

# VARIATION IN EPIFAUNA COMMUNITY AND EPIPHYTE COVER AMONG MARINE ALGAE

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**Abstract.** Algae function as a habitat for both faunal and floral communities by adding spatial complexity and increasing microhabitat spaces that provide refuge from physical stress, protection from predators, and a source of food for epifauna. This study reports on quantitative investigations of differences in the epifaunal community composition, relative abundance of epifauna, diversity of epifauna, and percent coverage of epiphyte among five different marine algae. Algae used in this study were collected from the fringing reef of Cook's Bay, on the island of Moorea, French Polynesia. Experimental results revealed that amphipods, tanaids, and gastropods were the most abundant epifaunal taxa. Significant differences in epifaunal community composition, relative abundance of epifauna, diversity of epifauna, and percent coverage of epiphyte were also observed. The results suggest that the assemblages of epifaunal and epiphytic community differ based on the structural morphology and sediment retention capacity among macroalgal species. Understanding the differences in epifaunal and epiphytic communities can provide insight into the amount of biodiversity present at a microhabitat level.

**Key words:** *epibionts; phytal communities; algal host; seaweed; Turbinaria ornata; Sargassum mangarevense; Halimeda sp.; Amansia rhodantha; Dictyota sp.; Moorea, French Polynesia*

## INTRODUCTION

Algae are important organisms at the base of the food web that also contribute to habitat structural complexity and heterogeneity in shallow water communities (Vázquez-Luis et al. 2012). Marine macroalgal species have been found to serve as both primary space holders in communities, competing for spatial resources (Cacabelos et al. 2010), as well as a secondary substratum, acting as biological habitat structure by changing physical properties of substrates or chemical environments that provide suitable habitats for more abundant and diverse organisms (Jones and Andrew 1992, Chemello and Milazzo 2002, Wikström and Kautsky 2004, Hauri et al. 2010, Wallentinus and Nyberg 2007).

By creating biological substrates, macroalgae function as foundation species by increasing microhabitat space available for other organisms. For example, macroalgae are known to provide breeding habitat for many fishes, as well as protection for juvenile fish against tidal currents, waves, and large predators (Mukai 1971). Similarly, many invertebrates also strongly depend on macroalgae as refuge from physical stress caused by unfavorable environmental

conditions including desiccation or wave impact, protection from predators, and a source of food (Duffy 1990, Bell 1991, Viejo 1999). Additionally, the physical structure of macroalgae can provide habitat for epifauna (Fishelson and Haran 1986, Cacabelos et al., 2010).

Epifaunal and epiphytic communities on algae, also referred to as the "phytal" in the sense of Remane (1993), have been extensively studied across different macroalgal hosts in different regions, although most studies have been conducted in temperate and subtropical zones (Mukai 1971, Hicks 1980, Fishelson and Haran 1986, Chemello and Milazzo 2002). Anandavelu et al. (2013) found that the distribution and abundance of epifauna on five morphologically distinct intertidal seaweeds differed based on the structural morphology of the macroalgal species. This same study also found that the most dominant animal phylum found across all algal species examined was Arthropoda, and the most abundant order present was Amphipoda. Fishelson and Haran (1986) also found differences in epifaunal communities across four different algal species collected from the Israeli Mediterranean shore and hypothesized that the differences were due to the variation in thallus structure of the algae and the

availability of nourishment on the host plant. In another study conducted in the Mediterranean Sea, Chemello and Milazzo (2002) showed that the abundance and diversity of the molluscan assemblages were significantly different between macroalgae with different algal architectural characteristics including degree of branching and algal width. Additionally, Gibbons' (1988) study on the West coast of South Africa found that the structure of the harpacticoid copepod community varied among intertidal algal species that differed in the amount of sediment accumulation. Algae provide a habitat for many invertebrates including Platyhelminthes, Annelids, Crustaceans, Molluscs, and Echinoderms (Fishelson and Haran 1986). The taxonomically and morphologically diverse invertebrates living on algal hosts exhibit a range of trophic habits from filter feeding, grazing on epiphytic algae, eating detritus, preying upon other epifauna, to consuming the host plant itself (Caine 1977, Roland 1978, Zimmerman et al. 1979, Brawley and Fei 1987, Duffy 1990) – all suggesting that the physical structure provided by macrophytes has important ecosystem consequences.

In addition to phytal animal communities, macroalgae also provide a hard substrate that serve as possible settlement sites for smaller algal epiphytes (Wahl 1989). Different macroalgal hosts differ in their suitability as substrates for epiphytes depending on multiple factors including the morphological characteristics of the base, the degree of branching, the roughness and texture of the surface, the production of allelopathic substances such as mucilage, and the thallus growth rate (Lobban and Harrison 1997). A previous study on epiphytic host-specificity on the brown algae *Padina boryana*, conducted in Moorea, French Polynesia, found that epiphytic communities exhibit host-specificity and the type substrates may influence the associated epiphytic community (Flynn 2011).

