

# FLOWING WITH THE TIDE: EPIPHYTIC HOST-SPECIFICITY AND PHENOTYPIC PLASTICITY OF THE BROWN ALGA *PADINA BORYANA*

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**Abstract.** Epiphytic algae form complex communities on their macroalgae hosts. The brown alga *Padina boryana* acts as a host for epiphytic algal communities, yet no studies have determined whether the community is host-specific. To test for epiphytic host-specificity, four substrates were placed in Cook's Bay and, after a three-week period, I examined the epiphytic community on each. My findings demonstrate that there is host-specificity and that substrate may influence the construct of epiphytic communities.

In addition to hosting epiphytes, *P. boryana* exhibits phenotypic plasticity – it adopts different morphs in response to environmental conditions. In order to understand how *P. boryana* responds to its environment, I observed where the distinct morphs occurred and attempted a transplant experiment to induce morph change. Furthermore, I compared the epiphytic communities on both morphs. My results support the hypothesis that the foliose morph occurs in shallower waters, while the turf morph is present in deeper water. These results provide evidence that *P. boryana* utilizes its phenotypic plasticity as a defense mechanism against predators. Moreover, the morphs affect the epiphytic communities that colonize *P. boryana*, substantiating the findings that substrate texture plays a role in the establishment of epiphytic communities.

**Key words:** *algae; Padina boryana; epiphytes; phenotypic plasticity; host-specificity; French Polynesia*

## INTRODUCTION

Epiphytic communities are present in both the terrestrial and marine environments. Epiphytes are plants or algae that colonize the surfaces of larger organisms. These diminutive species must rely on a host for survival and adjust to the chemical and physical characteristics of their host's environment (Burns and Zotz 2010). Epiphytes colonize larger species for a variety of reasons, including shelter from inhospitable environments and protection from herbivores (Ortuño-Aguirre and Riosmena-Rodriguez 2007). Although minute in size, epiphytes play an important ecological role in primary production (For example: Brock 1970, Finke and Seely, Jr. 1978, D'Antonio 1985). They act as a major food source for various organisms, such as snails, fish, and other invertebrates (Reyes-Vasques 1970, D'Antonio 1985). In addition, they contribute to reef biodiversity by increasing species richness (Ballantine 1975, Huston 1994).

Marine epiphytic algae communities are found on macroalgae species. The thalli (algae "leaves") of larger species provide ample space for colonization and house minuscule

epiphytic algal communities (Ortuño-Aguirre and Riosmena-Rodriguez 2007). Many studies have focused on how epiphytes affect the host-plant (D'Antonio 1985, Asaeda et al. 2004, Van Elven et al. 2004, Bittnick et al. 2010). However, there have been few studies that address whether these epiphytic communities are host specific. Moreover, most host-specificity studies focus on terrestrial, rather than marine epiphytes (Bernal et al. 2005, Laube and Zotz 2006).

The genus of brown algae *Padina* has a morphology that is conducive to colonization by epiphytic algae. A study documented the presence of epiphytic algal communities on *Padina* and determined percent cover of epiphytic algae increase with thallus size (Ortuño-Aguirre and Riosmena-Rodriguez 2007).

The epiphytic community associated with *Padina boryana*, a species of *Padina* that is found in Mo'orea, French Polynesia, has yet to be thoroughly studied. The foliose thalli of this species provide habitat for epiphytic algae, as well as micro-invertebrate species (personal observation). The epiphytic species involved and the specificity of colonization

surrounding this particular host-epiphyte interaction have yet to be assessed.

This study examined a subset of the *P. boryana* population in Cook's Bay to identify the epiphytic algal community that uses it as a host. I wanted to determine whether the algae that settle on *P. boryana* are specific to the host or whether they colonize the thalli opportunistically, as the algal propagules happen to drift in that direction. I hypothesized that the epiphytic community of *P. boryana* is host specific, due to its unique texture and calcified thalli.

In addition to hosting epiphytic algae, the genus *Padina* is known for its phenotypic plasticity – a phenomenon where individuals of the same genotype express varying phenotypes in response to environmental conditions (Bradshaw 1965). Morphological plasticity has been witnessed across clades in both terrestrial and marine environments (Spitze 1992, Thompson 1991, Callaway et al. 2002). Changes in *Padina* morphology occur in less than a week when predators are excluded (Lewis et al 1987, Diaz-Pulido et al. 2007). This morphological transformation has the potential to affect the epiphytic community that establishes on the *Padina* thalli. A study examining the morphological plasticity of *P. boryana* has yet to be conducted on Mo'orea.

