THE MICROHABITAT AND BEHAVIOR OF THE FORAMINIFERA *PENEROPLIS PERTUSUS* (FORSKÅL) ON FRINGING REEF, MOOREA, FRENCH POLYNESIA

WHITNEY N. BERNSTEIN

College of Chemistry, University of California, Berkeley, California 94720 USA

Abstract. Foraminifera are sensitive to the physio-chemical properties of their environment, and can therefore be utilized in paleoclimate research and environmental monitoring. The microhabitat of the larger symbiont-bearing reef foraminifera, *Peneroplis pertusus* (Forskål), occurring on the fringing reefs of Moorea, French Polynesia was described. The geo-taxic and bleaching behavior of *P. pertusus* was observed and analyzed. *P. pertusus* demonstrated a preference for coral rubble substrate over Halimeda (t-stat=6.068, DF=29.26, $p<0.0001$). Its distribution within the fringing reef flat in Cook's Bay did not correlate strongly with depth ($r^2=0.112$, $p=0.07$) or temperature ($r^2=0.05$, $p=0.2$). *P. pertusus* showed a preference for exposed surfaces ($X^2=20.16$, critical value=3.84) but did not demonstrated positive geotaxis ($X^2=30.22$, critical value=3.84). *P. pertusus* houses red algal symbionts in its calcium carbonate test, and it bleaches when under thermal stress (F ratio=267, $p=0.0001$). *P. pertusus* showed recovery after bleaching under a 34 deg C treatment. *P. pertusus* is an interesting candidate for further research on symbiosis in reef taxa.

Key words: foraminifera; Peneroplis pertusus; *microhabitat; bleaching, geotaxis, French Polynesia*

INTRODUCTION

Foraminifera are testate protozoans that occur in marine environments worldwide, (Culver 1993). Foraminifera make up a large portion of benthic biomass in marine environments (Culver 1993). Additionally, these protozoans take part in a variety of trophic interactions as predators and prey (Culver and Lipps 2003, Lipps and Culver 2002). Moreover, larger reef foraminifera play an important role in the carbon cycle. Throughout the world's reefs, approximately 43 million tons of calcium carbonate is produced each year by reef foraminifera (Langer et al. 1997). This accounts for about 4.8% of the global carbonate reef budget (Langer et al. 1997). Although the reef systems in which these calcifying foraminifera live cover only 0.17% of the world's oceans, the calcium carbonate contribution by reef foraminifera to the world's oceans comprises approximately 0.76% of the total oceanic calcium carbonate production (Langer et al. 1997). Hence, reef foraminifera are important members of marine ecosystems.

Reef foraminifera are interesting scientifically, because they are useful tools in paleoenvironmental and biostratigraphical studies. Reef foraminifera often constitute 7-8% of the reefal sediment deposits (Langer et al. 1997). Because reef foraminifera contribute significantly to the composition of marine sediment, an understanding of the factors influencing foraminiferal distribution and assemblage composition has proven useful in paleoenvironmental study, sedimentology and geology (Culver 1990, Gray et al. 2006, Hallock 2005, Hoare et al. 2002, Venec-Peyre 1991). The physio-chemical and biological properties of habitat vary in space and time, and thereby influence the distribution of foraminifera on micro and macro scales (Kitazato 1994). Moreover, the microenvironment determines the isotopic composition of foraminiferal tests. Therefore, a clear description of the ecology and biology of particular foraminifera is

required in order to verify and calibrate isotope tracers as paleo-proxies (Fontanier et al. 2006, Loubere et al. 1995, McCorkle et al. 1990). Further study of the ecology of foraminifera will facilitate their continued use in paleontology and environmental monitoring.

Understanding microenvironments of foraminifera will not only elucidate past environmental conditions, but will also aid in understanding changes in current conditions. Due to their sensitivity to environmental conditions, foraminifera serve as useful bioindicators (Fisher et al. 2005; Hallock 2002, Hoare et al. 2002). Larger symbiont-bearing reef foraminifera are of particular interest because they share important characteristics with coral (Hallock 2006). Reef foraminifera are dependent on a complex and intimate relationship with autotrophic symbionts, such as algae, diatoms, and dinoflagellates. This symbiosis is similar in many ways to the symbiosis between coral and dinoflagellate zooxanthellae (Hallock 2006). In particular, under stressful conditions, foraminifer exhibit bleaching similar to that observed in coral (Hallock 2006). While larger symbiont-bearing reef foraminifera share these important characteristics with coral, they are of particular interest because, due to their small size and high abundance, statistically significant sample sizes are more quickly and economically studied (Hallock 2002). Additionally, the collection of foraminifera has minimal impact on the reef resources, and due to their relatively short life-span chronic water quality decline can be distinguished from short-term stress events (Hallock 2002).

With the imminent changes in climate that have been predicted and the current pollution of numerous near-shore environments, foraminifera should be fully utilized as paleo-proxies and bioindicators. First, geological and depth distributions and microhabitats must be clearly defined for potentially useful species. Then, the influence that macro and micro-environmental factors have on the foraminifera must be determined. Then the mechanism by which these factors influence the foraminifera must be probed.

This study aims to address several of these questions with regards to a particular larger symbiont-bearing reef foraminifer, *Peneroplis pertusus,* occurring in the fringing reefs of Moorea, French Polynesia. *P. pertusus* has a trochospiral test and hosts a red algal symbiont that is thought to be *Porphyridium purpureum* (UTEX 161) (Lee 1990) (Fig. 1). The distribution of foraminifera within the reef and associated environments around Moorea has been described (Langer and Lipps 2006, Le Calvez and Salvat 1980, Venec-Peyre 1991). *P. pertusus* occurs at depths shallower than 30m (Le Calvez and Salvat 1980, Venec-Peyre 1991). I described the microhabitat of *P. pertusus,* and I observed the behavior of *P. pertusus* in response to its microenvironment.

FIG. 1. *Peneroplis pertusus* has a trochospiral calcium carbonate test and houses red algal endosymbionts.

METHODS

Study site

Moorea is a high volcanic island of the Society Islands archipelago, French Polynesia, in the oligotrophic waters of the central Pacific. It is encircled by a fringing

reef, lagoon, and barrier reef. The research site is a shallow, calm segment of fringing reef in Cook's Bay on the north side of the island just outside the UC Berkeley, Gump Research Station (Fig. 2). I placed temperature recording buttons (Smart Button) on the reef in order to determine the temperature regime for 24-hour periods of the habitat.

FIG. 2. The study site is on the north side of Moorea as indicated by the star.

Sample and data collection

I collected a constant volume of coral rubble in zip-lock bags from each of 30 random points within my study site. The temperature and depth were recorded at each of these points. *Halimeda* was collected in a similar manner from 20 random points within my study site. I scrubbed and washed each bag of coral rubble and *Halimeda* for five minutes and sieved the material through a 50 m sieve. Two dishes of material, (about 30 ml in volume) were examined from each sample. I searched for *P. pertusus* in each dish for 5 minutes and tabulated the number of individuals found. I counted the number of dishes of material that made up each entire sample. I multiplied this number by the average of the number of individuals found per dish to get the estimated abundance of *P. pertusus* per bag.

Exposure preference

I shone a light over three pieces of artificial coral rubble (ACR) in a tank of water in order to make the "exposed" top surface distinct from the "unexposed" ledge. 15 *P. pertusus* were arranged around the top surface of each piece and 15 foraminifera were arranged along the ledge of each piece. The rubble pieces were removed three days later. I counted the *P. pertusus* that remained in exposed regions on the ACR and those that remained in the unexposed regions of the ACR. I repeated this procedure for a total of 6 replicates.

Colonization ability and site preference

ACR was constructed by sealing two tiles together with wax and lashing them together with zip-ties. On October 12, 2007, I laid 6 pieces of ACR in a circle on the reef flat. The ACR was removed after 33 days, on November 14, 2007, and the *P. pertusus* that had colonized the ACR were counted. I noted the position of the *P. pertusus*, and the level of exposure. A region shielded from direct light was considered unexposed, while a region in direct light was considered exposed.

Geo-taxis

I randomly selected 25 live *P. pertusus*. I tilted a tile in a tank of seawater, and arranged the foraminifera on a marked line across the tile. Then I covered the tank with plastic wrap in order to allow oxygen exchange but minimize evaporation. I removed the tile after 12 or 22 hours and counted the foraminifera above the line, below the line and on the line, and the distance they were found from the line. This procedure was repeated three additional times.

Bleaching of P. pertusus under thermal stress

P. pertusus with three or fewer white terminal chambers were considered unbleached. I placed ten unbleached *P. pertusus* in each of sixteen 5ml glass tubes and covered the tubes with plastic wrap.

Four tubes were suspended in a tank through which sea water flowed constantly. This was the control because the foraminifera were exposed only to their typical temperature regime. Four tubes were placed in a water bath at 34 deg C, the upper limit of their temperature regime. Four tubes were placed in a water bath at 40 deg C, and four were placed in a refrigerator that varied in temperature between 0.5 and 18.5 deg C. I visually assessed any changes that occurred in percent bleaching of the foraminiferal test after 1 and 2 days at each temperature. I placed all the tubes in the flow tank at the conclusion of the experiment and visually assessed the extent of bleaching after three days at normal sea temperature.

Data Analyses

The abundance of *P. pertusus* on coral rubble and *Halimeda* were compared using a t-test. The relationships between abundance and the physical parameters, temperature and depth, were analyzed using two simple linear regression analyses. Movement of individuals in the geotaxis experiment was analyzed using a one-sample chi-squared test. Bleaching under the four temperature treatments was compared using a one-way ANOVA and the means were compared with a Tukey test. The exposure level data for microhabitat was analyzed with a one-sample chi-squared test.

RESULTS

The habitat of P. pertusus

The study site is composed of three zones, a shallow sandy strip where loose leaves and algae accumulate, a reef flat consisting of coral sand, coral rubble, and massive corals, and a reef crest where the seafloor drops steeply. The site has an average depth of 1.4 meters. The temperature ranged from 28 to 34 deg C.

There is no correlation between depth and abundance within the study site (r^2=0.112, p=0.07). *P. pertusus* was most abundant in rubble between approximately 0.9 and 1.3 meters deep (Fig. 3).

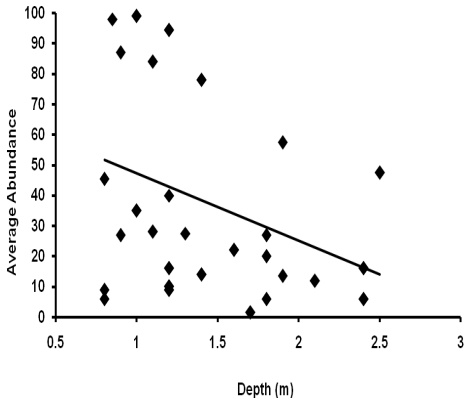

FIG. 3. There is no significant relationship between the average abundance of *P. pertusus* and depth within the study site (r^2=0.112, p=0.07).

The temperature measured during collection ranged from 28 to 30.5 deg C (Fig. 4). There is no correlation between abundance and temperature within my study site (r^2=0.05, p=0.2).

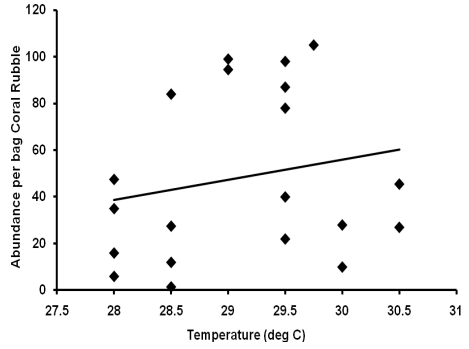

FIG. 4. There is no significant relationship between the average abundance of *P. pertusus* and depth within the study site (r^2=0.112, p=0.07).

Substrate type strongly influences abundance of *P. pertusus* (Fig. 5). The abundance of *P. pertusus* on coral rubble is statistically greater than that on *Halimeda* (t-stat=6.068, DF=29.26, p<0.0001). The mean estimated abundance per bag coral rubble was one order of magnitude greater than that for *Halimeda*.

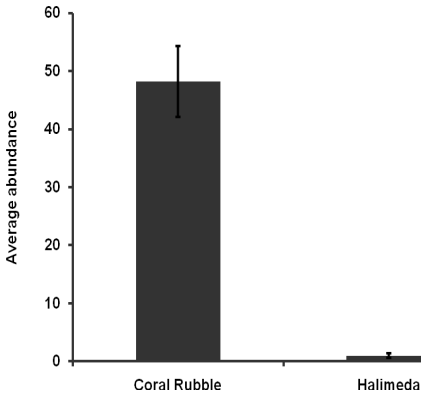

FIG. 5. Comparison of Average estimated abundance of P.Pertusus per bag substrate. The average abundance of *P. pertusus* on coral rubble is statistically greater than that on *Halimeda* (t-stat=6.068, DF=29.26, p<0.0001). Error bars are ±1 standard error.

Behavior of P. pertusus

At the conclusion of the exposure experiment, more individuals were found in exposed regions than in unexposed regions (X^2=20.16, critical value=3.84). *P. pertusus* were also found in other locations in the tank (Fig 6). Of the 180 foraminifera initially in the experiment, 10 were found on the walls of the tank, 18 were found on the bottom of the tank, 5 were found afloat, and 19 were never recovered.

In the colonization experiment, *P. pertusus* was the only species of larger reef foraminifera found on the ACR. A total of 11 individuals colonized the six pieces of ACR that were left on the reef for 33 days. All but one of these individuals were found in exposed positions.

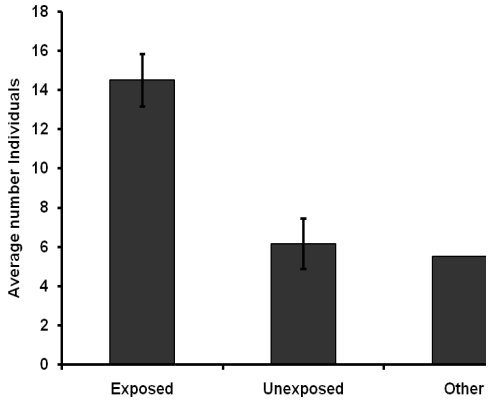

FIG. 6. More individuals were found in exposed regions than in unexposed regions (X^2=20.16, critical value=3.84).

In the geotaxis experiment, the net change in position was downward (Fig 7). The number of individuals that moved down was statistically greater than the number that moved up (X^2=30.22, critical value=3.84). The average movement, including individuals that did not move, was -1.9 ± 0.2 cm.

FIG. 7. The movement of individuals was averaged over four trials. Net movement was downward by -1.9 ± 0.2 cm (X^2=30.22, critical value=3.84).

Bleaching for *P. pertusus* under the four treatments were statistically different (F ratio=267, p=0.0001). Extensive bleaching was observed at 40 deg C (Fig 8). Intermediate bleaching was observed at 34 deg C and at cold temperatures. Little bleaching was observed in the control group at sea temperature. After the post-treatment period of three days at normal sea temperature, recovery was observed only in the group under the 34 deg C treatment. The extent of bleaching for this experimental group was similar to that for the control group after the post-treatment period (Fig 9).

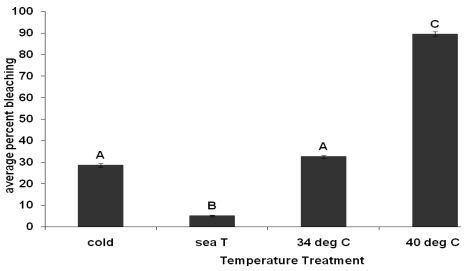

FIG. 8. Average percent bleaching of test after two days under several temperature treatments. Letters designate how the results of the treatments were statistically different from one another (F ratio=267, p=0.0001).

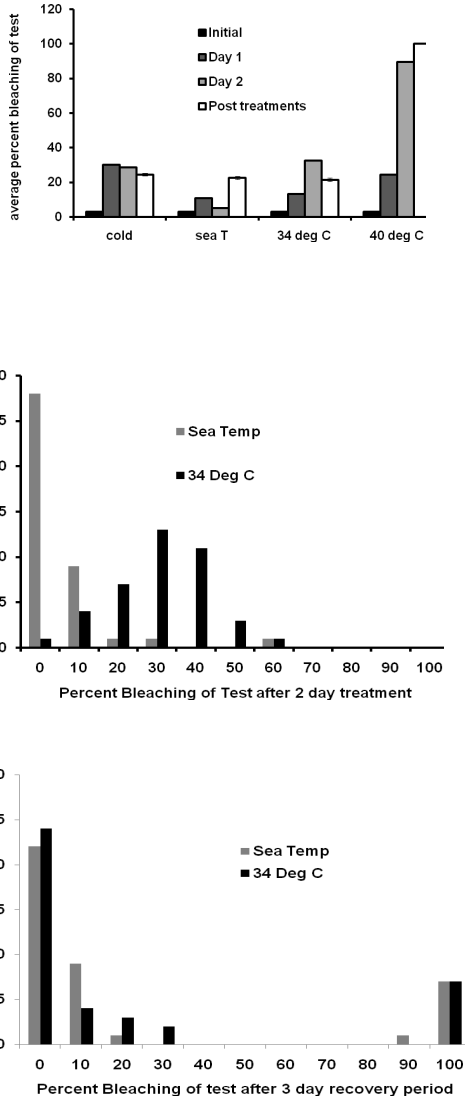

FIG. 9. Bleaching occurred under thermal stress after 1 and 2 days (top). A lower percentage of test bleaching was observed in the group submitted to the 34 deg C treatment and then returned to normal sea temperature conditions as illustrated by middle and bottom figures.

DISCUSSION

Microhabitat and microenvironment

The distribution of *P. pertusus* throughout the study site is not governed by depth or temperature. Light attenuation is considered the most important factor governing depth trends in the distribution of larger foraminifera, housing autotrophic endosymbionts (Hohenegger et al. 1999). Water energy also decreases with depth, and may be another cause for depth trends in foraminiferal distribution (Fujita 2004). *P. pertusus* occurs up to a depth of 30 meters (Fujita 2004 Hohenegger et al. 1999, Le Calvez 1980, Saraswati et al. 2003, Venec-Peyre 1991). The distribution of *P. pertusus* does not show a depth trend over 1 to 3

meters. The light is evenly distributed throughout the depth range of my study site and energy is low and fairly constant from the surface to the reef floor. The uniformity of the study site with regards to light and energy supports the finding that the distribution of *P. pertusus* is also uniform across the depth range.

Temperature within the study site is highly variable in both space and time. The distribution of *P. pertusus* within my study site is not driven by temperature. *P. pertusus* appears to be adapted to living in a highly variable thermal environment ranging in temperature from 28 to 34 deg C. The distribution of *P. pertusus* within the study site is governed by substrate type. *P. pertusus* prefers coral rubble over *Halimeda* as a habitat substrate. This is consistent with a previous studies, which found that *P. pertusus* prefers hard substrates (Hohenegger et al. 1999) and that foraminiferal abundance drops where *Halimeda* is abundant (Culver 1990). Perhaps *Halimeda* does not allow sufficient light exposure for algal endosymbionts to photosynthesize. Alternatively, *P. pertusus* may choose to live on coral rubble, rather than *Halimeda* to optimize food acquisition (Linke and Lutze 1993). I often observed that individuals would attach themselves to pieces of algae that had been brushed off the surface of the coral rubble and incorporated in the sample. *P. pertusus* would also collect algal matter in its pseudopodia. Fujita (2004) summarizes that small-scale foraminiferal distribution is influenced by light, water-motion, substrate type, food availability, and predation. Kitazato (1994) adds water chemistry to this list of variables. Light availability, water-energy, food availability, predation, and chemical properties may all be substrate-specific and any combination of these factors may be the impetus for the evident preference of *P. pertusus* for coral rubble substrate. Further experimentation and observation may bring to light the specific variables that drive *P. pertusus* to live on coral rubble.

In the exposure experiment, the number of individuals in exposed regions on ACR changed very little. However, the number of individuals in unexposed regions decreased significantly. Many foraminfera were found in other places within the tank that had exposure levels equivalent to the top surface of the rubble. It seems that those originaly in full exposure were content to remain there, and those who were unexposed left their original position, and attained a new position of higher exposure. *P. pertusus* prefers exposed microhabitats over unexposed habitats.

The colonization experiment supported this finding. Of the 11 individuals found on the colonized substrate, only one individual was found in an unexposed region. In the only other study that has been done on small-scale distributions of foraminifera on coral rubble, Peneroplids exhibited the same preference for exposed microhabitat (Fujita 2004). This preference may be attributed to positive phototaxis (Fujita 2004) or positive geotaxis, because *P. pertusus* houses algal endosymbionts. However, *P. pertusus* did not exhibit positive geotaxis in the lab. An informal trial demonstrated that *P. pertusus* may be positively phototaxic. Compared to the geotaxis results, more individuals moved up when a light was shone over a tilted tile across which foraminifera were arranged (W. Bernstein, personal observation). Further research should be done on phototaxis in *P. pertusus*.

As an alternative explanation for the patterns observed in colonization, only the top surface of the ACR was heavily colonized by epiphytes, which may have facilitated attachment to the top surface rather than the sides and ledges of the ACR (Fujita 2004). Additionally, these epipytes may have provided cover from predation, shelter from wave and current motion, or a food source that was not present on the sides and ledges of the ACR (Fujita 2004). Indeed, *P. pertusus* was often observed with a bolus of organic material collected in the pseudopodia. This organic material was the same as that found on the top surface of the ACR.

Behavior of P. pertusus

Very few individuals colonized the ACR. There are several explanantions for this. First, the ACR was deposited as a clean smooth surface. The colonization period may not have been long enough for the necessary succession to occur that would make the surface hospitable to foraminifera or conducive to attachment (Alve 1999, Fujita 2004). Alternatively, these results may be based on the mechanism of colonization. For example, if colonization is primarily driven by dispersal of juveniles, then the rate of colonization would depend on the reproductive cycle (Alve 1999). If dispersal is driven by passive suspension, then in a low energy environment such as this study site, colonization would be slow (Alve 1999).

As noted before, *P. pertusus* did not exhibit positive geotaxis. Although the net change in position was downward, this does not necessarily mean that *P. pertusus* was negatively geotaxic. *P. pertusus* may have been unable to attach itself well enough to the substrate to control its movement. The foraminifera may have fallen or rolled downward. The experiment is inconclusive as the geotaxic nature of *P. pertusus*.

Bleaching

Coral reef bleaching is a stress response defined as "the temporary or permanent loss of photosynthetic microalgae and/or their pigments by a variety of reef taxa" (Glynn 1996). While bleaching may be associated with disturbances such as subaerial exposure, increased sedimentation, freshwater influx, pollution, and disease, it is most strongly correlated with changes in temperature and solar irradiance, which may act synergistically (Glynn 1996, Lesser 1997). *P. pertusus* is an interesting study organism for bleaching experiments because it houses a red algal endosymbiont, while coral houses dinoflagellates called zooxanthellae (Glynn 1996, Lesser 1997). Because corals live close to their upper thermal thresholds, an increase in mean temperature of a few degrees for an extended period of time can cause bleaching (Glynn 1996, Hallock 2006, Lesser 1997). *P. pertusus* was tested for similar sensitivity to temperature. A group was exposed to 34 deg C, the upper limit of their temperature regime, and the group showed intermediate bleaching, statistically greater than that observed in the control. Perhaps *P. pertusus*, like coral, lives near its upper thermal threshold, as well. A group was exposed to temperatures well below their normal temperature regime, and although the bleaching observed was statistically greater that that of the control, it was not statistically different from the bleaching at 34 deg C. This shows additional support for the hypothesis that *P. pertusus* lives close to its physiological upper temperature limit. A group underwent a treatment at 40 deg C, and extensive bleaching was observed, as would be expected, under such extreme conditions. The conditions were lethal, as the foraminifera did not recover from the treatment. In contrast, under a sublethal temperature treatment at 34 deg C, the foraminifera did recover from bleaching. The ability to recover after bleaching suggests that either a small amount of red algal symbiont remains in the test, even when bleached, and multiplies when normal conditions are reestablished, or the symbionts are in the ambient water and recolonize the test when normal conditions resume. Also, this suggests that perhaps bleaching in foraminifera is a dynamic response to perturbations in the environment analogous to the response observed in coral (Douglas 2003).

CONCLUSIONS

The distribution of *Peneroplis pertusus* within my study site is not governed by depth or temperature, but it is governed by substrate type. *P. pertusus* prefers the exposed top surface of coral rubble over *Halimeda*. *P. pertusus* did not demonstrate positive geotaxis, but it may be positively phototaxic. Further experimentation is need on the phototaxis of *P. pertusus*. *P. pertusus* bleaches under thermal stress. However, after exposure to sublethal temperature

treatments, it may recover when returned to normal thermal conditions.

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TENTACLES AND THE PHOTOTROPISM OF THE BIVALVE MOLLUSK, *L. FRAGILIS* IN MOOREA, FRENCH POLYNESIA

Alvaro Palacios Casanova

Environmental Science, Policy and Management

University of California, Berkeley, 94720, USA

alvaro_casanova@berkeley.edu

Abstract

Tentacles are used by animals for variety of reasons, such as feeding, mating and locomotion. Although the uses of tentacles on a myriad of species have been described, the function of the tentacles found on *Limaria fragilis* is unknown. It has been previously observed that the tentacles on *L. fragilis* secrete a sticky mucus and can be automized (Donovan et al. 2004, Gilmour 1967). Observations from other studies have noted that species of Limidae have shown to be light sensitive (Cozier 1921). My study will test this hypothesis and examine if the tentacles on *Limaria fragilis* may be used to sense light. This study consisted of two experimental samples; *L. fragilis* with tentacles and *L. fragilis* without tentacles. Light was applied to each sample and the results indicate that *L. fragilis* is photonegative with tentacles. The results also suggest that *L. fragilis* has a substrate preference, perhaps indicating that its photonegativity is an adaptation to locate preferred habitat.

Keywords: Limaria fragilis, tentacles, phototropic, Limidae

Introduction

Evolutionary theory puts forth the concept that anatomical structures in animals serve a function for an organism's fitness. Many organisms develop phenotypic characteristics to adapt to their abiotic environment. One such anatomical structure is the tentacle. Many marine animals have tentacles that perform a variety of functions. For example some species in the phyla Cnidaria and Ctenophora (jellyfish, sea anemones and comb jellies) have tentacles, which facilitate feeding. (Lutz 1986).

The phylum Mollusca has species that have tentacles, such as the squid and nautilus (Lutz 1986). Within this phylum is the class Bivalvia. Bivalves can be characterized by their laterally flattened body with bivalve shells that are held together at the dorsal end by adductor muscles (Giribet et al. 2002). Within this class is the family Limoidae which has the species *Limaria fragilis*, *Lima scabra*, and *Lima hians* and are commonly known as file shells. Limids can be found near reefs, living underneath rocks and coral and in tropical and temperate waters. Limids are able to swim by quickly clapping their valves (Fauna of Australia 1987) and have long tentacles that extend from the mantle margins and secrete a sticky mucus. The tentacles on Limids contain radial and longitudinal muscles. The tentacles cannot be retracted into the valves and are found on the anterior and antero-ventral surface of the mantle margins (Gilmour 1962).

Previous studies on *L. hians* found that the tentacles on this species can be automized, secrete mucus when predated upon and help with locomotion (Gilmour 1967). Crozier (1921) observed that *L. hains* was sensitive to light and that its behavior was photonegative. Although we know the function of the tentacles on *L. hains,* we do not know the significance of the tentacles on the species *L. fragilis.* This study will test the hypothesis that Limids are

phototropic and to determine if the tentacles found on *L. fragilis* have dermal photoreceptors that facilitate light sensing.

Materials and Methods

Collection of Study organism

Fifty Eight *Limaria fragilis* individuals were collected from Haapiti (17° 33′ 49.47″ S, 149° 52′02.03″ W), Moorea, French Polynesia. All sampling was done in water less than 1 meter in depth. *L. fragilis* was collected by snorkeling and were caught with aquaria nets from the underside of partially embedded rocks and were immediately returned to aquaria at the Richard B. Gump field station in Moorea, French Polynesia. The organisms were kept in separate aquaria (57cm x 38cm x 41cm), containing fresh running sea water, sand and rocks and were kept on site until used for experimentations.

Removal of tentacles

The tentacles were removed from (n=20) *L. fragilis* with scissors. These specimens, where returned to their aquaria for a 24 hour period, before the experiments.

Experimental design

The experiment consisted of placing each *L. fragilis* specimen in a clear aquarium tank (25cm x 15 cm x 17 cm) next to a lamp (20 cm away) containing an 80 watt incandescent light bulb. The light was then turned on, and the behavior and distance moved by the individual was recorded in seconds and centimeters, with observation periods of 5 minutes each. The behaviors recorded were swimming, clapping, foot out, tentacles extended and tentacles retracted (Table 1, Appendix). The clear tanks that were to be used for the experiments had a metric grid drawn underneath the tank to measure the distance moved and activity levels. For two nights, *L.fragilis* (n=58) were observed for a period of ten minutes to evaluate their behavior under laboratory conditions. All experiments were done in a dark room at night.

Photo sensory

The first experiments were conducted from 10/18/ 2007 to 11/14/2007. These experiments were to determine if *L. fragilis* has photo sensing capabilities. The experimental *L. fragilis* (n=20) had tentacles and were given a light treatment. The control *L. fragilis* (n=20) had tentacles and received no light.

Photoreception of Tentacles

The experiments were conducted from 10/18/2007 to 11/14/2007. The purpose of these experiments was to determine possible photo sensing properties of the tentacles on *L. fragilis. L. fragilis* (n=20) had their tentacles removed, while the control (n=20) retained their tentacles. All the test organisms had light applied.

Substrate Selection

This experiment was conducted on 11/16/2007. *L.fragilis* (n=5) were placed in an aquarium (80 cm x 43 cm x 52 cm) one at a time, for a period of ten minutes. The aquarium contained sand, one cobble size basalt rock and one large piece of coral rubble to simulate its natural habitat. This was done to investigate the possible substrate preference of *L. fragilis,* which may indicate possible chemo-reception.

Statistical Analysis

For the experimental organisms, the time spent swimming (seconds) and the distance moved (cm.) were compared using a paired t-test; for both experimental samples. The control organisms received the same statistical analysis. The statistical computer program JMP 5.1 was used for the analysis of the data.

Results

Behavioral Analysis

L.fragilis were observed to be more active at night, where they were observed swimming, filter feeding, tentacles extended and several had their tentacles retracted. Under

laboratory conditions, some *L. fragilis* were found towards the top of the tank (water line) filter feeding with their valves open, tentacles extended. *L. fragilis* appeared to be "feeling" a rock with its tentacles, the tentacles would bend backwards "feel" the rock before swimming underneath it. During the day they were observed under rocks, with their tentacles retracted and at times appeared to be filter feeding underneath the rocks, but no other activity was observed. Prior to swimming, the tentacles would go straight up and sway back and forth.

Photo sensory

The frequency of the behaviors was variable between the test organisms. Observations during the experiments indicated that *L. fragilis* was sensitive to light and swam away from the light source, in some instances it went towards the light. When light was applied, *L. fragilis* specimens spent more time swimming, (P >0.0004, Fig.1) had a greater distance moved (P > 0.0007, Fig. 2)and spent less time with its tentacles out (P > 0.0023, Fig. 3) than specimens in the dark.

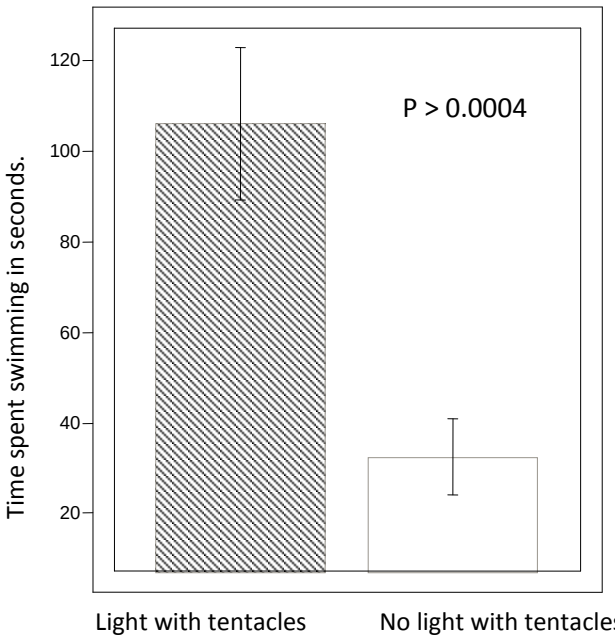

Figure 1. Mean time spent swimming by *L. fragilis,* with and without light.

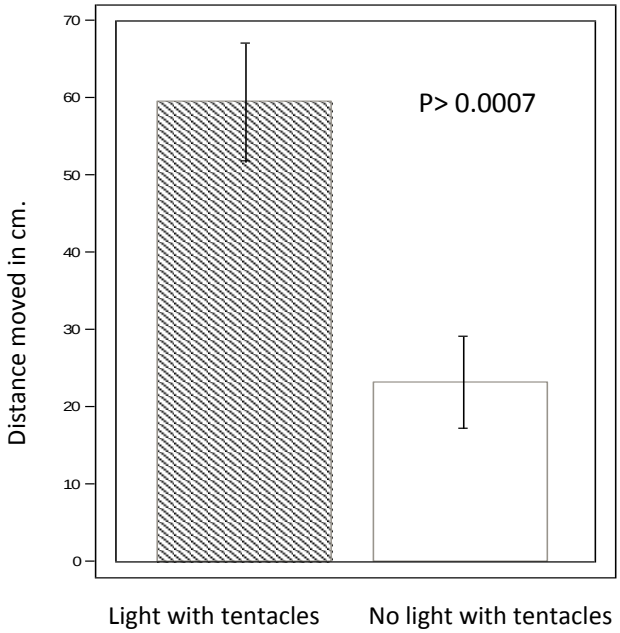

Figure 2. Mean distance moved by *L.fragilis*, with and without light.

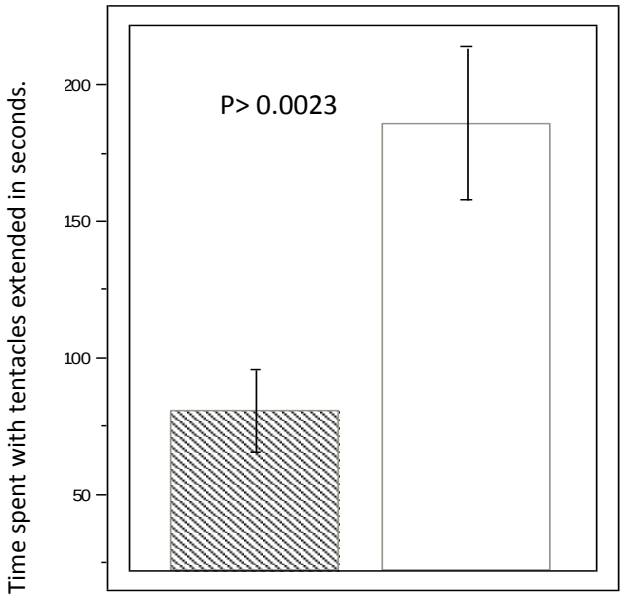

Figure 3. Mean time spent by *L. fragilis* with its tentacles out.

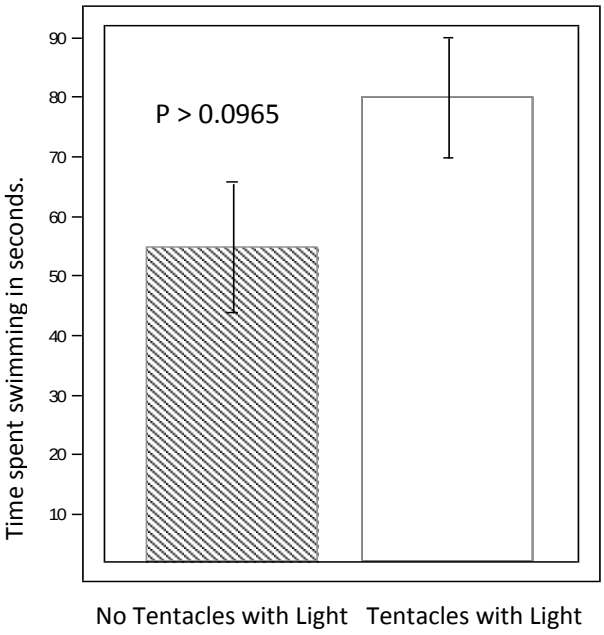

Figure 4. Mean time spent swimming by *L. fragilis,* with and without tentacles.

