unmanipulated shoots. We removed invertebrate grazers were removed from the shoots upon collection.

2.4 Sampling shoot characteristics: morphometrics and microbiota

For all shoots collected for the transplant experiment (N = 12 treatment shoots + 2\*X ambient control shoots) and environmental surveys (N = 120), we measured the following shoot characteristics: leaf length, leaf width, biomass (dry weight, after 48 hours at 60°C), and microbiota. For shoots collected as part of environmental surveys, we also counted the number of blades per shoot. Shoots were brought to the lab, where epiphytes were gently scraped off with a microscope slide and grouped taxonomically (*Smithora*, *Porphyra*, and periphyton). *Z. marina* shoots and associated *Smithora* epiphytes were then dried at 60°C for 48hrs to obtain dry weights.

To quantify the diversity and composition of each shoot’s external microbiota, bacterial samples were taken before and after the transplant, as well as from ambient shoots collected at the time of transplant retrieval. We sampled microbiota from a standard location on each shoot - an area halfway up the shoot that was free of *Smithora*. This area was rinsed with filtered sterilized seawater for 10 seconds, and then a Puritan® sterile swab was used to swab the area for ten seconds, avoiding any *Smithora* basal thallus cushions. Swabs of *Smithora* blades were taken as above for comparison. The swab was stored in an individual sterile cryovial (VWR) and placed on ice for transport back to the lab, and were transferred to -80˚C for storage within 8 hours.

DNA was extracted from swabs and water filters using the MoBio PowerSoil®-htp 96 well DNA extraction kit (Carlsbad, CA) following the manufacturer’s recommended protocol. The V4 region of 16S rRNA in Bacteria and Archaea was targeted for amplification using redesigned versions of the primers 515f/806r (Caporaso et al. 2012): 515f: 5’–GTGYCAGCMGCCGCGGTAA–3’, 806r: 5’–GGACTACNVGGGTWTCTAAT–3’. Forward primers were tagged with a 12bp Golay barcode to facilitate sample pooling. Each PCR contained 10µl of 5-Prime Master Mix, 1µl of each primer (final concentration = 0.2µM each), 0.5µl of peptide nucleic acid (PNA) chloroplast blocking primer (Lundberg et al. 2013; 0.2µM final concentration, purchased from PNA Bio Inc., Thousand Oaks CA), 2µl of DNA, and PCR grade water to a final volume of 25µl. PCR was carried out with an initial denaturation step at 94˚C for 3 minutes, followed by 25 cycles of denaturation at 94˚C for 45 seconds, PNA clamping at 75˚C for 60 seconds, primer annealing at 50˚C for 60 seconds, and extension at 72˚C for 90 seconds, with a final extension step of 72˚C for 10 minutes. PCR products were quantified using Quant-IT Pico Green® ds DNA Assay Kit (Life Technologies). Equal amounts (25ng) of each sample were pooled and then purified using the MoBio UltaClean® PCR clean-up kit. Pooled library quantitation and paired-end Illumina MiSeq sequencing (2 x 300bp) was carried out at the Integrated Microbiome Resource facility in the Centre for Genomics and Evolutionary Bioinformatics at Dalhousie University (Halifax, Canada).

Raw sequencing reads were demultiplexed using split libraries within the Quantitative Insights into Microbial Ecology (QIIME v.1.9) analysis pipeline (Caporaso et al. 2010b), and then then trimmed to 250 base pairs using FastX Toolkit (<http://hannonlab.cshl.edu/fastx_toolkit/>). Reads were then clustered into “species” level operational taxonomic units (OTUs) using Minimum Entropy Decomposition (MEDs; Eren et al. 2015), with the minimum number of reads per MED node set to 90 (-M parameter). All other parameters were run with default settings; the maximum variation allowed per node (-V) was automatically set at three nucleotides.

Taxonomy was assigned to MED-nodes (hereafter referred to as operational taxonomic units; OTUs) using uclust (Edgar 2010) as implemented in the Assign Taxonomy function of QIIME v.1.9 retrained on the GreenGenes (gg\_13\_8) database (DeSantis et al. 2006). OTUs annotated to either chloroplast or mitochondrial sequences were removed as putative host contamination. Additional OTUs were removed if they occurred in only a single sample. Representative sequences for the remaining OTUs (n = 1984) were aligned with PyNAST v.1.2.2 (Caporaso et al. 2010a) using the GreenGenes 13\_8 alignment as a template, and a tree was constructed using FastTree (Price et al. 2010) as implemented in QIIME v.1.9. Samples with fewer than 1000 reads were removed from the analysis. Sequence data and MiMARKs compliant metadata are deposited at the European Bioinformatics Institute, accession number (XXXXXXXX).