In addition to examining epiphytic host-specificity, I used this study to discover more about the phenotypic plasticity of *P. boryana* and its two morphs. I strived to understand how the morphs of *P. boryana* responded to increasing water depth and distance from shore. Since other species of *Padina* express phenotypic plasticity (Lewis et al. 1987, Diaz-Pulido 2007), I hypothesized that the foliose morph would be present in shallower waters and that with greater depths and distances from shore, the turf morph would become more abundant. Furthermore, I desired to understand how the two morphs of *P. boryana* affected the epiphytic community. Due to the difference of substrate textures, I hypothesized that the foliose morph would have a greater number of species and larger species diversity than the turf morph.

The final aspect of my study attempted to determine whether a morphological change would occur when herbivores were excluded from the ecosystem. This question was addressed with a non-reciprocal transplant experiment in which individuals of the turf morph were placed in a habitat dominated by the foliose morph. Due to the absence of herbivores in this region, I hypothesized that

the turf morph would then transform to the foliose morph when in a region free of herbivores.

## METHODS

### *Study site*

The first study site was located at the Richard B. Gump Field Station in Cook's Bay, Mo'orea, French Polynesia (17°29'25.92"S, 149°49'34.30"W). The algal community at this site is dominated by the foliose morph of *P. boryana* from the shoreline until a depth of approximately 2 meters. All host-specificity experiments were conducted at this field site.

The second field site was Pineapple Beach, which is located on the west side of Mo'orea near the town of Haapiti (17°33'50.16"S, 149°51'58.05"W). This site was selected because the turf morph of *P. boryana* is found there. All studies involving this morph were conducted here. Fieldwork at both sites was conducted from October 2011 to November 2011.

### *Study organism*

*P. boryana* is a brown alga that inhabits warm ocean environments (Wichachucherd et al. 2010). It is found in depths of up to 2 meters, but it occurs in higher densities in shallower waters. The genus *Padina* has the unique ability to adopt two morphs (Plate 1). *P. boryana* is preyed upon by herbivorous fishes (Lewis 1985) and combats that by changing morphs. If herbivores are present, the algae assume a less palatable turf morph (Lewis et al. 1987). However, if there is no threat of herbivory, the algae display a foliose morphology that increases the surface area of the thallus and provides ample room for the settlement of epiphytic algae (Lewis et al. 1987).

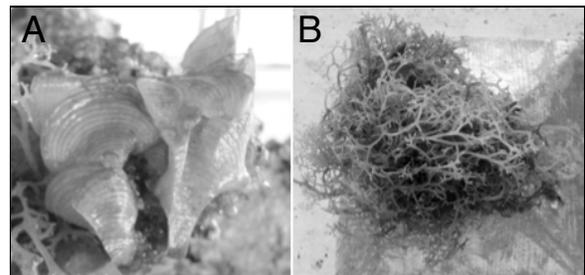


Plate 1. Two morphs of *P. boryana*: (A) foliose morph that is present when herbivores are absent and (B) the turf morph, which occurs when herbivores are present.

### *Epiphytic community assessment*

In order to assess the epiphytic community that colonizes *P. boryana* of Cook's Bay, I first mapped the perimeter of the field site using Global Positioning System (GPS). Once the perimeter of the *P. boryana* population was established, I ran a total of 12 transects throughout this defined area and destructively collected one *P. boryana* individual at the appropriate meter mark (Table 1). Three individuals were collected along each transect. At each collection site, the substrate and depth were noted. In addition to the 36 individuals collected from Cook's Bay, I also used the data collected from the uncleaned thalli of the host-specificity experiment to increase the sample size. In total, I examined 132 *P. boryana* thalli.

I transported the *P. boryana* individuals to the laboratory for epiphytic algal identification. I removed and examined four thalli from each individual using a dissecting microscope. The epiphytes were distinguished using a morphotype approach – I classified the epiphytes present based on morph alone. Species were recorded on a presence absence basis. This sampling method allowed for an initial characterization of the epiphytic population that acted as a resource for the experiments on epiphytic host-specificity.

TABLE 1. Location of transects conducted in Cook's Bay.