Photoreception of tentacles

Specimens of *L. fragilis* with their tentacles removed showed less reaction to light than those with tentacles. Those without tentacles exhibited lower distances moved ($p < 0.0307$, Fig.5) and less swimming behavior ($p< 0.0965$, Fig. 4) than control specimens with tentacles. *L. fragilis* with no tentacles was found to have a higher variability in its reaction to light; while many swam or clapped as the light was turned on some had no reaction.

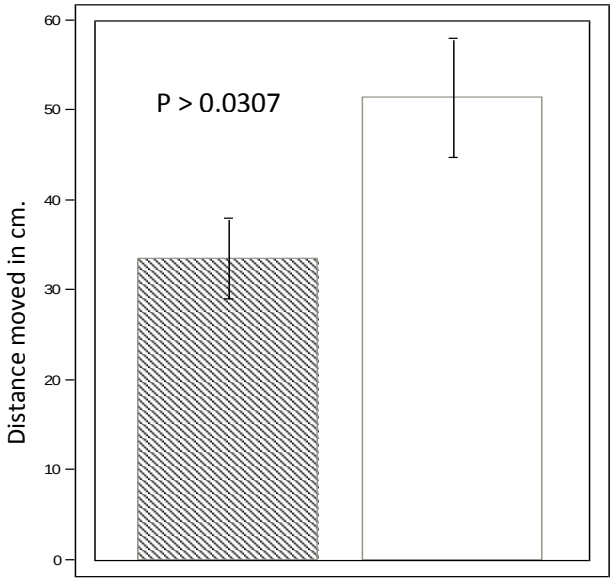

Figure 5. Mean distance moved in L. fragilis with and without tentacles

Substrate Selection

There was no variance in the substrate selection in *L. fragilis.* It chose the basalt rock five out of five times, all of the specimens had tentacles.

Discussion

The photo sensory results suggest that *L. fragilis* is photosensitive. The behavior displayed by *L. fragilis* indicates that Limids are photonegative, supporting Cozier's hypothesis. The distance moved also supports the observation that *L. fragilis* is photonegative. Having light sensing capabilities may be an adaptation to the organisms' habitat. Being able to detect light in shallow water may allow it to flee when a predator flips over a rock (such as a rock flipping fish). It may also have something to do with feeding, my observations that *L. fragilis* is more active at night, may point to a night feeding behavior, therefore making it necessary to detect when there light is present, to know when to feed.

The experiments that were done on *L. fragilis* to determine if the tentacles have dermal photoreceptors showed large differences between specimens with tentacles and those without, indicating that the tentacles may have important photoreceptive properties. Those without tentacles moved less far than those with tentacles, when subjected to light ($p < 0.0307$, Fig.5). Similarily, specimens without tentacles showed lower swimming behavior, though this relationship did not show a statistical significance at the .05 level.

The experiments on the tentacles suggest one of two things, either the lack of tentacles makes swimming inefficient or that the tentacles have photoreceptors. The photo sensory data supports this as *L. fragilis* spent more time with its tentacles out then the control. The results were not statistically significant to indicate that the tentacles have photoreceptors. However, the distance moved was significant.

The family Limoidae (Bivalvia) has been shown to have a complex lip structure, facilitating feeding and also aiding in swimming (Morton 1979). Morton (2000) also, discovered pallial eyes on the mantle margins of the species *Ctenoides floridanus*. Waller (1975) notes that the species *Lima lima* has eyes at the base of the tentacles, pallial eyes on *L. fragilis* has not been described. Morton describes the pallial eyes on *C. floridanus* being slightly pigmented. Observations of *L.fragilis* (A. Casanova, Personal Observations) indicate that it may have pallial eyes, as *L. fragilis* has red pigmentation at the base of the tentacles and throughout the mantle. The results from my substrate preference experiments, suggest that *L. fragilis* does have a substrate preference. My personal observations of *L. fragilis* and the "feeling" behavior of its tentacles, may point to possible tactile cells in the tentacles. This may be indicative of it being able to determine the type of substrate it prefers. The preference of *L. fragilis* for basalt rock over coral rubble, a common substrate, may be due to their chemical composition; as one contains calcium carbonate. There needs to be further investigations to determine if *L. fragilis* can chemo-sense substrate via their tentacles. Cozier (1921) noted that *L. hains* tentacles were reactive to acetic acid, giving evidence to possible chemo-sensing. Field observations after a tropical storm noted less fish and that the abiotic environment had been changed drastically. One test organism was caught on this particular day, the coral rubble and rocks were redistributed, making it difficult to find the organism. Perhaps, the amount and type of substrate available maybe a limiting factor in the abundance and distribution of *L. fragilis*. Further research should be done on the function of the tentacles on *L. fragilis*, for possible chemo and electro sensing and future research should look at the mantle for possible pallial eyes.

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Appendix

Table 1

Swimming	Tentacles extended	Tentacles retracted	Clapping	Foot out
Moving from one point to another.	Tentacles extended straight out.	Tentacles curled in.	Valves clapping, causing movement in a vertical direction, but not to another point.	Foot extending out of valves and "feeling."

TROPICAL RHODOLITHS: ABIOTIC FACTORS INFLUENCING MORPHOLOGY, ABUNDANCE DISTRIBUTION AND CALCIUM CARBONATE CONTRIBUTION IN SHALLOW WATER LAGOONS ON MOOREA, FRENCH POLYNESIA

JASMINE C. DECOSTA

Department of Earth and Planetary Sciences Berkeley, University of California, Berkeley CA 94720
jasminedecosta@berkeley.edu

Abstract. Free living, calcareous red algae, rhodoliths, inhabit a wide range of climate zones extending from the arctic to the tropics. Living and dead rhodolith beds are of significant scientific interest. Fossil rhodoliths may be used as paleoenvironment indicators with radiometric dates providing geologic history narratives. Studies of living beds provide evidence of environmental factors dictating morphology, distribution, and species. This study examines the habitat of rhodoliths. Located on the volcanic island of Moorea, French Polynesia, research was conducted to distinguish relationships between water motion, morphology, and density distribution along a depth gradient. Field measurements helped examine rhodolith calcium carbonate contribution in the shallow water reef lagoon.

Key words: *rhodolith, coralline, distribution, calcium carbonate contribution, Moorea, French Polynesia*

INTRODUCTION

Rhodoliths—free living, morphologically diverse calcareous red algae—occur globally over various longitudinal and depth ranges (Bosence, 1983b; Foster, 2001; Stellar and Foster, 1995; Konar, 2006). Two abiotic factors control the distribution of rhodoliths, light and temperature (Boscence, 1983; Marrack,1999; Foster, 2001). Additionally, the benthic habitat needs water motion to support movement and prevent the burial of the coralline algae (Bosence, 1976; Marrack, 1999). Physical conditions, such as current velocity, may play an important role in the general morphology of rhodoliths (Marrack, 1999; Foster and Stellar, 1995). The taxanomic identity of a rhodolith based on morphology alone is impossible. The surface area of the red algae is subject to change over the life span in reaction to changes in the environment. The preservation of rhodoliths over time has allowed for studies of their fossilized nature. Fossil rhodoliths have been used as indicators for paleoenvironments (Frantz et al, 2000; Brandano et al, 2005). Radiometric dating using ^{14}C provides a geologic time period in which the rhodoliths occured. Morphological analysis together with species identification gives insight on the conditions present at the time of growth. To better assist in understanding how morphology may be used as indicators for paleoenvironments, further studies of the impacts of water motion is needed on living rhodolith beds.

Rhodolith beds are distributed globally, in some regions acting as primary producers and providing a habitat for a diverse selection of fauna (Foster, 2001; Konar, 2006; Marrack, 1999; Stellar et al, 2003). Although the surface area occupied by reef communities in the ocean is minor, the contribution of calcium carbonate from coralline algae producers is very large. The role of rhodoliths in the calcium carbonate production is of interest since the biochemical production of calcium carbonate leads to the release of carbon dioxide into the atmosphere (Maier-Reimer, 1987). While the role of CO_2 release by the red algae appears to be non-influential, only playing a minor role in comparison with the release of CO_2 from anthropogenic influences, understanding the ocean's carbon cycle essential. As threats to coral reefs continue to raise question to the future of reef systems, knowledge of the role red algae occupies would give great strength to the biochemical engineer.

This study examines the links between both water motion and rhodolith morphology as well as water depth and rhodolith abundance, or density. This study quantifies the calcium carbonate contributed by rhodoliths in a shallow water reef community on Moorea, French Polynesia.

METHODS

Site Description

Within the Society Island Archipelago lies Moorea, the second youngest volcanic island, which has high elevations. A barrier reef intersected by twelve passes surrounds the island. A lagoon extends from the barrier reef to the island's shore. Inside the shallow water of the lagoon, scattered beds of coral, macroalgae, coralline algae, and sand compose the benthic habitat.

To examine the field environment of rhodolith bed distribution, surveys were conducted in the channel between motus Tiahura and Fareone, located off the northwest coast of Moorea (GPS S 17° 29.328', W 149° 54.783').

Field Methods

Fieldwork was performed during the months of September, October and November 2007. A handheld GPS *eTrex*™ garmin was used to map the distribution of rhodoliths. A total of twelve thirty meter transects were performed. Six randomly selected meters along each transect were chosen for analysis. A total of fifty-four rhodoliths were collected from the bed to be used in further lab analysis. In accord with each meter on the line, each rhodolith that was intercepted by the line, data recordings included dimensions of volume, wet weight, morphology, ground coverage, water depth, and distance from shore. Three types of morphologies were recorded including: branched (B), rounded (R) (columinar) and mixed (M), meaning a display of both branched and rounded. To aid in the distribution characterization of rhodoliths, bed regions were defined to being near, middle, and far shore. Extending perpendicular from the shore, the representation of the regions were defined by distance from shore, with the near shore region at 0-10 meters, the middle shore region at 11-20 meters, and the far shore region at 21-30 meters. The regional depiction of zones allowed simple analysis of factors affecting the bed distribution.

Density of each rhodolith was obtained by using the equation $\rho = m/v$. Weight measurements in the field included bonus weight from water, fauna, and epiphytes. To account for this weight difference, fifty rhodoliths were re-weighed once dried and free of debri. The JMP™ IN 5.1.2, a bivariate model fit of dry by wet weights was used to examine the relationship. The equation was applied to each recorded wet weight, yielding dry weights. With the dry weight and the volume, an estimate of the rhodoliths density may be determined. To look at the distributed density of rhodoliths along the depth gradient, continuous rhodolith density measurements were examined with the corresponding depth data using Microsoft® Excel®. Density and depth readings were placed together on a scatter plot. In each region (near, middle, and far) calculations of the total rhodolith density were determined.

Examination of water motion on rhodolith morphology was performed. Flow measurements were taken along the thirty meter transects at 5 m, 15 m, and 30 m. Grouping of the flow measurements allowed the regions (near, mid, and far) to be assigned a flow rate within range. To measure the water current near the substrate, fluorescein dye was injected into the water using a syringe. With the aid of a stopwatch, the dye traveled through a known distance, of 5m, yielding a flow rate. The flow rates were recorded in meters per second. A total of ninety flow measurements were used to determine an average flow rate. To quantify the effects of water motion on morphology, data collected concerning rhodolith morphology in conjunction with water motion, were analyzed using JMP™ IN 5.1.2. An ANOVA test searched for relationships among the three groups. A tukey test determined the relationship established by the ANOVA.

Calcium carbonate composition analysis required both field and lab work. Field measurements of weight and volume provided a rough estimate of individual densities. . To refine this estimation, further lab analysis investigating the complete composition of the rhodolith was required. Of the six sectioned specimens, an average percentage of $CaCO_3$ composition was

determined. An newly calculated density, relating to calcium carbonate contribution was calculated. To determine the role of red algae calcium carbonate contribution in the lagoon channel, Excel® analysis of percent coverage of coral, marcoalgae, coralline red algae, and sand were analyzed.

Laboratory measurements

Six rhodolith were dissected using a table saw. The samples were sanded down to a fine, smooth surface. Under a dissecting microscope, the complete composition of each rhodolith was determined. Surface area analysis separated core composition from the red algae calcium carbonate production.

An analysis of rhodolith growth rates was performed. Alizarin red dye was used to stain 10 rhodoliths. Five rhodoliths inside a weighted mesh bag were placed in the field. The remaining five rhodoliths were placed inside a container with saltwater. The rhodoliths were kept inside the wet lab on a table. The rhodoliths were undisturbed for a period of 21 days. Once removed from the water, the rhodoliths were dried and sectioned for further laboratory analysis. Using a dissecting microscope, rhodoliths were examined for recordings of the alizarin red dye.

RESULTS

Inside the shallow channel, GPS mapping (Fig. 1) of the rhodolith distribution is defined by a region extending approximately 150 m by 30 m parallel to the west shore of Motu Tiabura .

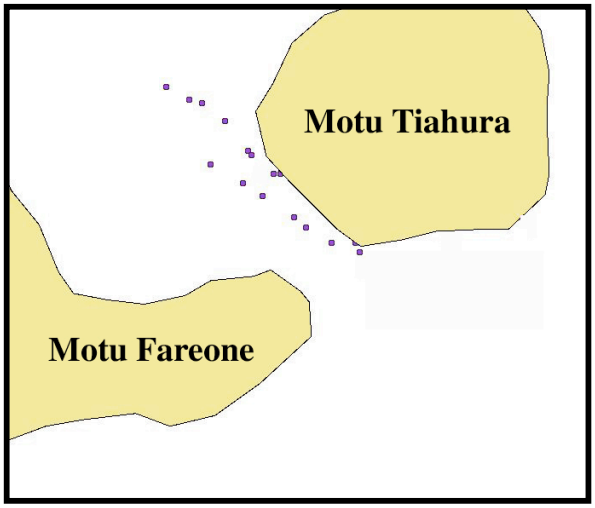

FIG. 1. Located off the north west coast of Moorea, lie Motu Fareone and Motu Tiahura. The channel shared by the motus contains shallow water reef communities. A red algae bed extends 150 m x 30 m parallel to Motu Tiahura.

The channel contains shallow water rhodolith beds. Rhodolith distribution occurs offshore. Inside the channel, depth variation and flow gradients are present. The distribution of rhodoliths is widespread within the channel; however the abundance of rhodoliths is not constant across the bed. Inside the mapped bed, depth ranged from 1 - 219 cm. Each region was assigned depth ranges (Table1).

Table 1. Water depth ranges from > 300 field measurements of depth (cm) assigned to each region (1-30 m). Depth readings were taken at various tides to reflect accurate variance, reducing possible error.

Near Shore (0-10 m)	1-84 cm
Middle Shore (11-20m)	50-170 cm
Far Shore (21-30 m)	60-219 cm

The linear regression model fit by dried versus wet weights (Fig. 2) performed with JMP™ IN 5.1.2 shows a strong relationship exists (r^2 value = 0.78 and $p<0.0001$). The equation representing the best fit line, $y = 0.75x + 2.63$, once expressed to the remaining wet measurements, an average weight difference of 28 grams was established.

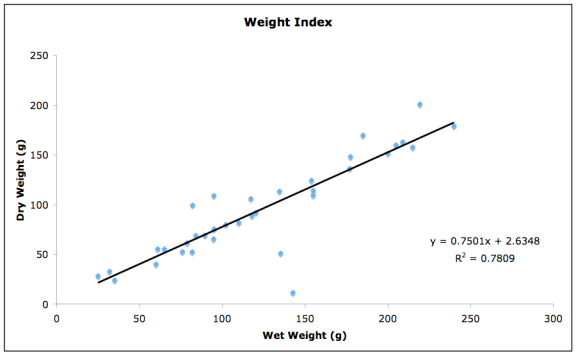

FIG. 2. Rhodolith weight index to determine average weight difference. Linear regression model of dry and wet weights, $p<0.0001$.

Using the Excel® software, a XY scatter plot graph depicts the density distribution (Fig. 3). The density distribution of the rhodolith bed shows variance along the depth range. Density abundance is highest in the far and middle regions, at water depths of 50-150 cm. Almost no density coverage is found in the near shore region.

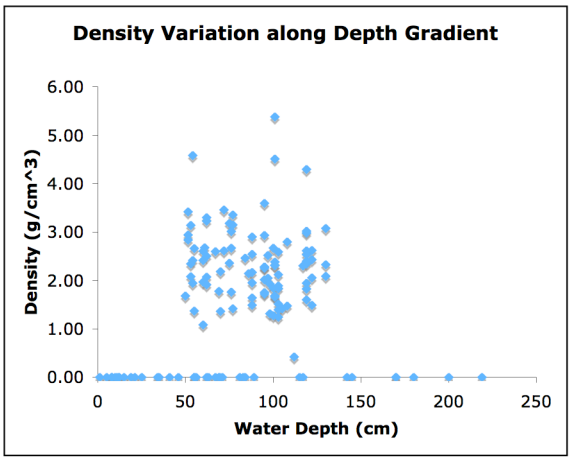

FIG. 3. Distribution of density along depth gradient. The highest densities occur in the depth range of 50-140 cm. Depth ranges found in the bed between the middle shore (11- 20m) and far shore (21-30m) regions.

Field observations of ninety flow measurements determined the average flow rate. Use of the Excel® software assisted in gaining knowledge of the relationship between the flow measurement and the distance from shore. Flow rates increased as distance from shore increased (Fig. 4).

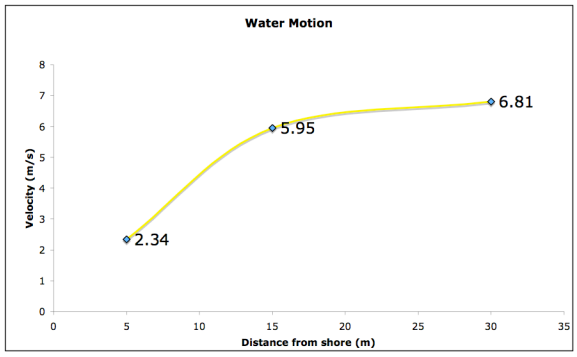

FIG. 4. XY scatter representation of flow (m/s) increase moving further from shore in meters. The flow increases as distance from shore increases.

Using the statistical software JMP IN 5.1.2., an ANOVA test (Fig. 5) showing relationships between categorical morphologies proved to be of interest. To further test the relationship discovered by the ANOVA, the Tukey test revealed a significant difference in branched and rounded morphology occurences at different distances from shore.

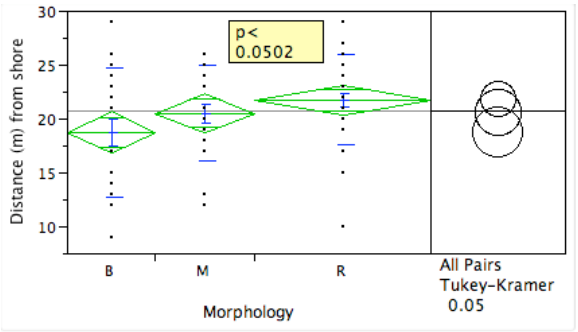

FIG. 5. Morphology distribution among the bed. Distance measured from shore in meters. Morphology identified as branched (B), mixed (M), and rounded (R). Tukey test reveals difference between occurrence of branched and rounded morphologies along the bed.

Field observations of ground coverage (Table 2) showed a high percentage of sand covering in each region of the bed. Coralline red algae coverage is highest in the middle shore region (11-20 m). Coral and carbonate platform coverings had the highest percentage in the far shore (21-30 m) region.

Table 2. Percent area coverage of bed by sand, coralline red algae, coral, marcoalgae, and carbonate platform. Sand dominates bed coverage. Of the calcium carbonate contributors, coralline red algae has the highest percent coverage.

(Table 2 at end of document)

An average 88% calicum carbonate composition was determined for each of the six sectioned specimens (Fig. 6). The work done with the dissecting microscope revealed core compositions to be coral or shell fragments.

FIG. 6. Cross section of a rounded morphology. Notice the concentric banding corresponding to growth. Rhodolith production of $CaCO_3$ composes approximately 90% of the volume.

Within the 150 m x 30 m rhodolith bed, an estimation of calcium carbonate contribution was produced for each bed region- near, middle, far shore. The highest percentage of $CaCO_3$ contribution is in the middle shore (11-20 m) region.

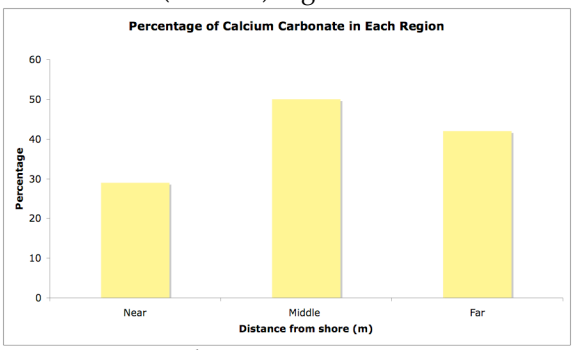

FIG. 7 Graphical representations of distributed contributions shows regional variance in calcium carbonate productivity.

DISCUSSION

Over the nine weeks of research tremendous field data was collected. The results represent many indications of abiotic factors in control of rhodolith bed distribution. The 150 m x 30 m region surveyed showed variation in the ground covering. A zoning occurred inside the bed, sand the near shore region, a high occurrence of rhodoliths in the middle and far shore regions, and the presence of coral solely in the far shore region. The regions, defined by distance from shore suggest different abiotic factors control the zoning.

The distribution across the bed varied in density. Higher densities of red algae occurred in regions corresponding to water depths of 50-140 cm, suggesting water depth to be a control in abundance distribution. Lab analysis revealed the composition of the rhodolith. 88% of each surveyed section showed concentric bands, implying growth and secretion of $CaCO_3$. The performed weight index, showing 28 gram average difference, supporting error reduction on density calculations.

Calcium carbonate contribution showed regions of higher productivity. The calcium carbonate contribution has been represented to be more successful in the middle and far shore regions. Water depth and flow rate represent abiotic influences attributing to the high percentage of calcium carbonate contribution in the middle and far shore region of the bed. As the reef systems experience threat, especially to corals, knowledge of the calcium carbonate budget gives revealing predictions for the future. The moderate flow rate provides protection for the rhodolith. Literature on red algae suggest rhodoliths are in need of water motion (Bosence, 1976; Marrack, 1999). In the middle and far shore regions the strong current prevents burial. The current remains weak enough to prohibit displacement. In the near shore region water depth may be too low for rhodolith survival. In the near shore region the flow rate of 2.34 m/s may be too calm. The near shore region is dominated by sand coverage suggesting that the region is not appropriate for red algae populations. An ANOVA test showed the rounded, columinar morphology highest distributed through 17-24 m, regions middle and far. The pevious Excel® graph shows high flow in the middle and far shore regions. The rounded morphology may be the response to the high flow as the surface area experiences movement from the current. The ANOVA showed the branched morphology greatest distributed in the near and middle shore region. The higher flow rate, greater depth, and less light exposure of the far shore region may prevent the growth of branched morphologies. Laboratory analysis of the stained

specimens provided no results on the growth rate. Possible sources of error include the short period of the experiment. Rhodoliths were not left in their native setting (the motu channel) for the experiment. Placed outside the station in Pao Pao Bay, the turbidity of the water did not match that of the Motu Channel. The inability to see a stained record of the Alizarin dye suggests the experiment may have provided error or rather the growth rate is not fast enough to be observed in the 21 day period granted.

Conclusion

The current research available on red algae suggests more work needs to be done. Rhodoliths require exposure to light and water motion for their survival. Research of abiotic factors in control of the distribution are valued. Living and dead rhodolith beds provide great knowledge of present and past environments. Future studies on the abiotic factors influencing morphology may provide more detailed narratives of the geologic record. Studies of living beds in tropical climates including red algae growth rates and distribution is of great interest. Further tropical studies include the environmental changes experienced in red algae beds during the dry and wet seasons. Continued research on living red algae beds will provide more insight on the reef communities supporting life in our oceans.

ACKNOWLEDGEMENTS

I thank James Bartolome, Rosie Gillespie, Carol Hickman, Jere Lipps, and George Roderick. My appreciation is extended to you for providing the opportunity and support for the conducted research. I would like to express the greatest appreciation to the Gump Station, on Moorea, French Polynesia. Special thanks for the use of the library, laboratories, and dormitory. I am grateful for the financial assistance from the University of California, Berkeley. I thank Jere Lipp's laboratory for the permitted use of equipment. Thank you to Mr. Aaron Lui for help with pictures and scanned images. To Jennifer Renee Witherspoon, thank you for your help in the laboratory. I possess immense gratitude to the Earth & Planetary Science department for their gracious relations concerning my research. To each of my field companions Bianca Giusto, Angela Minnameyer, Matt Harris and Greg Gillette, a huge thank you.

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(Insert Table 2)

Average Percent (%) Coverage					
REGION	**SAND**	**Coralline Red Algae**	**CORAL**	**ALGAE**	**Carbonate Platform**
NEAR 0-10m	70	29	1	0	0
MIDDLE 11-20m	42	50	0	1	5
FAR 21-30m	49	42	3	0	12

DISTRIBUTION AND ROLE OF *HALIMEDA* (BROPSIDALES/HALIMEDACEAE) IN CARBONATE PRODUCTION ON REEFS IN MO'OREA, FRENCH POLYNESIA

Nina B. Fitch

Department of Earth and Planetary Sciences University of California, Berkeley 94704 USA

Abstract. Coral reef ecosystems worldwide are increasingly threatened by produce enough reef-building calcium carbonate ($CaCO_3$) to keep up with rising sea level due to global warming. Calcareous algae and other non-coral $CaCO_3$ producing organisms play an equally important role in the reef-building process as the stony corals. In this study, the production of $CaCO_3$ by various species of the green algal genus, *Halimeda* (Bropsidales/Halimedaceae) was estimated by analyzing abundance and distribution from transect data on three different reef environments: algal ridge, fringing reef, and barrier reef in Mo'orea, French Polynesia. These field surveys were complemented with a series of laboratory experiments that determined the relative $CaCO_3$ of the ten Halimeda species found in Mo'orea *Halimeda* was found to cover an average of 7.8% of Mo'orea's reefs. Species varied widely in their $CaCO_3$ production, but averaged 90% $CaCO_3$. From these data, the potential $CaCO_3$ contribution of *Halimeda* to reef systems in Mo'orea was estimated to be 4,169,880 kg. Although *Halimeda* diversity and abundance are lower in French Polynesia than in other parts of its range, *Halimeda* likely contributes significantly to reef carbonate deposition. Because of *Halimeda's* importance to the reef building process, more attention should be paid to it when making predictions for the future of carbonate reef systems.

Key words: Halimeda, *calcium carbonate, fringing reefs, barrier reefs, algal ridge, macroalgae, lagoon substrate, Mo'orea, French Polynesia*

INTRODUCTION

Coral reefs systems are endangered by anthropogenic threats on both local and global scales (Hallock 2005). On a local scale, coral reefs are affected by increased nutrification, sedimentation, and over-fishing. Although slight nutrification has been proved to actually increase coral productivity and calcification, the excess nutrients also promote the growth of macroalgae (Edinger *et. al* 2000). Over-fishing has caused the herbivorous fish populations to collapse allowing macroalgae to out-compete the coral for the sunlight it needs to photosynthesize. This causes a "phase shift" from a coral dominated ecosystem to an algae dominated ecosystem (Hughes *et. al* 2007). Increased sediment from logging and urban runoff also contributes to coral's inability to photosynthesize (Edinger *et. al* 2000).

On a global scale, coral reefs are suffering the consequences of increased greenhouse gases and global warming. Rising sea surface temperatures contribute to coral bleaching events throughout the world (McNeil *et. al* 2004). Sea surface temperatures also affect the saturation level of $CaCO_3$ in seawater. The International Panel on Climate Change (IPCC) estimates predict that aragonite and calcite (various forms of $CaCO_3$) saturation states of tropical surface seawater will decrease by 39% from 1880 to 2100 (Gattuso *et. al* 1999). Another problem is ocean acidification, which affects coral's ability to produce $CaCO_3$ (Gattuso *et. al* 1999). These stresses potentially affect corals ability to grow and produce $CaCO_3$. If Coral reef's cannot grow fast enough to keep up with rising sea level due to global warming, then the coral will not be able to photosynthesize and will "drown"(Hallock 2005). In fact, the Coral Reef Symposium in 2000 predicted that current human populations would be the last to view coral reefs. This is why it is important to understand these diverse ecosystems and the organisms that help them grow.

Coral are not the only producers of $CaCO_3$, other carbonate-producing organisms such as algae, foraminifera, mollusks, and miscellaneous invertebrates are important to the reef building process as well. *Halimeda* (Bryopsidales/Halimedaceae) is a genus of green macroalgae widespread throughout the tropics and subtropics (Payri 1987). The genus has been an important primary and $CaCO_3$

producer on worldwide reefs since the mid-Jurassic Period (Multer 1987). Its abundance and diversity are due to its ability to reproduce both sexually and asexually (Walters *et. al* 2002), survive harsh conditions such as depth (Littler *et. al* 1988), temperature, and sedimentation (Walters *et. al* 2002), and physical and chemical defenses arm *Halimeda* against herbivory (Schupp and Paul 1994). Algal contributions to $CaCO_3$ production on reefs worldwide range from 0-61% (Wefer 1980) and in many cases *Halimeda* are the most productive contributors (Payri 1987). In some systems, it has been argued that *Halimeda* contributes more to the construction of the reef than the corals and crustose algae (Stoddart 1969; Milliman 1974).). In addition to $CaCO_3$ production, *Halimeda* and other calcifying algae contribute to reef building by forming the sand "cement" that in glues together the framework built by coral (McNeil *et. al* 2004).

The organisms that build the reefs must be better understood if we hope to protect the dwindling coral reefs of the world. This study focuses on *Halimeda* in shallow water reef systems on the island of Mo'orea, French Polynesia. Although there are seven species of *Halimeda* documented on Mo'orea as documented in a study by Claude Payri in 1987, it is possible that more species have found their way to the island since that time. In her study Payri found that although *Halimeda* is the highest carbonate producer (64%) among the calcifying algae, coral still dominates accounting for 57% of the total carbonate budget. Several studies have found that *Halimeda* $CaCO_3$ production rate differs among species (Multer 1987, Payri 1987). Because species often show habitat preference, $CaCO_3$ production should differ amongst different reef environments. Thus, in order to estimate the total amount of $CaCO_3$ produced by *Halimeda* in a system, the distribution of the various *Halimeda* species, their growth rates, and their $CaCO_3$ makeup must be taken into account.

The main objective of this study is to approximate the how much *Halimeda* contributes to Mo'orean reefs. The main objective was divided into smaller objectives to better answer this big question. The first of these smaller objectives was to assess the distribution and abundance of *Halimeda* on three common reef environments (fringe reef, barrier reef and algal ridge). The second objective was to provide data on the $CaCO_3$ production of individual species by analyzing growth rates and the mass percentage of $CaCO_3$. The goal of this research is by gathering data on $CaCO_3$ production and distribution on Mo'orean reef systems we can gain a greater understanding of the role of *Halimeda* elsewhere.

METHODS

Project Location

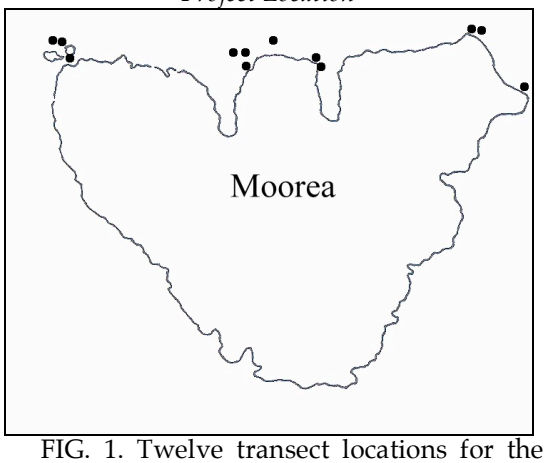

FIG. 1. Twelve transect locations for the distribution and abundance survey

Mo'orea (GPS location: S 17°30', W 149°54') is a high volcanic island that is a member of the Society Archipelago in French Polynesia. Because of its age, approximately 1.5 million years, Mo'orea has formed a barrier reef that circumscribes the island creating a network of lagoons, channels and reef. For this study three reef types were chosen on which to establish transects and gather data: fringe reef, barrier reef, and algal ridge. Fringing reefs are located adjacent to the shore, barrier reefs are separated from the fringing reef by a deep channel where water can flow in and out of the lagoons, and the algal ridge is the shallow zone located at the edge of the barrier reef where the reef meets the open ocean (Figure 2). There are many other reef types on Mo'orea, however these three are the most common.

For each reef type—fringing reef, barrier reef, and algal ridge—four different locations were chosen to establish transects (Figure 1). Fringing reef transects were laid out at Motu Tiahura in front of the old Club Med (M), At the channel marker in Pao Pao bay by Gump Station (GS), At the channel Marker in between the Sheraton and Pao Pao (PP), and at Opunahu Public Beach (O). Barrier Reef transects were sampled in front of Motu Tiahura, Opunahu Public Beach, Point Aroa (PA), and in front of the Sheraton (S). Algal

ridge transects were sampled in front of the Motu, by the Opunahu reef pass, at Tamai (T), and at Point Aroa.

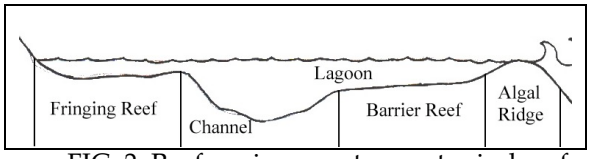

FIG. 2. Reef environments on a typical reef

Distribution and Abundance

At each location three 50 meter transects were laid out. On each transect quadrants were placed at five meters and repeated every five meters until the end of the transect line was reached for a total of ten quadrants per transect. In each .25m^2 quadrant the percent coverage and variety of *Halimeda* was recorded, along with the depth, percent coverage of coral, conglomerate rock/dead coral, sand, rubble, and other algae. The transects were laid out depending on the width and orientation of the reef.

After all three transects were complete five to ten minutes were spent snorkeling around the transect site collecting random samples of all the varieties found in the area. These samples were brought back to the lab, washed, labeled by variety, date collected, and location collected, and left out to dry to be photographed and used for $CaCO_3$ experiments.

Species Identification

All the samples brought back to the lab were dried, labeled and photographed. Initially, the individual species were unknown. In order to avoid confusion, the samples were organized into different varieties based on morphology. The varieties were *Halimeda* 1-10, however *Halimeda* 3 was divided into *Halimeda* 3 Long and 3 Short (see Appendix A). Later a student paper by Steve Hatosy on phylogenetic distribution of *Halimeda* on Mo'orea was used to identify several species. *Halimeda oputina, Halimeda distorta, Halimeda borneensis, Halimeda discoidia, Halimeda minima, and Halimeda taenicola* replaced *Halimeda* 1, 2, 3 (long and short), 4, 6, and 9 respectively. The other varieties (5,7,8, and 10) still remain unidentified.

Calcium Carbonate Experiments

Freshness and Size Test

Because some of the *Halimeda* specimens were collected earlier in the two-month period than others, a test was run to determine if the age of the specimens affected the mass % of $CaCO_3$. In order to test this fresh samples and older samples of two different *Halimeda, H. borneensis* and *H. discoidia,* were put in labeled paper bags and left in the drying oven for 48 hours. The dry samples were then removed, placed in jars, and the $CaCO_3$ was dissolved using hydrochloric acid. When the samples stopped reacting the samples were rinsed and re-dried in the drying oven. Finally the mass was taken again and the percent $CaCO_3$ was calculated by using the following equation:

(initial mass-final mass/ initial mass) x100

From this it was discerned that the older specimens could still be used for experimentation and for accurate results the sample should be between 6 to 10 grams.