**2.5 Statistical analyses**

To compare seagrass density and *Smithora* biomass at the edge vs. interior, one-way ANOVA was used with R. 325 statistical software. *Smithora* biomass and shoot density fit a normal distribution and so a linear model was used to fit the data.

To compare bacterial community composition among treatments, we constructed a dissimilarity matrix on rarefied data (5000 sequences/sample) using the UniFrac metric, which takes phylogenetic distance, but not relative abundance, into account (Lozupone & Knight 2005), to compare microbiota composition among sites and before and after transplanting of shoots. The matrix was constructed in Phyloseq (McMurdie and Holmes 2013) within R. Beta-diversity patterns were visualized with non-metric Multi Dimensional Scaling (NMDS) plots created in Phyloseq. A two-way PERMANOVA (Permutational Analysis of Variance) was used to compare the effect of *Smithora* presence, transplant, and their interaction on bacterial community. We did not include bacterial families with relative abundances lower than 0.02.

We compared epifaunal invertebrate abundance between edge and interior plots with ANOVA fit using a gamma generalized linear model. We used NMDS plots to visualize invertebrate community dissimilarity based on a bray-curtis dissimilarity metric. Invertebrate community data was analyzed in the Vegan 2.3-4 package in R (Okansen et al. 2016). A PERMANOVA was used to test the effect of Smithora, Location (edge vs. interior), and month (June vs July) on invertebrate communities. A one-way ANOVA compared amphipod abundance at the edge vs. interior locations. All R analyses used R 3.2.4.

**3. Results**

3.1 How do *Zostera, Smithora* and associated epifuanal and microbial species assemblages vary between meadow edge and interior?

Across eight sites at the landward side of the Choked Pass eelgrass meadow, *Smithora* presence and abundance on eelgrass shoots varied strongly from site to site (two-way ANOVA: site type (interior vs edge): F = 63.46, df = 1, p = < 0.001; Site: F = 8.06, df = 6, p = < 0.001, residuals: df = 108). There was a significant difference in *Smithora* abundance on *Z. marina* between meadow edge and interior sites (Figure 1C).

Additional, plot-scale sampling at the Wolf Beach site, where the experiment was conducted, revealed similar patterns of high *Smithora* abundance at the meadow edge and less in the interior in June 2017 (Figure 2). Shoot density was higher at the edge vs the interior (one-way anova: F = 15.29, df = 1, 10, p = 0.003; Appendix A), and so was *Smithora* load (one-way anova: F = 6.57, df = 1, 10, p = 0.028).

Epifaunal grazer abundance varied significantly over time and with shoot density across quadrats (Figure 2C). Grazer density on epiphytes increased significantly over the course of the experiment, between June and July (t=2.754, p=0.0079), and with shoot density (t=2.522, p=0.0268). Epifaunal invertebrate community composition also varied over time (PERMANOVA F=4.3221, df=1, p=0.065) and with *Smithora* abundance (PERMANOVA F = 4.7201, df = 1, p=0.048).

*Initial microbial assemblages.* Blades with *Smithora* harbor significantly different communities that blades without (p=0.027, pseudo-F=2.03,df=1). (Figures ##)

3.3 Does location and abiotic environment explain variation in epiphyte and microbial communities living on Zostera?

At the end of the reciprocal transplant experiment, shoots at the meadow edge had high *Smithora* load regardless of source location (Figure 3; two-way anova with interaction term: Source (interior vs edge): F = 32.04, df = 1, p = < 0.001; Treatment (control vs unmanipulated: F = 0.28, df = 1, p = 0.61, Source X Treatment: F = 4.67, df = 1, p = 0.05; residuals: df = 11). Shoots transplanted from the edge to the interior site retained *Smithora,* while interior shoots that stayed in the interior were not colonized. Controls (uprooted but locally planted) and unmanipulated shoots did not differ in *Smithora* load at the time of the end of the experiment (two-way anova: Source (interior vs edge): F = 26.34, df = 1, p = < 0.001; Treatment (control vs unmanpulated: F = 1.59, df = 1, p = 0.27, residuals: df = 10).