Transect	Distance Along Shore	Distance from shore	Frequency of Collection
A	0	8 to 14	3
B	10	44 to 50	3
C	70	40 to 60	10
D	130	10 to 30	10
E	160	10 to 30	10
F	190	1 to 30	10

*Notes:* All distances were measure in meters. Frequency of collection indicates how often (in meters) individuals were collected along transects. 0 meter corresponds to 15 meters north of the Fare Pote'e, a Gump Station landmark.

I conducted a similar study at Pineapple Beach to assess the epiphytic population of *P. boryana* at that location. However, instead of

sampling individuals solely for an epiphytic community assessment, I also used the data collected to understand the epiphytic community of the two morphs. I did this to prevent unnecessary destructive collecting of *P. boryana* individuals.

### *Host-specificity*

To determine whether the epiphytic algal community that colonizes *P. boryana* is host-specific, I placed four different substrates in a *P. boryana* habitat. These four substrates provided habitats of different textures as a test for host-specificity. The 4 substrates were as follows: an algae settlement plate, uncolonized *Turbinaria ornata*, *P. boryana* with clean uncolonized thalli, and *P. boryana* with uncleaned thalli. The brown alga *T. ornata* was selected because it is present in high densities in neighboring locations and has a texture that differs from *P. boryana*. The *T. ornata* was cleaned to rid it of its epiphyte population. I then tethered it and the settlement plate to a cement block using zip ties (Plate 2).

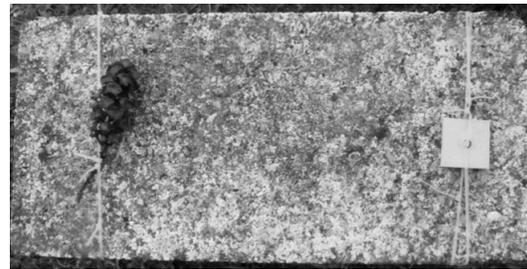


Plate 2. Cement block with tethered *T. ornata* (left) and the settlement plate (right). Both were secured using zip ties.

The additional substrates were both *P. boryana*. I cleaned one of the *P. boryana* substrates to provide a blank slate for colonization and left the other intact with its existing epiphytic population. I selected 12 plot locations at varying distances from shore—six in water below a depth of 0.85 meter and six in water deeper than 0.85 meter (Table 2). After a three-week period, I collected the substrates from each block and examined them within a two-day period in the lab to identify their respective epiphytic algae using the dissecting microscope.

### *Epiphytic community of different morphs*

As both the foliose and turf morph of *P. boryana* are found at Pineapple Beach, I used transects to determine whether morphology is

associated with depth and distance from shore. I conducted transects from six different points on shore to a distance of 50 meters. Transects were 30 meters apart along the shoreline. Every five meters I noted the morph of *P. boryana* individuals present, the depth of water, and the percent cover of *P. boryana* using a 0.5 by 0.5 meter quadrat.

TABLE 2. Distance from shore and depth of cement blocks.

Block Number	Distance from Shore	Depth
3	25	0.62
4	45	0.92
5	65	0.91
6	85	1.31
7	28	0.66
8	38	0.81
9	58	0.9
10	78	1.4
11	78	1.2
12	55	0.79
14	35	0.65
15	15	0.54

Notes: distance and depth are measured in meters.

I compared the epiphytic communities on the two morphs of *P. boryana* using foliose and turf individuals collected from Pineapple Beach. The individuals were sampled along the same transects originating at the shoreline and extending 50 meters. I collected focal individuals at varying depths and distances for a total of 20 individuals. I selected focal individuals approximately every 15 meters. If no *P. boryana* individuals were present, I would follow the transect until I found one. I examined four thalli from the foliose morph and four clumps of branches from the turf morph. In an attempt to standardize the size of the clump of turf morph examined, I cut rectangular chunks with an average width of 3.3 centimeters and an average length of 2.9 centimeters. The epiphytic algal communities of the two morphs were compared using species diversity and species richness. I documented the epiphytic algae present using a dissecting microscope and recorded them on a presence absence basis.

#### Non-reciprocal transplant experiment

To test the morphological plasticity of *P. boryana*, a non-reciprocal transplant experiment was conducted. I collected 20 individuals of the turf morph from Pineapple Beach and replanted them in Cook's Bay by securing the individuals to eight-centimeter metal plates. I then placed them near the cement blocks of the host-specificity experiment to locate them easily. The transplanted individuals sat in Cook's Bay for a period of two weeks. Algae individuals were photographed before and after the transplant experiment so that morphological changes could be determined visually. To ensure that removing the turf morph from its substrate did not negatively affect the growth of the algae, I carried out a procedural control on 15 turf individuals. I removed them from their substrate and then returned to the field site twice, one and two weeks after removing them, in order to verify their survival.