Calcium Carbonate Comparison between Species

This experiment was designed to determine if the percent of $CaCO_3$ varies between different varieties of *Halimeda.* To test this specimens collected from the transects were put in 11 paper bags each labeled for each of the variety/morphologies found during the two month period. The bags were dried in the drying oven and then divided into five samples. A few of the varieties were not abundant enough to divide into five samples so they were only divided into two. Afterward the $CaCO_3$ was dissolved using the same procedure described previously. The samples were rinsed, dried and the re-massed.

Calcium Carbonate Comparison between Reef Types

To compare various reef types it is important to know if varieties of *Halimeda* found in multiple reef environments vary in percent $CaCO_3$. *Halimeda oputina* and *H. distorta* are common on all reef types. Specimens of each variety were collected on all three reef types on the same day at the Opunahu Public Beach and at the Pao Pao Fringe reef. The percent $CaCO_3$ was calculated using the same method as the comparison between species except that there were only three samples for each bag.

Analytical Methods

Distribution and Abundance

The data from each quadrant was recorded as percents (% coral, % rock/dead coral, % rubble, % sand, % other algae, % *Halimeda* total and the percentages of the individual varieties of *Halimeda* All statistical analyses were done with JMP 5.1 (SAS Institute Inc.) Data collected on *Halimeda* distribution on reef types were not normally distributed, so a non parametric Kruskal Wallis test was used. The same method was used to determine the distribution of the most common *Halimeda* varieties, *Halimeda distorta, H. oputina, and H. discoidea*, on the reef types.

Single factor ANOVA and Tukey-Krammer HSD tests were used to compare the various substrates on each of the reef types. A PCA was performed on the suite of five substrate types against the total *Halimeda* to determine which environmental factors influence *Halimeda* growth. The Eigenvectors from the PCA are shown in Table 1.

Calcium Carbonate Tests

The mass percentage of $CaCO_3$ for each of the 11 varieties was compared in a one-way ANOVA tests. A Tukey-Kramer HSD test was used to compare the means. The two most common *Halimeda* varieties are found on all three reef environments, the $CaCO_3$ percentages of two different varieties of Halimeda from different reef types were entered into a spreadsheet. ANOVA tests were done on each variety to determine if the % $CaCO_3$ was significantly different between the reef environments.

RESULTS

Distribution

Halimeda is common on all three reef types sampled in this study: algal ridge, barrier reef, and fringing reefs. The percent coverage of total *Halimeda* is 3.5, 4.8, and 15.1 respectively (Figure 3). Over all reef types the average *Halimeda* abundance is 7.8%, however, three species—*H. oputina, H. distorta,* and *H. discoidea*—account for 90.65% of the *Halimeda* coverage. The seven other species found during this study were much less abundant, some of the species (*Halimeda spp.* 7 and *Halimeda Taenicola*) were so rare that they never appeared on the transect lines. They were only found during the collection around the transect location. Even so, most of the *Halimeda* species are not evenly distributed over all reef types. In fact many species are found only in one or two reef environments (Figure 5 and Table 2) For example *Halimeda oputina*, the most abundant species accounting for half of the *Halimeda* on the transects covers 9.98% of the area on the fringing reef and only 0.51% on the barrier reef and 0.12% on the algal ridge. *H. distorta*, the second most abundant species is more evenly distributed throughout the reef types, however like *H. oputina*, *H. distorta* is most abundant on the fringing reef. Only four species were found in all three reef environments, one species was found in two of the three, and four species were restricted to only one reef type.

It is apparent that the various species of *Halimeda* show preference toward their environment in the ANOVA tests, where most of the species had significant P-values (Table 3) showing that distribution of *Halimeda* based on reef type is statistically significant. In order to better understand why *Halimeda* might have a preference for one reef type or another the reef environment was also surveyed on the transects. *Halimeda* is an alga that anchors itself to the substrate; therefore the environmental factors focused on were substrate type. It was found that the all five substrate types (rock/dead coral, living coral, sand, rubble, and other algae) were significantly different for each reef type (Table 4). The fringing reef is dominated by rock/dead coral, living coral and sand, the barrier reef is dominated by coral and coral rubble, and rock/dead coral and other algae dominate the algal ridge (Figure 6). The substrate data was also compared to *Halimeda* coverage using a PCA to determine which substrates influence *Halimeda* abundance. It was found that *Halimeda* growth is correlated with the presence of $CaCO_3$ rock/dead coral, living coral, and the presence of other algae. However, with the exception of the sand dwelling species, *Halimeda borneensis*, *Halimeda* is negatively correlated with the presence of coral rubble and sand. Field observations show that most of the *Halimeda* species are dependant on rocky substrate in order to grow, however some species have developed a rhizoidal anchor that allows them to grow in lose substrate, such as sand. Field observations also showed that *Halimeda* is abundant where there is abundant epiphytic algae, and less abundant where there was abundant macroalgae such as *Turbinaria* and *Sargassum*.

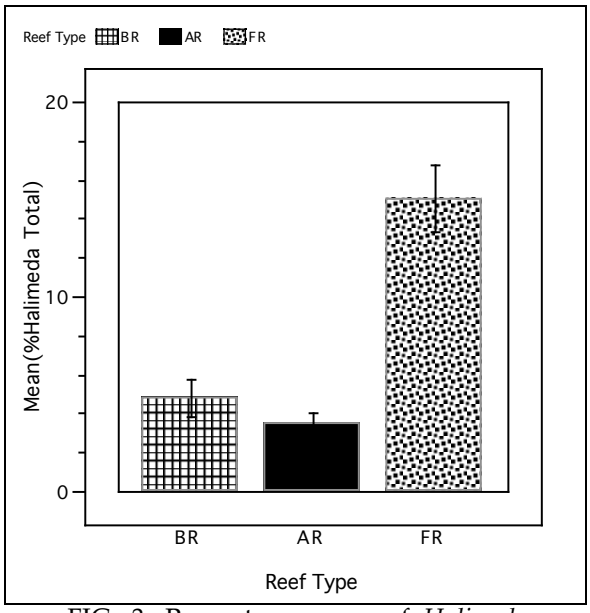

FIG. 3. Percent coverage of *Halimeda* on the three reef environments, barrier reef, algal ridge, and fringing reef.

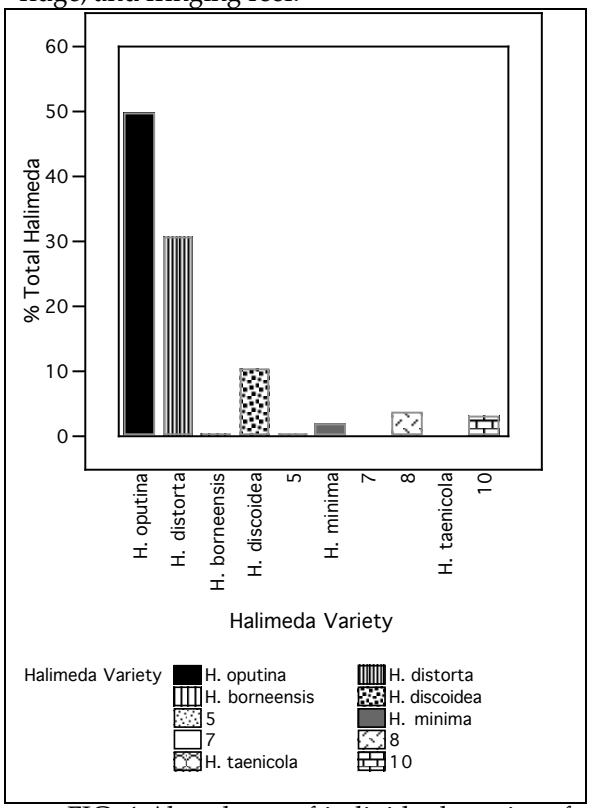

FIG. 4 Abundance of individual species of *Halimeda* in relationship to total *Halimeda.*

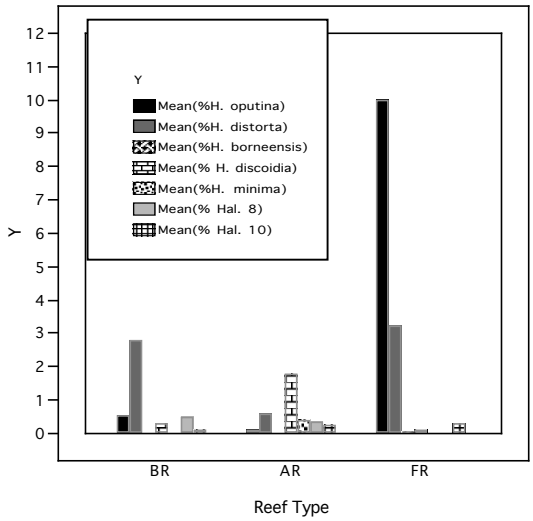

FIG. 5 Percent Coverage of the most abundant species of *Halimeda* on the three reef types.

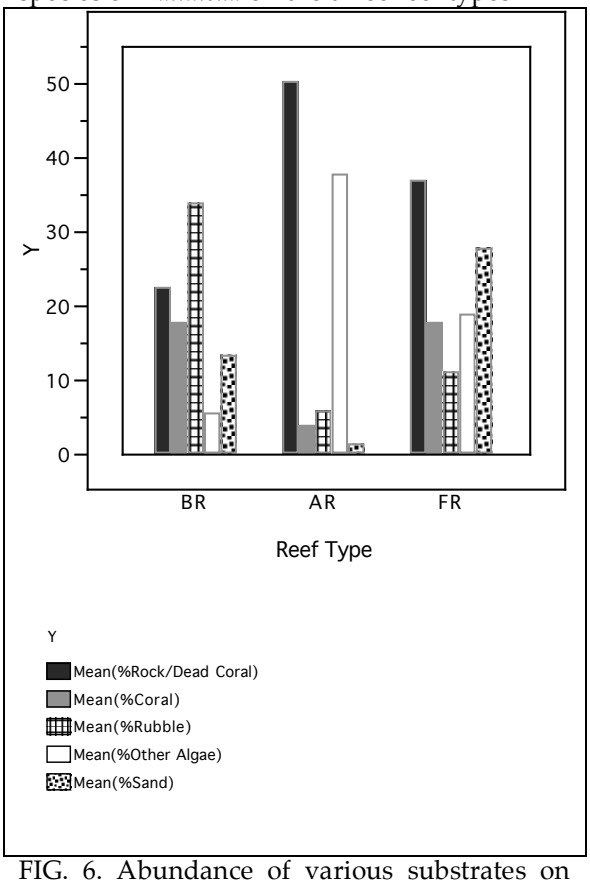

FIG. 6. Abundance of various substrates on the different reef types: barrier reef, algal ridge, and fringing reef

Calcium Carbonate Tests

Calcium Carbonate by Species

On average *Halimeda* is about 88% $CaCO_3$ dry weight. Carbonate makeup differs widely between the various species ranging from 90.24±3.63% for *Halimeda distorta* to 69.54±3.34% for *H. discoidea* (Figure 7). The ANOVA showed that the species are statistically different in their carbonate makeup, P-value=<.0001, and the F-ratio is 25.69. A means comparison analysis determined that the only species significantly different from all of the other species is *H. discoidea.* (Figure 7). However the Tukey-Krammer HSD showed that the six species which %$CaCO_3$ ranged between 95.7-88.4% (A) were statistically equivalent. The nine species that ranged between 95.5-86% $CaCO_3$ (B) were showed no significant difference. Finally the four species with a range of 88.4-79.3% (C) were not significantly different. (Table 2)

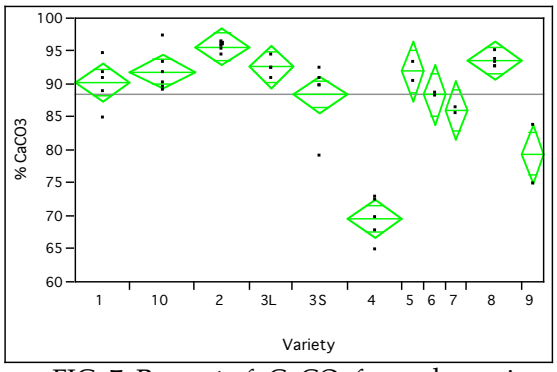

FIG. 7. Percent of $CaCO_3$ for each species.

Calcium Carbonate Comparison between Reef Types

The $CaCO_3$ makeup of *Halimeda* does not vary depending on reef environment. *Halimeda oputina* and *H. distorta* percent dry weight of $CaCO_3$ was not influenced by reef environment. Samples of *H. oputina* collected on an algal ridge did not significantly differ from samples collected on a fringing reef (P-value=.7076, F-value .391); likewise samples of *H. distorta* collected at all three reef environments did not show a significant difference (P-value=.087, F-value 3.365). (Figure 8 and 9).

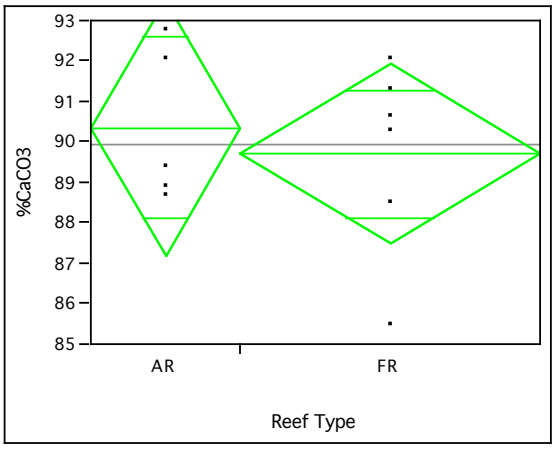

FIG. 8. Percent of $CaCO_3$ for *Halimeda oputina* on two different reef types: algal ridge and fringing reef.

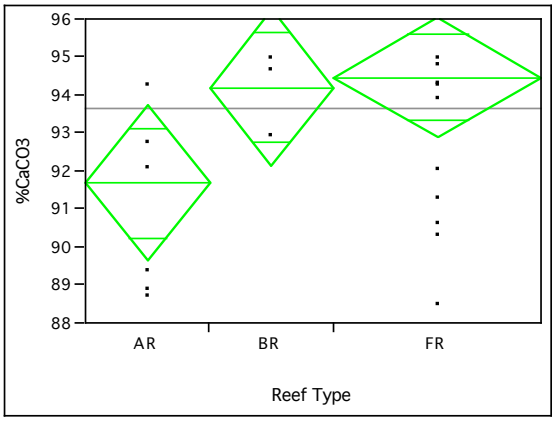

FIG. 9. Percent of $CaCO_3$ for *Halimeda distorta* on all three reef types: algal ridge, barrier reef, and fringing reef.

DISCUSSION

The main objective of this study was to approximate how much *Halimeda* contributes to the reefs in Mo'orea. In order to answer this question the study was divided into two smaller studies, one to assess the abundance and distribution of *Halimeda* on various reef types, and the second to determine the $_{CaCO3}$ makeup of the various species of *Halimeda.*

The objectives for the first study were to assess how many species of *Halimeda* there are on Mo'orea, how much of the reef does *Halimeda* cover, and on what reef environments does *Halimeda* prefer to grow. Ten species were found in this study, however because only six of the species were identified, some of the unidentified species may only be different morphologies of the known species. Claude Payri documented only seven species in 1987, and a student Steve Hatosy found six

Table 1. Eigenvectors from a Principal Component Analysis (PCA) of Various Substrate Types. PC 1 is loaded by the percent coverage of rock and dead coral, PC2 by % rubble, PC 3 by % other algae, PC 4 by % Coral and PC 5 is a repetition of PC 1, however since PC 1 is stronger PC 5 was discarded.

Substrate	PC 1	PC 2	PC 3	PC 4	PC 5
%Rock/Dead Coral	**-0.66762**	-0.02484	-0.43639	-0.22197	**0.56033**
% Coral	0.38490	0.19910	-0.48549	**0.67109**	0.35517
% Rubble	0.39232	**-0.74200**	0.15818	-0.15345	0.49695
% Other Algae	-0.34581	0.09412	**0.70874**	0.50169	0.34286
% Sand	0.36420	0.63271	0.21571	-0.47448	0.44201

Table 2. Abundance and percent $CaCO_3$ for the individual Halimeda species

Halimeda Species	% cover AR	% cover BR	% cover FR	% cover total	% $CaCO_3$	Tukey-Krammer HSD
H. oputina	0.12	0.51	9.98	**3.54**	90.24±3.63	A,B
H. distorta	0.59	2.77	3.21	2.19	**95.65±0.79**	A
H. borneensis S	0	0	.067	.022	88.36±5.33	B,C
H. borneensis L	-	-	-	-	92.56±1.45	B,A
H. discoidea	1.79	0.28	0.12	.73	69.54±3.34	D
Hal 5	0	0.083	0	.028	91.95±2.10	A,B
H. minima	0.38	0	0	.13	88.40±0.24	A,B
Hal 7	**0**	**0**	**0**	**0**	86.01±0.74	C
Hal 8	0.33	0.46	0	.27	93.50±1.05	B,C
H. taenicola	**0**	**0**	**0**	**0**	79.36±6.17	B,C
Hal 10	0.26	0.11	0.30	.22	91.86±3.10	A,B
Hal Total	3.51	4.83	15.08	7.80	88.35	

Table 3. Results from ANOVA test comparing the most abundant individual species and total *Halimeda* to reef type.

Species	P-value	F-Ratio	Mean Value
H. oputina	<.0001	48.7531	3.54
H. distorta	.0296	3.5548	2.19
H. borneensis	.1516	1.8964	.0222
H. discoidia	<.0001	12.8047	.731
H. minima	.0347	3.3934	.128
H. spp. 8	.2646	1.3347	.267
Total *Halimeda*	<.0001	28.5106	7.80

Table 4. Results from ANOVA test comparing substrate type to reef type.

Substrate	P-value	F-ratio	Mean	Tukey HSD BR	Tukey HSD FR	Tukey HSD AR
Rock/Dead Coral	<.0001	13.84	34.95%	A	B	C
Live Coral	<.0001	9.6	14.3%	A	A	B
Rubble	<.0001	26.9	18.35%	A	B	B
Sand	<.0001	27.54	14.65%	A	B	C
Other Algae	<.0001	28.32	20.94%	A	B	C

species in 1995. The increase in species richness in this study may be due to species migration during the past decade, or due to the fact that both Payri and Hatosy had fewer study locations, for example Payri's experiment was exclusively on Tiahura reef. Of the ten species found 3 species accounted for 91% of the total *Halimeda*, this result is also similar to Payri's study in 1987 where three species accounted for 99% of the total *Halimeda.* However the dominant species in this study differed from the 1987 study where *Halimeda incrassata* (now *H. borneensis*) has been replaced by *H. distorta.*

The distribution and abundance study also found that Halimeda covers an average of 7.8% of Mo'orea's reefs, which is slightly higher than Payri's result of approximately 5% at Tiahura in 1987. However, *Halimeda* coverage varies significantly by reef type. *Halimeda* covered and average 15% of the fringing reefs studied. This abundance might be a result of potentially higher levels of nutrients near the shore, but further testing would need to be run in order to prove this. On the contrary, the algal ridge, named for the abundance of macroalgae found there, had significantly less *Halimeda*, 3.5% (Table 2). It seems contradictory that a macroalgae such as *Halimeda* should be so low in abundance on the algal ridge, but there is an explanation. Other uncalcified, faster growing species of macroalgae such as *Turbinara* and *Sargassum* must be out competing *Halimeda* for substrate to attach onto and for sunlight to photosynthesize. As for the barrier reefs, it is unclear why *Halimeda* occurs at such a low abundance except for the fact that *Halimeda* does not tend to grow on coral rubble, which is an abundant substrate for this type of reef.

The objectives for the second part of the study were to determine the $\%CaCO_3$ for each of the species found in the distribution study, and to determine if the $\%CaCO_3$ was dependant on the reef environment or the species. It was found that the $\%CaCO_3$ was highly dependant on species and not on the reef environment where it grows. The $\%CaCO_3$ varies between 96% and 69% for the individual species. The $\%CaCO_3$ for all the species was 88%. If species abundance is taken into consideration than the average $\%CaCO_3$ for Mo'orea is 90%.

The last objective was to take the information from this study and compare it to similar studies from other reef systems. Because French Polynesia is a geographically isolated location, it tends to be species poor (Payri 1987). *Halimeda* exemplifies this pattern. On Mo'orea *Halimeda* has low species richness, with a few species making up a large percentage of the *Halimeda* biomass, when compared to other areas such as Australia or the Caribbean. Still, *Halimeda* is the dominant $CaCO_3$ producer amongst calcifying algae, providing 1.4 kg $CaCO_3/m^2/year$, and makes up 11% of the total algal covering (Payri 1987). Small and Adey found in 2001 found in their microcosm experiment that whole ecosystem calcification at 4.0±0.2 kg $CaCO_3/m^2/year$ is related to its principal components—stony coral 17.6%, *Halimeda* 7.4%, *Tridacna* 9%, algal turf, coralline and foraminifera 29.4%, and miscellaneous invertebrates 36%. In another experiment on carbonate production by *Halimeda* in Antigua, Wefer estimated in 1988 that sediment accumulation due to Halimeda is 61.3g $CaCO_3/m^2/year$. In order to compare this study to these other studies an estimate of how much $CaCO_3$ *Halimeda* produces on Mo'orea must be made. However, making an estimate of $CaCO_3$ production is complex and difficult.

Assuming that the average percent cover found in this study (7.8%), the average $\%CaCO_3$ (90%) and the approximate area of reef on Mo'orea, 27 km^2 (Payri 1987), the growth rates for individual species would still have to be calculated. Calculating growth rates for *Halimeda* is a complex task. The growth rates are dependent on species, age, and season (Multer 1987), data that this study did not account for. As an alternative, a calculation of the mass of $CaCO_3$ present in living *Halimeda* on Mo'orea can be made. Assuming that the relationship between percent cover and biomass for *Halimeda oputina* from Payri's study makes a good approximation for the rest of the species, and assuming that the percent cover calculated in this experiment is a good approximation for the rest of Mo'orea's reef then the biomass of *Halimeda* in Mo'orea would be 171.6 gdw/m^2. Taking the approximate area of reef on Mo'orea then there is 4,633,200 kg dry weight of *Halimeda* on Mo'orea. If 90% of that dry weight is $CaCO_3$, then there is 4,169,880 kg of $CaCO_3$ tied up in living *Halimeda* on Mo'orea. If the $CaCO_3$ production rates determined by the Payri, Small and Adey, and Wefer studies are applied to the 27km^2 of Mo'orea's reefs than *Halimeda* would produce 37.8, 7.99, and 1.66 million kg $CaCO_3/year$.

Studies like this show that more attention needs to be paid to the other carbonate producers in reef system when predicting the effects of conditions on reefs worldwide, many of these other reef building organisms, like *Halimeda* are not as sensitive to environmental changes as are coral. If the mechanisms for reef building are better understood than more accurate predictions for the future of carbonate reef systems can be made, and from better predictions, better solutions can be made.

FURTHER RESEARCH

There is very little research on the growth rates of multiple species of *Halimeda*, and why the growth rates of sand-dwelling species are slower than species that prefer rocky substrate. There is also very little research on the deep-water species of *Halimeda* on Mo'orea. It would be beneficial to study sexual and asexual reproduction, lifespan, competition with other species of macroalgae, and yearly growth patterns of individual species. Finally one could study the fate of the sandy sediment that *Halimeda* produces, including, decomposition, transportation, and how it helps to produce reef rock.

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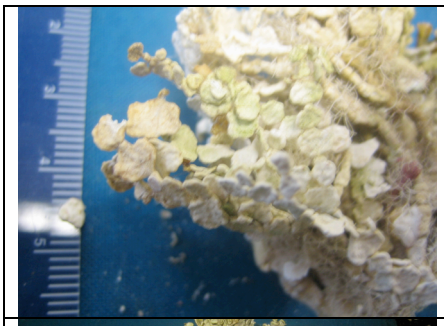
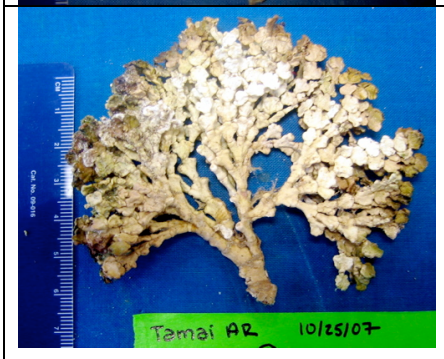
APENDIX A

Halimeda of *Mo'orea*

	*Halimeda oputina* This species has small angular segments (width: 3-5mm). Thallus is sprawling on rocky substrate and forms loose bushy clumps, also found in sandy areas. Rhizoidal holdfast attaches it to rocky bottom. Most common species on Mo'orea
	*Halimeda distorta* Small round segments (width: 3-5mm). Thallus branching is in one dimension. Thallus forms dense mats on rock and in rock crevices. Usually found on the underside of coral heads or large rocks.
	*Halimeda borneensis* formerly *Halimeda incrassata* Found in sandy substrate, has a bulbous rhizoidal holdfast. Similar to *H. distorta* in morphology except with larger segments and tends to grow in clumps.
	*Halimeda discoidia* Fleshy species commonly found on the algal ridge. Broad leathery segments (8-10mm) usually grow in clumps, basal segments form a fan like structure and the end segments are convoluted.
	*Halimeda spp.* 5 (unidentified) This variety is a stringy, large segmented species that found growing between two coral heads on the motu barrier reef. It was also found on the Opunahu barrier reef but was unable to bring it back as a sample. The segments are spaced apart and do not branch often. May be the same as Halimeda 8 since I have not found very much of it.

	*Halimeda minima* Similar to *H. oputina* but with smaller segment size (2-3mm). Thallus forms compact bushy structure attached to rocky substrate with a single holdfast, only found on the Algal ridge.
	*Halimeda spp.* 7 (unidentified) Sage green variety with large, thick, round segments. Collected on the Sheraton barrier reef. Very similar to *H. discoidia* and *H. taenicola.*
	*Halimeda spp.* 8 (unidentified) This variety has large, hard, segments that look similar to *H. oputina* but much bigger. It grows in large clumps that are not very dense. Found on most reef types, common on the Point Aroa Algal ridge
	*Halimeda Taenicola* Fleshy species, large round segments, grows attached to the rock, flexible thallus.
	*Halimeda spp.* 10 (unidentified) Easily mistaken for Halimeda 1. The top segments are similar to *H. oputina* but the basal segments are thick and columnar. It grows in very dense patches and found on the Tamae and point Aroa algal ridges.

EPIPHYTE DISTRIBUTION WITH RESPECT TO MICROHABITATS IN MO'OREA, FRENCH POLYNESIA

ELAINE FOK

Department of Environmental Science, University of California, Berkeley, CA 94720 USA

Abstract. Epiphytes contribute significantly to the biomass of forest canopies; however, in the tropics, epiphytes have been greatly understudied. This study seeks to better understand the effects of forest edge on the distribution of epiphytes as well as describe general characteristics of epiphytic communities on *Inocarpus fagifer* in Mo'orea, French Polynesia. It was found that species richness was relatively similar throughout the study site. While there was no significant difference between locality on buttress root or trunk of the host tree, moss communities in particular were significantly affected by distance from forest edge and proximity to perennial streams. Ferns were found to be somewhat correlated with their proximity to streams while liverworts and lichens were not greatly affected. Overall, location of epiphyte communities relative to edge or at different heights on the host tree did not play a large role in the establishment of epiphytes.

Key words. epiphyte communities; edge effects; microhabitats; *Inocarpus fagifer*; Mo'orea, French Polynesia

INTRODUCTION

Vascular and non-vascular epiphytes are essential contributors to the biomass of tropical and neotropical forest canopies (Nadkarni 1984). True epiphytes are autotrophic, and thus must absorb atmospheric moisture (Hietz 1998). In particular, vascular macroepiphytes, such as orchids and bromeliads, are often very different from microepiphytes such as bryophytes (Gradstein and Pocs 1989). Non-vascular microepiphytes, such as lichens, lack mechanisms for the regulation of water, making them more susceptible to abiotic stress (Renhorn 1998). However, non-vascular epiphytes tend to out-compete their vascular counterparts in wetter and cooler environments (Benzing 1998).

While much research has investigated forest fragmentation in temperate zones (Kivisto and Kuusinen 2000, Lindlar and Frahm 2002, Znotina 2003, Baldwin and Bradfield 2007, Echeverria *et al*. 2007), tropical zones have not been thoroughly studied (Nadkarni 1984, Frahm and Gradstein 1991). Fragmentation and agricultural management has been shown to negatively affect epiphytic communities in Brazilian forests (Pereira-Alvarenga and Porto 2007) but the effects of fragmentation and management have yet to be examined in many other tropical areas. Fragmentation creates microclimates because wind speed, solar radiation, air temperature, and relative humidity are often modified at forest edges (Chen *et al*. 1993, Esseen and Renhorn 1998). These edge habitats tend to discourage certain epiphyte growth as wetter, more suitable epiphyte habitats can often be found within a forest stand away from a clearing (Ghuman and Lal 1987).

In addition, the management of forest stands lead to lower species diversity and abundance of macrolichens and bryophytes (Andersson and Gradstein 2005). While most results are species specific, epiphytes respond negatively to habitat modification

and disturbance (Benavides *et al*. 2006). Because tropical rain forests are home to nearly 30% of the world's non-vascular epiphytes (Gradstein and Pocs 1989), examining growth patterns of epiphytes can help us understand how habitats altered by forest fragmentation and management affect this important portion of the community. Understanding growth conditions is necessary to restore species diversity and abundance in epiphyte communities following disturbance. Additionally, investigating colonization processes can help us understand natural changes in communities and monitor epiphyte response to fragmentation.

In Mo'orea, French Polynesia, several species of epiphytes grow on *Inocarpus fagifer*, also known as the Tahitian Chestnut or *mape* (De Sloover 1994, d'Artenay *et al.* 2006). Previous studies of epiphyte growth on Mo'orea have measured factors including canopy cover, aspect, host tree diameter, and height of trunk growth *Metrosideros collina* (Cushing 2002, Dobbs 2006). Finding abundance correlated with canopy cover, size of tree and trunk height.

This study seeks to describe general characteristics of epiphyte growth on *Inocarpus fagifer*. It examines how epiphyte communities are affected by forest edge, locality and distribution on trees. Because little is known about *I. fagifer* and its associated epiphytes, this study also examines two aspects of epiphyte communities: ecological succession and growth conditions. While effects are species specific (Hilmo and Holien 2002), I hypothesize that communities further from the edge and closest to running water are characterized by greater growth rates and species richness. In contrast, host trees closer to the edge of the stand have slower epiphyte growth and lower species richness. I also predict that epiphyte communities growing at different trunk heights on *I. fagifer* would be composed of different dominant species.

METHODS

Study organism and site

All field work was conducted between 8 October 2007 and 16 November 2007. Work was completed near the Tetiiroa Marae immediately below the Belvedere in Mo'orea, French Polynesia (UTM coordinates X199566 Y8058975). The marae was amid mid elevation cloud forest, dominated by *mape*, a Polynesian introduction to Mo'orea (Lepofsky 1994). *Mape* was planted extensively in the mid-1900s to prevent erosion in mid and high elevations (Jennifer Kahn, personal communication). Unique climates associated with high net precipitation characterize these cloud forests and contribute to moisture gradients within the stand.

Sampling design

Transects were established that sampled a range of distances from forest edge and streams. Three linear transects of 75m were established that started at the parking lot at the edge of the stand and ended past a stream in the middle of the stand. A fourth transect of 75m was sampled along the lower reach of stream. Epiphytes were sampled every 10m along transects, on trees within a 5m radius of the transect point. Because species associations between *Inocarpus* tree size and epiphyte diversity was not known, samples were limited to trees with buttressing 2m high with circumferences no larger than 150cm at height 1.5m. I recorded species present along a circumferential transect at height 1.5m and along transects on the two largest buttresses at height 0.75m. Epiphyte species present were recorded every 2cm along the top of the measuring tape. I estimated the aspect of epiphyte growth around the trunk, and noted the aspect of the buttress face.

Experimental design

In order to test the effects of microclimates, an edge-interior transplant was performed, following a technique modified from Renhorn *et al*. (1997) after initial sampling. I removed 9cm diameter circles of bark from trees on the edge of the stand and transplanted them on Petri dishes to the interior of the stand, and vice versa. One sample from the four cardinal directions was transplanted from each location in addition to four control samples that were transplanted to trees within the same location. Species were collected, cleaned of debris, weighed individually, and the species present were identified for individual samples. Samples were then mounted to Petri dishes with botany paste and reattached to trees using fishing line and nails on in late October. After twenty three days, samples were brought back to the lab for weighing and assessment of growth.

A second experiment was conducted to examine influential factors on epiphyte colonization. Colonization experiments were completed at both the interior and exterior of the forest stand. Epiphytes were removed from the tree while the bark remained intact. I cleared a 9cm diameter circle from four trees on the exterior of the stand and from four trees on the interior of the stand, one at each cardinal direction, respectively. Epiphytes present were catalogued before clearing and after twenty three days, any epiphyte growth was also noted.

Organisms were identified with keys by Gradstein (1989), D'Artenay *et al*. (in press), Murdock and Hinkle (1999), and De Sloover (1994). Mosses and ferns were identified to species level. Lichens, liverworts, and algae were identified to the genera level. Voucher specimens of all epiphytes were submitted to the University of California and Jepson Herbaria. Fern specimens were also submitted to the Herbarium of Tahiti.

Statistical analysis

Species diversity along each transect was calculated using the Shannon Diversity Index. Because my response variables were percent values, I used an arcsine transformation to convert the data. Additionally, I used a Bonferonni correction to adjust my p-value. With four responses tested separately, my significant p-value was 0.0125. I performed t-tests between buttressing and trunk height to test for differences in species richness on *I. fagifer.* Because some of my data could not be normalized, I used Wilcoxon tests between buttressing and trunk height. I also performed a two-way ANOVA test to examine the effects of edge and colonization height on microhabitats. All statistical tests were completed using JMP 5.1 (©2004).

RESULTS

A total of eleven epiphyte species were sampled more than once, consisting of three lichens, four ferns, two mosses, two liverworts, and one alga (Appendix A). On average, lichens were most abundant,

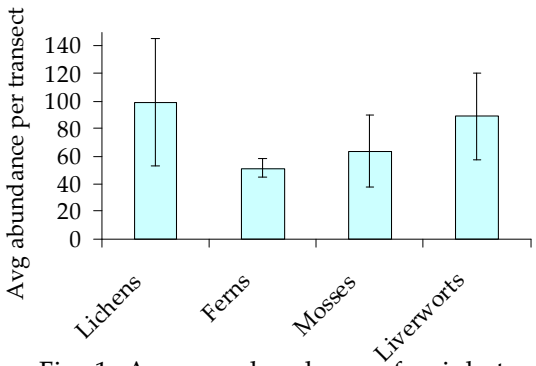


Fig. 1. Average abundance of epiphytes between transects was greatest for lichens, but lichens also had the most variance. Ferns were least abundant between transects and had lowest variance.

followed closely by liverworts (Fig. 1). Lichens had the greatest variance between transects while ferns had little variation (Fig.

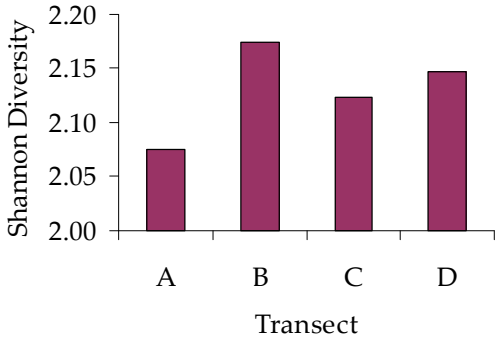


Fig. 2. Transect B had greatest diversity while Transect A had lowest diversity value. There was no significant variance between transects.

1). Mosses and liverworts varied about the same between each transect (Fig.1).

Looking at species richness, transect B showed the greatest diversity with a Shannon Diversity Index of 2.17 and transect A had the lowest diversity of 2.07 (Fig. 2). Transect C had a diversity of 2.12 and transect D had a diversity of 2.14 (Fig. 2). There was no variance between transects.