In Moorea, previous studies have also explored the phytal animals living on macroalgal hosts (Naim 1988, Hanson et al. 2002). For example, Naim (1988) studied the distributional patterns of mobile fauna associated with three different species of the green alga *Halimeda* on the Tiahura coral-reef complex and found differences in the faunal communities across the three species of algae. The epifaunal organisms were also hypothesized to take an active part in the

preservation of the thallus of the macroalgal host by multiple processes including consuming the superficial film of organic matter on the algal surface, restricting the amount of sediment trapped by the thallus, and grazing on microphytes that inhibit photosynthesis on the macrophyte (Naim 1988). In another study on epifaunal assemblages on macroalgae, Hanson et al. (2002) found that the most abundant group of epifauna present on the invasive brown alga *Turbinaria oranata* was crustaceans. Both studies have provided insight on the epifaunal community structure on two different genera of macroalgal hosts individually, but no previous work has explored both epifauna and epiphytic communities across multiple macroalgal hosts in Moorea.

The overall goal of this study is to characterize epifaunal communities and describe epiphyte coverage on the five most abundant marine algal species in the fringing reef zone of Cook's Bay, Moorea, French Polynesia. Specifically, this study aims to answer two questions: 1) Does epifaunal community composition, relative abundance, and diversity differ among multiple algal host taxa? And 2) Does epiphyte coverage differ among multiple algal host taxa? Because the five algae selected in this study differ in aspects of architecture, thallus structure, and sediment retention capacity, I hypothesized that there will be a difference in the epifaunal community composition, relative abundance, and diversity. Taxonomically distinct groups of invertebrates are more likely to prefer colonizing different algae depending on their feeding habit and differences in morphological structures. I hypothesized that amphipods would be the most abundant epifaunal group present across all the algal hosts. Additionally, I hypothesized that the percent coverage of epiphyte will differ among multiple host species because of epiphytic host-specificity and differences in substrate structure that the different macroalgal hosts can provide.

## METHODS

### *Study site*

Sampling was conducted between October 23<sup>rd</sup> and November 9<sup>th</sup> at the edge of the fringing reef of Cook's Bay on the island of Moorea, French Polynesia (Fig. 1).

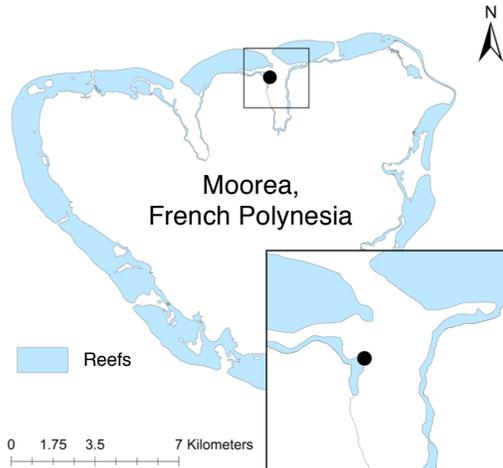


FIG. 1. Map of Moorea, French Polynesia showing the sampling site (17°29.166'S 149°49.503'W) on the fringing reef of Cook's Bay

#### *Algal Collection*

The five macroalgal hosts from which the epifauna were analyzed in this study were selected based on high abundance on rocky substrates in the area. The algae were collected from the same area to prevent effects from confounding variables such as wave action, depth, temperature, pH, and salinity. Each bundle of algae was removed carefully with minimal disturbance. The entire structure including the blade, stipe, and holdfast were placed in a Ziploc bag with as little water as possible and stored in the -80°C freezer to prevent them from deteriorating. Ten replicate samples of five species of algae were collected in total. Each of the five algal taxa are morphologically distinct, and were identified using Payri et al. (2000). See Appendix 1 for photographs and distinguishing characters.

#### *Epifauna and Epiphytes*

Each algal sample was defrosted and rinsed with fresh water for 10 seconds then filtered through a 500 µm sieve to capture epifauna. The sieve and the algae were examined under a dissecting microscope for 30 minutes. Invertebrates were removed with forceps and placed into a 4 mL glass vial with 70% ethanol. Epifauna were then categorized into taxonomic groups and the number of individuals for each group was recorded. The groups were broken down as follows: gastropods, bivalves, amphipods, isopods,

decapods, tanaids, copepods, ostracods, polychaetes, oligochaetes, and ophiuroids. See Appendix 2 for photographs.

Percent epiphyte coverage for each algal sample was then estimated by examining four pieces of algae with area approximately 2 cm<sup>2</sup> under the dissecting microscope.

#### *Density Calculation*

The algal samples were dried in a drying oven at 75°C for 72 hours and the dry weight of the algae were recorded. Because the different algal samples collected had different dry weights, the epifaunal counts for each taxonomic group had to be normalized with the dry weight.

#### *Statistical Analysis*

The data collected in this study was analyzed using R-Studio (R Development Core Team 2013).

A PERMANOVA (Anderson 2001) test was done in R using the vegan package (Oksanen et al. 2007) in order to determine whether there is a significant difference in epifaunal community composition among the different algal species. The PERMANOVA was performed on both the raw epifaunal count data as well as the normalized density calculations for (a) all five algal species and (b) a subset of three algal taxa. Normalized density data on community composition for all five algal species was then visualized in multidimensional space using a non-metric multidimensional scaling (NMDS) plot with the vegan package (Oksanen et al. 2007). Ordilipses were used to create a confidence ellipse around each of the algal taxa.

The relative abundance of epifauna, measured as the number of organisms per 100 g of dry algae, was calculated using the following formula:

$$\text{relative abundance} = \frac{\text{total number of organisms}}{\text{dry weight of algae (g)}} \times 100$$

The Shannon-Wiener Diversity Index (Shannon 2001) for each of the algal samples was calculated in R using the vegan package (Oksanen et al. 2007). The percent epiphyte coverage was found by averaging the estimated epiphyte coverage of the four replicates for each algal sample.