#### Statistical analyses

All statistical analyses were run in the statistical program R unless otherwise noted (R Development Team 2007).

**Epiphytic community assessment:** A Principal Component Analysis (PCA) was used to understand the distribution of epiphytic algae within the *P. boryana* population and to help determine whether patterns in the epiphytic community existed in different regions of the bay. A species accumulation curve was composed, which aided in determining how many epiphyte species colonized the thalli of *P. boryana*.

**Host-specificity:** A PCA analysis contributed to understanding whether the epiphytic algae that colonizes *P. boryana* is host-specific. This accounted for the presence or absence of particular epiphytic species and clustered the substrates with more similar epiphytic populations. An Adonis test (a non-parametric permutation MANOVA) was run to determine whether the communities on the substrates differed significantly.

**Epiphytic community of different morphs:** Since depth of water and distance from shore are highly correlated, those two factors were combined into one Principal Component in the statistical program JMP 9 ©. In JMP, A chi-square test was run to determine whether the morph of *P. boryana* changed in relation to this newly constructed Principal Component.

Non-reciprocal transplant experiment: Due to the failure of this aspect of the experiment, no statistical analyses were necessary.

## RESULTS

### *Epiphytic community assessment*

I identified 32 distinct morphotaxa of epiphytic algae on 132 thalli of *P. boryana* sampled from Cook's Bay. According to a small 95% confidence interval at 132 samples, most of the epiphytic species that occur on *P. boryana* at this location were sampled. At Pineapple Beach, 29 distinct morphotaxa of epiphytic algae were observed on the thalli of *P. boryana*. Similarly, according to a small 95% confidence interval at 78 samples, most of the epiphytic species were observed.

### *Host-specificity*

Each different substrate that was placed in Cook's Bay had a unique community associated with it (Fig. 1). The epiphytic communities on each were significantly different from one another (Adonis – a non-parametric permutation MANOVA –  $DF_{3,94}$ ,  $F=14.168$ ,  $P<0.00002^*$ ).

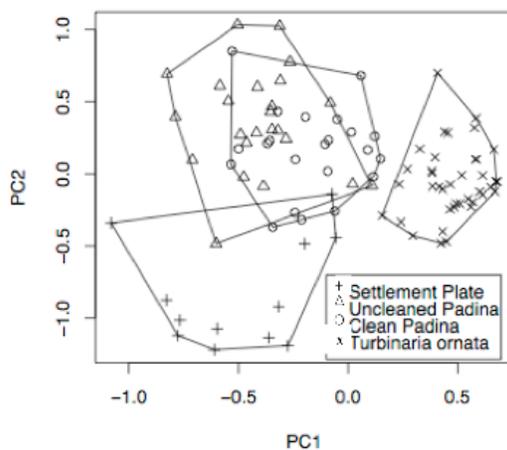


FIG. 1. Host-specificity of the epiphytic community on the four substrates placed in Cook's Bay. Each shape corresponds to a different treatment. The two-overlapping clusters (uncleaned *Padina* and cleaned *Padina*) show that same host substrate result in similar epiphytic communities, while the other two clusters (settlement plate and *Turbinaria ornata*) do not overlap with each other and thus have distinct epiphyte communities. The figure was generated using a Principal Component Analysis in R.

### *Epiphytic community of different morphs*

The morph of *P. boryana* changes with distance and depth from shore (Fig. 2). When compared, the morphs present differed with changing distance and depth (Chi-square test,  $\chi^2=73.64$ ,  $df=2$ ,  $P<0.0001^*$ ). Depth of water and morph were compressed into one principal component for all analyses.