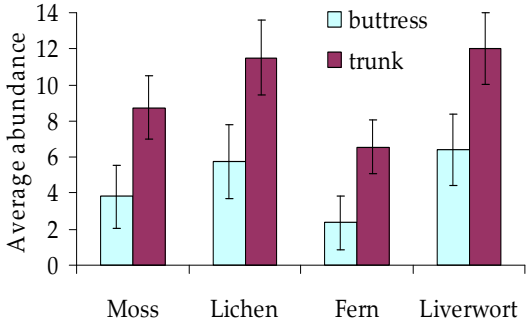


Fig. 3. Average abundance of epiphytes was twice as great on trunks than on buttresses. Liverworts had greatest abundance, followed by lichens, mosses, and ferns.

Results of a t-test to examine species richness showed that it was not significantly different in epiphytes at trunk or buttressing height for liverworts (p=0.7672) or lichens (p=0.8168, Fig. 3). Similarly, results of a Wilcoxon test found non-significant differences in fern richness (p=0.2566) and moss richness (p=0.6524, Fig 3). All calculated p-values were less than the critical value (p-value$\leq$0.0125), thus the null hypothesis could not be rejected.

By a two way ANOVA, there was no significant difference between buttressing and trunk height on lichen (p=0.5166), fern (p=0.3823), moss (p=0.5495), or liverwort (p=0.7248) coverage (Fig. 4). Distance from a stream or edge had no significant effect on lichen growth (p=0.6353), or liverwort growth (p=0.1766, Fig. 4). As communities were sampled closer to a stream, there was a significantly positive effect on mosses (p=0.0033) and a positive loose correlation with ferns (p=0.0631, Fig. 4). The cross-factor between the trunk height and location showed no significant effect on coverage of lichens (p=0.8826), ferns (p=0.8461), mosses (p=0.9861), or liverworts (p=0.6560, Fig. 4).

Most experimental transplants decreased in weight by the end of the study, whether control or experimental plate. The internal East control plate was the only plate to increase in weight, gaining 1.9g. Exterior control plates decreased by 0.9g on average compared interior control plates which decreased by 2.3g on average (Fig. 5). Exterior plates transplanted to the interior location decreased by 2.4g on average, and interior plates transplanted to the exterior location decreased the most on average by 2.6g (Fig. 5).

There was no growth due to colonization after twenty three days, on any of the eight cleared areas.

DISCUSSION

Overall, I did not expect great differences in species composition or

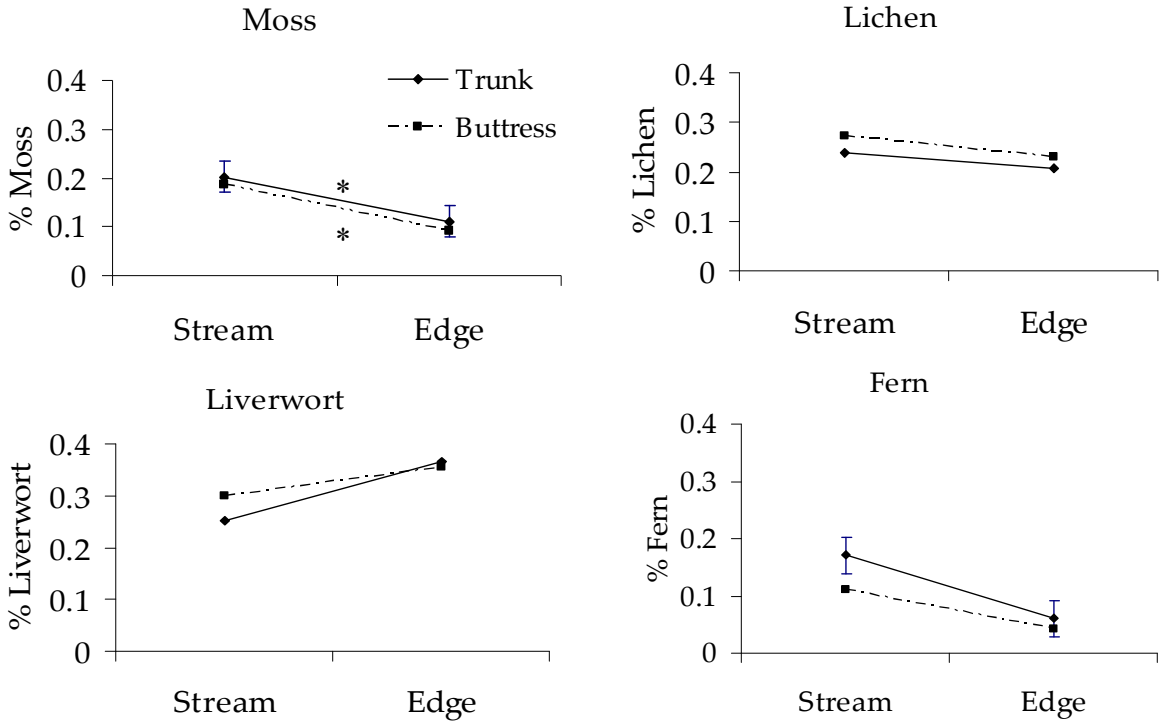


Fig. 4. Percent coverage by epiphyte species as a response to habitat (stream vs. edge) and tree position (trunk vs. buttress). Error bars represent ± 1 standard error. Vertical bars indicate lack of significance between position; asterisks indicate significant difference between habitat.

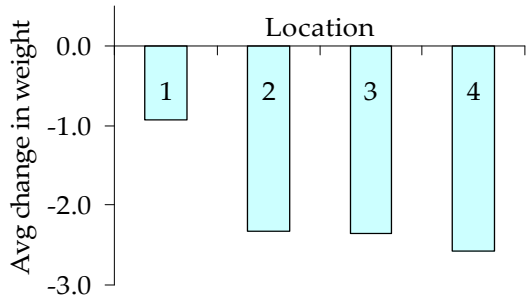


Fig. 5. Average change in weight by location for control and experimental transplants. 1=external control, 2=internal control, 3=external transplant, 4=internal transplant

diversity as all transect sampling was completed in the same area. However, I noticed that edge microhabitats had greater lichen richness which quickly disappeared as sampling continued along transects. These edge environments had the greatest constant light exposure and typically had the least canopy cover which may explain the surge in lichen richness.

In regards to total epiphyte abundance, the patterns in variance between transects support the idea that microhabitats are conducive to growth of specific epiphytes. Lichens seem to tolerate the greatest range of habitats, while ferns are less tolerant of certain microhabitats. Mosses and liverworts seem to be somewhat generalists in their ability to flourish in varying habitats.

I predicted that microhabitats on tree buttresses would differ from that of tree trunks because of the amount of light, canopy cover, and moisture. However, the species richness was not significantly

different between the two heights. This may be due to a variety of factors including host preference, or it may be that the two heights were not far enough apart for comparison. There may be a greater difference in richness between epiphyte communities in the under-story as compared to epiphytes 40m high in the *I. fagifer* canopy.

Although there was similar richness, I found that the average abundance of epiphytes at trunk height was twice as great as buttressing height. This could be attributed to age of communities on the host tree. It would be interesting to see if this trend continued at greater heights on the trunk.

Statistically, only mosses were significantly affected by the distance from the stream. This was surprising because mosses are typically more tolerant to desiccation. Although ferns are the most susceptible to desiccation, there was only a loose correlation between fern growth coverage and stream distance. I expected more of a correlation between fern growth coverage and stream distance. Perhaps a larger sample size is needed to examine this correlation more thoroughly. It is possible that certain species of mosses and ferns are more or less affected by distances from streams, an aspect that this study did not examine. Liverwort and lichen coverage was not significantly affected by distance from the stream. Other than considerable lichen richness at the edge, I did not notice any other trends in liverwort or lichen growth as I sampled along transects. Based on these results, there is not enough evidence to support the idea that variation in stream proximity plays a significant role on epiphyte growth.

Decreased average weight in the transplant experiment was likely due to overall water loss by epiphytic individuals. As mentioned above, the internal East control plate, transplanted from one tree to another in the same location, was the only one to increase in weight. The composition of this plate was 90% lichen coverage with some liverwort and algal growth. This was the only transplant that increased in weight. It is difficult to determine whether this increase was due to productivity, water retention, species present, or other factors, as there was no defining element that differentiated this plate from the other control and experimental plates.

In addition, most specimens, despite full exposure to outdoor elements, had mold growth at the end of the transplant period. This may be due to a contamination introduced during the transplant or in the materials. However, it is worth noting that two transplant plates that only contained *Coenogium* lichen had no mold growth. It may be that this particular genus interacts differently with the environment as compared to other epiphytes on the transplant plates.

There was no epiphyte colonization on any of the cleared areas. Colonization often depends on fertilization cycles and environmental factors, among others, thus it is understandable that growth did not occur. If conditions were favorable, it is possible there may have been some epiphyte growth noted in the short time that this study was conducted. However, most colonization experiments, including Cobb *et al*. (2001), occur over greater lengths of time with estimations of biomass increase noted annually.

CONCLUSIONS

Overall, stream proximity primarily affected moss coverage in epiphyte communities on *Inocarpus fagifer*, while forest edge environments were favorable for lichen abundance. The distribution of epiphyte communities at varying tree heights was not correlated with richness but rather abundance. Because there are many environmental factors that affect epiphyte growth, more specific measurements of abiotic conditions such as relative humidity

could lead to a more detailed understanding of growth patterns. Also, canopy access would allow for a broader look at the range of epiphytic communities on *I. fagifer* as light, humidity, and temperature differ at the canopy level. Future studies could investigate seasonal effects on epiphyte and bryophyte communities in tropical habitats because it has not been well studied. Seasonal differences in rainfall may contribute to the success of vascular and nonvascular plant communities. In addition, the life cycles epiphyte communities have not been well documented as reproductive structures are often elusive to the naked eye. As *I. fagifer* is considered a Polynesian introduction, a comparison of epiphytes on *I. fagifer* between islands in French Polynesia would be an interesting study to examine the possibility of speciation.

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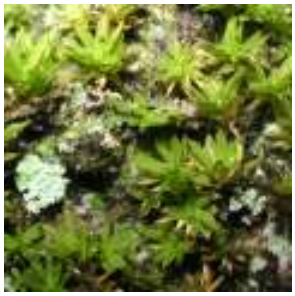
APPENDIX A

Epiphytes found on *Inocarpus fagifer* in Mo'orea, French Polynesia



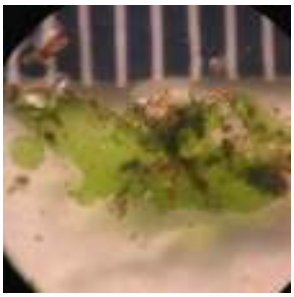
Vesicularia aperta/calodictyon

Orthorrhynchium cylindrium

Trentepohlia sp.

Plagiochila sp.

Rectolejeunea sp.



Fern gametophyte

Trichomanes tahitense

Crepidomanes humile

Crepidomanese bipunctatum

Lepraria sp.

Coenogium sp.

Lichen H

INVERTEBRATE SUCCESSION WITHIN THE FRUIT OF TAHITIAN CHESTNUT *Inocarpus fagifer* IN MOOREA, FRENCH POLYNESIA

GREG GILLETTE

Department of Integrative Biology, University of California, Berkeley, California 94720

Abstract: The process of succession takes place over a broad range of magnitudes and timescales. Studies of animal succession within short-lived microhabitats are few in number, making it an important addition to the ecological literature. The decomposing fruit of the Tahitian Chestnut tree *I. fagifer* represents such a microhabitat. In this study, chestnut fruits from the island of Moorea, French Polynesia, were collected at different stages of decomposition, and the invertebrates inside were catalogued and identified to the most specific taxonomic category possible. Pitfall traps were set up at each location where chestnuts were collected in order to ensure that the dynamics of the chestnut habitat were different than the dynamics of the forest floor. Species richness and diversity for the chestnuts and pitfall traps were calculated and compared in order to test for trends of succession. There were no significant differences in richness or diversity for the pitfall traps, but significant differences did occur across stages for the chestnuts. Predictable trends of succession were interpreted from these results, suggesting that some form of facilitative succession was taking place.

INTRODUCTION

The process of succession is the orderly and predictable change of species composition and structure within ecological communities through time (Pickett and Collins 1987). It takes place in habitats that have either been recently disturbed, or previously unoccupied, since this leaves open ecological niches for new species colonization(Connell and Slatyer 1977). As the species change, so do the characteristics of the habitat since different species interact with the environment in different ways. The habitat change influences colonization by new species whose preferences are met by the newly created conditions. This process of continuous species replacement occurs across a broad range of timescales and habitat types. Practically any newly created or heavily disturbed habitat will undergo some form of succession, making the process an important focus of ecological study (Bazzaz 1979).

Researchers typically distinguish between primary and secondary succession. Primary succession refers to the predictable change in community composition after a new habitat has formed (Chapin 1994). The formation of new habitats is constantly occurring at different scales, such as retreating glaciers that leave large areas of exposed land, or a leaf that has recently fallen to the ground. These examples, while extremes in magnitude, both act as blank canvasses for the colonization of new species, and therefore are starting points for primary succession. Secondary succession refers to the predictable change of community composition in a habitat that has been disturbed, perhaps by natural causes like a fire or flood, or human-induced causes like forest clearing. In this case the

habitat already existed, but the disturbance opened up niches for the colonization of new species (Guevara 1986). There have been a number of pathways or mechanisms through which the sequences of succession have been observed to take place (Connell and Slatyer 1977). One of the most common mechanisms, although there are many more, is referred to as facilitative succession, where a colonizing species affects the habitat in such a way making it more suitable for future successional species to thrive (Chapin 1994).

Some of the earliest studies of succession within insect communities focused on primary succession, and how insect communities changed within the habitat of decomposing carcasses (Bornemissza 1957). Today, decomposition is still a major focus for the field of forensic entomology which uses the predictable sequence of insect colonization on corpses to determine the time of death in criminal investigations (Andersen 2001). Many things in nature, such as fallen fruit from a tree, are potential candidates with which to study primary succession of invertebrate communities, but outside of forensic entomology, relatively little research has been done.

On the island of Moorea in French Polynesia, I observed the Tahitian Chestnut tree *Inocarpus fagifer* (Hammes and Putoa 1986) bears a fruit that when fallen, becomes infested with a number of insects and invertebrates throughout its decomposition. This decomposing fruit acts as a microhabitat which changes radically over a relatively short timescale. Studying such a habitat provides insight into a changing community structure with a large number of potential replicates. This allows for a comparison of species richness and diversity at different stages of decomposition in order to see what kind of trends of invertebrate succession are taking place.

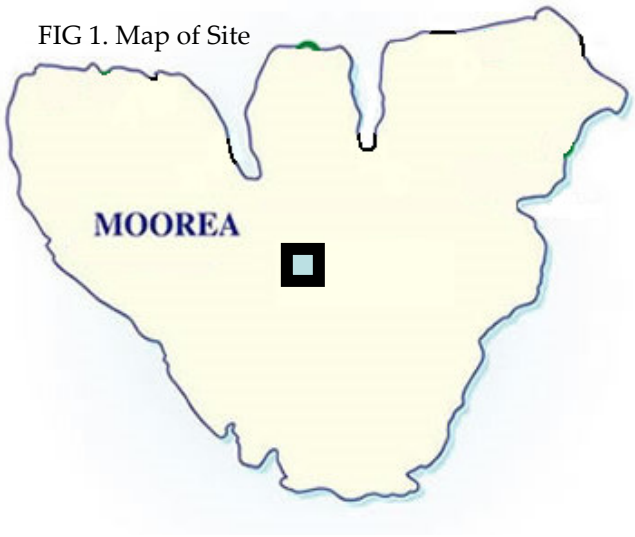
I proposed that some form of succession was occurring within the decomposing fruit of *I. fagifer*. To test this hypothesis I developed a study where a large number of *I. fagifer* fruit samples were collected at different stages of decomposition, and the invertebrate communities within them were catalogued and identified. The species richness and diversity between stages were then compared to test for trends of succession within the timescale of the fruits' decomposition and see if specific successional pathways could be observed.

MATERIALS AND METHODS

Site description

Eight separate plots were chosen on Moorea at mid-elevations (200-250m) between the upper Oponuhu and Pao Pao Valleys (Figure 1).These eight plots were all in one general area in order to minimize factors that could alter species composition such as elevation, precipitation, etc. Each plot consisted of a ten meter radius circle in an area of dense *I. fagifer* forest, where the canopy cover varied from about 85-90%.

FIG 1. Map of Site



Classification of decomposition stages and assessment of classification accuracy

Based on field observations between the eight sites, I developed a classification key identifying six stages of *I. fagifer* fruit decomposition. Eight freshly fallen chestnuts were collected from within my site and monitored once a week for six weeks to determine whether the classification system correctly identified the progression of decomposition. The timescale of decomposition was also assessed through this monitoring.

Chestnut collection and invertebrate identification

I selected chestnuts within my plots by randomly generating six azimuths and picking the first chestnut that corresponded to each of my six decomposition groups. I set up a pitfall trap at every collection point in order to compare invertebrates found around the fruit, and those found on or within it. The pitfall traps were 6 cm diameter plastic cups filled with a soapy water solution, and buried so the edge of the cup was flush with the ground. They were collected after two days and their contents were catalogued and identified in the lab.

Once the study chestnuts were collected, each sample was frozen separately in order to immobilize the invertebrates that may have easily escaped. After freezing, a census was carefully performed on each sample, cataloguing the invertebrates found inside. The invertebrates were identified to different extents. Many were identified to family, some were identified more specifically, and some were qualitatively described as different morphospecies. A microscope picture was taken of each new invertebrate observed so there would be an accessible record of what was found. Specimens were also taken and packaged in an ethanol preservative. All voucher specimens will be deposited in the Essig Museum of Entomology at the University of California, Berkeley.

Analysis of data

Once the data were collected, functional roles were assigned to a subset of the invertebrates found, and their changes through time were observed. I calculated a value for species richness (S), as well as a Shannon diversity index (H`) averaged over each stage for the eight plots. I compared the biological diversity index, which measures species evenness, with values for species richness. This is a common step in analysis of successional studies (Whittaker 1994). I used Jump Version 5.1 (SAS Institute Inc.) to visualize a plot of the mean species richness and diversity indexes against the six stages of decomposition. A Tukey-Kramer HSD test was performed on these plots to see if there were statistically significant differences between the community compositions at different stages. I analyzed the results to see if trends of succession could be observed.

In order to compare the invertebrates collected within the chestnuts, and those collected in the pitfall traps, I also calculated a mean value for species richness and diversity for the pitfall trap communities averaged over each stage. The pitfall results were compared with the chestnut results to see if changes in chestnut species richness and diversity were significantly different than the background richness and diversity of the forest floor.

RESULTS

Classification of decomposition stages

Based on field observations, I developed a timeline consisting of six stages to characterize the decomposition of the *I. fagifer* fruit (Figure 2). This timeline represents three possible routes of decomposition; the fruit decomposes relatively undisturbed, the fruit begins to decompose undisturbed until it germinates, or the fruit is cracked open by a

Timeline of Decomposition

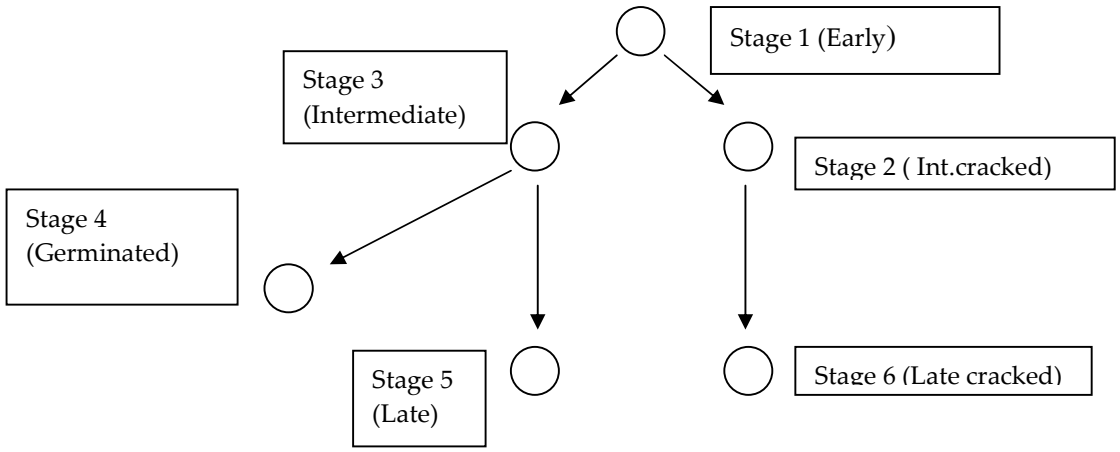


FIG 2. Stage 1 represents a freshly fallen fruit with hard outer skin. Stages 2 and 3 represent an intermediate decomposition with a mixture of hard skin and fibrous husk. Stage 4 represents a chestnut that has germinated. Stage 5 and 6 represent a late stage of decomposition where the chestnuts are completely brown and fibrous

rat or bird leaving it prematurely exposed to the forest floor.

The fruits which most recently fell from the trees were characterized by a hard and glossy green and yellow skin surrounding a thick husk that protected the endosperm in the center. They would go on to an intermediate stage of decomposition where their outer skin would retain the original characteristics in some parts, while in other places the hard outer skin was gone, leaving the brown soft husk exposed. This stage was also observed with the fruits that were cracked open, but they were counted as separate parallel stages since the two habitats were so different. The final stage of decomposition was characterized by only the fibrous brown husk being present, and this too was the final stage for cracked fruits. The one other stage I defined was when the seed germinated, which appeared to take place sometime after the intermediate decomposition since they always had the fibrous brown husk.

Assessment of classification accuracy

The eight freshly fallen chestnuts were monitored for six weeks and all decomposed at roughly the same rate. There were some fluctuations in appearance from week to week, but by the end they all looked the same. The hard outer skin was still present on all of them, but it was brown and no longer hard. The fibrous husk was also visible in parts, indicating that after six weeks these fruits were all in a stage of late intermediate decomposition. This experiment suggests that the timescale of decomposition is much higher than six weeks since none of the fruits reached the final stage of decomposition.

Species composition and trends through time

A total of forty six morphospecies were observed from all the chestnuts collected. Of these forty six morphospecies,

TABLE 1. Taxonomic groups, number of morphospecies and hypothesized functional groups from collected chestnuts across decomposition stages.

Name	Number of morphospecies	Predicted Functional Group
Staphylinidae spp. (Rove Beetle)	3	Predator
Acarina (Mite)	3	Herbivore
Dipluran spp.	1	Herbivore
Small Orange Beetle	1	Herbivore
Small Larva	1	Herbivore
Tineidae Larvae	1	Herbivore
Scotlytidae spp.	1	Herbivore
Pheidole (Ant)	2	Forest Floor
Amphipod	1	Forest Floor
Microgastropod	3	Forest Floor
Centipede	1	Forest Floor
Millipede	3	Forest Floor
Cryptophlebia pallifimbriana	1	Herbivorous Colonizer

twenty two were placed in to functional groups for further analysis (Table 1). The remainder of the individuals were either found so infrequently as to be considered insignificant, or functional groups could not be determined. The functional groups included herbivores, predators, herbivorous colonizers and forest floor individuals. The herbivorous colonizers group refers to one species (*Cryptophlebia pallifimbriana)* that appears to play a major role in the system and will be further discussed in detail. The forest floor individuals refer to the morphospecies found in the chestnuts that overlap with morphospecies predominantly found in the pitfall traps. A graph was generated to show how these functional groups proportionally varied on average across stages (Figure 3). This was done by calculating what percent of the community the individuals in each functional group represented and then averaging across the eight plots.

The early stages of the fruits' decomposition were dominated by a colonization of the larvae of the moth *Cryptophlebia pallifimbriana* (Hammes and Putoa 1986*)*. This species is described by the group of herbivorous colonizers and in the first stage they represented, on average, about fifty percent of the individuals found. These larvae would bore into the inner fruit at a very early stage, possibly even while the fruit was still on the tree. It was observed that in later stages the tunnels of these larvae were still noticeable, long after their departure from the microhabitat of the fruit. The possible role of these larvae will be discussed in detail later.The non-cracked intermediate stage did not exhibit any prominent trends, other than the proportional reduction of *C. pallifimbriana* by about half. None of the cracked open

TABLE 2. Mean Abundance of Individuals Across Stages

Stage	Mean Individual Abundance
Early	28
Intermediate Cracked	40
Intermediate	19
Germinated	3
Late	52
Late Cracked	10

Note: There was one plot where over 100 individuals of ants were found in the early stage, resulting in a major outlier and a high average number.

chestnuts at this stage were found to have *C. pallifimbriana.* They also had a surprisingly low proportion of forest floor individuals considering they were so exposed to that habitat

The germinated seeds had the lowest average number of individuals of all the stages (Table 2). For these chestnuts the endosperm was always completely intact, with no signs of previous tunnels by *C.pallifimbriana*.

The later stages of decomposition were characterized by large numbers of mites, small orange beetles and other small herbivores. These orange beetles were often very great in number and appeared to feed on the decomposing husk and frass. Millipedes were frequently observed, as well as smaller larvae from the family Tineidae. The cracked chestnuts in this stage were similar, but had smaller proportions of herbivores and a much higher proportion of forest floor individuals such as microgastropods, millipedes and ants.

Species richness and diversity were calculated for each stage and averaged over the eight plots for both the chestnuts and pitfall traps (Figures 4a-4b). The pitfall trap results showed no significant difference between stages for species richness (p=0.92) or species diversity (p=0.98). The chestnuts did have significant differences between stages for species richness (p=0.0001) and species diversity (p=0.0009). The general trends between the two measurements were very similar. The first stage and germinated stage had the lowest species richness (S_{early} = 1.75 and S_{germ} = 2) and lowest diversity ($H`_{early}$ = 0.40 and $H`_{germ}$= 0.49). The two cracked stages had the highest diversity ($H`_{int\ cracked}$ = 1.20 and $H`_{late\ cracked}$ = 1.25), followed closely by the last stage of decomposition ($H`_{late}$ = 1.11). These three stages also had the highest species richness ($S_{int\ cracked}$ = 5.00, $S_{late\ cracked}$ = 4.38, and S_{late}= 5.75).

DISCUSSION

The *I. fagifer* fruit is a unique habitat to study for successional dynamics because it is a relatively closed system with its hard outer skin, as compared to a more exposed habitat like a fallen leaf or decomposing body. The *C. pallifimbriana* larvae are the first macro-

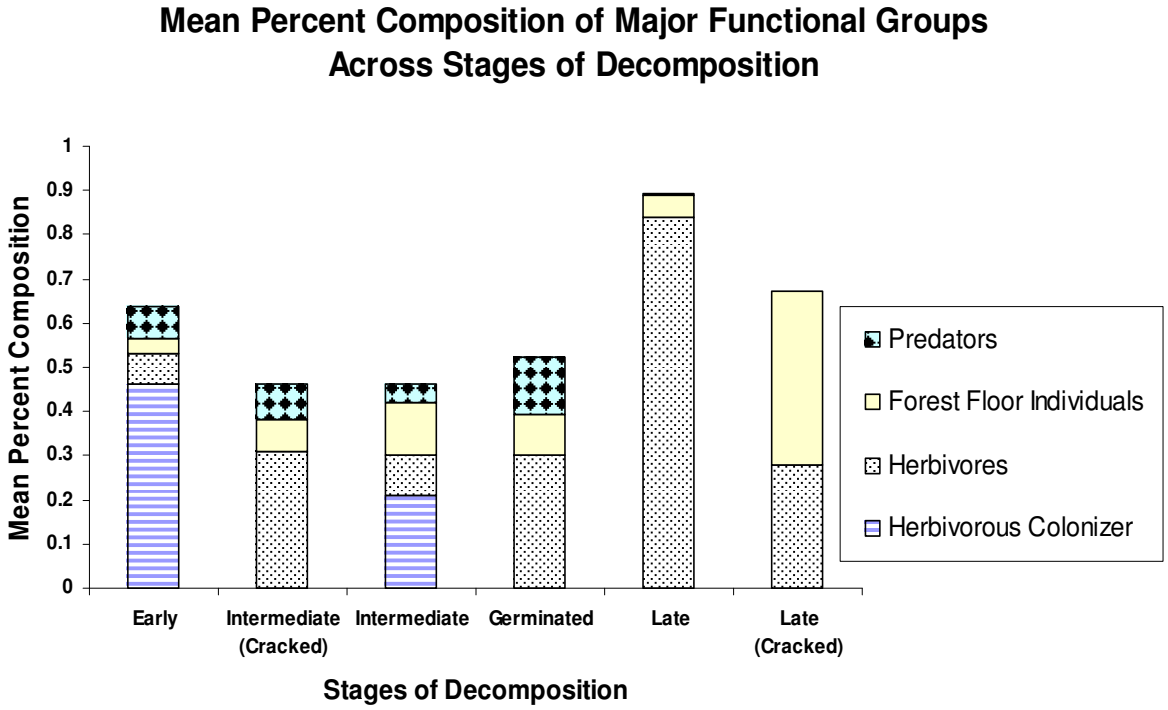


FIG 3. Shows average percent composition of the difference functional groups through time. The herbivorous colonizer is the species *Cryptophlebia pallifimbriana.* Note the numbers do not add to one hundreded because these represent only the major functional groups.

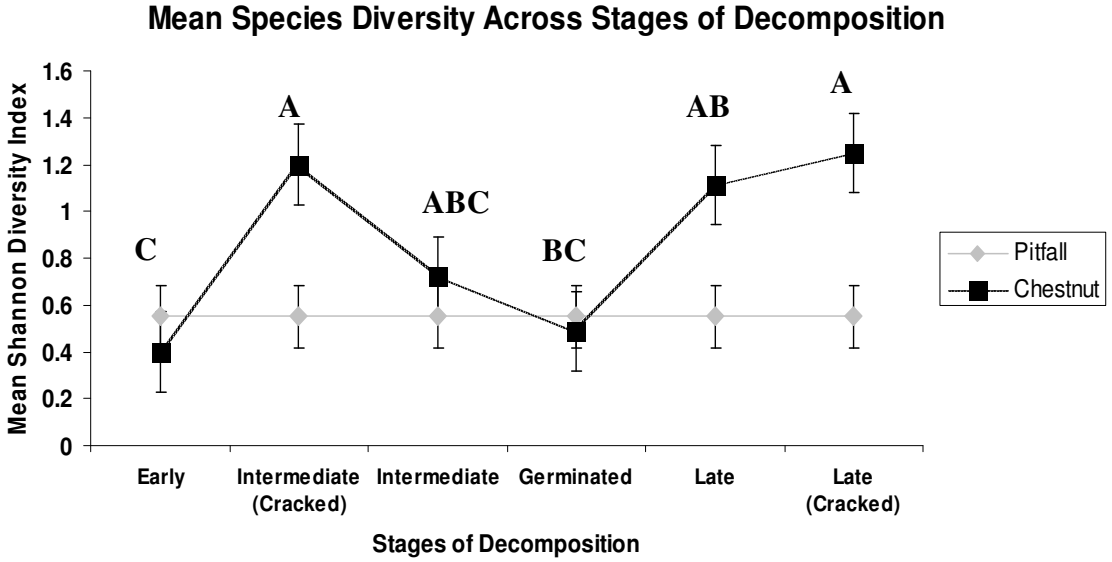


FIG 4a. Because the Tukey test showed no significant differences between stages for the pitfall traps, and they are meant to show general background richness, an average line was generated. Different letters reflect significant differences between stages for chestnut results ($p = 0.0009$).

organisms to bore into the fruit and by doing this they make the interior accessible to all future species. The data suggest that these larvae are the crucial colonizing species in a facilitative succession within the fruit.

The first stage had the lowest diversity, which is characteristic of diversity in early succession since the habitat is only suitable for the colonizing species at that early time. In this case it is dominated by *C. pallifimbriana* which makes the habitat accessible, digests the fruit, and leaves frass for small insects to feed on. Further evidence for facilitative succession is given by two of the early stage chestnuts I collected that had nothing found inside. The larvae were not present, and neither was any trace that they had been present, so nothing was able to access the habitat.

Results from the germinated chestnuts also support this interpretation. Based on the condition on the outside of the germinated fruits, which resembled the characteristics of

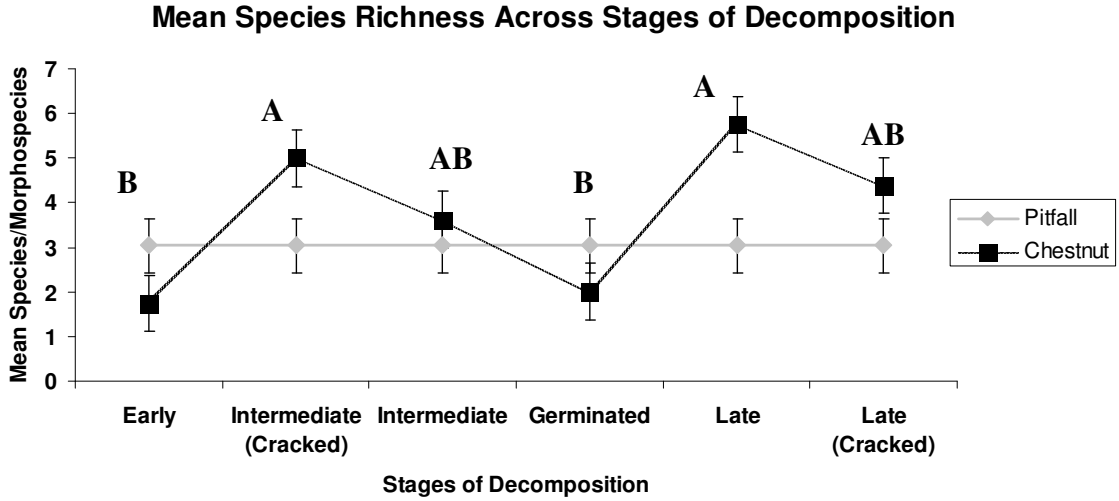


FIG 4a. As in previous figure, pitfall results showed no significant difference so an average line was generated. Different letters reflect significant differences between stages ($p = 0.0001$).

late decomposition, these fruits have been on the forest floor for a long time. The late stage of decomposition was characterized by high diversity and large numbers of small herbivores, and it could be expected that a chestnut that has been on the forest floor for a similar period of time would exhibit the same trends. However, the mean diversity of this stage was almost as low as the first stage and consistently had the lowest number of individuals compared to other stages (see Figures 3 and 4 and Table 2). When the chestnuts were cut open, the endosperm was completely intact, indicating that colonization by *C. pallifimbriana* never occurred. This could suggest that the larvae represent some limiting factor for *I. fagifer* seed germination. The absence of caterpillars ensures the absence of future species, allowing the endosperm to remain intact and able to germinate.

Further manipulative experiments could be performed to strengthen these interpretations. It would be useful to know if the caterpillars do anything other than allow access to the fruit to make it more suitable for future species, such as making the endosperm more digestible, or leaving frass. Germination experiments could also be conducted to see to what extent the absence of caterpillars promotes germination.

The pitfall traps were set up as a control to test that there were changes in species composition within the fruit, independent of the background species composition of the forest floor. My data confirm this as seen by comparing the graphs of the two mean indexes. In the non-cracked samples there were very few species that were found in both the chestnuts and the pitfall traps. Ten morphospecies out of a total forty six were found to overlap with morphospecies collected in the pitfall traps, suggesting that the organisms inside the fruits are not moving in high frequencies from fruit to fruit.

Succession refers to a predictable and orderly change in species composition through time. As previously discussed, the early trends were predictable. The late trends were also predictable as herbivores came to dominate the habitat. The intermediate decomposition stages were less predictable because there did not seem to be any species that dominated the system across all eight plots. This could be because the habitat was going through a transition as the colonizing larvae leave and all of a sudden the system is open to a large number of species. The cracked chestnuts had the highest diversity because they contained the species of two habitats; the interior of the fruit and the forest floor. Not counting the cracked or germinated stages, there is an almost linear increase in diversity through decomposition. It would be beneficial to create a more stringent classification for decomposition to get a clearer picture of how the communities change. Little additional information could be taken from my experiment to assess the accuracy of my classification system. The results showed that the timescale of decomposition is longer than six weeks, but any guess of how long it would take is pure speculation.

Trends of succession were observed in the fruits, but many more tests and experiments could be done to strengthen the hypothesis. Functional roles within a family can be highly variable, and the groups I placed certain species in were by no means definitive. A more complete description of functional groups within the chestnut would be advantageous for further study of succession since many species may differ, but their roles within the habitat stay the same. Despite these limitations, there does appear to be some form of predictable species replacement taking place, as well as patterns that resemble facilitative pathways, suggesting that my hypothesis should not be rejected.