*Bacterial results on transplanted shoots.* There was a significant effect of transplant and *Smithora* presence on shoot level bacterial community. Following the transplant *Smithora* presence continued to be correlated with different bacterial communities (p=0.027, pseudo-F=2.03,df=1), but dispersion was not different (PERMDISP p=0.441). There was no significant difference in blade communities by origin of blades (PERMANOVA for start location p=0.583,pseudo-F=0.800,df=1) or by destination (PERMANOVA for destination p=0.573,pseudo-F=0.94, df=1). All August comparisons include ambient samples. Microbial taxonomic richness at the end of the experiment time point was not significantly different on blades with or without *Smithora* (t-test p=0.59) or by destination location (t-test p=0.60), or starting location (t-test p = 0.664).

Microbial community composition shifted from July to August (NMDS\_before\_after; PERMANOVA for date p=0.001, pseudo-F=4.818, df=1). This is unlikely to be a result of the transplant itself because the ambient samples from August group solidly within the August transplant samples.

**4. Discussion**

We tested the question / hypothesis that *something about hosts and their associated flora and faunal communtieies*…. We found that *Smithora* abundance did not change to match its environment when transplanted in one direction (from meadow edge to interior) but it did change in the other direction (interior to edge). Thus, we reject the hypothesis that in this case, local environmental factors determine *Smithora* abundance on Zostera shoots. This indicates that there is something unrelated to shoot level microbiome and local environment that is limiting *Smithora* dispersal into the interior of the meadow.

We observed that shoots with and without Smithora have different microbial communities in the field. *This might merit a little more discussion – was this a surprise, or is there any precedent for this in the litarture?*

The distinct microbial communities on shoots without *Smithora* did not prevent *Smithora* from colonizing clean shoots transplanted into a high *Smithora* area. Bacterial communities changed following the transplant, suggesting that algal colonization could be influencing bacterial community differences. not variation among individual shoots as consistent with outher studies our results did not show a significant effect of shoot location in microbial community (Ettiner et al. 2017) but all microbial communities changed for both colonized and non-colonized shoots following. This could also be related to an influence of time on the microbial communities over the 1 month transplant or a change in shoot health due to uprooting. Zostera marina can maintain its own epifaunal microbial community and the extent to which this community is influenced by environment (Meja et al. 2016). Rather than ‘more research is needed’ try to identify the actual knowledge gap.

In general we found that *Smithora* biomass and *Zostera* biomass and density differed between edge and interior sites. It is unclear why there is consistently more Smithora biomass at the edge of the meadow. The adult sexual stage of Smithora is unknown and it could be that the diploid stage of Smithora is a conchocelis phase that grows outside the seagrass meadow in shell fragments (Harlin,Hawkes). This could explain why there is higher Smithora biomass at edge areas facing the rocky intertidal and why we see high abundances of Smithora on *Phyllospadix* spp. in the intertidal. It could be that the dispersal distance of Smithora propagules is quite small and so it settles relatively quickly into the seagrass meadow.

Our final comparison between high and low Smithora sites was a grazer community comparison. We expected grazer abundances to be positively correlated with Smithora abundance. *Smithora* abundance did not explain the variation seen in epifaunal invertebrate abundances but it was correlated with a shift in community structure while location (edge vs. interior) was not. This indicates that *Smithora* providing more substrate on the blade surface is not necessarily what is driving the community changes between blades with and without *Smithora*. It could be that Smithora provides a specialized habitat to a unique assemblage of invertebrates or is an important food source to certain species. Juvenille rockfish are also abundant in these high Smithora areas and so they could be selectively reducing certain grazing species and altering the community composition (Olson 2017). Grazer communities vary between the edge and interior as well (Tanner 2005\*add a few more) and further research is needed to determine the extent to which these patterns of edge effects in seagrass meadows are driven by changes in substrate, predation, or food availability.

In summary our research highlights some important community forming processes happening at the edges of seagrass meadows. We noted differences in Smithora abundances between the edge and interior of meadows, and we showed that different seagrass microbial communities are correlated with this variation in abundance. We also showed that grazer communities vary with these changes in algal abundances. It is unclear whether all three communities are influenced by the same edge effects or they are interacting together to form the ecological pattern we are noting. Understanding community forming processes in seagrass epifaunal communities at small spatial scales is important for recognizing large scale patterns in seagrass communities.