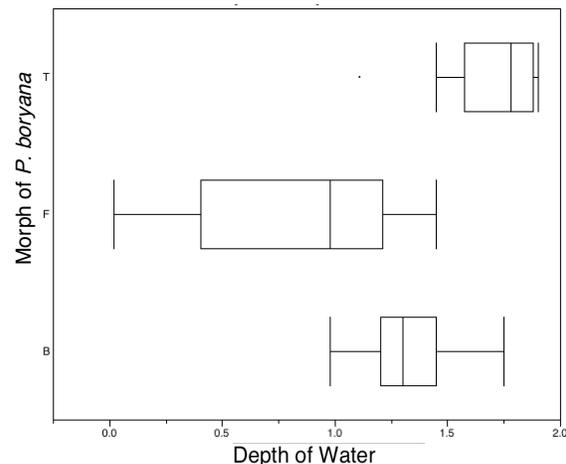


FIG. 2. The morph of *P. boryana* changes in relation to water depth. The foliose morph (F) is present in the shallower water (below 1.1 meter) and the turf (T) morph is present in deeper water (greater than 1.1 meter). There is an interim distance where both morphs (B) are present. The error bars represent standard error. The pattern seen in this graph is analogous to the relationship between distance from shore and morph present. This figure was generated using JMP 9.

Epiphytic communities differ between the two morphs of *P. boryana* (Fig. 3). There was difference in the epiphytic community on the two morphs of *P. boryana* (Constrained Redundancy Analysis,  $Df_{1,29}$ ,  $F=1.1931$ ,  $P<0.00005^*$ ). However, the average species diversity and average species richness for both morphs are relatively the same. (Fig. 4 and 5).

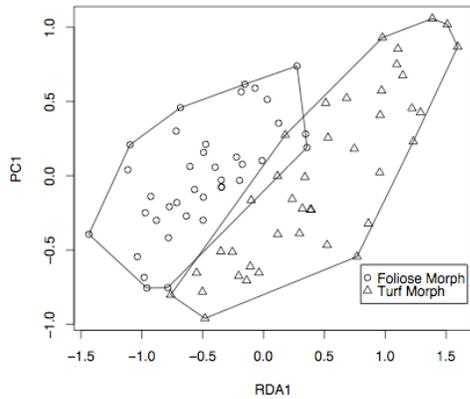


FIG. 3. The epiphytic communities on the two morphs of *P. boryana* differ significantly. The clusters representing the two morphs (denoted by the circles and triangles) do not overlap, indicating the epiphytic communities have different characteristics and are distinct. The figure was generated using a Constrained Redundancy Analysis in R.

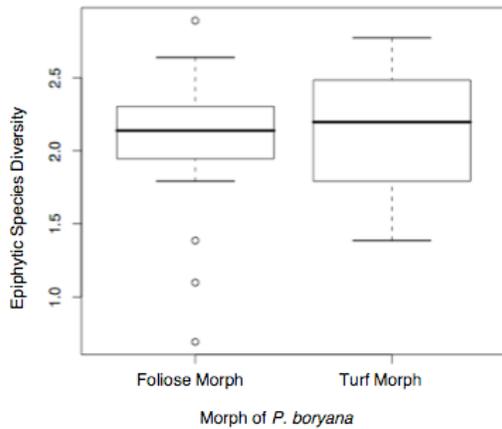


FIG. 4 Epiphytic species diversity for both morphs of *P. boryana*. The black bars indicate the average species diversity, the circles represent outliers, and error bars represent standard error. The average species diversity for each morph is relatively the same, but the outliers on the foliose morph make the communities significantly different. The graph was constructed using the statistical program R.

### Non-reciprocal transplant experiment

Over a two-week period, no morph change was observed in the turf morph individuals that were transplanted from Pineapple Beach to Cook's Bay. The 15 algal individuals of the procedural control survived for a period of two-weeks.

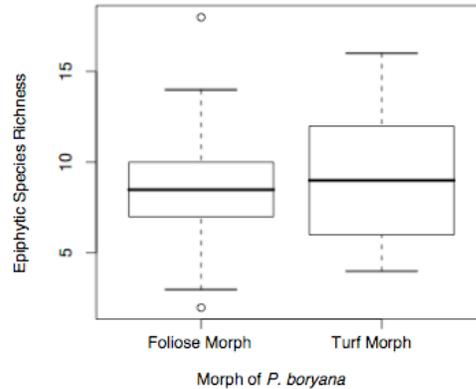


FIG. 5. Epiphytic species richness for both morphs of *P. boryana*. The black bars indicate the average species richness, the circles represent outliers, and error bars represent standard error. The average species richness of both morphs is relatively the same, but, similar to the species diversity, the outliers result in overall different communities. The graph was constructed using the statistical program R.