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THE DIVERSITY AND DISPERSAL OF ESTUARINE INFAUNA IN MOOREA, FRENCH POLYNESIA

BIANCA GIUSTO

Department of Integrative Biology, University of California, Berkeley, California 94720 USA
giusto@berkeley.edu

Abstract. Studies examining benthic macrofauna of estuaries are becoming more prevalent in the scientific community but none have yet been conducted on the island of Moorea, French Polynesia. The present field study surveyed four estuaries on the island: the Papeahi, Paopao, Urufara and Vaihana Rivers. Organisms were collected and abiotic factors (including sediment type, depth, temperature, water flow, salinity, pH and dissolved oxygen) were measured to find correlations between species diversity and species abundances and the physical conditions that surround them. Abundance of taxa varied considerably among estuaries. Correlations were found between diversity and temperature and between gastropod abundance and depth/salinity. Many correlations reported in previous studies were absent; however this is most likely due to low abundances, small sample sizes and time constraints.

Key words: estuary, infauna, benthic macroinvertebrates, community assemblage, diversity

INTRODUCTION

Estuaries are unique and important natural ecosystems with significant economic values (EPA 2007). The brackish water and tidal range create an environment dividing the freshwater from the ocean, and organisms that live in these habitats are permanently subjected to stressful conditions (Rosa-Filho et al. 2004). The benthic macroinvertebrates of estuarine communities are critical components of the community, making up a substantial portion of estuarine biomass (Bailey-Brock et al. 2002). Benthic macroinvertebrates play an essential role in the food web as primary consumers (Salgado et al. 2007) and as a food source for other animals (Bailey-Brock et al. 2002). There is a pressing need to catalogue the distribution and abundance of macrobenthic species in estuaries, both as an indispensable tool for ecological studies (Martin et al. 1993) and as a compilation for comparative purposes in the future (Bailey-Brock et al. 2002).

Multiple factors may influence the diversity and dispersal of estuarine infauna. Some of these factors are abiotic and change with the physical surroundings (Kumar 2002, Ysebaert et al. 2002, Bailey Brock et al. 2002, Rosa-Filho et al. 2004). When these factors change, does the community assemblage change? This question can be analyzed by looking at different aspects of a community: the diversity, taxonomic group distribution and functional group distribution. Martin et al. (1993) and Salgado et al. (2007) grouped the species present in an estuarine community into trophic guilds, but did not investigate their relationship to abiotic factors. Analyzing dispersal and abundance of species based on their feeding guilds may give insight into the niche partitioning and limiting resources of benthic macrofauna.

The infauna in the estuaries on the island of Moorea have been little studied and I could not find any extensive published record of the macrobenthic community. The goal of this study is to describe the benthic

macrofauna species composition of 4 estuaries on Moorea and to better understand the habitat preferences and dispersal of the macrofauna in relation to multiple abiotic factors. Based on previous studies (Martin et al. 1993, Ysebaert and Herman 2002, Anderson et al. 2004, Gimenez et al. 2006), I hypothesized that sediment type would have the greatest effect of the abiotic factors in determining species distribution and diversity.

METHODS

Study Sites

Four estuaries were surveyed on the northern coast of Moorea: the Papeahi, Paopao, Urufara and Vaihana Rivers (Figure 1). The criteria for choosing the estuaries were sediment composition, length of the year the estuary was present, and location. All of the estuaries sampled were permanent, meaning that the river consistently ran all the way to the ocean. I chose estuaries as close together as possible to reduce community variability that might exist if I had sampled from all sides of the island. All of the estuaries were contained physically by constructed features, including rock walls on both sides of the rivers until they reached the bay or lagoon.

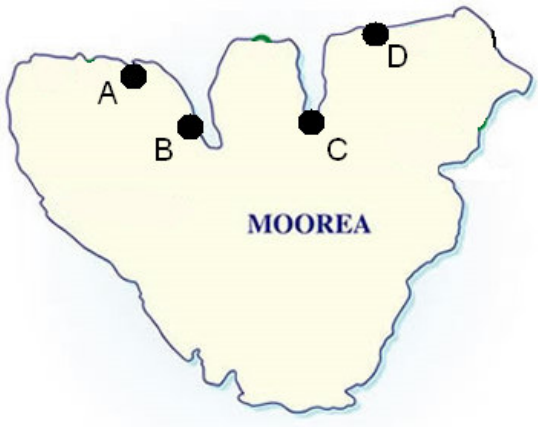

Figure 1. Sampled estuaries on the island of Moorea. A-Vaihana, B-Urufara, C-Paopao, D-Papeahi.

Biological Sampling

The goal of sampling was to obtain a representative sample of the distribution and abundance of organisms in the estuaries. The lengths of the estuaries were measured from the mouth to the end of the brackish water, determined by using a refractometer that measured salinity by parts per thousand. I positioned five line transects per estuary across the width of the channel (Figure 2). The location of each transect was determined by dividing the estuary into 4 equal segments and placing a transect at each interval. The first transect sampled was at the mouth of the estuary and the last was at the end of the brackish water. The estuaries were sampled on different days, but at each estuary, I collected all the data and samples within one day.

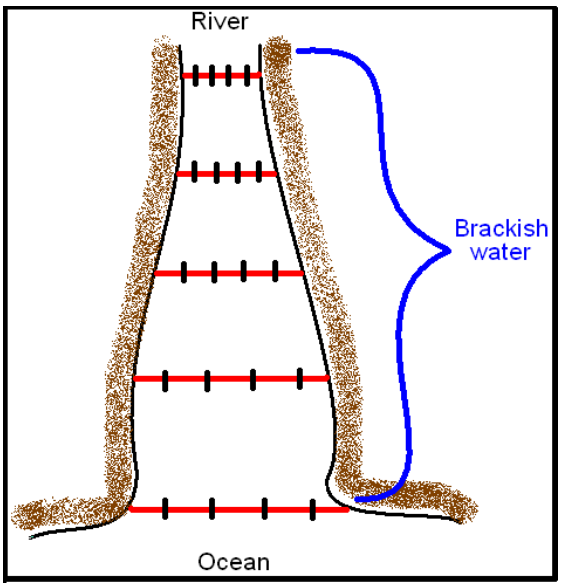

Figure 2. Bird's eye view of an estuary. Horizontal lines represent where the transects were placed. Tick marks represent where samples were taken along each transect.

It was not possible to sample at the very edge of the estuary because of the rock walls. To ensure that sample sites would not

be placed at the very edges of the estuary, four sediment cores were taken at separate, equidistant sites along each transect (Figure 2). These points were selected by dividing the length of each transect into 5 segments and sampling along the inner-intervals. The corer used was a cylinder, 15cm deep and 9.5cm in diameter. When there was solid rock at the sample site that could not be cored or collected, I collected sediment off the surface of the rock that was able to be cored. The most prevalent sediment size in each sample was recorded. The sediment size descriptions were based on categories described by the Wentworth Grain Size Scale (Leeder 1982) (Table 1). The cored sediment was sifted through 1mm mesh and the remaining sediment was transported to the lab in plastic bags. The organisms in the sediment were analyzed within 24 hours. All individuals were counted and identified to the greatest taxonomic description.

Sediment categories	Size range (mm)	Wentworth size class
Rock	64 mm and larger	Boulder Cobble
Pebble	2mm – 64mm	Pebble Granule
Sand	0.125mm – 2mm	Very coarse sand Coarse sand Medium Sand Fine sand
Silt	0.125mm and smaller	Very fine sand Coarse silt Medium silt Fine silt Very fine silt Clay
Solid Rock	N/A	N/A

Table 1. Sediment categories compared to the Wentworth size class. These are the sediment categories used in this paper and their corresponding sizes in mm and Wentworth size classifications (Leeder 1982).

Abiotic Factors

The water depth, water temperature, dissolved oxygen level, salinity and water flow were measured at each location before a sediment core was taken and as close to the sediment core as possible. Water flow was measured by releasing a fluorescent liquid, made from Fluorescin sodium salt, at the surface of the sediment and calculating the time it took to travel a measured distance. Weather conditions, sunlight exposure, containment by human action, pollution levels and other general observations and descriptions were also recorded. Water samples were collected at each sediment core location. I measured the pH of every sample and I randomly selected two water samples from each transect, one to be tested for nitrate (LaMotte Nitrate-Nitrogen testing kit) and the other for phosphate (LaMotte Phosphate testing kit, Model VM-12). I used sub-samples because I assumed that the nitrate and phosphate levels would be similar for every location across each transect.

Data Analysis

All statistical analyses were performed using JMP 7.0 (SAS Institute Inc., Cary, NC).

Principal Component Analysis (PCA)

I used Principal Component Analysis (PCA) to summarize the abiotic factors, except sediment type. I did not include the nitrate or phosphate levels in the PCA because nitrate was not present in any of the tested water samples and phosphate was present at 1ppm in only 2 samples.

The purpose of PCA is to combine my correlated abiotic variables into new, uncorrelated variables. The principal components are listed in order of how much of the variation of the data they describe (Table 5, Appendix A). PC1 describes the majority of the data, PC2 describes less, and so on. I decided to include the first 5 principal components in my statistical analyses because they represent all factors being tested. PC6 was left out because it repeats PC1.

Diversity

I computed the diversity of taxa at each location using the Shannon Diversity Index (Shannon 1948). Spirorbidae was left out of the diversity index calculations because I was not able to tell whether the organism was alive or dead. Their accumulation of calcium carbonate shells on the rocks is a misrepresentation of the living population. The first five principal components from the PCA were included in a Stepwise Fit test with diversity to find the components that significantly describe diversity. A Bivariate Fit was performed with these principal components and diversity.

The relationship between sediment type and diversity was analyzed in a One-way Anova. Because I had many more samples of rocky sediment type, I had to randomly sub-sample these points so that the number of rocky samples was closer to the rest.

Taxonomic Groups

Organisms were grouped into four taxonomic groups according to class: Gastropoda, Bivalvia, Polychaeta and Malacostraca. I used a Manova to find correlation both between the abundances of these groups and the Principal Components and between these groups and sediment type. Rocky sediment was sub-sampled.

Functional Groups

Organisms were grouped into five trophic guilds: planktivores, detrivores, herbivores, carnivores and omnivores (Table 2). I used a Manova to find correlation both between the abundances of these groups and the Principal Components and between these groups and sediment type. Rocky sediment was sub-sampled.

Species	Functional Group	Citation
Neritidae spp. A	Herbivores	Beesley et. al 1998
S. porcellana	Herbivores	Beesley et. al 1998
C. spinosa	Hrebivores	Beesley et. al 1998
N. turrita	Herbivores	Beesley et. al 1998
Diastomidae spp. A	Omnivores	Beesley et. al 1998
Diastomidae spp. B	Omnivores	Beesley et. al 1998
Cerithiidae spp. A	Herbivores	Beesley et. al 1998
Cerithiidae spp. B	Herbivores	Beesley et. al 1998
Ostreidae spp.	Planktivores	Nelson 1923
Mytilidae spp.	Planktivores	Widdows et al. 1979
Amphinomidae spp. A	Omnivores	Marsden 1963
Amphinomidae spp. B	Omnivores	Marsden 1963
Nereididae spp. A	Detrivores	Beesley et. al 2001
Nereididae spp. B	Detrivores	Beesley et. al 2001
Pisionidae spp. A	Carnivores	Beesley et. al 2001
Pisionidae spp. B	Carnivores	Beesley et. al 2001
Lacydoniidae spp.	Unknown	Beesley et. al 2001
Spionidae spp.	Detrivores	Fauchald 1979
Spirorbidae spp.	Planktivores	Fauchald 1979
Orbiniidae spp.	Detrivores	Beesley et. al 2001
Maldanidae spp.	Detrivores	Fauchald 1979
Cossuridae spp.	Detrivores	Fauchald 1979
Hemigrapsus spp.	Omnivores	Ledesma and O'Connor 2001
Paguroidea spp.	Omnivores	N/A

Table 2. Lists of species and the functional group to which they belong.

RESULTS

Taxonomic Composition

In the present study, 24 distinct taxa were differentiated and identified (Table 3, Appendix B). Out of 12,678 specimens collected (1,083 without *Spirorbidae spp.*) Annelida (50%) was the most important group in number of species, followed by Mollusca (42%) and Arthropoda (8%). Gastropoda (85%) was the dominant group in terms of abundance, exceeding Annelida (6%) and Arthropoda (4%). (All the above

calculations were computed without including *Spirorbidae spp.*).

Taxa differed between the estuaries (Table 4). The χ^2 (Chi-squared) test of independence gave a chi-squared value of 12,677.24, which is much greater than 84.82, the critical value allowed for 69 degrees of freedom. This concludes that the four estuaries are independent from each other in taxa composition.

Species	Vaihana	Paopao	Urufara	Papeahi
Neritidae spp. A	4	0	327	3
S. porcellana	256	22	149	92
C. spinosa	0	3	0	2
N. turrita	1	6	6	4
Diastomidae spp. A	0	3	0	0
Diastomidae spp. B	2	0	0	4
Cerithiidae spp. A	3	0	1	0
Cerithiidae spp. B	0	11	0	0
Ostreidae spp.	4	0	5	0
Mytilidae spp.	9	0	0	0
Amphinomidae spp. A	9	1	0	0
Amphinomidae spp. B	5	0	0	0
Nereididae spp. A	3	0	0	0
Nereididae spp. B	4	13	0	2
Pisionidae spp. A	0	0	1	0
Pisionidae spp. B	0	0	1	0
Lacydoniidae spp.	1	0	0	0
Spionidae spp.	1	0	0	0
Spirorbidae spp.	11595	0	91	0
Orbiniidae spp.	2	1	5	0
Maldanidae spp.	0	0	7	0
Cossuridae spp.	3	0	0	0
Hemigrapsus spp.	4	5	3	4
Paguroidea spp.	3	0	1	3

Table 4. A list of taxa found and the number of individuals in each estuary. (Note: Spirorbidae spp. abundances include all shells found on rocks, some of which do not contain living organisms.)

Data Analyses

Principal Component Analysis

The purpose of PCA is to combine the correlated abiotic variables into new, uncorrelated variables. Table 5 (Appendix A) shows what abiotic factors each Principal Component is dominated by. PC1 is loaded by depth and salinity. PC2 is loaded primarily by dissolved oxygen, PC3 by pH, PC4 by flow rate and PC5 by temperature. PC6 is loaded by depth and salinity, the same as PC1.

In PCA, the principal components are listed in order of how much of the variation they describe. Although PC1 describes the most of the variation (38.37%), I decided to include the first 5 principal components in my statistical analyses because they represent all factors being tested. PC6 was left out because it repeats PC1.

Diversity

The Stepwise Fit of Principal Components 1-5 and diversity showed that PC5 was the only one significant in describing diversity, with a P-value of 0.04. Principal Components 1-4 were insignificant, with P-values of 0.25, 0.60, 0.14 and 0.29, respectively. A Bivariate Fit of diversity by PC5 confirmed the Stepwise Fit with a significant P-value of 0.04 but also low overall correlation (r^2=0.05) (Figure 3). Because PC5 describes very little of the variation of the abiotic factors, we must be cautious of assuming that this is a truly significant relationship.

The One-way ANOVA of diversity and sediment type (Figure 4) showed no significance (r^2=0.06, P=0.54).

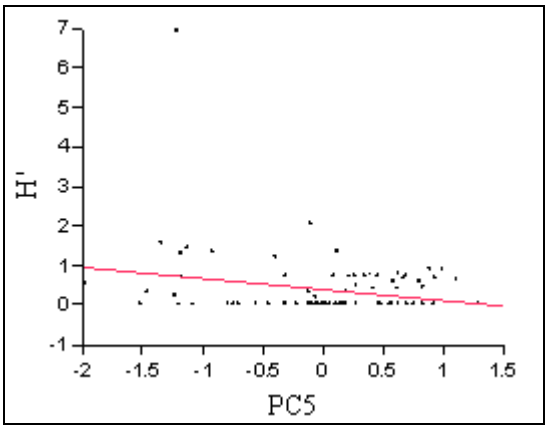

Figure 3. Bivariate Fit of Diversity (H') and Principal Component 5 (r^2=0.05, P=0.04).

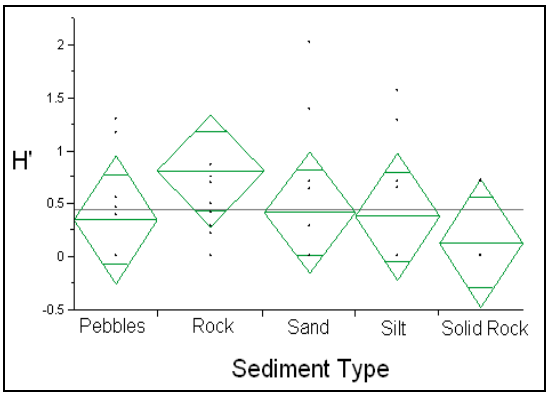

Figure 4. One-way Anova of Diversity (H') by Sediment Type. The diamonds represent the mean diversity values, none of which are significantly different from the others (r^2=0.06, P=0.54).

Taxonomic Groups

The Manova of the abundance of organisms in each taxonomic group and Principal Components 1-5 gave a Pillai's Trace Test P-vale of 0.0165 for the whole model, but the only Principal Component that showed a significant correlation (P=0.0009) was PC1. PC2 through PC5 had P-values of 0.95, 0.26, 0.32 and 0.09, respectively. A Least Squares Fit of all four functional groups by PC1 revealed that the only significant correlation was between PC1 and the abundance of Gastropoda (P=0.0002). A Bivariate Fit of Gastropoda by PC1 had a P-value of 0.0002 (Figure 5).

Manova was used to find the effect of sediment on abundance of the four different taxonomic groups. Pillai's Trace test gave a P-value of 0.5958 for the whole model, showing no significant correlation.

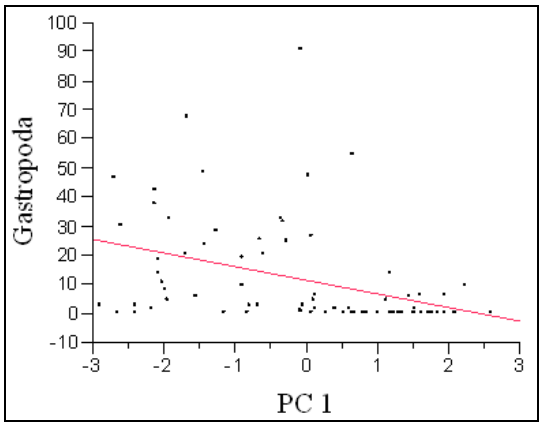

Figure 5. Bivariate Fit of Gastropoda abundances by PC1.

Functional Groups

The Manova of the abundance of organisms in each functional group and Principal Components 1-5 gave an insignificant Pillai's Trace Test P-value of 0.0913 for the whole model.

Manova was used to find significant effect of sediment on abundance of the five different functional groups. Pillai's Trace test gave a P-value of 0.1988 for the whole model, showing no significant correlation.

DISCUSSION

The diversity of taxa in the estuaries studied on Moorea is different than other estuaries that have been studied. The diversity was much lower on Moorea and taxa were found in smaller abundances. However, most estuaries in the literature cover a much larger area, are in different parts of the world and are not physically contained by rock walls like the estuaries on Moorea (Inglis and Kross 2000, Anderson et al. 2004, Rodrigues et al. 2007, Salgado et al. 2007). For this reason, I was unable compare

the taxa found in these estuaries with the estuaries on Moorea.

The patterns observed in this study differed from those expected. The results indicate an inverse relationship between diversity and Principal Component 5, which is loaded by temperature (Figure 3). However, PC5 describes very little of the variation of the abiotic factors so this may not be a truly significant correlation. The other abiotic factors had no correlation with diversity. The only taxonomic group whose abundance correlated with abiotic factors was Gastropoda. The data show that no functional groups' abundance was correlated with abiotic factors. My hypothesis was not supported because sediment type did not show significant correlation with diversity, taxonomic group abundance or functional group abundance.

The correlations that were discovered are consistent with previous studies. There are findings that temperature is correlated with faunal abundance (Kumar 2002) and that salinity and depth are main factors structuring spatial distribution (Gaudencio and Cabral 2007). Gastropod abundance decreasing with increasing depth and salinity may reflect the preferences of the certain species involved, and more research should be conducted on this subject. Many trends that previous studies have found were not significant in this study. This is most likely due to the limitations of this project, rather than the different geographical location.

A limitation of these data was the species richness and abundance of organisms found in each sediment core. Many sediment cores had one or no species, bringing the diversity to zero. With the very small range of diversity levels, it is possible that there was not enough data to be able to find correlations between diversity and the abiotic factors. There are similar problems with the taxonomic abundances and functional group abundances. Gastropoda had the largest number of individuals, and a correlation was found. If there were more individuals of every group, there may be a greater possibility of correlation. Other kinds of statistical analyses might be able to find more correlations, also.

A restriction of the sediment type analysis arose because of the unequal samples of each sediment type. I originally wanted equal samples of each sediment type. Unfortunately, a fine silt sediment estuary was unavailable so I chose to sample one that had a rockier composition. As mentioned previously, I was forced to sub-sample the rock samples in order to obtain unbiased test results. However, I believe the number of samples analyzed in each sediment type category was not sufficient to find correlations with the rest of the data.

The time constraints of this class posed a problem for this study also. I was not able to sample as many estuaries as needed. The results would be more stable if I could have sampled over a longer period of time and repeated sampling sites. Tracking the abiotic factors and sampling frequently to get averages of those values over time would provide more data to work with and solidify the findings.

Although the data did not support my hypothesis, it has fulfilled this study's goal to document the benthic microorganisms that live in estuaries on the island of Moorea. This information is now available for use in future research on these organisms or estuaries. Some species that are present in these estuaries may be used as bioassay organisms or pollution indicators (Pocklington and Wells 1992, Galope-Bacaltos and San Diego-McGlone 2002). Tracking changes in the community assemblages can tell us the health of the system. Expanding our knowledge of estuaries can keep us from destroying them in the future.

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APPENDIX A

Abiotic Factor	**PC 1**	**PC 2**	**PC 3**	**PC 4**	**PC 5**	**PC 6**
Depth (cm)	**0.561465**	0.103234	0.067213	-0.30423	0.332398	**-0.68303**
Flow rate (m/s)	0.276231	0.147168	-0.53368	**0.773228**	0.09546	-0.10116
Salinity (ppt)	**0.553269**	-0.24286	-0.11431	-0.18824	0.369721	**0.67061**
Temp (℃)	0.4934	0.356134	0.04931	-0.09726	**-0.77514**	0.130362
D.O. (mg/l)	-0.17778	**0.878742**	-0.06319	-0.16107	0.343672	0.219452
pH	0.165221	0.0984	**0.831373**	0.488593	0.157336	0.091439

Table 5. Eigenvectors from Principal Component Analysis. PC1 is loaded by depth and salinity, PC2 by dissolved oxygen, PC3 by pH, PC4 by flow rate and PC5 by temperature. These were all included in the statistical tests involving diversity, taxonomic groups and functional groups because every abiotic factor being analyzed was loaded within these principal components. PC6 is loaded by depth and salinity and was left out of the other tests because those factors were already present in PC1.

APPENDIX B

MOLLUSCA
Gastropoda
Orthogastropoda
Neritopsina
Neritoida
Neritidae
Neritidae spp. A
Neritinae
Theodoxini
Septaria
S. porcellana
Clithon
C. spinosa
Neritini
Neritina
Neritina
N. turrita
Apogastropoda
Caenogastropoda
Sorbeoconcha
Cerithiimorpha
Cerithioidea
Diastomidae
Diastomidae spp. A
Diastomidae spp. B
Cerithiidae
Cerithiidae spp. A
Cerithiidae spp. B
Bivalvia
Ostreoida
Ostreina
Ostreoidea
Ostreidae
Ostreidae spp.
Pteriomorpha
Mytiloida
Mytilacea
Mytilidae
Mytilidae spp.

ANNELIDA
Polychaeta
Palpata
Aciculata
Eunicida
Amphinomidae
Amphinomidae spp. A
Amphinomidae spp. B
Phyllodocida
Nereididae
Nereididae spp. A
Nereididae spp. B
Pisionidae
Pisionidae spp. A
Pisionidae spp. B
Lacydoniidae
Lacydoniidae spp.
Canalipalpata
Spionida
Spionidae
Spionidae spp.
Sabellida
Spirorbidae
Spirorbidae spp.
Scolecida
Orbiniidae
Orbiniidae spp.
Maldanidae
Maldanidae spp.
Cossuridae
Cossuridae spp.

ARTHROPODA
Crustacea
Malacostra
Decapoda
Pleocyemata
Brachyura
Grapsoidea
Grapsidae
Hemigrapsus
Hemigrapsus spp.
Anomura
Paguroidea
Paguroidea sp

Table 2. A list of species found in all estuaries that were sampled. Organisms that could not be identified to species are labeled as a species of the lowest taxonomic group they identified with.

SURFACE ZOOPLANKTON ABUNDANCE AND DIVERSITY, AND THE SALINITY TOLERANCES OF THE SUBCLASS COPEPODA AND CRUSTACEAN NAUPLII IN MO'OREA, FRENCH POLYNESIA

MATTHEW W. HARRIS

Environmental Science, Policy, and Management, University of California, Berkeley, California 94720 USA

Abstract. Surface plankton tows were completed at select reef passes and lagoons over five weeks on the island of Mo'orea, French Polynesia. Differences in zooplankton species richness and abundance were analyzed based on location, salinity, and tide. Reef passes and lagoons varied in the average abundance of zooplankton as well as having different species prevalence. Lab experiments tested individual groups' tolerance to varying salinity levels that were found in Cook's Bay. There was a significant drop in copepod and crustacean nauplii populations when exposed to lower salinity levels.

Key words: Moorea, French Polynesia; Copepods; Veligers; Crustacean Nauplii; Crustacean; zooplankton abundance; zooplankton diversity; reef pass; lagoon; salinity tolerance

INTRODUCTION

Plankton is in the primary trophic level of the marine food web and constitutes a significant portion of the diet of many smaller marine organisms (Nybakken 1993) Zooplankton, in particular, plays a significant role in the transfer of energy to larger organisms (Lafontaine Y, 1994). Gathering data on zooplankton assemblages is important in understanding local marine productivity because of the role it plays in the marine food web. Certain conditions, such as low salinity levels due to increased rainfall, can affect zooplankton populations leading to a suit of effects on the entire marine ecosystem.

Plankton species and abundance differ with currents, depths, time of day, seasons, temperatures, and salinity (Otero and Carbery, 2005). Patterns of diel vertical migration show that different groups of plankton travel to different depths throughout the day (Ramos-Jiliberto and Gonzalez-Olivares, 2000). Accordingly, it is often difficult to get a representative sample of plankton, because surface daytime tows may miss the species that move between depths. Currents and seasonal weather shifts may also move plankton into habitats where they are not usually found. Extreme weather, such as hurricanes or large swells, can be very important in the transport of pelagic plankton into lagoons and vice-versa (Kaartvedt and Svendensen, 1990).

Identifying zooplankton species can be extremely difficult, especially because they may have different morphologies depending on the season and the geography. Significant morphological changes can also occur within their life cycle so that identifying plankton at different stages of development can be extremely challenging (Steedman 1974). For ecological comparisons on a large scale, such as in the comparison of passes and lagoons, species and genus within classes are generally combined and counted together because they often share similar characteristics and behaviors (Canepa, 1996).

The reef geography is crucial in the understanding of plankton distribution and

abundance for islands surrounded by a barrier reef, such as Mo'orea. Passes have much more water movement with swell, wind and tide conditions while lagoons are generally less affected by pelagic waters. Sampling the sites of Opunohu and Pao Pao reef passes can provide a good indication of what kinds of zooplankton may be entering and exiting bay environments. One would predict that the differences in environmental and geographical conditions at reef passes and lagoons should cause a consistent and measurable change in zooplankton abundance and richness. I hypothesize that diversity should be higher in the lagoons because not only will there be species endemic to the shallower water but also currents, waves, and wind can bring in pelagic zooplankton. Population densities should be highest at the reef passes because tidal changes and currents bring surface water from many locations into a much smaller, narrow area before being dispersed into either the open ocean with an outgoing low tide, or the lagoons/bays with the incoming high tide.

I tested the copepod and crustacean nauplii for different salinity tolerances. I expect that there will be a lower survival rate the more the treatment is comprised of freshwater. The importance of this experiment lies in that there are many streams on Mo'orea and storm activity often results in increased brackish waters in river mouths and bays. I want to better understand the physiological ability of zooplankton to react to a rapid increase of freshwater. Further implications may help in the prediction of changes caused by climate change on zooplankton populations due to an expected increase in storm activity and rainfall.

MATERIALS AND METHODS

Study sites

Five sites on the island of Mo'orea, French Polynesia, Temae public beach, Pao Pao Pass, Opunohu Pass, the Sheraton Hotel lagoon, and the channel between Motu Fareone and Motu Tiahura (Fig. 1) were sampled six each for surface zooplankton. Plankton tows were completed on peak high and low tides during the same day for each location using the tides for Fare Ute Point on Tahiti around 25 km away.

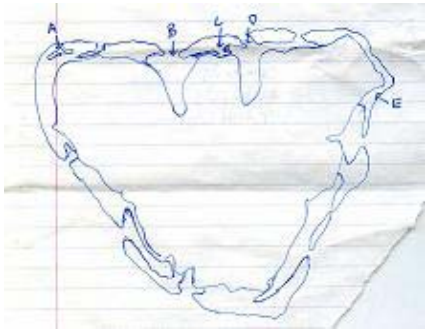

FIG. 1. Plankton drag sites around Mo'orea. "A" is the channel between Motu Fareone and Motu Tiahura. "B" is Opunohu Pass, "C" is the lagoon outside the Sheraton Hotel, "D" is Pao Pao Pass, and "E" is Temae

Sampling

In a two seat kayak, I would lower a plankton net 0.3m in diameter with 64 micron mesh, so it would be fully submerged and 15 feet behind the boat, then paddle for one minute in a predetermined direction based on where I could go in a straight line without having the net strike any underwater obstacles such as coral heads or buoys. Both kayaks had similar paddling speeds, an average of 60 meters per minute. This was tested in 10 trials for each kayak using a 100 meter transect tape. Each trial was within plus or minus one meter of 60 meters.

At the site, one 50ml water sample was collected for turbidity and salinity measurements while another 1.7 liters of

ocean water was placed in a two liter ice cream container to be mixed with the plankton sample from the PVC bucket. 1.7 liters allowed the bucket to be fully emerged in water; and to extract the plankton four complete spin cycles were done underwater and then tipped into the container. The container was then homogenized using ten rapid shakes and a 50 ml subsample was taken incorporating all vertical layers of the sample by slowly filling the vile in a swooping motion. Half of this subsample was analyzed and all zooplankton were counted on the same day as collected to try and avoid any predation and the breakdown of organism tissue.

Species Identification

Identification tables and pictures found in *Coastal Marine Zooplankton* and *A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae* were used to identify organisms. Pictures of samples were taken for future identification (Fig. 2). For this study, identification to the most accurate taxonomic level was used to reduce the error of misidentification.

Sampling regimen

The five sites were re-sampled two and four weeks later keeping tidal fluctuations similar. The tows also incorporated new and full moon's because of their affect on plankton activity (Canepa 1996**)**. The month difference in tows was also designed to show seasonal changes in plankton numbers and assemblages. Although the rainy season (December through March**)** had not fully started, heavy rain storms did provide different conditions to test in. To fully explore salinity changes on zooplankton, lab experiments were conducted to test specific group's tolerances.

Statistical tests

Two way ANOVA tests were used to compare the factors of tide, salinity, and location as well as the correlation between them, to overall zooplankton abundance, richness, and average numbers found of each of the four main groups; copepods, veligers, crustacean nauplii, and plankton "B" (Fig. 2).

FIG. 2. Zooplankton "B"

Salinity manipulations

The Subclass Copepoda and crustacean nauplii were tested by exposing them to different salinity levels. Samples were 25ml of water, enough to be homogenized and tested every 15 minutes over 1 hr but small enough so that analysis could be completed in the allotted 3 minutes per subsample. Every replicate would have one vial with 25 ml of salt water, one vial with 20 ml of saltwater and 5 ml of freshwater, one with 15 ml of saltwater and 10 ml of freshwater, and one with 5 ml of saltwater and 20 ml of freshwater. These solutions were chosen based on real salinity levels found in Cooks Bay. A plankton tow outside of the station or off the dock provided adequate live samples to test. Three vials with ocean water mixed with a plankton sample were used as an initial test to see if similar percentages of living target subjects would be found. All three had similar percentages so the plankton sample was homogenized and added equally to the four treatments. After adding between 75-125 target organisms

into the solutions, 5ml samples would be taken from each every 15 minutes for analysis. The first sample at 0 minutes was taken before being mixed with the solution to have a reference as to how much the population declined. Vials were kept at a constant temperature of 28 degrees Celsius in the wet lab.

Species would be classified as alive and active, or as dead. Five replicates were completed for each species and a MANOVA test was used to look for significance over the entire hour. ANOVA and Tukey-Kramer HSD tests were used for each time period to test for significance between the means for each treatment.

RESULTS

Drag samples

There is a statistically significantly higher average number of zooplankton found in reef passes than in the lagoons as demonstrated by a p-value of 0.0098. The average mean at the passes and lagoons were 308 and 174 organisms, respectively. The tide was not found to have a significant influence on abundance with a p-value of 0.9808 and an average mean of 241 zooplankton found at high tide and 240 zooplankton found at low tide. There was no significant correlation between the factors of tide and lagoon/pass (Table 1). A good explanation of this is that there may be other variables that my study did not account for that affect abundance.

The four most prevalent groups had mixed results when comparing tide and location to their respected abundance. Copepods were found significantly more often at the reef passes (an average of 51 copepods) than the lagoons (an average of 26 copepods). The p-value was 0.0359. Tides and the relationship between tides and location were not significant, with a p-value of greater than 0.05 (Table 2) and an average abundance of 39 copepods at high tide and 38 copepods at low tide.

TABLE 1. ANOVA results for overall zooplankton abundance. Significant values are in bold and underlined.

	F Value	D.F.	P Value
Reef Pass/ Lagoon	7.7785	1	**0.0098**
High/Low Tide	0.0006	1	0.9808
Lagoon/pass *high/low	0.8457	1	0.3662

TABLE 2. ANOVA results for Copepod abundance. Significant values are in bold and underlined.

	F Value	D.F	P Value
Reef Pass/ Lagoon	4.8948	1	**0.0359**
High/Low Tide	0.0216	1	0.8844
Lagoon/pass *high/low	0.0307	1	0.8622

TABLE 3. ANOVA results for Veliger abundance

	F Value	D.F	P Value
Reef Pass/Lagoon	1.4760	1	0.2353
High/Low Tide	0.5907	1	0.4491
Lagoon/pass *high/low	2.82	1	0.1048

Location and tides and the correspondence between the two did not play a significant role in veliger abundance (Table 3) as there was an average of 124 and 86 veligers found at reef passes and lagoons respectively while there was an average of

92 and 118 veligers found at high and low tide, respectively.

Passes had significantly higher numbers of crustacean nauplii with a p-value of 0.0004 and a mean number of 91 per sample found at passes while only 12 on average were collected in the lagoons. Tide (65 and 37 crustacean nauplii found on average at high and low tide, respectively) and the correlation between tide and location did not have a significant role in its distribution (Table 4).

TABLE 4. ANOVA results for Crustacean Nauplii abundance. Significant values are in bold and underlined.

	F Value	D.F.	P Value
Reef Pass/Lagoon	16.8230	1	**0.0004**
High/Low Tide	2.0573	1	0.1634
Lagoon/pass *high/low	1.2754	1	0.2691

Only plankton "B" was found in significantly higher numbers in lagoons (a mean of 19 organisms as compared to only an average of 7 found in the pass samples) with a p-value of 0.0361, and once again tide (a mean of 8 and 19 plankton "B" found at high and low tide per sample, respectively) and tidal relations with location show no significant differences (Table 5).

There was a range of 7 to 13 species found in the tows, but their means had no significant differences when the factors of location, tide, and salinity (along with the interaction between each) were analyzed (Table 6).