The following tests were performed independently to determine whether relative abundance, diversity, and percent epiphyte coverage all vary between algal species. The

Shapiro-Wilk test for normality (Shapiro and Wilk 1965) was done to show that the data was not normally distributed. The non-parametric Kruskal-Wallis Test (Feir-Walsh and Toothaker 1974), using the PMCMR package in R (Pohlert 2014), was then performed to test the significance of the differences between the mean relative abundance, mean Shannon diversity index, and percent epiphyte coverage among different algal species. Lastly, a posthoc pairwise comparison using the Tukey and Kramer (Nemenyi) test (Nemenyi 1962) with Tukey-Dist approximation for independent samples from the PMCMR package (Pohlert 2014) was done in order to investigate differences between each of the algal species pairs.

## RESULTS

### *Epifaunal Community Composition*

A total of 2280 organisms were found on the 35 algal samples observed. The three most abundant epifaunal taxonomic groups across all the algal hosts are amphipods, tanaids, and gastropods (Fig. 2). Together, these three groups make up 66% of all the epifauna found in this study.

Epifaunal community composition among the five algal taxa is different (Fig. 3). Amphipods are the most abundant epifaunal group on *Turbinaria* (35%), *Sargassum* (41%), and *Amansia* (33%), decapods are the most abundant epifaunal group on *Halimeda* (25%), and gastropods are the most abundant epifaunal group on *Dictyota* (46%) (Fig. 3).

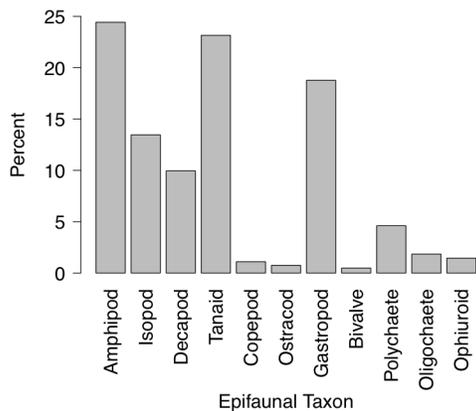


FIG. 2. Percent of total animals found belonging to each taxon, pooled across all algal hosts. See appendix for better descriptor of each epifaunal taxon.

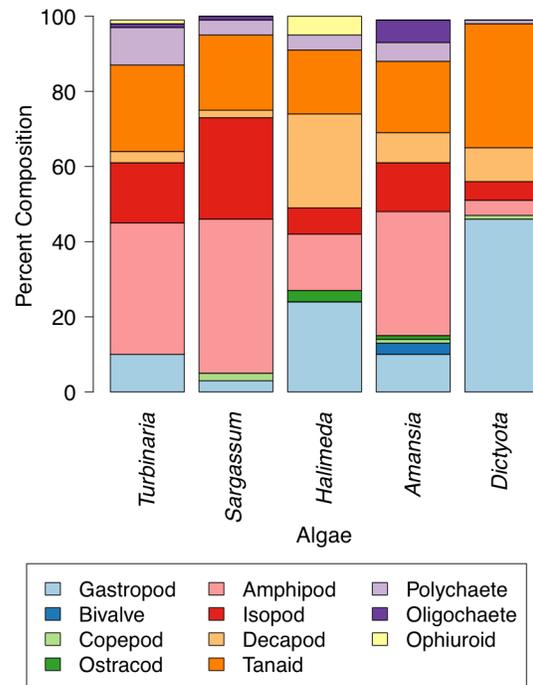


FIG. 3. Stacked barplot of the percent composition of each epifaunal taxon for the five algal species.

The results of the PERMANOVA test on both the raw epifaunal count data as well as the density data (number of organisms corrected by dry weight of algae) showed that there was a significant difference in the epifaunal community composition among the algal taxa ( $p < 0.0001$  for both data sets). In the non-metric multidimensional scaling (NMDS) plot, the *Dictyota* and *Halimeda* ellipses did not overlap with any of the other algal species, whereas the *Turbinaria*, *Sargassum*, and *Amansia* ellipses overlap with one another (Fig. 4). The additional PERMANOVA test on the epifaunal density data of only *Turbinaria*, *Sargassum*, and *Amansia* showed no significant differences in epifaunal community composition among these three groups ( $p = 0.29$ ).

### *Epifaunal Relative Abundance*

The relative abundance of epifauna was significantly different among the five algal groups (chi-squared=20.8,  $df=4$ ,  $p < 0.0005$ ). The average relative abundances range from a high in *Dictyota* ( $5183.6 \pm 2984.5$  organisms/100g algae) to a low in *Halimeda*

( $314.7 \pm 171.2$  organisms/100g algae) (Fig. 5). The average relative abundance and standard deviation for *Dictyota* was 16.5 times and 17.43 times larger than the average relative abundance and standard deviation for *Halimeda*, respectively (Fig. 5).