### DISCUSSION

The results provide evidence for epiphytic host-specificity. The epiphytic communities on the different substrates placed in Cook's Bay, as well as on the two morphs of *P. boryana*, demonstrated that each host has a distinct epiphytic community.

The species accumulation curves of the epiphytes on *P. boryana* from both Cook's Bay and Pineapple Beach begin to saturate with increasing thalli samples, demonstrating that most of the epiphytic species at each location were observed. At Cook's Bay, 32 distinct morphotaxa were observed, while at Pineapple Beach 29 species colonized the algae. To reach these points of saturation, it was necessary to analyze 132 thalli from Cook's Bay and only 78 thalli from Pineapple Beach. This implies that the epiphytic community of *P. boryana* is more diverse at

Cook's Bay than the population at Pineapple Beach. These data indicate the thalli of *P. boryana* act as a habitat for a diverse and speciose epiphytic algal community. This is a phenomenon that is seen across many species of macroalgae. The brown alga *Sargassum muticum* acts as a host for 48 epiphytic algal species and the brown alga *Fucus vesiculosus* houses a total of 27 epiphytic and mobile algae species (Aguilar-Rosas and Galindo 1990 and Kersen et al. 2011).

The results of my study support my hypothesis that the epiphytic algae that colonize *P. boryana* are host-specific. My results clearly indicate that the three different substrates – *P. boryana*, *T. ornata*, and the settlement plates - act as habitats for distinct epiphytic communities. Both the uncleaned and cleaned thalli of *P. boryana* had similar community assemblages, while the other two substrates have their own communities. The presence of unique epiphytes contributed to these distinct communities – certain epiphytic species were found only on one of the 4 substrates. Although many of the same epiphytic species were found on these four substrates, the communities were distinct in the frequencies at which epiphytic species were found. For example, I found the epiphyte defined as "green O" on both the clean and uncleaned *P. boryana* 10 and 20 percent of the time, respectively. I never observed it on *T. ornata* and it was present on the settlement plates 75 percent of the time. Close proximity of all substrates ensured that epiphytes had access to all surfaces. The varying frequencies show the substrates were equally accessible, but epiphytes only colonized particular ones.

The difference in substrate texture may influence the epiphytic community. Each substrate had different architectural traits, such as calcified foliose thalli or a smooth hard surface, which may influence epiphyte community structure. Similar results were seen when the epiphytic community of *Padina consecrens* was examined. Different epiphytic communities were found on the thalli of *P. consecrens* and plastic algal mimics (Ortuno-Aguirre and Riosmenda-Rodriguez 2007). In addition, the plant architecture of two species of freshwater algae affected the quantity of colonizing epiphytes (Cattaneo et al. 1998) and greater numbers of epiphytes colonize substrates with more rugose textures (Jennings and Steinberg 1997). The host characteristics, which include substrate texture, may influence epiphytic communities (Cacabelos et al. 2010, Jones and Thornber

2010). Certain species of epiphytes may have an affinity for specific textures, leading to the construct of host-specific communities.

The depth of water and distance from shore affected which morph of *P. boryana* was present at Pineapple Beach. The foliose morph was found in shallower waters and the turf morph occurred in deeper waters, which supports my hypothesis that the foliose morph would be present in shallower water depths and the turf morph would occur in deeper water. The transition of phenotypes from the palatable foliose to the unpalatable turf morph is likely the result of the increased presence of herbivores (Lewis et al. 1987, Diaz-Pulido et al. 2007). The turf morph is the less edible version of the two morphs. With increasing water depth, larger fish are present and grazing frequency intensifies. The heightened level of herbivory exerts a pressure on the algae forcing it to transform into the turf morph. This phenotypic plasticity is thus a survival technique employed by the algae in response to the higher numbers of herbivores (Lewis et al. 1987, Diaz-Pulido et al. 2007).

The epiphytic communities that colonize the foliose and turf morphs are significantly different, which supports the initial hypothesis that the communities on each morph would differ. This result was unanticipated because the average species diversity and richness for the two morphs were relatively similar. However, the foliose morph has a wider spread of species, which leads to the overall difference in epiphytic communities. These results support the idea that substrate texture influences epiphytic communities – the two morphs have distinct textures and rather different epiphytic communities.