TABLE 5. ANOVA results for plankton "B" abundance. Significant values are in bold and underlined.

	F Value	D.F.	P Value
Reef Pass/ Lagoon	4.8877	1	**0.0361**
High/Low Tide	3.8399	1	0.0608
Lagoon/pass *high/low	0.2627	1	0.6126

TABLE 6. ANOVA results for average species diversity

	F Value	D.F	P Value
Salinity T/C	0.0323	1	0.8588
Salinity*high/ low tide	0.2254	1	0.6395
Salinity*reef pass/lagoon	1.4462	1	0.2414
Lagoon/pass *high/low tide	3.2249	1	0.0857
Lagoon/pass	0.8066	1	0.3784
High/low tide	2.2371	1	0.1483

Higher salinity levels significantly increased total zooplankton numbers with a p-value of 0.0018. When salinity was tested

TABLE 7. ANOVA results for overall zooplankton abundance. Significant values are in bold and underlined.

	F Value	D.F	P Value
Salinity	12.1017	1	**0.0018**
Salinity*High/ Low Tide	0.0531	1	0.8196
Salinity*Lagoon/ pass	1.8226	1	0.1886

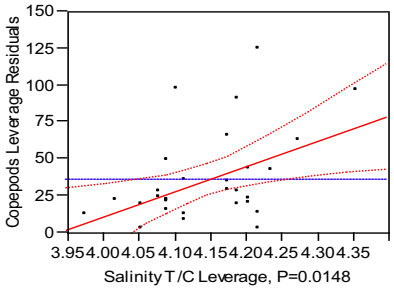

FIG. 3. ANOVA results showing a positive correlation between higher salinity levels and a greater abundance of copepods

with tide and with location (separately) there was no significant difference in abundance (Table 7). Of the four zooplankton groups, only copepod and crustacean nauplii were found in significantly larger quantities with an increase in salinity. The p-values were 0.0018 and 0.0045, respectively (Fig. 3 and Fig. 4). The relationship between the factors of salinity and tide and salinity and location had no significant change in the organisms' abundances (Appendix 1).

Salinity Manipulations

Copepod populations decreased significantly when salinity approached fresh water levels. Table 8 shows that there is a

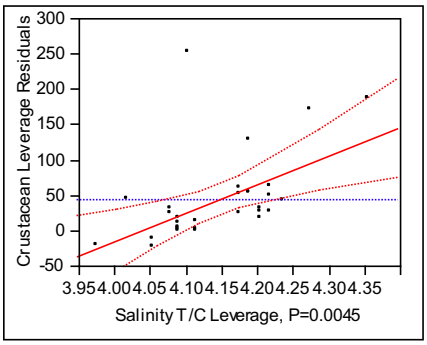

FIG. 4. ANOVA results showing significant positive correlation between higher salinity levels and a greater abundance of crustacean nauplii.

TABLE 8. Repeated measures ANOVA results for Copepod survivorship

	F Value	D.F	P Value
Between (F Test)	33.1417	3	**<0.0001**
Within (Wilks' Lambda)	6.6489	12	**<0.0001**
Time (F Test)	105.6726	4	**<0.0001**

statistical difference in the percentage of living copepods over the different treatment levels for the one hour. The Wilks'-Lambda test demonstrates a p-value of less than 0.0001. Fig. 5 shows that for the control of 0ml freshwater, the percentage of living copepods stays between 60% and 70%. It also demonstrates that the 5ml of freshwater treatment drops about 25% in the first 15 minutes, and then stays constant at around 40% living population for the next 45 minutes. The 10ml of freshwater treatment falls around 45% to around about 20%

TABLE 9. Repeated measures ANOVA results for Crustacean Nauplii survivorship

	F Value	D.F	P Value
Between (F Test)	62.0229	3	**<0.0001**
Within (Wilks' Lambda)	7.7921	12	**<0.0001**
Time (F Test)	48.0796	4	**<0.0001**

where it plateaus for the next 45 minutes. The 20ml treatment dramatically falls around 65% to about 0% living copepods where it levels off as well.

Crustacean nauplius populations died off significantly more when salinity approached fresh water levels. The Wilks'-Lambda statistical test demonstrates a statistically significant p-value of less than 0.0001 (Table 9). Although initial living populations were between 50% and 55% (Fig. 6) they follow similar paths as the copepod tests (Fig. 7), with the 5ml freshwater treatment falling to around 40%, the 10ml treatment dropping to around 20% and the 20ml freshwater treatment decreasing all the way to about 0% living population. More tests should be conducted to test for significance of the similarities between the two experiments' results.

For both experiments, individual ANOVA tests and Tukey-Kramer tests were run at each time point. Significant differences in means between the treatments were found except for a select few cases (primarily between the treatments of 5ml and 10ml of freshwater) when the Tukey-Kramer test showed no statistical significance. The ANOVA test still demonstrated a statistical significance overall and so the few non-significant relationships were not important to the experiments' significant results as a whole.

DISCUSSION

Reef passes and lagoons have significant differences in overall as well as individual group zooplankton abundance. Some groups (such as copepods and crustacean nauplii) are found more at the passes, while plankton "B" is found more often in the shallower lagoon waters. Yet other groups, such as veligers were found in similar quantities in both areas. My results support my hypothesis that passes have, on average, a greater number of zooplankton. It may be due to passes being a point of exchange in pelagic and lagoon waters. It may also be because the deeper water is a more suitable habitat for zooplankton, or one of many other variables.

Individual differences in numbers found are important because it may mean that some of the groups travel more than others. More research is needed to really understand the extent of these migrations as well as the fact that all groups are found in both locations, just in different numbers. The outliers of the data may be due to human error. One possibility is that if I did not homogenize the sample well enough, then the sample would have different species abundance and diversity. Along with the possibility of not having representative data, another variable in need of further study is the idea that zooplankton may be social animals, and may congregate together in swarms (Hamner and Carleton 1979). If this holds true in Mo'orea, then the large numbers of one group found may be due to towing through one of these "swarms". In reverse, some of the samples where I expected to find more organisms than I did may have been because I missed these swarms or even that they swam out of the path of the plankton net (Hamner and Carleton 1979). Towing in the same location and using the same speed during each tow

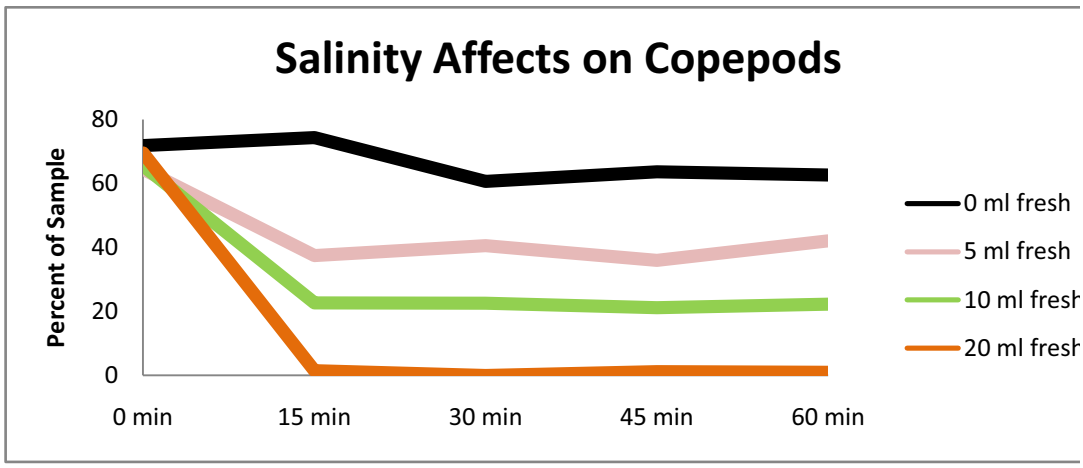

FIG. 5. Copepod living percentage with different salinity treatments

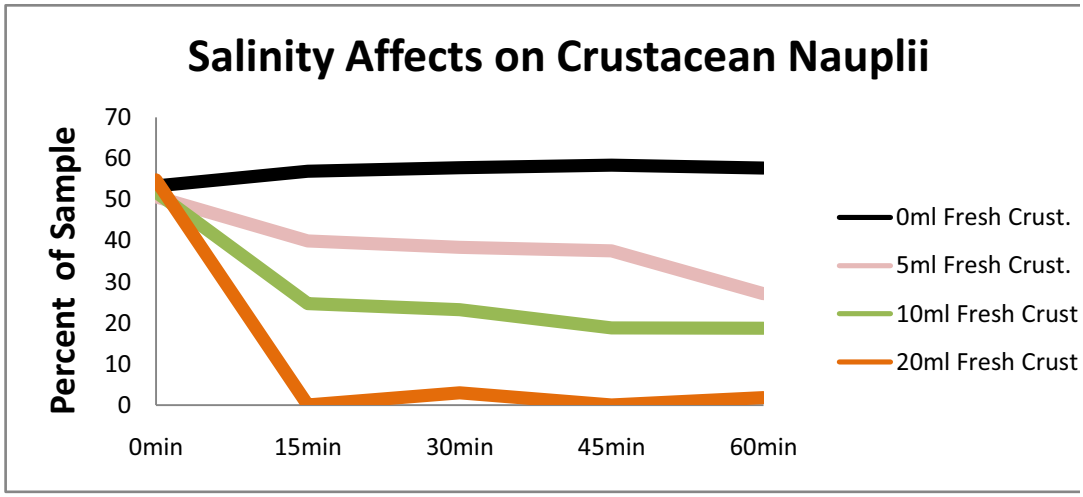

FIG. 6. Crustacean nauplii living percentage with different salinity treatments

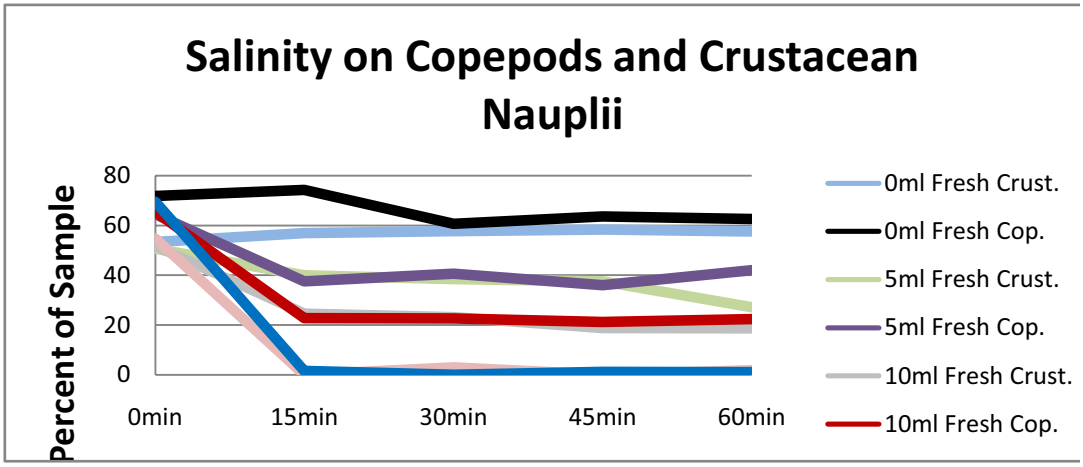

FIG. 7. Comparison of Copepod and Crustacean nauplii living percentage with different salinity treatments

was designed to cut down on sample error, but this did not control for zooplankton's ability to swim away.

Although the data is not conclusive about species diversity when compared to different factors, it still is of interest for different factors, it is of interest for further research. It is apparent that some species prefer either the passes or the lagoons, and there was a slight trend towards having more species found at lower tide especially in the passes. My data does not support my hypothesis that lagoons have greater species richness, but more data, especially from different depth ranges as well as time changes, is needed to check for statistical significance.

An increase of freshwater lowers the percentage of copepods and crustacean nauplii that are able to survive (Fig. 7), supporting my hypothesis that there is a positive correlation between lower salinity levels and an increase in death rates. Copepods and crustacean nauplii are two of the three most abundant species I found around Mo'orea, meaning that any large influx of freshwater may have devastating impacts on the marine environment.

The lack of significance between some treatments at the same testing time may be corrected with more replicated. Some of the samples may have been exposed to heavier shaking for homogenization, and since they are not being replaced or used in other treatments, each organism has its own tolerance to salinity and to disturbance so small amounts of variation are expected.

Copepods are one; if not the most, important group in the transformation of energy to higher marine levels (Hamner and Carleton 1979), meaning that any large drop in population will have significant affects on the rest of the ecosystem with a major drop in food availability for small marine organisms. The significant results in the two groups' stress test are a good indicator that other marine organisms may be affected by salinity levels in similar ways. This is important when considering current climate changes, because if there is increased storm activity on a large scale, then the increased flow of freshwater flow into the ocean may have an impact on plankton composition. More research is needed to see whether increased rainfall and storm activity will affect the zooplankton populations.

Zooplankton is an underexplored key group of small animals; therefore there are almost infinite possibilities for further research. Looking into energy transformation between phytoplankton to zooplankton, then on to higher trophic levels is one topic to look into. Also, different observational studies are necessary to better understand the social structure of different groups. Studying the few organisms that seem to be healthy and fine in the 20ml of freshwater treatment could lead to interesting discoveries on individual tolerances. Lifespan studies, physiological studies, and exploring how great a distance they can travel could further the understanding of the importance of zooplankton. More stress tests could give scholars a better idea of what to be careful of in the future if natural conditions continue to change. More studies could be focused on the interactions between different species at different levels of development, and different zooplankton hierarchies could be established based off of predator/prey interaction.

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APPENDIX 1. ANOVA results for Copepod, Veliger, Crustacean Nauplii, and plankton "B" abundance. Values in bold and underlined represent a statistically significant level of below 0.05.

	Source	F Value	D.F.	P Value
Copepods	Salinity	6.8183	1	**0.0148**
	Salinity*lagoon/reef pass	3.1384	1	0.0882
	Salinity*High/Low tide	3.6038	1	0.688
Veligers	Salinity	1.71	1	0.2024
	Salinity*lagoon/reef pass	0.1283	1	0.7231
	Salinity*High/Low tide	0.1007	1	0.7535
Crustacean Nauplii	Salinity	9.6654	1	**0.0045**
	Salinity*lagoon/reef pass	0.9416	1	0.3408
	Salinity*High/Low tide	3.5619	1	0.0703
Crustacean "B"	Salinity	2.6112	1	0.1182
	Salinity*lagoon/reef pass	2.5047	1	0.1256
	Salinity*High/Low tide	0.0246	1	0.8765

CHEMICALLY STIMULATED BEHAVIOR OF THE HERMIT CRAB *CALCINUS LATENS* (RANDALL 1840) AND THE ROLE OF CHEMICAL SIGNALING AS A MODE OF SENSORY PERCEPTION WITHIN THE CORAL RUBBLE HABITAT OF MOOREA, FRENCH POLYNESIA

ILYSA S. IGLESIAS

Department of Integrative Biology, University of California Berkeley, California 94720 USA

Abstract Aquatic invertebrates utilize multiple forms of sensory perception including chemical signaling, to evaluate their surrounding environment. The hermit crab *Calcinus latens* is able to detect external chemical cues within the complex coral rubble habitat. These discrete chemicals whether emanated from a potential predator, competitor or conspecific are received through chemosensory structures and elicit a specific behavioral response. This study examines the effect of four chemical treatments (control-ambient sea water, predator-Octopus bocki, potential competitor-Saron marmoratus and conspecific-Calcinus latens) on the number of times an individual *Calcinus latens* is observed in active, exploratory behavior verses stationary, defensive behavior. The results demonstrate a significant difference in the amount of time observed in defensive behaviors by the hermit crabs exposed to the treatment containing octopus chemical cues when compared to the other treatments. Across the four chemical treatments, there was a significant difference in the observed use of six specific behaviors, indicating a patterned behavioral response, unique for each treatment. Additionally, an experiment testing the response of *Calcinus latens* individuals to artificially introduced treatment species, (octopus Octopus bocki, shrimp Saron marmoratus as well as conspecifics) in which tested individuals could utilize all modes of sensory perception, was compared to the chemically stimulated behaviors. Analysis of the response behavior to chemical cues verses multimodal sensory assessment of actual treatment species demonstrated a statistically significant similarity in elicited behavior which underlines the importance of chemical signaling in modulating the behavior of *Calcinus latens* within the coral rubble microhabitat.

Keywords: chemical cues, *Calcinus latens*, hermit crab behavior, Moorea, French Polynesia, coral rubble microhabitat

INTRODUCTION Multimodal sensory perception is critically important for organisms in assessing their surrounding environmental conditions. The ability of organisms to garner and synthesize information from any combination of visual cues, tactile senses, sound perception and chemoreception, near-range to considerable distances away (Mellon 2007) allows for informed behavioral decisions. This is especially true for organisms living within topographically complex habitats such as coral rubble where complex distributions of microhabitats have lead to high invertebrate species diversity and distribution (Kohn 1983, Kohn and Leviten 1976, Abele 1974, Gischler 1997, Turra and Denadai 2002, Choi and Ginsburg 1983).

The coral rubble habitat is a common hard substrate on most coral reefs (Gishler 1997, Choi and Ginsburg 1983) and the biotopes created within its cavities offer refuge from predators and physical disturbances (Choi and Ginsber 1883), as well as create feeding sites of settled detritus (Turra and Denadai 2002), and prey abundance. These factors allow for sympatric species from discrete trophic levels to coexist in close proximity (Monteforte 1987, Poupin 1998). The community structure and spatial distribution observed within these microhabitats is influenced by complex species behavior and interactions dependent upon sensory perception; namely the influence of chemical cues (Reese 1999, Brooks 1991, Chiussi et al 2001, Hazlett 1981, Gilchrist 2003).

Within the coral rubble habitat, the dynamic fluid movements of the surrounding aquatic environment, combined with local low light conditions and turbidity has lead to the ubiquity of chemical signaling (Marcotte 1999) both at close range and over great distances (Briffa and Williams 2006, Mellon 2007). Aquatic crustaceans, one of the most represented groups in this environment, have developed diverse chemoreceptive structures to process chemical signals for surrounding environment. The interpretation of chemosensory inputs occur by means of cuticular sensilla on the body and appendages (Mellon, 2007), specifically through

the antennules and chemoreceptive units on walking legs in decapod crustacea (Mesce 1993). Receptors receive and process chemical input from surrounding currents, which elicit responses of feeding, predator avoidance, settlement, and intraspecific communication in the individual (Herring 1979). The ability of individual prey organisms to chemically detect the presence of potential predators, surrounding competitors and neighboring conspecifics influences behavior and life history strategies.

One common chemoreceptive organism of the coral rubble environment of Moorea, French Polynesia is a hermit crab species *Calcinus latens* (Randall 1840). In addition to structures on antennules and walking legs, hermit crabs have developed chelar simple setae and ambulatory dactyls (Hazlett 1971 and Mesce 1993) to receive chemical signals. Hermit crabs are known to modulate their behavior in response to surrounding chemical signals as a strategy of predator avoidance (Brooks 1991, stone crab Rittschof and Hazlett 1997, green crab Rotjan et al 2004, fish juice Chiussi et al 2001, predatory crab Mima et al 2003, lobster model Scarrat and Godin 1992 and fish juice Hazlett 1971), identifying conspecifics (Rittschof et al 1992, Gherardi and Tiedemann 2004, Gherardi and Atema 2005, Gherardi et al 2005 and Briffa and Williams 2006), to mediate exploratory shell seeking behavior (Hazlett and Rittschof 2005, Rittschof et al 1992, Pezzuti et al 2002, Gherardi and Atema 2005 and Orihuela et al 1992) and orientation of visual cues (Briffa and Williams 2006, Chiussi et al 2001, Diaz et al 1994, and Orihuela et al 1992). However, little is known about the comparative effects of chemical cues emanating from a predator, competitor and conspecific as they relate to the stimulated behavior of *Calcinus latens*.

To quantify and contrast stimulated behavior of tested *Calcinus latens* individuals in response to four chemical treatments, an ethogram of defensive (stationary) verses exploratory (active) behavior will be used to determine the impact of the following four chemical treatments: 1. Ambient seawater 2. Chemical cues from the marbled shrimp *Saron marmoratus* (Olivier, 1811), an invertebrate whose distribution in the coral rubble habitat overlaps with that of *Calcinus latens*, and is thus assumed to interact in some capacity 3. A pygmy octopus *Octopus bocki* (Adams, 1941), a predator of *Calcinus latens* within the coral rubble habitat. 4. Chemical cues from conspecifics of the hermit crab species *Calcinus latens.*

This study aims to quantify the differential behavioral response (namely amount of time observed in specific behaviors) of *Calcinus latens* to treatments of water containing various chemical cues with the hypothesis that the predator odors (of *Octopus bocki*) will elicit a more severe response in exploratory verses locomotory behavior than those treatments of a potential competitor odor (*Saron mamoratus*) and conspecific (*Calcinus latens*).

The second facet of this study aims to investigate the associations between the chemically stimulated behavioral responses of C. *latens* individuals and the elicited behavior in response to the artificial introduction of actual treatment species individuals. The actual interactions of hermit crab *Calcinus latens* individuals with *Saron marmoratus*, *Octopus bocki* and conspecifics will allow tested individuals to utilize all of their modes of sensory perception (mainly tactile, auditory, visual and chemical cues) to assess their environment and respond accordingly. Using the same behavioral criterion as in the chemosensing experiment, I plan to compare and analyze the response behavior of *Calcinus latens* between chemical cue and actual interaction experiments in order to compare the relative importance of chemical signaling (between individuals of the same species, competitors and predators) to other modes of environmental perception in modulating the activity and behavior of *Calcinus latens* to sympatric species of the coral rubble habitat.

METHODS

Study site

Fieldwork took place on the French Polynesian island of Mo'orea. A volcanic island that is a part of the society island chain, Mo'orea has extensive marine habitats and immense biodiversity. Lab work was conducted at the Richard Gump field station in Cook's bay.

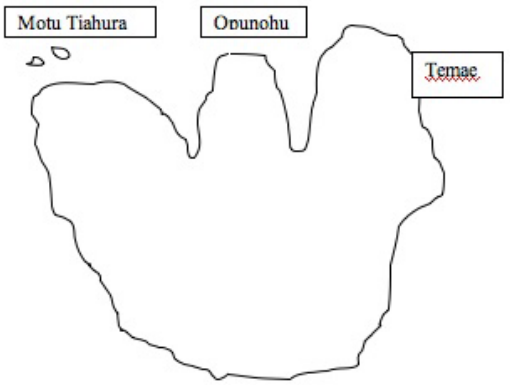
Focal Species Biology

Calcinus latens (the white tip hermit crab) is a common species within the lagoons of Moorea and has the spatial distribution ranging from the infralittoral fringe to the sublittoral (Gherardi and Nardone 1997, Reese 1969) and predominantly aggregates under dead coral rubble (Reese 1969, Personal Observation). *Calcinus latens* has been observed in the field to demonstrate complex shell selection behavior which often permeates many aspects of observed

behavior and biology (Shih and Mok 2000, Kosuge and Imafuku 1997). As with most hermit crab species, *Calcinus latens* is an omnivorous detritvore, opportunistically foraging for a variety of energy sources within its range (Hazlett 1981). Although an indepth description of interspecific species interactions of *Calcinus latens* is currently not available in the literature, personal observations indicate a predator-prey relation ship between *Octopus bocki* and *Calcinus latens*.

Collection

Species of interest from the coral rubble habitat (*Octopus bocki, Saron mamoratus* and *Calcinus latens*) were collected from inside the reef crest regions in the coral lagoons at the following sites around the island of Moorea, French Polynesia: Temae bay, outside Opunohu public beach (near the Sheraton), and the lagoon outside Motu Tiahura (See Figure1). I fastened a number of buckets to the top of a large kayak and filled the large bins with porous coral rubble ranging in size from 5 to 50 centimeters in diameter. The rubble was then left to drain for approximately 30 minutes at which point I would search through the contents on the bottom of the bucket for desired organisms. Animals were transported back to the Richard Gump field station via aerated plastic containers.



Care at the Station

Calcinus latens and *Saron mamoratus* were stored in individual plastic containers so as to aid in identification and prevent interactions and fighting between individuals. Both species were fed every other day on fish food pellets. Water was cleaned on a daily basis from the running seawater system in the wet lab. *Octopus bocki* were stored in 2 Liter plastic containers with ample holes in the lids and fed every other night with various crustaceans gathered from the coral rubble (predominantly xanthid crabs, stomatopods and various shrimp sp.). Water was changed daily.

Chemosensing Experiments

Two series of 40 *Calcinus latens* individuals (for a total of 80 crabs) were collected from the field and numbered. Twenty individuals were used per treatment and selected using Excel random number generator. There were a total of four chemically stimulated behavior tests, each one varying in their chemical treatment:

1. *Control Chemical Treatment* Three 2 Liter containers were each filled with 750 mL of ambient seawater taken from the source in the wetlab. The three containers were then left to sit for a total of 14 hours (overnight). This procedure was repeated until all twenty individuals were tested.
2. *Predator (Octopus bocki) Chemical treatment* The same three 2 Liter plastic containers were each filled with 750 mL of plain sea water and then an adult *Octopus bocki* was added to the container and allowed to sit for 14 hours in the container without feeding or other known chemical inputs.
3. *Potential Competitor treatment* (*Saron mamoratus*) Same procedure as for *Octopus bocki* but instead one *Saron marmoratus* was added per container.
4. *Conspecific treatment* (*Calcinus latens*) Same procedure as above but one hermit crab of the species *Calcinus latens* was added per container.

Experimental Procedure: Chemically stimulated behavior

All of the experiments were conducted between the hours of 8am and 12pm and held within a small, indoor room to ensure similar activity levels of test species and minimum disturbance from outside factors. An individual hermit crab (selected randomly) was placed in a 14-cm diameter clear Petri dish placed above a paper grid and allowed to acclimate for a total of 60 seconds. Following the 60 seconds, 150mL of a chemical treatment (one of the four listed above) was then added to the Petri dish. The subsequent behavior of the hermit crab was noted every 10 seconds for a total of 300 seconds (Although only the first 60s were used in behavioral comparisons and data analysis). An ethogram of exploratory behavior (adapted from Briffa and Williams 2006 and combined with personal observations) was used to describe behavior with the following six behaviors recorded, the first three being grouped as stationary positions, the latter three considered locomotory positions:

Withdrawn all arms withdrawn into the shell *Stationary* no observed movement but appendages visible *Stationary-appendage movement* while the whole body remained in the same position, appendages were still waved around *locomotion* moving around in any direction *climbing* attempts to climb the side of the Petri dish and *shell raising* the behavior of physically lifting the shell up against the side of the Petri dish (similar to climbing but appendages remain on the bottom of the pi-tri dish). Following the 300 seconds, the *Calcinus latens* individual was returned to its cup and stored for the second experiment involving interactions.

Experimental Procedure: Artificial Introduction of actual treatment species

This set of experiments was designed to observe the behavior of hermit crabs *Calcinus latens* stimulated in response to an introduced treatment species individual. Tested individuals could utilize all modes of perception (namely visual, tactile, auditory and chemical cues) in gaining information about their experimental environment and the species artificially placed within it. First, each 2 Liter container (same ones used in above experiment) was filled with 750 mL of ambient seawater collected from the wet lab. Of 80 individuals collected, 20 were used per trial for a total of four trials and 80 individuals and were selected randomly using Excel random number generator. The test crab was placed into the container with the plain seawater and left to acclimate for one minute. After 60 seconds, either one adult *Octopus bocki* one *Saron marmoratus*, plain seawater or one *Calcinus latens* was physically added to the container already holding the focal hermit crab. Using the same ethogram as the chemical sensing tests, behavior was recorded every 10 seconds for a total of 60 seconds (for a total of 7 data points). This procedure was then repeated 20 times for every four treatments until the behavioral response of all 80 individuals was documented.

RESULTS

Preliminary Observations

In preliminary experiments, an observation of the feeding behavior of *Octopus bocki* upon *Calcinus latens* was repeatedly attempted. Although actual feeding was never observed (most likely as a result of the intrusive procedure for feeding the octopus in lab conditions), when left overnight the hermit crab shell in the morning was either empty, indicative of its consumption by the octopus, or the hermit crab was observed maintaining a withdrawn position, in which it stayed until returned to an individual container with ambient sea water.

Another preliminary experiment designed to test the relationship of individual *Calcinus latens* within the coral rubble habitat involved placing multiple individuals in a container containing one piece of coral rubble and observing latency to approach and behavior upon arrival to the substrate. In all cases the *Calcinus latens* individuals approached the hunk of coral rubble immediately upon introduction into the container and selected cavities on all surfaces of the coral rubble large enough to allow shell fit. In some cases individuals would actually climb on top of each other, vying for the desired position within the rubble, while those that could not fit on the small piece of dead coral aggregated around the substrate.

A final preliminary observation involved the simulation of natural conditions for the three treatment species in order to gain insight of their interactions in the field. A large container was filled with coral rubble (collected from above mentioned collection sites) and all three treatment species, *Calcinus latens, Saron mamoratus and Octopus bocki* were added simultaneously to the arena. Observations were made over a thirty-minute period. During the whole 30 minutes of observation, none of the individuals were seen to physically interact as each species immediate sought refuge in the abundant coral rubble interstices and remained for the duration of the time. While experiment was not reproduced or continued over a greater amount of time, it demonstrated the importance of coral rubble cavities as refuges to interactions in field conditions.

Chemical cue experiments: Behavioral responses to chemical stimuli

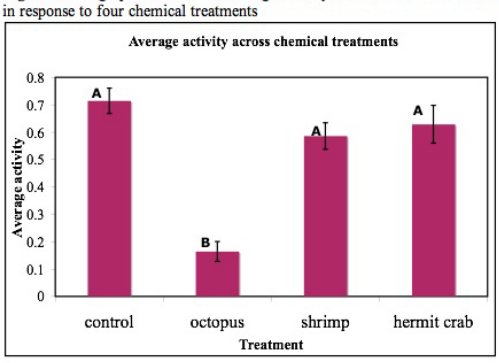
A behavioral activity bioassay was conducted to compare the response of hermit crabs exposed to ambient sea-water, predator odor (*Octopus bocki*), potential competitor chemical cues (*Saron mamoratus)* as well as conspecific cues (other *Calcinus latens*). Using the behavioral ethogram outlined in the materials and methods section, average activity levels (measured in number of times observed in a locomotory position for the first 60 seconds of observation) were compared across treatments (figure 2) and analyzed using one-way analysis of variance (ANOVA) statistical test on JMP 5.1.2 software (see table 1). The results (df=3, F ratio= 22.7

and Prob>F of <0.0001) demonstrate a significant difference in the average activity levels across chemical treatments. Further examination of the data using a Tukey-Kramer HSD comparison test revealed that the chemically stimulated behavior of focal hermit crabs, measured in number of times observed in a stationary vs active position responded to the chemical cue of a predator (*Octopus bocki*) by spending significantly greater time in a stationary behavior than the hermit crabs in the other chemical treatments that were comparatively more active.

Table 1 Analysis of Variance (ANOVA) results:

Experiment	DF	F ratio	Prob> F
Average activity across chemical treatments	3	22.7104	<0.001
Withdrawn behavior compared across chemical treatments	3	14.5891	<0.001
Stationary behavior compared across chemical treatments	3	10.0918	<0.001
Stationary with Apendage movement behavior compared across chemical treatments	3	0.04424	0.7233
Locomotory behavior compared across chemical treatments	3	21.3370	<0.001

Figure 2 This graph describes the average activity of hermit crab individuals in response to four chemical treatments



Comparison of specific behaviors across chemical treatments

Although the above test demonstrated a significant difference in the amount of time focal hermit crabs were observed in stationary vs locomotory behaviors in response to varying chemical cues, specifically predator odors, it does not describe the specific behaviors demonstrated. A comparison of the percentage of times individuals were observed in particular behaviors gives detailed information about hermit crab behavior in response to these specific cues (see figure 3). A comparison of the number of times the specified six behaviors (withdrawn, stationary, stationary with arm movements, locomotion, climbing and shell raising) were observed was analyzed using a contingency chi-squared test on JMP 5.1.2 software (the climbing and shell raising categories were combined because of such low frequency). The Pearson test value (chisquared= 181.535, df=12, P<0.0001) (see table 2) revealed that the types of behaviors observed were significantly different across the four treatments. Next I analyzed the average number of times specific response behaviors were observed across chemical treatments:

Figure 3 This graph describes the frequency of six specific observed behavior across four chemical treatments

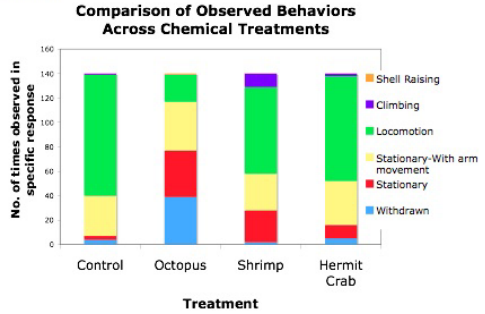


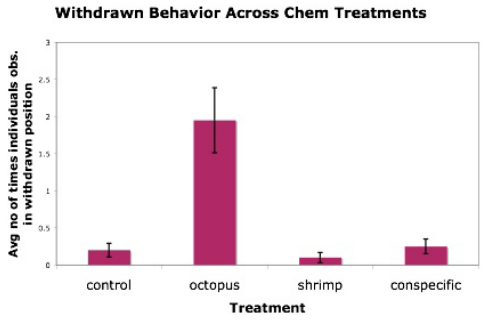
Table 2 Chi squared analysis : the comparison of six specific observed behaviors across chemical treatments

Source	DF	RSquare (U)
Model	12	0.1169

Test	Chisquare	Prob> Chisq
Pearson	182.042	<0.0001

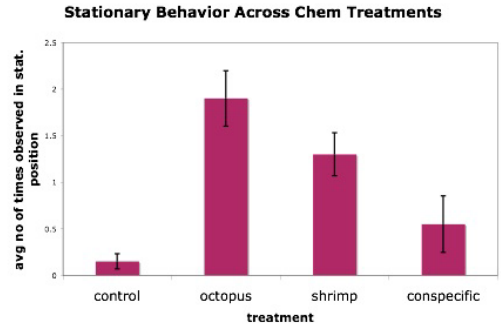
Withdrawn Behavior A one-way ANOVA run on JMP 5.1.2 software demonstrated a significant difference in the amount of time the withdrawn behavior was stimulated across the four treatments (df=3, F ratio 14.5891, Prob>F <0.0001) (table 1). Further analysis using a Tukey-Kramer HSD analysis on JMP 5.1.2 software showed that the hermit crabs exposed to treatments containing octopus chemical cues spent significantly more time in the withdrawn position that the hermit crabs from the other three treatments (control, shrimp and conspecific)(see table 1 and figure 4).

Figure 4 Graph comparing the number of times treatment *Calcinus latens* elicited **withdrawn** behavior in response to four varying chemical treatments



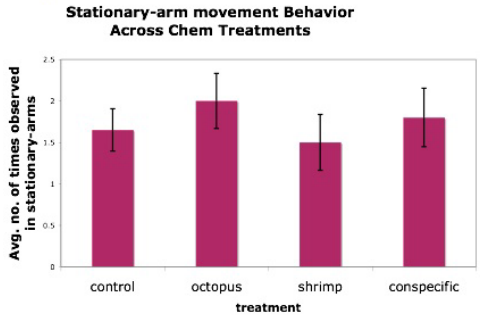
Stationary Behavior A comparison of the average number of times tested hermit crabs were observed in a stationary position across treatments was analyzed using a one-way ANOVA on JMP 5.1.2 software (table5 and figure 5). The results (df=3, F ratio 10.0918 and Prob>F <0.001) indicate that the variance in observed stationary behavior was significant across treatments. Further analysis using the Tukey-Kramer HSD analysis on JMP 5.1.2 software demonstrated there was no significant difference in the observed stationary behavior between the hermit crabs exposed to octopus and shrimp treated water, the shrimp and conspecific treatments and between the control and conspecific chemical treatments. There was a significant difference however between the observed stationary behavior of hermit crabs exposed to control and conspecific verses the octopus and shrimp treatments.