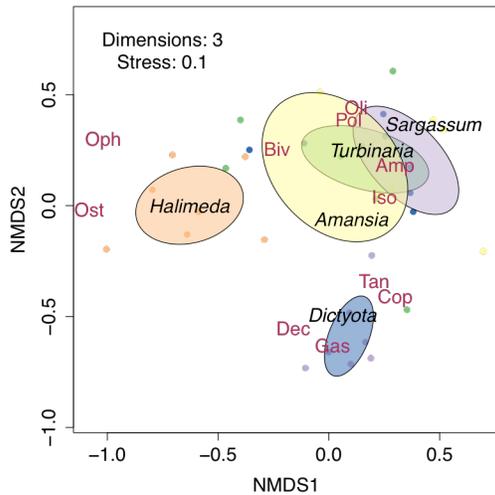


FIG. 4. NMDS plot showing differences in epifaunal community composition for the five algal hosts. The following terms for the epifaunal groups have been abbreviated: Amphipod (Amp), Isopod (Iso), Decapod (Dec), Tanaid (Tan), Copepod (Cop), Ostracod (Ost), Gastropod (Gas), Bivalve (Biv), Polychaete (Pol), Oligochaete (Oli), and Ophiuroid (Oph).

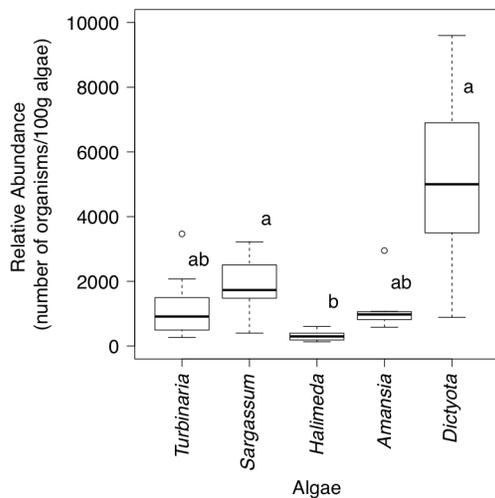


FIG. 5. Boxplot of relative epifaunal abundance for the different algal taxa. Algal taxa sharing a common subscript letter are not significantly different from one another using the pairwise Tukey and Kramer (Nemenyi) posthoc test.

### Epifaunal Diversity

The epifaunal Shannon Diversity Index was significantly different among the five algal groups (chi-squared=20.9,  $df=4$ ,  $p < 0.0005$ ). The Shannon Diversity Index ranges from a high in *Halimeda* ( $1.71 \pm 0.07$ ) to a low in *Sargassum* ( $1.16 \pm 0.23$ ) and *Dictyota* ( $1.21 \pm 0.13$ ) (Fig. 6). The average epifaunal diversity for *Halimeda* was 1.48 times and 1.41 times larger than the average epifaunal diversity for *Sargassum* and *Dictyota*, respectively (Fig. 6). *Halimeda* has the smallest standard deviation compared to all other algae.

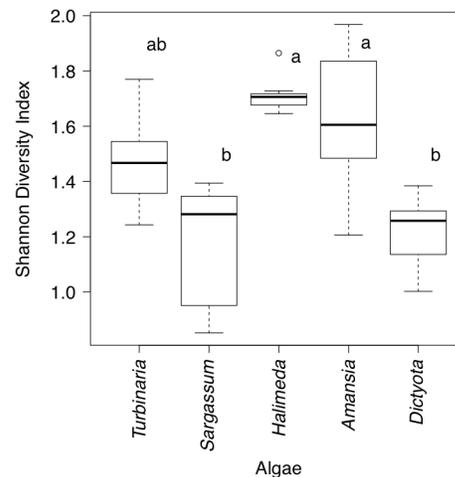


FIG. 6. Boxplot of Shannon Diversity Index for the different algal taxa. Algal taxa sharing a common subscript letter are not significantly different from one another using the pairwise Tukey and Kramer (Nemenyi) posthoc test.

### Percent Epiphyte Coverage

The percent epiphyte coverage was significantly different among the five algal groups (chi-squared=16.4,  $df=4$ ,  $p < 0.005$ ). The Shannon Diversity Index ranges from a high in *Turbinaria* ( $52.7 \pm 10.61$ ) to a low in *Halimeda* ( $9.29 \pm 2.69$ ) and *Amansia* ( $20.43 \pm 18.66$ ) (Fig. 7). The average percent epiphyte coverage for *Halimeda* was 5.68 times and 2.58 times larger than the average percent epiphyte coverage for *Halimeda* and *Amansia*, respectively (Fig. 7). *Halimeda* has the smallest standard deviation compared to all other algae.

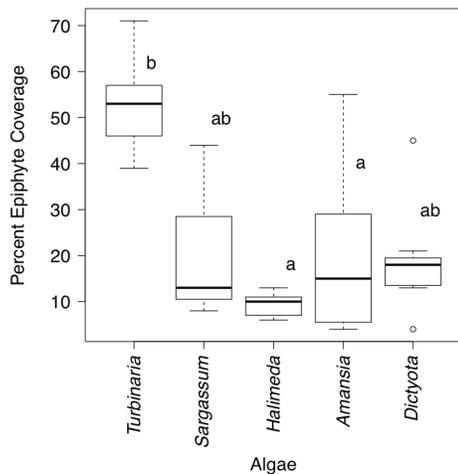


FIG. 7. Boxplot of Percent Epiphyte Coverage for the different algal taxa. Algal taxa sharing a common subscript letter are not significantly different from one another using the pairwise Tukey and Kramer (Nemenyi) posthoc test.

#### DISCUSSION

This study showed that the epifaunal community composition, relative abundance of epifauna, diversity of epifauna, and percent coverage of epiphytes all varied among different macroalgal hosts.