However, since the diversity and richness of the two morphs do not differ significantly, epiphytes may colonize *P. boryana* for reasons other than purely substrate texture. Chemical composition of host plants can influence epiphytic communities (Pereira et al. 2010). In addition, abiotic factors, such as exposure to waves or other elements, contribute to the formation of epiphytic communities (Kersen et al. 2011). These studies demonstrate that the formation of epiphytic communities do not rely solely on texture.

Additional studies on epiphytic host-specificity would aid in understanding how these miniscule communities function. Increasing the number of host substrates and including algal mimics would clarify whether

epiphytic communities are influenced exclusively by substrate texture or whether chemical composition of the host affects the community construct.

None of the 20 individuals that were transplanted from Pineapple Beach to Cook's Bay changed morph within two weeks. Only 10 individuals remained tethered to the tiles, while the other 10 disappeared. Other studies on the genus *Padina* found that when herbivores were excluded, the algae changed morph in less than a week (Lewis et al. 1987, Diaz-Pulido 2007). This phenomenon was not seen in my transplant experiment. The transformation may not have occurred because a large storm pelted Cook's Bay for a period of 4 days, causing massive quantities of sediment to infiltrate the bay. Sediment has the potential to affect photosynthesis, as well as plant reproduction (Chapman and Fletcher 2002, Wichachucherd 2008, Wichachucherd 2010). This run-off coated the algae with a layer of dirt particles and may have prevented them from receiving the environmental cues to which the other *P. boryana* individuals in Cook's Bay normally respond.

In addition, the algae may have not transformed due to a dearth of environmental cues. Two other species of *Padina* transformed from foliose to turf morph when herbivores were excluded, but those results were obtained by fish exclusions and not transplant experiments (Lewis et al. 1987, Diaz-Pulido 2007). In addition, other algae that exhibit phenotypic plasticity respond to cues from herbivorous zooplankton, but not from carnivorous species (Lurling 2003). Thus, even though there was a lack of *P. boryana* predators, the failure of individuals to transform may have been due to the absence of other necessary environmental cues.

In order to understand the intricacies of *P. boryana*'s phenotypic plasticity, further studies must be conducted. Experiments incorporating herbivore exclusions, rather than transplant experiments, would allow for morph transformation in the organism's own habitat. This would alleviate any stress the algal individuals experienced during transportation and transplantation, as well as control for other abiotic factors, such as water depth and sediment deposition.

The results of this project contribute to the understanding of epiphytic communities. They demonstrate that there is some level of host-specificity. Moreover, this study supports the idea that members of the genus *Padina* utilize the biological phenomenon of

phenotypic plasticity to defend themselves against ravenous herbivores.

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#### LITERATURE CITED

- Aguilar-Rosas R and Galindo AM. 1990. Ecological aspects of sargassum-muticum (fucales, phaeophyta) in Baja-California, Mexico - reproductive phenology and epiphytes. *Hydrobiologia* 204:185-90.
- Asaeda T, Sultana M, Manatunge J, Fujino T. 2004. The effect of epiphytic algae on the growth and production of *Potamogeton perfoliatus* L. in two light conditions. *Environ Exp Bot* 52(3):225-38.
- Ballantine, DL and Humm HJ. 1975. Benthic algae of the Anclote Estuary I. Epiphytes of seagrass leaves. *Florida Scientist*. 38:150-162.
- Bernal R, Valverde T, Hernandez-Rosas L. 2005. Habitat preference of the epiphyte *Tillandsia recurvata* (bromeliaceae) in a semi-desert environment in central Mexico. *Canadian Journal of Botany* 83(10):1238-47.
- Bittick SJ, Bilotti ND, Peterson HA, Stewart HL. 2010. *Turbinaria ornata* as an herbivory refuge for associate algae. *Marine Biology* 157(2):317-23.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advance Genet* 13:115-55.
- Brock, TD. 1970. Photosynthesis by algal epiphytes of *Utricularia* in Everglades National Park. *Bull Mar Sci* 20:952-956.