Figure 5 Graph comparing the number of times treatment *Calcinus latens* elicited **stationary** behavior in response to four varying chemical treatments



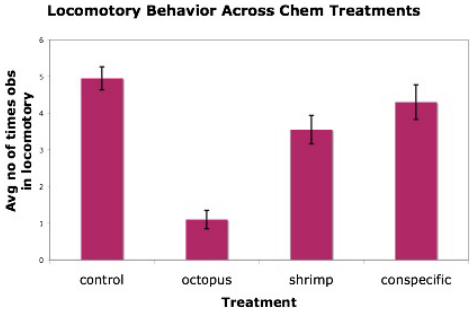
Stationary-Appendage movement behavior The graph depicts the average number of times hermit crabs from each chemical treatment were observed in a stationary-with appendage movement. A oneway ANOVA carried out on JMP 5.1.2 software gave a p value of 0.7233 (df=3, F ratio 0.4424, Prob>F, 0.7233, see figure 6), which indicates there is no significant difference in the observed stationary with appendage movements across the four chemical treatments.

Figure 6 Graph comparing the number of times treatment *Calcinus latens* elicited **stationary-appendage movement** behavior in response to four varying chemical treatments



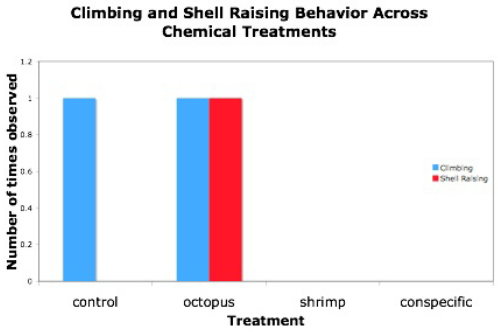
Locomotry Behavior The average number of times hermit crabs were observed in a locomotry position across four chemical treatments (control, octopus, shrimp and conspecific) was graphed (figure 7) and analyzed for statistical significance using a oneway ANOVA on JMP 5.1.2 and Tukey test. There was a significant difference (Prob>F, <0.0001) in the amount of time hermit crabs exposed to the octopus chemical cues compared to the other three treatments. There was no significant difference between the locomotory behavior of hermit crabs exposed to the control and conspecific treatment and the shrimp and conspecific chemical cues.

Figure 7 Graph comparing the number of times treatment *Calcinus latens* elicited **locomotory** behavior in response to four varying chemical treatments



The remaining two behaviors, shell raising and climbing were observed with such low frequency that no statistical analysis could be run (see figure 8 for a graph of number of times observed). However, it is important to note that shell-raising behavior, although only observed 13 times across all individuals and treatments, was observed 10 times in the shrimp chemical cue treatments. Shell raising behavior was only observed once in all trials and was in response to treatment containing octopus chemical cues.

Figure 8 Graph comparing the number of times treatment *Calcinus latens* elicited **climbing or shell raising** behavior in response to four varying chemical treatments



Comparison of elicited behavioral response between chemical treatments and actual interactions

In order to compare the behavioral response of *Calcinus latens* to chemical treatments with their reaction to actual treatment species, intended to simulate natural conditions (see figure 9), I ran a two-way ANOVA on JMP 5.1.2 software in order to determine the similarities and differences in elicited behavioral response between chemical treatments and actual interactions with the species. As the graph of observed activity levels across chemical treatments and actual interactions illustrate, there was no significant difference in the average activity levels across experiments (chemical and actual) (df =3, Prob 0.973) (table 3). Whereas there were significant differences between treatments, specifically between the average activity of individual hermit crabs in response to octopus and octopus chemically treated water when compared to the other preparations.

Figure 9 Graph comparing the response behaviors of tested *Calcinus latens* individuals from the chemosensing experiment and "actual interaction" experiments, across chemical treatments

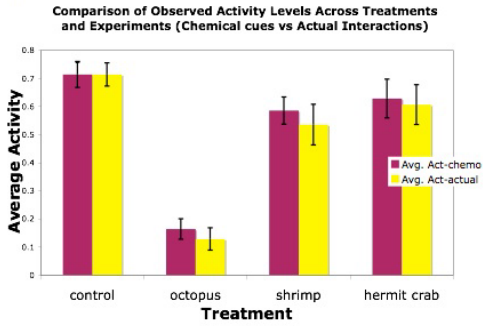


Table 3 Analysis between two experiments: Actual interactions experiment compared to Chemosensing experiment: and compared across four chemical treatments (control, predator, shrimp and conspecific) MANOVA statistical test:

Source	DF	F ratio	Prob> F
Treatment	3	41.4735	<0.0001
Actual Interactions	1	0.4745	0.4920
Actual Interactions*Treatment	3	0.0752	0.9732

DISCUSSION

The chemically stimulated behaviors of the hermit crab *Calcinus latens* to treatments containing the chemical cues of sympatric species within the coral rubble habitat (predator *Octopus bocki*, a potential competitor, *Saron marmoratus* and conspecifics) agree with previous findings on other species of hermit crabs that individuals are capable of detecting and responding to chemical signals in the surrounding aquatic environment (Brooks 1991, Gherardi and Atema 2005, Pezzuti et al 2002, Rittschof et al 1992, Mima et al 200, Orihuela et al 1992, Diaz et al 1994, Chiussi et al 2001 and Hazlett 1970). The first experiment observed behaviors of hermit crabs in response to different treatments of chemical cues, and demonstrated a difference across the four treatments in the amount of time individuals were observed in stationary, defensive positions compared to active, exploratory behaviors. The predator chemical cues (*Octopus bocki)* had the single greatest effect on the amount of time individuals were observed in defensive behaviors, as predicted in the hypothesis. A more detailed comparison of six specific observed behaviors indicates that the grouping of behavior into stationary or locomotory showed a difference in frequency across treatments for three of the six behaviors. The withdrawn and stationary behaviors appear to be associated with defensive positions, and are displayed with the greatest frequency by hermit crabs exposed to octopus or shrimp chemical treatments. The stationary with appendage behavior conversely is equally observed across all treatments, which suggests its common use in facilitation of chemical reception. Further, the high frequency of locomotory behavior shown in the control and conspecific chemical treatments accentuates the frequent foraging and shell seeking behavior of individuals who do not perceive a threat in their surrounding environment. Finally, the remaining two behaviors, although not displayed with great frequency give details on the plasticity of behavior of the *Calcinus latens* hermit crab.

The first major finding of this study is the significant difference in the average activity level of tested hermit crabs across chemical treatments. Those individuals exposed to predator (*Octopus bocki)* chemical cues are more likely to be observed in stationary positions then active ones. The literature on hermit crab behavior describes stationary behavior as a defensive position, most often demonstrated in

response to predators or predator cues (Rotjan et al 2004, Scarratt and Godin 1992, Mima et al 2003). Active, exploratory behavior on the other hand, is typically observed in hermit crabs displaying foraging behavior or shell seeking behavior. In a natural setting, hermit crabs must change shells as they increase in size or suppress their body size growth to compensate (Sato and Seno 2006). Additionally, predators select for hermit crabs inhabiting shells of inadequate size, in one study preferentially eating hermit crabs in shells that were too small (Vance 1972). These pressures to find an adequate shell, combined with a limited supply of gastropod shells in any environment is responsible for the frequency of observed locomotory shell seeking behavior of hermit crabs, in the absence of a perceived predation threat. Some hermit crab species aggregate around gastropod kill sites to facilitate exchange of shells (Pezzuti et al 2002 Rittschof et al 1992, Gherardi and Benvenuto 2001), others simply spend more time in locomotion, fast and meandering, in order to increase their chances of encountering empty shells or conspecifics (Tricarico and Gherardi 2006). This explains the active, exploratory behavior observed in the three treatments where the tested individual did not receive chemical cues indicating any threat in their surroundings and thus wandered around the Petri dish either exhibiting foraging or shell seeking behaviors.

The second comparison of observed behaviors across chemical treatments considers six elicited behaviors outlined in the methods (withdrawn, stationary, stationary-arm movement, locomotion, climbing and shell raising.) The first specific behavior examined across the four chemical treatments is withdrawn behavior. The number of times individual hermit crabs are observed in a withdrawn position when exposed to chemical cues of the predatory octopus *O. bocki* varied from the other treatments, which rarely display this behavior. When hermit crabs are faced with the chemical cue of a predator, they have two typical antipredator behaviors: fleeing from the area or seeking refuge in their acquired gastropod shells (Scarratt and Godin 1992, Mima et al 2003). The frequency of hermit crabs withdrawing into their shells for protection against predators is influenced by the shell fit of the hermit crab (crabs with a large shell fit tend to withdraw more often than flee Scarrat and Godin 1992), and the quality of the shell it occupies (some shells are better adapted to defend against predation). Hermit crabs have been documented actively selecting gastropod shells better adapted for physical protection against potential predators when there is selective pressure from predators on a population (Bertness 1981) or when exposed to predator chemical cues and other shells are available for occupation (Rojan et al 2004, Mima et al 2003). Although both shell fit and shell type could describe the observed frequency of withdrawn behavioral response to octopus chemical treatments, I believe it is elicited as a behavioral adaptation to their environment. The complex substrate of the coral rubble habitat affords *Calcinus latens* refuge within its cavities and attempting to flee from potential predators incidentally may compromise this refuge and make the individual more exposed and vulnerable to attack. A comparison of antipredator success comparing fleeing verses withdrawing behavior in the coral rubble habitat would be an interesting topic for future research and might explain the preference of this antipredator tactic in *Calcinus latens.*

Another specific response behavior of tested *Calcinus latens* individuals compared across the four chemical treatments is stationary behavior (where an individual was out of its shell but not observed moving). The two treatment groups that display this behavior with the greatest frequency are the individuals tested from the octopus and shrimp treatments. Although stationary behavior is not a direct antipredator response, the refrain from locomotion, which could put the individuals in a position more vulnerable to predation, demonstrates that tested hermit crabs can detect and respond to chemical signal differentially. The groups displaying stationary behavior the least are the hermit crabs exposed to treatments of control water and conspecific chemical cues. A study by Briffa and Williams (2006) with the hermit crab *Pagurus bernhardus* demonstrated that focal crabs spent less time in a stationary position and a greater proportion of time on locomotion when cues from conspecifics were present (as long as they were previously non-fighting crabs) (Briffa and Williams, 2006). If *Calcinus latens* individuals exposed to the conspecific chemical signals are stimulated into locomotory shell seeking behavior, then they would not be expected to demonstrate high instances of stationary behavior. An examination of the specific locomotory behavior (movement of focal crabs in any direction) of tested *Calcinus latens* individuals across treatments illustrates this, see figure 8. Another reason for the observed locomotory behavior of hermit crabs

exposed to conspecific odors could be due in part to their ability to recognize the odor of other *Calcinus latens* individuals (Gherardi and Tiedemann 2004, Gherardi et al 2005 and Briffa and Williams 2006). A study by Gherardi et al in 2005 found that individual hermit crabs of the species *Pagurus longicarpus* could chemically distinguish between larger crabs inhabiting higher-quality shells and smaller crabs inhabiting lower-quality shells if they had some past association. Not knowing the previous interactions of tested individuals (due to random collection methods), it is possible that the potential previous encounters could influence the observed behavior within these treatments. However, because the hermit crabs exposed to the control treatment of ambient seawater had no statistical difference to the elicited behavior of hermit crabs in the conspecific treatment, we can assume that the potential influence of previous encounters does not have a severe impact on the recorded behaviors.

Another specific response behavior examined across chemical treatments is "stationary with appendage movement. These experiments demonstrate that this behavior is elicited equal across all four chemical treatments. Although little literature reports on this specific response behavior in hermit crabs, considering the location of chemoreceptive structures on hermit crabs, the movements of appendages (typically the front chelar structures as well as walking legs) could be a means for the individual hermit crab to generate mini currents around its sensors in order to detect the presence of chemicals within its environment. Because I only examined the behavioral responses of *Calcinus latens* to the four treatments within the first 60 seconds of exposure to the treatment, the ubiquitous use of this behavior across treatments supports the postulation that arm moving behavior is a means to distinguish chemical cues when placed in a novel environment as the tested individuals of this study are. It would be interesting in the future to compare the frequency of this behavior over a longer amount of observation.

The chemosensing experiment demonstrates that hermit crabs *Calcinus latens* is capable of detecting chemical cues and can modulate its behavioral based on whether it is sensing chemical signals from conspecifics, predator or potential competitors. *Calcinus latens* responds strongest to the chemical cues of its predator *Octopus bocki* by spending a significant amount of time in a withdrawn behavior to avoid predation. These predator-induced changes in behavior may have implications for population dynamics and interspecific interaction within the coral rubble habitat.

The results of the second experiment conducted in this study demonstrate that the behavioral responses of individual *Calcinus latens* to actual treatment species artificially introduced to the same containers as individual hermit crabs, had no impact on elicited behavior when compared to the chemically stimulated behaviors in the first set of experiments. The similarity of these "actual interactions", which allow for multimodal sensory perception (namely auditory, visual, chemical and tactile cues) to the chemically stimulated behavior experiment, in which tested hermit crab individuals were only able to discern perceived threat through chemoreception, underlines the importance of chemical signaling to *Calcinus latens* in perceiving their environmental surroundings.

The observed response behavior of tested *Calcinus latens* individuals to the forced introduction of a treatment species (namely *Octopus bocki, Saron marmoratus* and conspecific) mirrors the cross treatment results of the chemosensing experiment: hermit crabs exposed to the treatment containing chemical cues from the predatory octopus were observed in stationary, defensive behaviors with greater frequency compared other chemical treatments. The response behavior of *Calcinus latens* individuals to these "actual interactions" compared to chemical sensing experiments demonstrate that they are not distinguishable from one another. The experimental design of the chemosensing experiments were intended to eliminate the ability of hermit crab individuals to utilize multiple modes of sensory perception. The clear Petri dish without contained no visual or auditory information, forcing the individuals being tested to rely on their ability to detect chemicals in the surrounding environment. To contrast, the second set of experiments, which physically placed a treatment species individual into a container of ambient sea water with the hermit crab being tested allows the use of visual cues to aid in directional orientation, auditory cues between species and tactile stimulation all in addition to chemical sensing information. The fact that tested *Calcinus latens* individuals respond the same whether they have all sensory faculties or only chemical perception underlines the importance of chemical signaling in

evaluating the proximate environment and responding with appropriate behavior.

Although hermit crabs have a range of sensory tools for interpreting their ambient environment, often one cue is not enough to establish directional orientation. In lab experiments, shape discrimination, background pattern, and other visual orientation cues have been tested either in the presence or absence of chemical signals representative of background cue, for example, the availability of a shell combined with calcium cues, and gastropod haemolymph extract or environment sea grass scent corresponding to a stripped background, and found that the response behavior of the hermit crab being tested are activated by chemical cues (Orihuela et al 1992, Diaz et al 1994, Chiussi 2001). Further, one study which additionally observed orientation of a tested hermit crab individual to a predator (fish odor) chemical cue discovered that the orientation away from a target (indicating an avoidance response) was only observed following the presence of predator odor (Chiussi et al 2001).

The requirement of chemical cues in synthesizing other sensory inputs to process information about surrounding conditions indicates the importance of chemical cues in determining directional orientation within a complex environment. Within the complex interstices of the coral rubble environment, there is a need to know the location of predators, food, mates and availability of shells without compromising a position in a refuge, or risking predation by sympatric predatory species. However, due to low light conditions, physical disturbances and complex microhabitats, many of the potential sensory cues can be obstructed by environmental conditions. Chemical sensing however, appears to be a relatively important mode of perception in these complex environments because of the observed specificity in signaling and the ability to garner information from proximate to distant ranges.

Hermit crabs are able to distinguish between the four chemical treatments of this study and modulate behavior according to the perceived threat. When a threat is received in the form of chemical cues emanating from a predator, appropriate antipredator tactics are induced in the individual, and other potential behaviors are not observed. This may have implications for the shell selection behavior of Calcinus, *latens* in the coral rubble habitat, as well as affect their locomotory behavior within their range. Future studies should consider the a priori shell fit and quality shells occupied by individuals when comparing behaviors. It would also be interesting to compare the results of this study to an experimental design mimicking natural conditions to get a better understanding of hermit crab behavior in their natural, dynamic environment. This study also outlined the importance of chemical cues, in combination with other sensory modes, as well as the only means of evaluating environment conditions with the demonstration of chemical cues in determining directional orientation to sympatric species presence. This observation would benefit from future research on the comparative roles of other sensory modes of perception within this complex habitat to better understand the plasticity of behavior and sensory perception modes of *Calcinus latens* in the coral rubble microhabitat.

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DISTRIBUTION AND HABITAT FEATURES OF THE SEDGE *KYLLINGA NEMORALIS* ON THE POLYNESIAN ISLAND OF MO'OREA

CHRISTINA M. JOHNSON

Genetics & Plant Biology, University of California, Berkeley, California 94720 USA

Abstract. This study focuses on the current distribution and habitat preferences of the sedge *Kyllinga nemoralis.* It is a weed on Mo'orea, but an invasive to other islands of the Pacific. Annual precipitation, temperature, water availability, soil moisture, soil type, canopy cover and elevation are shown to influence the distribution of this species. A minor transplant study affirms its preference of full sun locations to those with low light due to canopy cover.

Key words: Sedge; Cyperaceae; Kyllinga nemoralis; rangelands; roadsides; Mo'orea, French Polynesia

INTRODUCTION

Invasive plant species are problematic to native plant populations worldwide (Vitousek et al. 1996). A plant becomes invasive when, after dispersal to a new range, its progeny reproduces, thrives and persists (Elton 1958). Invasives enter a population by filling seasonally or habitually empty niches, then out-competing their native counterparts (Davis 2000). *Kyllinga nemoralis* (Forst.) exhibits characteristics common to the success of an invasive species such as asexual spreading, positive reaction to human-caused disturbance (Mack 2000), early and consistent reproduction, and small seed mass (Rejmanek 1996). Several species of Cyperaceae are listed as highly invasive worldwide (Muyasa et al. 2001). Sedges of the genus *Kyllinga* are recognized for their invasive tendencies within tropical climates (Space 2002). This trend is exemplified by a related sedge, *Kyllinga polyphylla.* Whether due to later introduction rate or a reduced ability to spread due to differing environmental conditions, *Kyllinga* species exhibit a less aggressive distribution on Mo'orea. *Kyllinga nemoralis* (Forst.) is native to the Old World Tropics. It is a listed invasive introduction, and moderate invader to Hawaii (Whister 1994, SREP 2000), an invasive weed in Samoa (Whistler 2002) and is considered a benign "mauvaise herbe," or weed, in Mo'orea (Welsh 1984, Whistler 1995).

The first step in managing an invasive species is understanding its distribution and the abiotic factors affecting its distribution (Chornesky 2003). In this study, I assess the distribution of *K. nemoralis* in Mo'orea. Its distribution on Tahiti and other Pacific islands extends to 800 meters in elevations and is found along roadsides and in close proximity to human habitations (Whistler 1995). At first glance, *K. nemoralis* is not as extensively established on Mo'orea as it is in its neighboring island, Tahiti. I hypothesize that *K. nemoralis* has a preferred habitat type that includes zero or low canopy cover and ready moisture availability. I also propose that average annual precipitation, temperature, water availability, soil moisture, soil type, and elevation contribute to the presence of *K. nemoralis*.

METHODS

Study organism

K. nemoralis is a rhizome-spreading perennial sedge with angular stems, a brown to purple leaf sheath, and a globose terminal head (Whister 1995). With its three

to four long, distinct bracts and fluffy white inflorescence, this sedge is easily identified from surrounding vegetation. Other names for *K. nemoralis* include *K. cephalotes* (Jacq.) *K. monocephala* (Rottb.), and *Cyperus kyllingia* (Endl.). *K. nemoralis*, known as Mo'u upoo in Tahitian (Petard 1986). Samoans called this herb Tuisē (Whistler 2001) and mo'u upo'o (PIER). In Hawaiian, it is known as mau'u mokae, and to the Maori of the Cook Islands it is called maku 'ōniāni. While this species has been a trusted remedy to illness such as rheumatism (Petard 1986), today it appears as a common weed. It grows in full sun in lawns beside houses (Petard 1986), and pastures. It is also found alongside roads in ditches, thriving on the moist habitats formed by storm drainage.

Terms

The culm is the above-ground shoot, from which leaves and inflorescence diverge. The culm extends from the rhizome to the base of the inflorescence.

Distribution

Initial distribution study was conducted by way of planned habitat searches. Three searches were conducted of five minutes each for each of 34 localities. Localities searched included variation in elevation, average annual temperature, average annual precipitation, canopy cover, and soil type. Choice of localities was made by overlaying multiple map layers using ArcMap. Layers were produced by taking digital photographs of soil type, temperature, precipitation, and vegetation maps from OSTRAM's *Atlas de la Polynesie Francaise*, georeferencing them using ArcMap, georeferencing them, and layering them with a topographical map of Mo'orea, obtained from Berkeley's GIIS website. Noted and obtained from each locality was a GPS point, a 3cm x 1cm cylindrical soil core, average canopy coverage, presence or absence of *K. nemoralis*, and a list of present Cyperaceae. GPS point data was later used to infer the presence of *K. nemoralis* throughout the island (Image 8). Soil core samples extended only 3cm into the soil to correspond with average depth of root mass. Canopy cover percentages were collected to show the variation in canopy cover habitat preference.

Habitat Preference

Habitat preference was inferred from statistical analysis of presence/absence data of *K. nemoralis* within each habitat variable. Variables included: elevation, average annual temperature, average precipitation, water availability, canopy cover, vegetation type, soil moisture, and soil type. A transplant study then was used to confirm the hypothesis: while *K. nemoralis* prefers environments where moisture is readily available, it does not perform well in moist, densely shaded environments.

Transplant

One hundred rhizomes of *K. nemoralis* were taken from a thriving roadside population and placed in two habitat types where *K. nemoralis* was never found to be naturalized during the initial distribution study: within the *Inocarpus fagifer* and *Hibsicus tiliaceous* forests, under 60% - 100% canopy cover, within iron-rich, high-moisture content soils. Within the transplant sites, 10 plots measuring 15cm x 7cm x 7cm deep were formed every 5 meters along two 25 meter transects: one set of 10 plots in *Inocarpus fagifer* forest, the other set of 10 plots in *Hibsicus tiliaceous* forest. Each transplant site contained 50 total rhizomes. Transects ran perpendicular to a stream's edge. 10 healthy rhizomes were measured, labeled, and planted in each plot. Upon planting, soil from host site was rinsed off each rhizome to show bare roots, and measurements were taken of each rhizome's length in cm, with one

measurement of a culm length for each rhizome. Culm lengths were only taken at a distinct stage of flowering, to avoid discrepancies inherent in different stages of development. Within the host population, 20 culm lengths were measured and labeled at the time of transplant specimen removal. Upon completion of 20 days in each environment, rhizome and culm measurements were again taken of transplant specimens, and culm measurements alone for host population. Growth rate of shade-grown versus full-sun host population *K. nemoralis* was then shown through rhizome growth and culm growth.

Associated Species

Ten locations were chosen from the 20 located in the initial distribution study that showed presence of *K. nemoralis*. Sites were visited to gather additional data on associated species. Transects of 25 meters ran in a pre-determined randomized ordinal direction. Four 25cm^2 quadrats were taken at 7, 12, 19, and 25 meter marks. *K. nemoralis* was consistently found within 3 meters of the transect line, if not along the transect line.

Statistical Tests

The following tests were performed using the JMP 7 statistical analysis program: oneway ANOVA analysis of culm difference by transplant location, oneway ANOVA analysis of rhizome difference by transplant location, bivariate fit of presence/absence of *K. nemoralis* by percent canopy, bivariate fit of presence/absence of *K. nemoralis* by altitude, bivariate fit of presence/absence of *K. nemoralis* by water availability, bivariate fit of presence/absence of *K. nemoralis* by precipitation, and oneway ANOVA of soil moisture by soil type.

RESULTS

Distribution

K. nemoralis occurs on Mo'orea in moist, sunny, low-elevation locations. These areas also exhibit low-range precipitation levels and close proximity to roads. While distribution is limited to moist areas near human habitation, low average water availability levels are common among distributions of *K. nemoralis.* See Appendix 1 for statistical information.

Habitat Preference

The transplant study showed that culm and rhizome growth are not correlated. Rhizome growth rates between full-shade sites were not significant (fig. 1). *K. nemoralis* preferred full-sun to both dense-canopy environments (fig. 2). Intense soil moisture levels did not encourage growth of *K. nemoralis* in the absence of full-sun. Growth rates were often negative in full-shade plots, and positive in full-sun. Soil type and soil moisture were correlated., and *K. nemoralis* was more likely to occur in soil types 2, 5, 6, 8, and 9 than in type 11. It is not likely to occur in soils 12 and 7 (fig. 3). GIS projection of habitat preference on Mo'orea is shown in figure 4.

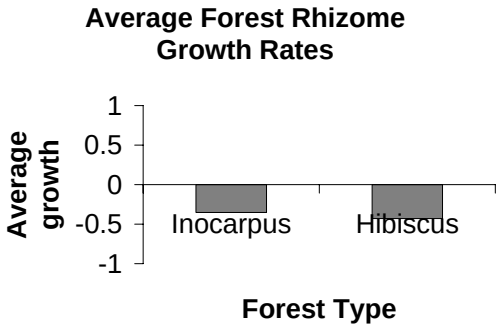

Figure 1: Average rhizome growth rates of *K. nemoralis* grown in *Inocarpus fagifer* and *Hibiscus tiliaceous* forests.

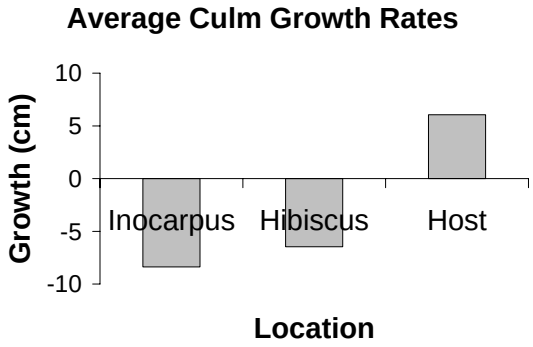

Figure 2: Average culm growth rates of *K. nemoralis* grown in *Inocarpus fagifer* and *Hibiscus tiliaceous* forests.

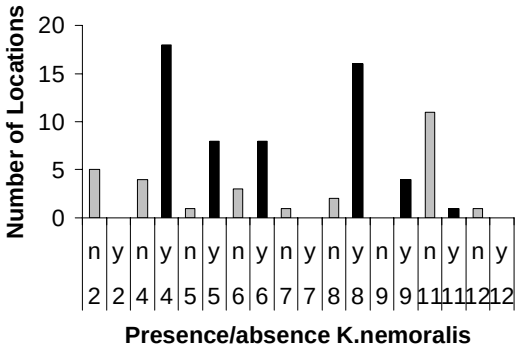

Fig. 3: Occurrence of K. nemoralis in common soil types found on Mo'orea. Soil type 2 is lithic, eroded by strong winds, 4 is alluvial, type 5 alluvial modeled into cliffs by water, type 6 is calcium/magnesium-rich, type 7 is humid and eutrophic, type 8 is ferralitic, type 9 is ferralitic and eroded, type 11 is podzolitic, type 12 is mesotrophic (translated from ORSTOM 1993).

Figure 4: Projected distribution of *K. nemoralis* on Mo'orea based on soil type, temperature, and precipitation data.

DISCUSSION

The current distribution of *K. nemoralis* on Mo'orea is influenced by temperature, soil type, precipitation, and canopy cover. While ecological studies on the invasive species of French Polynesia are common, no previous extensive digital mapping has been done on the ecology of an invasive plant on Mo'orea. This project was twofold: to explore the trends of *K. nemoralis* distribution, and to digitize the extant maps of Mo'orea, enabling others to perform additional studies on this island's worst invaders.

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APPENDIX A

RESULTS OF STATISTICAL ANALYSIS

Oneway Analysis of Culm Difference By Transplant Location
Oneway Anova
Summary of Fit

Rsquare	0.055084
Adj Rsquare	0.038932
Root Mean Square Error	18.31929
Mean of Response	-3.57242
Observations (or Sum Wgts)	120

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Transplant Location	2	2288.952	1144.48	3.4103	0.0363
Error	117	39264.788	335.60		
C. Total	119	41553.740			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
CJ7 roadside ditch	20	6.0630	4.0963	-2.05	14.18
Hibiscuss forest	50	-4.7200	2.5907	-9.85	0.41
Inocarpus forest	50	-6.2790	2.5907	-11.41	-1.15

Std Error uses a pooled estimate of error variance

Oneway Analysis of Rhizome Difference By Transplant Location
Oneway Anova
Summary of Fit

Rsquare	0.000134
Adj Rsquare	-0.01007
Root Mean Square Error	3.361285
Mean of Response	-0.3915
Observations (or Sum Wgts)	100

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Transplant Location	1	0.1482	0.1482	0.0131	0.9090
Error	98	1107.2271	11.2982		
C. Total	99	1107.3753			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
CJ7 roadside ditch	0	.	.	.	.
Hibiscuss forest	50	-0.43000	0.47536	-1.373	0.51333
Inocarpus forest	50	-0.35300	0.47536	-1.296	0.59033

Std Error uses a pooled estimate of error variance

Bivariate Fit of K.nemoralis (y/n) By % CANOPY

Linear Fit

K.nemoralis (y/n) = 0.7727088 - 0.0078749*% CANOPY

Summary of Fit

RSquare	0.273191
RSquare Adj	0.264218
Root Mean Square Error	0.408027
Mean of Response	0.662651
Observations (or Sum Wgts)	83

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	5.068846	5.06885	30.4461
Error	81	13.485371	0.16649	**Prob > F**
C. Total	82	18.554217		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.7727088	0.049028	15.76	<.0001
% CANOPY	-0.007875	0.001427	-5.52	<.0001

Bivariate Fit of K.nemoralis (y/n) By ALTITUDE (ft)

Linear Fit

K.nemoralis (y/n) = 0.7616211 - 0.00034*ALTITUDE (ft)

Summary of Fit

RSquare	0.203911
RSquare Adj	0.194082
Root Mean Square Error	0.427031
Mean of Response	0.662651
Observations (or Sum Wgts)	83

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	3.783402	3.78340	20.7474
Error	81	14.770815	0.18236	**Prob > F**
C. Total	82	18.554217		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.7616211	0.051664	14.74	<.0001
ALTITUDE (ft)	-0.00034	7.463e-5	-4.55	<.0001

Bivariate Fit of K.nemoralis (y/n) By HYDRO (m)

Linear Fit

K.nemoralis (y/n) = 0.7602717 - 0.000594*HYDRO (m)

Summary of Fit

RSquare	0.172839
RSquare Adj	0.162627
Root Mean Square Error	0.435285
Mean of Response	0.662651
Observations (or Sum Wgts)	83

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	3.206895	3.20690	16.9253
Error	81	15.347322	0.18947	**Prob > F**
C. Total	82	18.554217		<.0001

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	0.7602717	0.053347	14.25	<.0001
HYDRO (m)	-0.000594	0.000144	-4.11	<.0001

Bivariate Fit of K.nemoralis (y/n) By PRECIP

Linear Fit

K.nemoralis (y/n) = 1.2501546 - 0.0002097*PRECIP

Summary of Fit

RSquare	0.135996
RSquare Adj	0.125329
Root Mean Square Error	0.444874
Mean of Response	0.662651
Observations (or Sum Wgts)	83

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	2.523302	2.52330	12.7496
Error	81	16.030915	0.19791	**Prob > F**
C. Total	82	18.554217		0.0006

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	1.2501546	0.17163	7.28	<.0001
PRECIP	-0.00021	5.874e-5	-3.57	0.0006

Oneway Analysis of Soil Moisture By Soil Type

Oneway Anova

Summary of Fit

Rsquare	0.415494
Adj Rsquare	0.353967
Root Mean Square Error	0.521467
Mean of Response	1.316279
Observations (or Sum Wgts)	43

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Soil Type	4	7.345347	1.83634	6.7530	0.0003
Error	38	10.333258	0.27193		
C. Total	42	17.678605			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
4	12	1.36667	0.15053	1.0619	1.6714
5	8	1.18750	0.18437	0.8143	1.5607
6	8	0.71250	0.18437	0.3393	1.0857
8	11	1.90909	0.15723	1.5908	2.2274
9	4	1.00000	0.26073	0.4722	1.5278

Std Error uses a pooled estimate of error variance

APPENDIX B

Cyperaceae of French Polynesia		
Genus species	**Locality**	**Description**
Carex tahitensis	Tahiti (Fosberg)	Plants tufted perrenials, (20) 60-80 cm tall, the culms sharply 3-angled, the angles spinulose-serrulate; lowermost leaves bladeless, the blades elongated upward, finally to 60 cm long or more and much overtopping the inflorescences; inflorescence 10-20cm long, subteneded by foliose bracts to 25cm long, spikes pedunculate, 3-6 (or more), 1.5-3 cm long, 6-12mm thick, androgynous; peduncles 1-7cm long, the basal one the longest; lemma of staminate floret ca. 3mm long; lemma of pistillate floret ca 2.5mm long; perigynia 3-4mm long or more, irregularly biconvex, many-veined, the apex acute, the mith minutely bidentate, achene dull yellow to brownish, ca 1.7mm long. Socitey islands ; tahiti, Orofena, Mt. Marau, endemic. (Welsh)
Cladium jamaicense	Tahiti, Tetiaroa, Huahine, Tahaa, Maupiti, Tupai (Fosberg) Tahiti, Tupae, Huahine, Feie, Raietea, Tahaa, New World, Many pacific Islands, Asia. (Welsh)	Perenials from thick, spreading rhizomes; culm solitary, ca. 1.5-2.5 m tall, terete, often with extra-vaginal shoots at lower nodes; leaves cauline, the blades thick, coriaceous, serrulate-scabrous, the apex caudate; sheathes loose, shorter umbellate corymbs, these terminal and lateral, nearly as wide as the peduncle and rays flattened; bracts leafy, sheathing, much longer than their subtending corymb; congested in globose heads of 4-12, each one ovoid-ellipsoid; glumes broadly ovate, contracted to the obtuse or ovoid-globose, 1.8-2mm long, apiculate, rounded basally. Society Islands; Tahiti; Tupae; Huahine, Feie, wetland margin of lagoon; Raiatea,