Of the five algal taxa, *Turbinaria ornata* had the highest percent epiphyte coverage. This is most likely due to its erect upright thallus that has the ability to provide a hard substrate that serves as a platform for epiphytic growth. The most abundant epifaunal taxa found on *Turbinaria* were amphipods. Amphipods are known to prefer more highly branched, morphologically complex algal hosts because they are less susceptible to predation by fishes when living in algae that provide better protection (Holmlund et al. 1990). The stiff, erect thallus of *Turbinaria ornata* could therefore provide an ideal living condition for amphipods.

*Sargassum mangarevense* had the lowest average and highest variance for epifaunal diversity, which may be due to its soft flexible thallus and leaflike lateral branches not being able to support a variety of morphologically different epifauna. *Sargassum* also collects very little sediment, which could provide another explanation for the low epifaunal diversity. Additionally, *Sargassum* provides a better habitat for organisms that are suited to filter-

feeding (Fishelson and Haran 1987). Animals that require a nutritional factor or other abiotic factors that exists only on the reef platform will not be able to continue living on *Sargassum* after it detaches from the platform and floats without decaying or losing structure for a portion of its life cycle (Fishelson and Haran 1987).

*Halimeda*, a sediment trapping calcified green alga, had the highest average epifaunal diversity and the lowest average percent epiphyte coverage. Sediment trapping increases epifaunal habitat complexity and allows the algae to provide a microhabitat community for sediment-dwelling organisms (Anandavelu et al. 2013). This could explain the reason why decapods were the most abundant epifaunal taxa found in *Halimeda*. However, the presence of sediment also covers up the algal surface, which reduces the amount of open surface area available for epiphytes to grow on. This study also found that *Halimeda* had the lowest average relative abundance of epifauna, which may be explained by the variation in the dry weights of the different algal taxa depending on the composition of the algae and the amount of water retained in the thallus. This will be further discussed in comparison to the highest average relative epifaunal abundance in *Dictyota*.

*Amansia rhodantha*, a red alga with a thin compressed leafy thallus, had the second highest average epifaunal diversity. Additionally, *Amansia* also had the largest variance for both epifaunal diversity and percent epiphyte coverage, which could be explained by the variability of surrounding algae found near *Amansia*.

*Dictyota* had the second lowest average epifaunal diversity, possibly due to the thin ribbon-like compressed thallus that, like *Sargassum*, cannot support as many different kinds of organisms. However, in this study *Dictyota* was the alga with the highest average and largest variance for relative abundance of epifauna. The large difference in average epifaunal relative abundance for *Dictyota* and *Halimeda* is most likely due to differences in dry algal weight. Across the seven replicates, the average weights of the *Dictyota* samples were  $1.97 \pm 0.75$  g, while the average weights of the *Halimeda* samples were nearly 16 times greater ( $30.69 \pm 8.95$  g). Because the epifaunal counts were based on a timed effort sampling, the maximum number of organisms that can be removed from the algae within 30 minutes could have been reached for *Halimeda*. In other

words, increasing the amount of algae might not have increased the number of organisms found in *Halimeda*. Thus, a higher average dry weight for *Halimeda* compared to *Dictyota* resulted in a lower epifaunal density because the epifaunal counts did not increase proportionally with the increase in dry weight. This could also explain the large variance in epifaunal relative abundance in *Dictyota* because a slight difference in dry algal weight, for instance 1 g of algae compared to 2 g of algae, would result in a two-fold difference in relative abundance because the epifaunal counts are divided by the different algal weights. In the future, a possible way to avoid encountering this problem could be to either scale the epifaunal counts by surface area instead of by weight or collecting less algae so that the majority of the organisms living on the algae can be collected.

In addition to differences in epifaunal abundance and epifaunal diversity, the epifaunal community composition also varies among the five algae. This was expected because previous studies had shown that different macroalgal hosts provide specific microhabitat conditions that different invertebrate groups prefer, depending on the function of the host, which can range from providing a source of food to providing protection from both predators and environmental conditions (Duffy 1990, Bell 1991, Viejo 1999).

Here, it was found that amphipods are the most abundant epifaunal group on *Turbinaria*, *Sargassum*, and *Amansia*. As discussed earlier, the abundance of amphipods in *Turbinaria* is most likely due to the amount of protection the algae provides. The abundance of amphipods in *Sargassum* and *Amansia*, however, could be explained by the overlap in epifaunal community composition with *Turbinaria*. A possible explanation for this similarity in epifaunal community composition is that they are located spatially close to one another. The close proximity between these algal species could allow for movement of the invertebrates back and forth between the different algae. *Amansia rhodantha* was generally found to be on the rock platform underneath both *Turbinaria ornata* and *Sargassum mangarevense*, so the invertebrates could have been mistakenly captured in the Ziploc bags during collection.

*Turbinaria ornata* and *Sargassum mangarevense*, the two most abundant algal species, were also generally present alongside one another. Another possible reason for the

similarity in epifaunal community composition between these two algal species is that both of them undergo a phase in their life cycle where they detach and float on the water surface in the form of algal mats. This unique characteristic for these two algal species may play a role in defining what types of epifauna can use these algae as a habitat. Additionally, the ability to float without decaying or losing structure has also allowed *Turbinaria* and *Sargassum* to conquer the crest, barrier, and fringing reefs of the Society Islands of French Polynesia since the beginning of the eighties, and continue to be widely distributed with a high population density in Tahiti and other high islands of French Polynesia today (Payri and Naim 1982, Stiger and Payri 1997, Stiger and Payri 1999).