- Burns KC and Zotz G. 2010. A hierarchical framework for investigating epiphyte assemblages: Networks, meta-communities, and scale. *Ecology* (Washington D C) 91(2):377-85.
- Cacabelos E, Olabarria C, Incera M, Troncoso JS. 2010. Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. *Estuarine Coastal and Shelf Science* 89(1):43-52.
- Callaway RM, Reinhart KO, Moore GW, Moore DJ, Pennings SC. 2002. Epiphyte host preferences and host traits: Mechanisms for species-specific interactions. *Oecologia* 132(2):221-30.
- Cattaneo A, Galanti G, Gentinetta S, and Romo S. 1998. Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. *Freshwater Biology* 39: 725-740.
- Chapman A and Fletcher R. 2002. Differential effects of sediments on survival and growth of *Fucus serratus* embryos (fucales, phaeophyceae). *J Phycol* 38(5):894-903.
- D'Antonio C. 1985. Epiphytes on the rocky intertidal red alga *Rhodomela-larix* (turner) C agardh - negative effects on the host and food for herbivores. *J Exp Mar Biol Ecol* 86(3):197-218.
- Diaz-Pulido G, Villamil L, Almanza V. 2007. Herbivory effects on the morphology of the brown alga *Padina boergesenii* (phaeophyta). *Phycologia* 46(2):131-6.
- Finke LR and Seeley HW. 1978. Nitrogen-fixation (acetylene-reduction) by epiphytes of freshwater macrophytes. *Appl Environ Microbiol* 36(1):129-38.
- Huston, MA. *Biological diversity: the coexistence of species on changing landscape*. Cambridge university press, 1994.
- Jennings JG and Steinberg PD. 1997. Phlorotannins versus other factors affecting epiphyte abundance on the kelp *Ecklonia radiata*. *Oecologia* 109(3):461-73.
- JMP, Version 9. SAS Institute Inc., Cary, NC, 1989-2011.
- Jones E and Thornber CS. 2010. Effects of habitat-modifying invasive macroalgae on epiphytic algal communities. *Marine Ecology-Progress Series* 400:87-100.
- Kersen P, Kotta J, Bucas M, Kolesova N, Dekere Z. 2011. Epiphytes and associated fauna on the brown alga *Fucus vesiculosus* in the Baltic and the North seas in relation to different abiotic and biotic variables. *Marine Ecology-an Evolutionary Perspective* 32:87-95.
- Laube S and Zotz G. 2006. Neither host-specific nor random: Vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* (London) 97(6):1103-14.
- Lewis SM. 1985. Herbivory on coral reefs algal susceptibility to herbivorous fishes. *Oecologia* (Berlin) 65(3):370-5.
- Lewis SM, Norris JN, Searles RB. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. *Ecology* (Washington D C) 68(3):636-41.
- Lurling, M. 2003. Phenotypic plasticity in the green algae *Desmodesmus* and *Scenedesmus* with special reference to the induction of defensive morphology. *Ann. Limnol - Int. J. Lim* 39(2): 85-101.
- Ortuño-Aguirre C and Riosmena-Rodriguez R. 2007. Dynamics of epiphytism on *Padina concrescens* (dictyotales : Phaeophyta) from the southwestern coast of the Baja-California peninsula, Mexico. *Cienc Mar* 33(3):311-7.
- Pereira RC, Bianco EM, Bueno LB, De Oliveira MAL, Pamplona OS, Da Gama BAP. 2010. Associational defense against herbivory between brown seaweeds. *Phycologia* 49(5):424-8.
- R Development Core Team. 2007. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing. <http://www.R-project.org>
- Reyes-Vasquez, G. 1970. Studies on the diatom flora living on *Thalassia testudinum* Konig in Biscayne Bay, Florida. *Bulletin of Marine Science* 20(1) 106-134.
- Spitze K. 1992. Predator-mediated plasticity of prey life-history and morphology - *Chaoborus-americanus* predation on *Daphnia-pulex*. *Am Nat* 139(2):229-47.
- Thompson, DB. 1991. Consumption rates of the evolution of diet-induced plasticity in the head morphology of *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Oecologia* 89:204-213.

- Van Elven BR, Lavery PS, Kendrick GA. 2004. Reefs as contributors to diversity of epiphytic macroalgae assemblages in seagrass meadows. *Mar Ecol Prog Ser* 276:71-83.
- Wichachucherd B. 2008. Population structure of *Padina boryana* Thivy (Dictyotales, Heterokontophyta) in two locations in Phuket Province in Southern Thailand. Prince of Songkla University. Master's Thesis.
- Wichachucherd B, Liddle LB, Prathep A. 2010. Population structure, recruitment, and succession of the brown alga, *padina boryana* thivy (dictyotales, heterokontophyta), at an exposed shore of sirinart national park and a sheltered area of tang khen bay, phuket province, thailand. *Aquat Bot* 92(2):93-8.