Humans play a large role in modifying the environment by increasing the amount of nutrients present in bodies of water as a result of fertilizer use and agricultural runoff. The increase in available nutrients, such as nitrogen and phosphorus, leads to the process of eutrophication, where macroalgae such as *Turbinaria* and *Sargassum* become more abundant. A further consequence of the change in macrobenthic communities is the change in diversity and composition of epifaunal communities living on the algal hosts. This study provides a discussion of differences in epifaunal community composition that could be useful in predicting which invertebrate group may become more or less abundant and diverse in the future depending on which algae are more widespread.

Since there have been no previous studies comparing the epifaunal communities and epiphyte coverage among macroalgal hosts in Moorea, this research could contribute to the existing literature on the epifaunal guild. Another interesting area, which could be of interest for future studies, would be to separate epifauna found on algae into smaller taxonomic groups. Understanding the composition of epifauna on different algal hosts, especially at a higher resolution taxonomic analysis, can provide greater insight into the amount of biodiversity present at a microhabitat level. This could be interesting in terms of conservation as well as potentially understanding interactions between organisms and their algal hosts as well as interactions among the phytal communities themselves.

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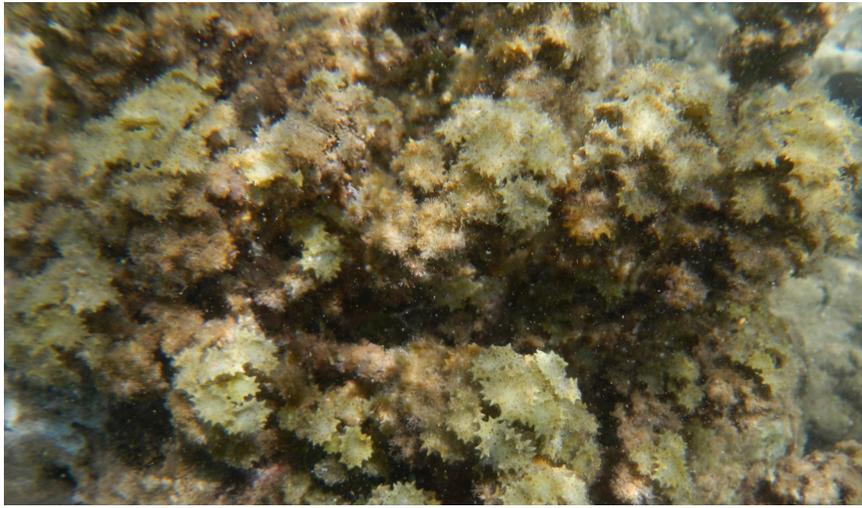
#### LITERATURE CITED

- Anandavelu I., R. Jayabarathi, G. Padmavati, and K. Jayaraj. 2013. Epifaunal assemblage on morphologically distinct intertidal seaweeds of Kodiyaghat (South Andaman), India. *Proceedings of the International Academy of Ecology and Environmental Sciences* 3:229-237.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Bell, S. S. 1991. Amphipods as insect equivalents? An alternative view. *Ecology* 72:350-354.
- Brawley, S. H., and X. G. Fei. 1987. Studies of mesoherbivory in aquaria and in an unbarricaded mariculture farm on the chinese coast. *Journal of Phycology* 23:614-623.
- Cacabelos, E., C. Olabarria, M. Incera, and J. S. Troncoso. 2010. Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. *Estuarine, Coastal and Shelf Science* 89:43-52.
- Caine, E. 1977. Feeding mechanisms and possible resource partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, USA. *Marine Biology* 42:331-336.
- Chemello, R., and M. Milazzo. 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. *Marine Biology* 140:981-990.
- Duffy, J. E. 1990. Amphipods on seaweeds: partners or pests? *Oecologia* 83:267-276.
- Feir-Walsh, B. J., and L. E. Toothaker. 1974. An empirical comparison of the ANOVA F-test, normal scores test and Kruskal-Wallis test under violation of assumptions. *Educational and Psychological Measurement* 34:789-799.
- Fishelson, L., and T. Haran. 1987. Epifauna of algae on a rocky platform near Mikhmoret (Mediterranean Sea, Israel): composition and dynamics. *Israel Journal of Zoology* 34:105-123.
- Flynn, S. M. 2011. *Flowing with the Tide: Epiphytic Host-Specificity and Phenotypic Plasticity of the Brown Alga Padina boryana*. Biology and Geomorphology of Tropical Islands, Student Research Papers. University of California, Berkeley.
- Gibbons, M. 1988. The impact of sediment accumulations, relative habitat complexity and elevation on rocky shore meiofauna. *Journal of Experimental Marine Biology and Ecology* 122:225-241.
- Hanson, C., K. Karr, and A. Kendall. 2002. Distribution and abundance of *Turbinaria ornata* on the north side of Moorea, French Polynesia. *Maine Ecology of Moorea, French Polynesia*, Student Research Papers. University of California, Santa Cruz.
- Hauri, C., K. E. Fabricius, B. Schaffelke, and C. Humphrey. 2010. Chemical and physical environmental conditions underneath mat- and canopy-forming macroalgae, and their effects on understory corals. *PloS ONE* 5:e12685.
- Hicks, G. R. 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of Experimental Marine Biology and Ecology* 44:157-192.
- Holmlund, M. B., C. H. Peterson, and M. E. Hay. 1990. Does algal morphology affect amphipod susceptibility to fish predation? *Journal of Experimental Marine Biology and Ecology* 139:65-83.
- Jones, G. P., and N. L. Andrew. 1992. Temperate reefs and the scope of seascape ecology. *Proceedings of the Second International Temperate Reef Symposium* 7:63-76.
- Lobban, C. S., and P. J. Harrison. 1994. *Seaweed ecology and physiology*. Cambridge University Press.
- Mukai, H. 1971. The phytal animals on the thalli of *Sargassum serratifolium* in the Sargassum region, with reference to their seasonal fluctuations. *Marine Biology* 8:170-182.
- Naim, O. 1988. Distributional patterns of mobile fauna associated with *Halimeda* on the Tiahura coral-reef complex (Moorea, French Polynesia). *Coral Reefs* 6:237-250.

- Nemenyi, P. 1962. Distribution-free multiple comparisons. *Biometrics* **18**:263.
- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, M. H. H. Stevens, M. J. Oksanen, and M. Suggests. 2007. The vegan package. Community Ecology Package. R package version 1.15-1.
- Payri, C., and O. Naim. 1982. Variations between 1971 and 1980 of the biomass and composition of macroalgae populations on the coral reef of Tiahura (island of Moorea, French Polynesia). *Cryptogamie Algologie* **3**:229-240.
- Payri, C. E., A. D. N'Yeurt, and J. Orempüller. 2000. Algae of French Polynesia. Au vent des îles.
- Pohlert, T. 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). R package.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria. Retrieved from <<http://www.R-project.org/>>.
- Remane, A. 1993. Verteilung und Organization der benthonischen Mikrofauna der Kieler Bucht. *Helgoländer Wissenschaftliche Meeresunters. (Abt. Kiel)* **21**:161-221.
- Roland, W. 1978. Feeding behaviour of the kelp clingfish *Rimicola muscarum* residing on the kelp *Macrocystis integrifolia*. *Canadian Journal of Zoology* **56**:711-712.
- Shannon, C. E. 2001. A mathematical theory of communication. *ACM SIGMOBILE Mobile Computing and Communications Review* **5**:3-55.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* **52**:591-611.
- Stiger, V., and C. Payri. 1997. Strategies of reef invasion by two brown algae in Tahiti (French Polynesia): reproduction, dispersion, competition. *Phycologia* **36**:108-109.
- Stiger, V., and C. Payri. 1999. Spatial and seasonal variations in the biological characteristics of two invasive brown algae, *Turbinaria ornata* (Turner) J. Agardh and *Sargassum mangarevense* (Grunow) Setchell (Sargassaceae, Fucales) spreading on the reefs of Tahiti (French Polynesia). *Botanica Marina* **42**:295-306.
- Vázquez-Luis, M., J. A. Borg, P. Sanchez-Jerez, and J. T. Bayle-Sempere. 2012. Habitat colonisation by amphipods: Comparison between native and alien algae. *Journal of Experimental Marine Biology and Ecology* **432**:162-170.
- Viejo, R. M. 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquatic Botany* **64**:131-149.
- Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Marine Ecology Progress Series* **58**:175-189.
- Wallentinus, I., and C. D. Nyberg. 2007. Introduced marine organisms as habitat modifiers. *Marine Pollution Bulletin* **55**:323-332.
- Wikström, S. A., and L. Kautsky. 2004. Invasion of a habitat-forming seaweed: effects on associated biota. *Biological Invasions* **6**:141-150.
- Zimmerman, R., R. Gibson, and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. *Marine Biology* **54**:41-47.

## APPENDIX 1

Algae used in this study. All photographs taken by the author.



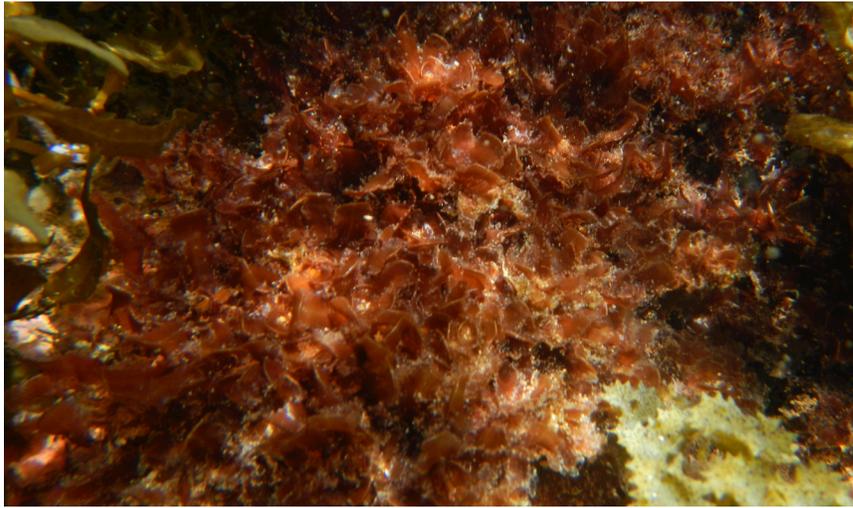
*Turbinaria ornata*:  
Brown algae with erect  
obconical thallus,  
obconical lateral  
branchlets, and a  
coriaceous texture



*Sargassum mangarevense*: Brown  
algae with erect  
densely branched  
thallus, leaflike lateral  
branches, and a  
coriaceous texture



*Halimeda* sp.:  
Green algae with  
calcified flattened  
segmented thallus



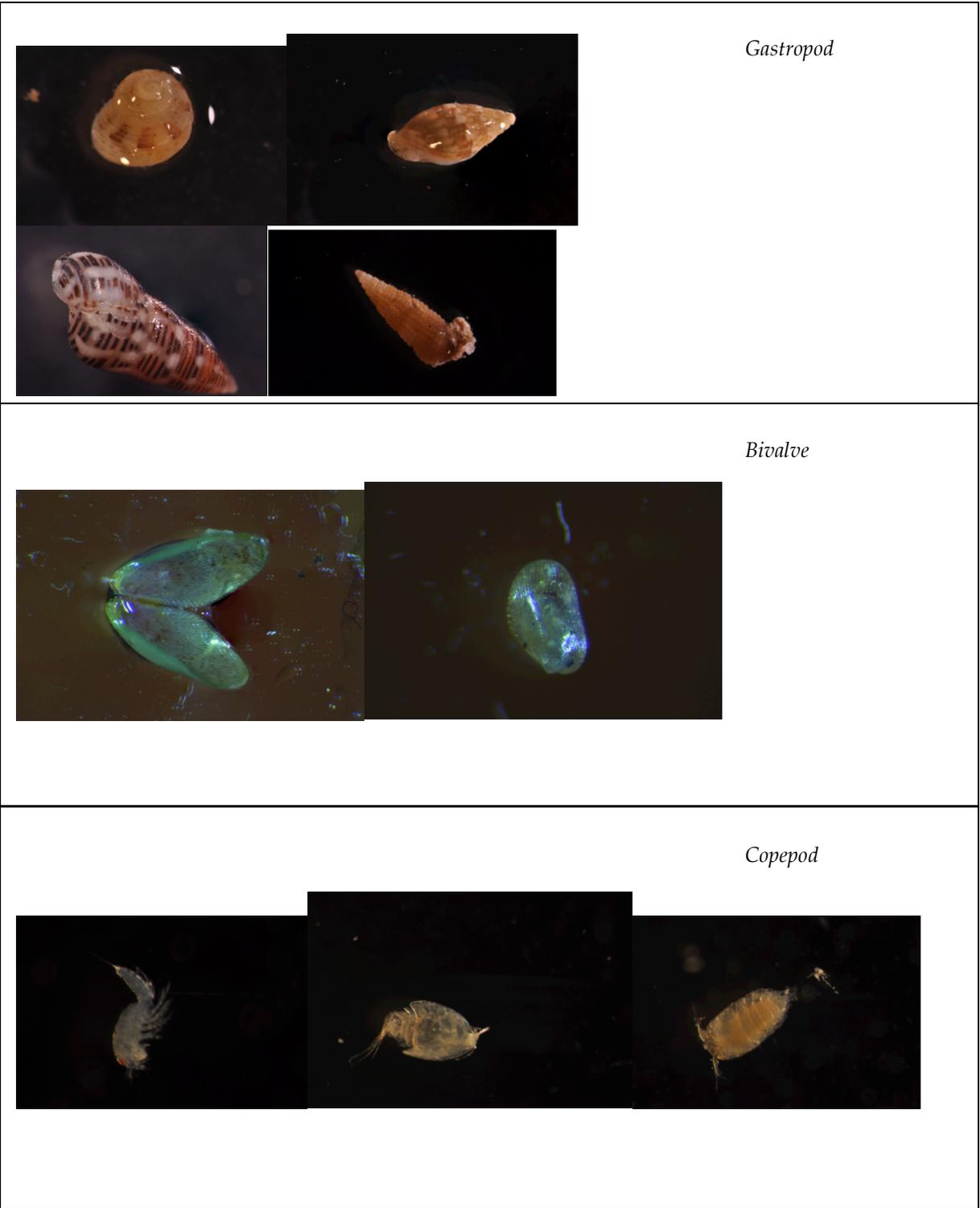
*Amansia rhodantha*:  
Red algae with thallus  
forming rosettes and  
leaf-like ultimate  
branchlets with a  
midrib and inrolled  
tips



*Dictyota* sp.:  
Brown algae with thin  
ribbon-like  
dichotomously  
branched thallus  
without a midrib

## APPENDIX 2

Epifauna observed on different algae for this study. All photographs taken by the author using a scientific camera attached to a dissecting microscope.



*Ostracod*



*Amphipod*



*Isopod*



*Tanaid*



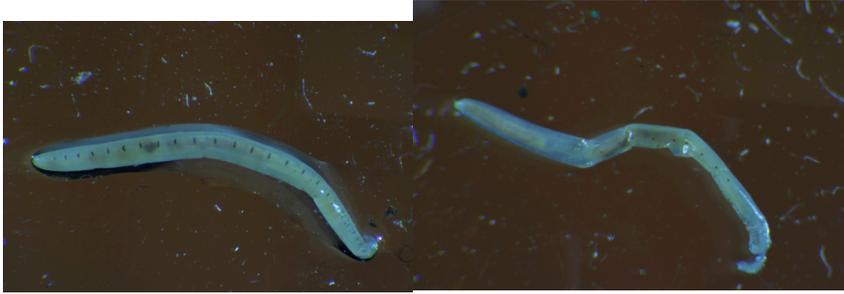
*Decapod*



*Polychaete*



*Oligochaete*



*Ophiuroid*