		Tahaa; widely distributed in the New World, many Pacific Islands, Asia. (Welsh)
Cyperus alternifolius/ flabelliformis	Tahiti, Raiatea (Fosberg) Society Islands; Tahiti, low, swampy land near Outo-maroro, Punaauia; introduced, cultivated and escaped; originally described from sw. Asia and adjacent Africa; Raiatea. A portion of this has been called C. papyrus. (Welsh)	Perennial, from short, woody rhizome; culms tufted, 5-15dm tall, trigonous to subterete, scabrous below the corymb; basal leaves reduced to bladeless sheathes; basal leaves reduced to bladeless sheaths; basal sheaths 10-20cm long, the lower ones yellowish brown; corymbs large, dense, decompound, 15-30cm in diameter, primary rays numerous, slender, 7-10cm long, each with 4-10 secondary rays, 1-1.5cm long, the lower ones yellowish brown; corymbs large, dense, decompound, 15-30cm in diameter, primary rays numerous, slender, 7-10cm long; involucral bracts numerous (12-20), stiff, flat, subequal, ca twice as long as the corymb, 2-12mm wide, the apex abruptly acute; spikelets clustered at apices of secondary rays, densely 6-to30-flowered, lanceolate-oblong to elliptic, flattened, 3-9mm long, 1.7-3 mm wide, the rachilla not winged; glumes pale green and variegated with rusty brown, membranous, ovate, 1.5-2mm long, 3-or 5-nerved, the keel prominent, acute apically; style subequal to length of achene;

		stigmas 3, elongate; achenes brown, trigonous, less than half as long as the glume; 2n=30,32. (Welsh)
Cyperus compressus	Tahiti, Maupiti (Fosberg) All main island groups (Whistler) Society Islands; Tahiti, Arue, introduced, pantropical, originally described from North America, Paea District; Mehetia; Meetia; Raiatea; Marquesas; cosmopolitan weedy species. (Welsh)	(Chlorocyperus c.) Tufted annual sedge with fibrous roots, culms erect, 3-sided, leaves basal, shorter than culm, spikelets 3-12 o up to 5 rays subtended by leaf-like bracts, fruit a 3-sided achene (Murdock's checkllist) Tufted annual sedge with fibrous roots, Culms erect, 4-60cm in height, 3-sided, glabrous. Leaves few, basal, blade linear, flat 1-3mm in diameter, shorter than the culms; leaf sheath membranous, pale brown, striate. Inflorescence umblliform with 3-12 spikelets on 2-5 rays up to 8 cm long, or sessile in dense clusters, subtended by 2-4 unequal, leaf like bracts 4-20cm long. Spikelets 3-12 per axis, lanceolate to oblong, 0.5-3.5m lolng, 15-40 flowered, laterally compressed, imbricate, green turning yellow. Glumes ovate, 3-3.5mm long, strongly folded with an acute keel, acute at the apex with a short mucro. stamens 3. Ovary superior, style 3-lobed. Fruit a broadly obovate, 3-

		sided achene 1-1.3mm long, shiny dark brown. (Whistler) Tufted annuals, with fibrous roots; culms spreading, 8-30dm tall, trigonous, smooth;leaves few per culm, basal, with blades pale green, linear, flat, shorter than the culm, 1-3mm wide; sheaths membranous, pale brown, striate; inflorescences umbelliform or congested, 2-10cm long and wide, rays (when present) 2-5, spreading, 0.8-5cm long, slightly compressed, the spikes with 3-10 spikelets on a shortened axis; involucral bracts 2-4, foliaceous, unequal, the longest 2-3times as long as the inflorescence; spikelets oblong-lanceolate, 10-25mm long, 2.5-3 mm wide, compressed, rachilla not winged; glumes herbaceous or thin and coriaceous, ovate or broadly so, 3-3.5mm long, strongly folded, the keel green, acute, 3-nerved on both sides, apex acute with a straight mucro ca 0.8mm long; style elongate; stamens 3; stigmas 3; achenes dark brown, siny, broadly obovoid, trigonous, 1-1.3mm long; 2n=96. (Welsh)

Cyperus elegans	Raiatea (Fosberg) Society Islands; Raiatea. Probably introduced (Welsh)	Rhizome short; stems many, caespitose, 30-60cm tall, rigid, obscurely trigonous; leaves equaling the stem, canaliculate-convolute, often viscosus, transversely septatenodose, with margins remotely dentate, the sheaths pale but reddish at base; bracts 3, foliaceous, finally spreading; inflorescence lax, 5- to 9-rayed, the rays spreading, unequal, to 10cm long, the raylets divaricate, to 2cm long, with short setaceous bracteoles; spikes 3, foliaceous, finally spreading, inflorescence lax, 5- to 9-rayed, the rays spreading, unequal, to 10cm long, the raylets divaricate, to 2cm long, with short setacous bracteoles; spikes 3-12 in a congested, radiate head, ovate-oblong or lanceolate-oblong 5-8mm long, 3mm wide, turgidly subcompressed, obtusish 8- to 12-flowered; rachilla rigid, elevated; glumes rather densely imbricated, chartaceous, 2 mm long, broadly obate, on the broad back green, acutely carinate, mucronate, the margins stramineous and often suffused purplish, obsoletely 7- to 9-nerved, cellular-reticulate; stamens 3; style long, deeply trifid, the three stigmas slender, exserted. (Welsh)

Cyperus iria	Tahiti (Fosberg) Tahiti, on the flanks of Pinai towards 800m; Raiatea, Faaroa Valley, Tepua Valley, Africa and Asia to Malaysia and Australia, USA, West Indies, and S. America. (Welsh)	Annual, with fibrous roots; culms solitary or tufted and few to several, erect, mainly 1-6dm tall, slender, trigonous, smooth; leaves 2 or 3 per culm, much shorter than the culm; blades linear, 2-5mm broad, weakly folded; sheaths reddish or purplish brown; corymbs mainly compound, 5-15 cm long, 3-10cm broad, with 3-7 unequal rays, these 2-12 cm long, each bearing 5-10 spikes; spikes often more or less inclined, 1-4cm long, bearing 4-20 spikelets; leafy bracts 4 or 5, the lowest 2 or 3 surpassing the corymb; spikelets rather loosely disposed, erect-spreading, linear-oblong or elliptic to lanceolate, 4-9 (11)mm long, 1.7-2mm wide, flattened, 6-to 22-flowered; rachilla conspicuously flexuous, hardly winged, the glumes somewhat loosely disposed, obovate-orbicular, 1-1.5mm long, truncate to shallowly retuse, the apex usually mucronulate, yellow or straw-colored, pale on hyaline upper margin, 3- or 5- nerved, convex; achenes obovate, trigonous, less than half as long as the achene; stigmas 3, stamens 4. (Welsh)

Cyperus papyrus	Tahiti (Fosberg) Society Islands; Tahiti; cultivated aquatic ornamental and botanical curiosity; noted in Papeete and Faa; native to Africa and adjacent areas. (Welsh)	Tall perennial herbs, from a short thick rhizome; culms tufted along the rhizome, mostly 1-2.5m tall, 1-3cm thick near the base, obtusely trigonous, naked or with bladeless sheaths at base, the basal sheaths coriaceous, brown, obliquely truncate at orifice, the sterile shoots sometimes bearing short-bladed leaves; corymb ample; bracts 4-10, narrowly lanceolate, much shorter than the corymb rays, these numerous, 1-3dm long, subequal in length, slender, a prophyll at base of rays 3cm long; secondary corymbs bearing 3-5 slender raylets and 3-5 bracteoles; spikes cylindric, 1-2cm long, 6-9mm broad, bearing many spikelets, these linear, 6-12mm long, ca 1mm wide, with 6-20 flowers; rachilla winged with lanceolate base of glumes; body of glumes ovate-elliptic or elliptic, winged, pale brownish and green on midvein; stamens 3; achenes oblong, trigonous, obtuse apically, maturing brownish; style 3-lobed; 2n= ca. 102. (Welsh)
Cyperus rotundus	Tahiti, Raiatea, Maupiti, Tahaa (Fosberg)	Perrenial sedge with long stoloniferous rhizomes arising from scaly tubers, leaves few, basal, inflorescence a loose cluster of up to 8 unequal rays subtended by 2-3 bracts, fruit a 3-sided achene. (Murdock's checklist) Perennial, with long, slender stoloniferous rhizome terminated by a globose-ovoid tuber; culms solitary or few, bearing a cormlike enlargement at base, erect, 1-4 (6) dm tall, slender, triquetrous, smooth, with leaves at base; leaves few, much shorter than culm; blade linear, 2-5mm broad, folded; sheaths light brownish, eventually breaking into brown fibers; corymbs simple to compound,

		loose, with 2-10 slender rays of unequal length... (Welsh)
Fimbristylis dichotoma	Mo'orea (digital flora project)	(F. annua, F. diphylla, F. polymorpha, Scirpus dichotomus, Scirpus diphyllus) Perennial sedge from short rhizome, culms thin, tufted, glabrous, inflorescence variously compound subtended by up to 5 bracts, 1 or 2 leaf-like, fruit a pitted achene. (Murdock's checklist) (more description and photo in Whistler)
Gahnia schoenoides	Tahiti, Aorai, Mo'orea; Raiatea.(Welsh) Mo'orea (digital flora project)	Rhizome thick, fibrous; culms clumb-forming, becomng large, 8-12dm tall; leaves cauline along much of the stem, the sheaths cylindric, scabrous through the upper part, the floral bracts of the same form, much surpassing the inflorescence; panicle 5-30cm long, slender, the spikes erect, ca 3-7cm long, slender, the spikes erect, ca 3-7cm long; glumes chestnut-brown to blackish, the body ovate, to ca 1cm long, with a long-aristate, scabrous awn-tip surpassing the body in length; stamens 4; style hispid at the base; achenes brown, shiny or somewhat punctate. (Welsh)

Kyllinga nemoralis		(Cyperus k., K. cephalotes, K. monocephala, Thyrocephaoln m.) Perennial, creeping via rhizomes, culms basally leafy, up to 50cm tall, though generally much shorter, inflorescence a white terminal globose head subtended by 3 or 4 spreading bracts, fruit an achene.(Murdock's checklist) (more description and photo in Whistler) It is a small, vivacious herb that is very abundant, found in the vicinity of human habitation. It has globose inflorescences that are 1cm in diameter. It is called mo'u upoo nui in Tahitian (Cyperaceae with a big head). The entire plant is used medicinally to treat a number of uses, including vaginal discharge, hemorrhoids, rheumatism, etc... (Translated from Petard p. 115)
Kyllinga polyphylla	Samoa, Tahiti, Fiji (Whistler)	Creeping perennial sedge up t 75cm in height. Culms 3-angled, glabrous, congested on the knotty, purple-scaled rhizome to form dense clumps. Leaves basal 2-4, linear and shorter than the culms, 2-4mm wide; lower leaf sheaths leafless, surrounding the culm base. Inflorescence a green, globose head 8-15mm in diameter, formed form 1-3 confluent spikes and subtended by 5-8 drooping, unequal, leaf-like bracts up to 15cm long and wider than the leaves. Spikelets green, densely packed on the head, 1-2 flowered, laterally compressed, narrowly elliptic, 2.5-3.5mm long. Glumes several, lanceolate to ovate, tip slightly curved. Stamens 3. Ovary superior, style elongated, 2-lobed. Fruit a dark, oblong to ovate, biconvex achene 1.5-2mm long. The 4-8 leaf-like bracts are wider than the leaves. Native to tropical

		Africa. Similar to Kyllinga brevifolia, but much more robust and has wider bracts. (Whistler)
Kyllinga spp.		TUISE (Samoan) Two sedges, one of ancient introduction, the other modern, common in disturbed spaces. The stems are used to clean out the ears. The name also applied to other sedges similarly used, which would otherwise remain nameless. (Whistler, 2001)
Mariscus cyperinus	Mo'orea (digital flora project)	Perennial; rhizomes short, woody, clothed with brown fibers; culms solitary or few, erect 2-7dm tall, trigonous, smooth, thickened at base; leaves several, basal, the blades linear, shorter than the culm, 5-7mm wide, flat, plicate; sheaths green, tinged purplish or pink; inflorescences umblliform, simple, open or sometimes almost headlike, solitary on each ray, cylindrical, narrowed at the base, 1.5-3cm long, 8-12mm wide, densely bearing numerous spikelets.... (Welsh)
Mariscus javanicus	Mo'orea (digital flora project)	Coarse tufted perennial, the rhizome short; culms robust, 4-11dm tall, 3-5mm thick, obtusely trigonous; leaves many, mostly surpassing culms; blades linear, 8-12mm wide, plicate below the

		middle, septate-nodulose, prominently cylindric, septate-nodulose; corymbs compound to decompound, 10-15cm long... (Welsh)
Pycreus polystachyos	all of the main island groups (Whistler)	Annual or perennial herb. Culms tufted, erect 16-100cm in height, 3-angled, smooth. Leaves few, shorter than the culms, blade linear, 1.5-3mm wide, stiff; leaf sheath reddish brown. Inflorescence a loose corymb with 2-6 rays up to 7 cm long, or condensed in to head-like clusters. 1.5-5cm across, subtended by 4-8 leafy, unequal bracts 1-30cm long, the lowest usually longer than the corymb. Spikelets digitately arranged, linear to linear-lanceolate, 7-12mm long, acute at the apex, flattened, 9-15 flowered... Uncertain origin. First recorded in Hawaii in 1888, listed as native to Hawaii.Synonym: Cyperus polystachyos. (Whistler)

THE DISTRIBUTION AND ROLE OF AN INVASIVE PLANT SPECIES, LANTANA CAMARA, IN DISTURBED ROADSIDE HABITATS IN MOOREA, FRENCH POLYNESIA

STEPHANIE LIN

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Invasive species are known to displace native habitat and threaten biodiversity. *Lantana camara* has invaded over 60 countries and island groups and is one of the top invasive plant species in French Polynesia. Few studies discuss the relationship between *L. camara* and anthropogenic disturbances, though it is known to be associated with disturbance. I surveyed the major roadsides of Moorea, French Polynesia for *L. camara* cover in association with environmental factors, resulting in an estimated *L. camara* roadside area cover of 1.99%. *L. camara* presence was significantly correlated to roadside habitat types, highest in areas of agricultural disturbance. *L. camara* presence and area cover were positively correlated to soil moisture and slope. Faunal species richness was higher in areas where *L. camara* was present. Germination experiments reared no results over six weeks. However, in a vegetative growth experiment, cuttings had greatest height growth over two weeks under the heaviest shaded of three light treatments. I predict that the current range of *L. camara* on Moorea could expand to shaded areas with sufficient soil moisture, slope, and intermediate disturbance, conditions typical of higher elevation habitats on Moorea.

Key words: Lantana camara, invasive species, anthropogenic distrbance, roadside habitat

INTRODUCTION

Invasive species pose a threat to the biodiversity and ecological structures of native habitats that may be of conservation value (Schei 1996, Mack et al. 2000). Disturbance is a major factor in determining the invasibility of native ecosystems (Hobbs 1991). For example, habitat disturbance caused by anthropogenic activity may free up light and nutrient resources to facilitate some invasive species establishment via broken canopies and bare soil, depending on disturbance type and frequency (Christen and Matlack 2006). Certain forms of disturbance, such as road construction that create edge habitat, are correlated with the establishment and distribution of some invasive plant species (Pauchard and Alaback, 2004).

Anthropogenic disturbance may also play a role in the invasion of French Polynesia by *Lantana camara* L., a thorny shrub thought to have originated in Central and South America, and naturalized in over 60 countries or island groups (Sanders 1987, Day et al. 2003). *L. camara* reached Tahiti in 1853 as an ornamental plant (Jacquier 1960, Swarbrick et al. 1995) and has since established on the Austral, Marquesas, Society, and Tuamotu islands (Meyer 1998). *L. camara* may be dispersed through faunal seed dispersal and vegetative growth throughout large ranges of elevation and climate (Rajendran et al. 2001, Swarbrick et al. 1998, Matthew 1971). The presence of *L. camara* is continuing to spread, and has been listed as one of the top threats to the biodiversity of French Polynesia (Meyer 2004) due to its potential to displace native habitat, increase fire disturbance intensity, and damage pastures and forestry (Swarbrick et al. 1995, Alfonso et al. 1982).

Biological control programs have been employed in the past century to deal with *L. camara* invasions in at least 33 countries to date (Julien and Griffiths 1998). *L. camara* was one of the first organisms tested with biological control agents in Hawaii in 1902 (Perkins and Swezey 1924) and has since been a major study organism for biological control methods including insect, fungal, and bacterial releases (Thomas & Ellison 2000). *L. camara* biological control programs have varied in success due to the organism's great climatic range and genetic diversity that goes beyond the target abilities of most biocontrol agents (Thomas & Ellison 2000).

Many *L. camara* studies focus on biological control applications approaches to preventing further invasions (Broughton 2000). Fewer studies have focused on the prediction and prevention of *L. camara* invasions through the management of land

use and anthropogenic activity, though some studies have found that the reproductive success of *L. camara* is significantly correlated to the size of anthropogenic forest gaps (Totland et al. 2005) as well as the intensity of natural and anthropogenic disturbances including overstory removal and fire (Duggins & Gentle 1998). Other types of anthropogenic activity known to be associated with *L. camara* include the construction of roads, railways, and canals, in addition to forest edges created by logging and fire (Day et al. 2003).

My study investigated the distribution and ecology of *L. camara* in disturbed roadside habitats and *L. camara* growth in a series of pot experiments to identify factors that may influence its invasion in Moorea and reveal its ecological role in these marginal habitats. Moorea, French Polynesia has a largely non-native low-elevation flora due to increased susceptibility of disturbed lowland habitats to invasive species establishment and persistence. The island of Moorea may serve as a model for studying the distribution and ecology of *L. camara* invasion since it occurs in a range of disturbed habitat types including forest edges, neglected land plots, agricultural areas, and gardens. I surveyed the roadsides of Moorea to determine the distribution and characteristics of *L. camara* establishment on a gradient of habitat disturbances to find a relationship between the success of *L. camara* and environmental factors associated to disturbed habitats such as increased levels of establishment in areas of increased levels of sunlight, moisture, and anthropogenic disturbance. I also surveyed the biotic communities supported by *L. camara* patches to investigate the relationship of *L. camara* to the faunal makeup of disturbed habitats to determine if *L. camara* presence has a significant affect on faunal species richness and diversity that may be important to the native faunal communities of Moorea. Furthermore, I examined the response of *L. camara* seeds and cuttings to a gradient of light treatments to isolate factors potentially contributing to establishment. With information on the distribution and establishment of *L. camara* in disturbed habitats, I will discuss possible implications for predicting and preventing further *L. camara* invasion into the remaining native habitat of Moorea, French Polynesia.

METHODS

Study site

Moorea is a high island located in the Society Islands of French Polynesia. This study was conducted alongside the major roads of Moorea, within a 50-m elevation range.

Field survey for distribution

A total area of 3 m (perpendicular to road) by 10 m (parallel to road) was surveyed alongside the island perimeter road, Route 91, at every 0.25 km over 5 randomly selected 2-km sections of the road. In addition, similar sites alongside three interior-reaching roads were surveyed (total survey area=1710 m^2). All sample areas were located on the hillside of the road (higher elevation location). The area of *L. camara* cover was recorded within the bounds of the sampling area. The greatest branch length of any *L. camara* occurrence within the sampling area was recorded in addition to the presence or absence of any flowering individuals as indicators of establishment success (Sharma et al. 2005). Semi-dominant plant species occurring within the sampling area were noted. The percent canopy cover was determined by using a densiometer along a 10-m long transect (parallel to road) through the middle of the sampling area, recording canopy presence or absence at every meter point. The light intensity was determined with a digital light meter, recording one measure at the 3-m point and one at the 5-m point of the 10-m transect line. Slope was visually assessed. Elevation and slope aspect were determined using a handheld GPS unit (Garmin E-trex). 10 mL of a soil profile were collected at every site and soil moisture was quantified using the gravimetric method by comparing the soil sample dry weight (soil dried in oven) to its original wet weight. Notes taken on each sampling area included the disturbed habitat type (1-forest edge, 2-neglected land plots, 3-agricultural land, 4-garden or yard, 5- paved area), adjacent habitat descriptions, and weather conditions.

Field survey for biotic community

To analyze the relationship between habitat and the establishment of *L. camara*, data from non-random survey areas for *L. camara* were used, in addition to data from the

distribution survey with *L. camara* presence. The non-random survey targeted *L. camara* patches of various sizes and locations, following the distribution survey methods. 17 non-random *L. camara* sites were also surveyed for fauna (mostly insect) by sweep netting and hand collecting one of every different organism seen. The organisms were later separated into morphospecies. Three pitfall traps (120-mL cups half filled with dilute dish soap water) were set out for 24 to 48 hours at five *L. camara* sites. Three pitfall traps were also set out next to each of the five sites in areas covered with the common invasive herb, *Wedelia trilobata*, and without *L. camara*.

Germination experiment

15 sets of 20 seeds of standard origin were potted in a random arrangement of three light treatments created by varying layers of shade cloth. Seeds were collected from fruiting *L. camara* individuals along Route 91 that occurred naturally on the island, whether ripe or unripe, and allowed to ripen before planting. The seeds were planted 6 cm beneath the soil surface of the pot in generic potting soil and left outdoors at 5 meters elevation, 50 meters from the shore in an open field. Pots were watered once a day except on rainy days, and signs of germination were quantified after six weeks.

Vegetative growth experiment

18 cuttings containing three nodes each were obtained from one naturally occurring *L. camara* individual from Moorea. Cuttings were planted in individual pots in generic potting soil, within 15 meters of the germination experiment and under similar conditions. Initially, all cuttings were allowed to establish under full sunlight for one week. The cuttings were then arranged into 6 rows and three light treatments created by varying layers of shade cloth to establish light treatment A (~2,000 lux), treatment B (~20,000 lux), and treatment C (~80,000 lux). Each cutting was measured for leaf number and height above soil surface over two weeks under light treatment conditions. The cuttings were watered once a day except on rainy days. The soil moisture of every pot was determined 24 hours after one of the waterings, using the gravimetric method. Dry root and aboveground masses were quantified using an electronic scale after three weeks.

Data Analysis

All statistical analysis was performed using JMP 7.0 (Copyright 2007 SAS Institute Inc.) Correlations between *L. camara* cover area and measured habitat conditions were analyzed using single regression analysis and ANOVA. *L. camara* percent cover on the roadsides was extrapolated from percent cover estimates made over all of the distribution sampling sties. *L. camara* presence (versus absence) over different roadside habitat types was analyzed using the likelihood-ratio test. Comparisons of species richness and diversity (Shannon Diversity Index) from pitfall trapping between areas of *L. camara* presence and absence were made with a paired sample t-test. Comparisons of leaf number, height, and belowground biomass between light treatments were made using a series of single factor ANOVAs; pairwise comparisons were made with Tukey HSD post hoc tests.

RESULTS

Field survey for distribution

L. camara was present in 24.6% of all distribution survey sites, covering a total of 1.99% of all distribution survey area. The L. camara cover area within the 30- m^2 survey areas ranged from 0.25 m^2 to 6.16 m^2. The mean cover in survey sites where *L. camara* was present was 19.8%, representing 5.956 m^2. *Wedelia trilobata* was highly associated with roadside habitats and was present in 47.4% of all distribution survey sites.

L. camara presence versus absence was correlated to edge type by the likelihood-ratio test ($p<0.0292$). *L. camara* presence occurred most in roadside habitats of agricultural areas (edge type 3) and least in roadside habitats consisting of highly disturbed and paved areas (edge type 5, Fig. 1).

Forest edge roadside habitats (edge type 1) also had least *L. camara* presence compared to agricultural roadside habitats (edge type 3). No significant relationship was found between *L. camara* cover area and light intensity and *L. camara* cover area and canopy cover. However, *L. camara* cover area was positively correlated with soil moisture levels ($p<0.0191$, Fig. 2).

When analyzing the area of *L. camara* on slopes greater than 0 degrees, there was a

significant positive correlation ($p<0.0498$, Fig. 3).

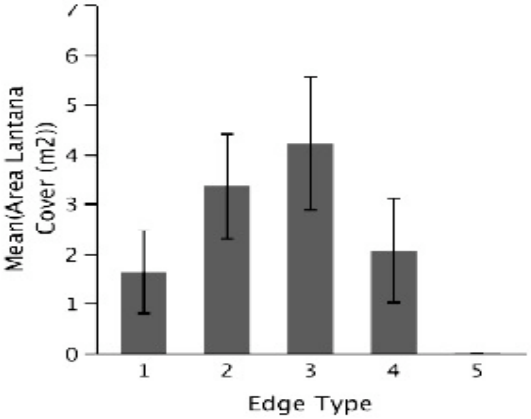

Fig. 1. Comparisons of area of *L. camara* cover between different roadside habitat types (1-forest edge, 2-neglected land, 3-agricultura l land, 4-garden or yard, 5-paved area). *L. camara* presence occurs most in agricultural areas (edge type 3) by the likelihood ratio test ($p<0.0292$, N=72).

Field survey faunal community makeup

The overall faunal species richness was significantly higher with *L. camara* presence versus absence by paired sample t-test ($p<0.0087$) (Fig. 4). Mean species richness was higher in sites with *L. camara* presence and was significantly different from sites without *L. camara* ($p<0.0087$). However, the biodiversity (Shannon Diversity Index) was not significantly different between sites with *L. camara* presence and absence.

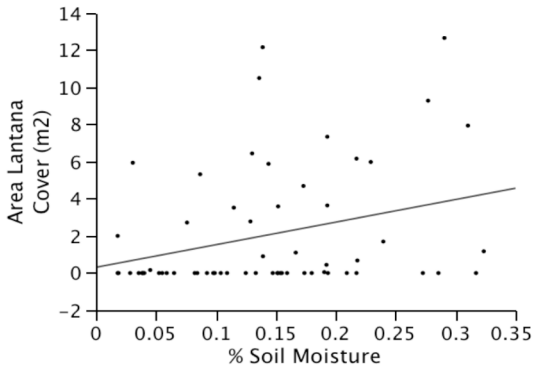

Fig. 2. Increasing area *L. camara* with increasing soil moisture levels ($p<0.0191$, $R^2=0.09$, N=61).

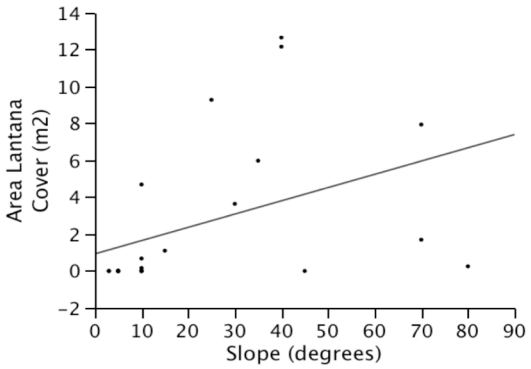

Fig. 3. Increasing area of L. camara with increasing slope ($p<0.0498$, R2=0.17, N=23).

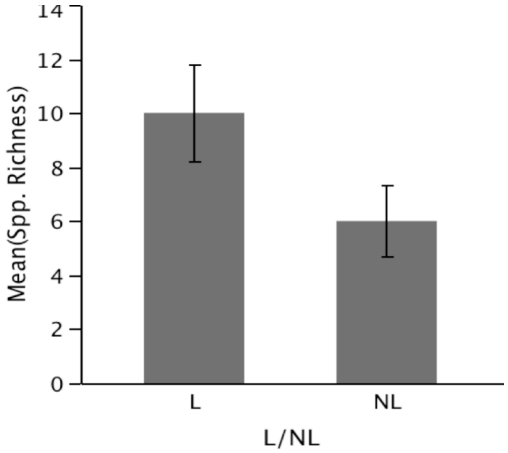

Fig. 4. Species richness is significantly greater in sites with *L. camara* presence (L) in comparison to sites without L. camara (NL) by paired sampling t-test ($p<0.0087$, N=10).

Germination experiment

No seeds germinated in any of the three light treatments within six weeks of planting. No signs of germination were found upon analyzing the potted soil after six weeks. Seeds remained either aborted or dormant.

Vegetative growth experiment

Leaf count growth did not differ significantly between the three light treatments (Treatment A-heavily shaded, Treatment B-lightly shaded, Treatment C-not shaded), though treatment B had the highest mean leaf number growth. Mean height growth significantly differed between the three light treatments. Mean height growth

was highest in light treatment A (heavily shaded) and lowest in light treatment C (not shaded) (Fig. 5). There were no significant differences of root mass growth and root mass to aboveground mass ratio between the three light treatments. The soil moisture of pots did not differ significantly between light treatments.

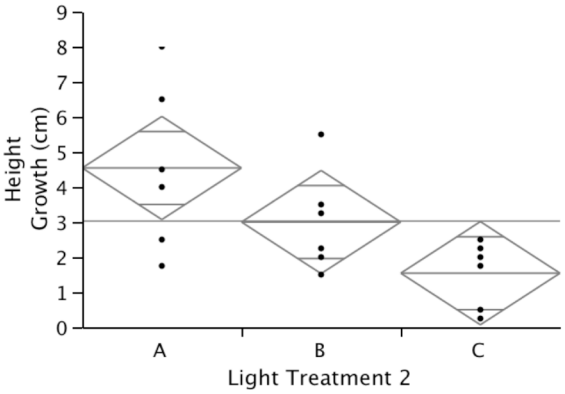

Fig. 5. The mean height growth differs significantly between light treatments. $P<0.0256$, $N=18$, R^2=value.

DISCUSSION

Because there is a significant area of roadside habitats occupied by *L. camara*, there is justified concern for the potential for the invasive species to displace and damage the remaining native habitats of Moorea, French Polynesia. The prevention of *L. camara* establishment may be effectively focused on areas where it may more likely establish, including areas of sufficient agricultural disturbance, soil moisture, slope, and shade.

L. camara appears to support a higher number of faunal species as compared to invasive species, *Wedelia trilobata* alone. The year-round flowering of *L. camara* in Moorea may account for a consistent biomass that may feed a faunal community that consumes the fruit, nectar, and leaves, adding a layer of structural complexity for faunal species to inhabit. Because *L. camara* often occurs simultaneously with *Wedelia trilobata*, the surveyed *L. camara* sites may have encompassed the species richness of a faunal community supported by both invasive species. The community supported by *L. camara* includes a number of invasive faunal species, including those of Formicidae and Apidae, which may have negative predatory effects on the native communities of Moorea. Future studies are needed to observe the interactions between invasive plant species and the faunal community they support, including aspects of species richness, species diversity, and native/invasive makeup of the community to assess the threat of *L. camara* and other invasive plant species on native faunal communities.

L. camara germination did not occur within six weeks of planting, though seed dispersal may still be an effective way for *L. camara* to establish in disturbed habitats due to the potentially large number of seeds produced by individuals year-round. In the vegetative growth experiment, the cuttings established without much difficulty under sufficient soil moisture and sunlight conditions. The heavily shaded light treatment was ideal for vegetative growth in terms of height, implying that vegetative growth in *L. camara* is shade tolerant to a certain degree, making *L. camara* establishment into shaded areas possible. Degraded forest edges with slight canopy damage may be vulnerable to *L. camara* establishment by vegetative growth and invasion.

Maintaining intact forests and decreasing anthropogenic disturbances including overstory removal may decrease the occurrence of *L. camara* on roadsides (Duggins & Gentle 1998), in addition to other invasive species such as *Wedelia trilobata*. Disturbed habitat created by roadsides may serve as starting points for *L. camara* to establish and spread into higher elevation and native habitats via roads and agricultural land where intermediate disturbance occurs through harvesting and grazing. This conclusion may be applicable to the management of higher elevation roads and gaps, where there is a higher occurrence of forest edge habitat types and intermediate disturbances (personal observation), by conserving remaining intact forest edges. The higher elevation areas of French Polynesia contain rare native habitats that are threatened by invasive species (Meyer 2004) and may be protected by the prevention of further invasive species establishment and expansion.

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DISTRIBUTION AND STAND DYNAMICS OF THE FALCATA TREE, *PARASERIANTHES (ALBIZIA) FALCATARIA* IN MOOREA, FRENCH POLYNESIA

ELISABETH LONG

Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA

Abstract. *Paraserianthes (Albizia) falcataria* is a dominant invasive alien tree species throughout the Society Islands, including on the island of Moorea, French Polynesia. Its invasive traits allow it to outcompete native vegetation and alter ecosystem level processes (Friedman 1994; Wagner et al. 1999; Sylvio 2007). No study to date has mapped the species' distribution on Moorea. This study uses geographic information systems (GIS) technology to map distribution and further analysis using Google Earth Pro shows that *P. falcataria* stands occur adjacent to disturbances such as roads, pine/other plantations, fields, and clearings 90.1% of the time. A subsequent stand level study characterizes 2 of the 202 mapped *P. falcataria* stands as dominated by non-native and invasive tree species and describes average diameter at breast height (dbh), trees per hectare (tpha), tree canopy levels by species, and understory vegetation composition in these stands. A comparison between *P. falcataria* stands and adjacent Caribbean Pine (*Pinus caribaea)* plantations finds differences in tree species composition and understory vegetation composition between these forest types, evidence of increased regeneration in the disturbed edge between Pine plantations and *P. falcataria* stands, and illustrates some of the tree's invasive characteristics.

Key words: invasive; agroforestry; forestry; Paraserianthes falcataria; Albizia falcataria; Falcataria moluccana; *distribution; mapping; GIS; disturbance; stand dynamics.*

INTRODUCTION

Biological invasions are increasingly prevalent worldwide and change ecosystems by causing species extinctions, habitat modifications, and altered ecosystem level processes (Vitousek et al. 1997; Sherley et al. 2000; Meyer 2000). Alien forestry and agroforestry trees can be very aggressive invaders. Such trees are planted because they grow faster than native species, are easier to manage silviculturally, possess greater seed availability, are better suited to planting on marginal lands, and many fix nitrogen (Richardson 1998). Their large seed banks, high seed viability and wide planting facilitate dispersal over large distances (Meyer and Malet 2002; McNeely 2004). Oftentimes, native vegetation competes poorly against these larger, hardier trees which can shade out other species with dense closed canopies and possess superior abilities to capture water and sunlight (Meyer and Malet 2002; McNeely 2004). Therefore, managing their capacity to invade is a critical conservation concern. The first step in effectively controlling invasions is mapping species distributions to provide a baseline for future monitoring and management.

Agroforestry invaders are particularly problematic on oceanic islands where they modify habitats and are partially responsible for high rates of extinction (Loope and Helweg 2004; Sherley et al. 2000). Invasives are implicated in more species extinctions (post-habitat destruction/modification) than any other cause, and these extinction rates are higher on islands than anywhere else in the world (Sherley et al. 2000). Species within delicate island ecosystems are particularly

prone to extinction and disturbance because here populations are small, isolated, and contain a large number of endemic species (Cox & Elmqyist 2000; Simberloff 2000; Hansen et al. 2002). Agroforestry trees threaten biodiversity in sensitive island ecosystems where they are often found in places that would otherwise be occupied by natural forests (McNeely 2004).

There are 38 invasive alien agroforestry trees across the Pacific Islands, 15 of which are noted as important invaders in French Polynesia (Meyer 2002). Most were planted after WWII with the advent of new afforestation policies (FAO 2003; Richardson 1998). Introductions have reduced structural diversity, increased forest biomass, altered nutrient cycling, and disrupted prevailing vegetation dynamics (Richardson 1998).

In Moorea, French Polynesia, two agroforestry trees, *Paraserianthes falcataria* and *Pinus caribaea* have become important invaders. *P. falcataria,* (Wagner et al. 1999) (synonyms *Albizia falcataria* (L.). Forberg (Little and Skolmen 1989) and *Falcataria moluccana* (Herbarium Pacificum 1998)) of the family Leguminosae is known commonly as Falcata in French Polynesia (it is called Albizia elsewhere). It is one of the most important threats to biodiversity in French Polynesia where it is classified as a "dominant invader," because it is widespread, forms dense stands, and significantly affects native biota (Meyer 2000; 2004). It is indigenous to Southeast Asia and invasive in the Cook Islands, French Polynesia, Guam, Hawaii and the Federated States of Micronesia (Meyer 2000; Elevitch and Wilkinson 2000). *P. falcataria* was introduced to French Polynesia for erosion control, reforestation, as a shade plant and windbreak in 1966 (Meyer 2000; FAO 2003; Gray 2007; Sylvio 2007). The need for a distribution study exists as few studies have mapped forestry trees in the Society Islands, and the current distribution of *P. falcataria* in French Polynesia is unknown (Meyer and Tetuanui 2000; Stoll and Capolini 2004).

Caribbean pine, *P. caribaea* plantations exist on Moorea, where the moderately invasive agroforestry tree is used for both erosion control and as a commercial species (Gray 2007; Sylvio 2007). Plantations disturb vegetation and break up canopy cover. Naturally occurring *P. falcataria* stands are associated with plantations edges and interiors (Sylvio 2007).

This study contributes to current vegetation surveys by mapping *P. falcataria* distribution on Moorea using GIS and Google Earth Pro. A subsequent categorization of the areas surrounding stands reveals the species is heavily linked to disturbed areas. A stand level study describes 2 of the 202 mapped *P. falcataria* populations. Measures of stand species composition, stem densities, average dbh, and a canopy description demonstrate that *P. falcataria* lives in areas of low diversity and endemism, dominating other species with which it co-occurs. Finally, a comparison of *P. falcataria* stands to adjacent *P. caribaea* plantations in the Opunohu Valley and the edge between the two species reveals differences in species composition and understory vegetation percentages that show the species' invasive potential.

METHODS

Study species

Paraserianthes falcataria grows up to 40m tall at all elevations on Moorea and has smooth or slightly warty white/gray bark (Meyer 2000; Meyer 2004). Its lateral branching pattern and large spreading crown allows it to quickly dominate at the canopy level and shade out competitors in the understory (Wagner et al. 1999). Growth rates can be as much as 4.5m per year and the tree's lightweight seed pods are wind-dispersed, establishing forests wherever seed trees are present (Little and Skolmen 1989; Elevitch and Wilkinson 2000). The tree is considered noxious throughout its non-native range because it consumes a great deal of water and

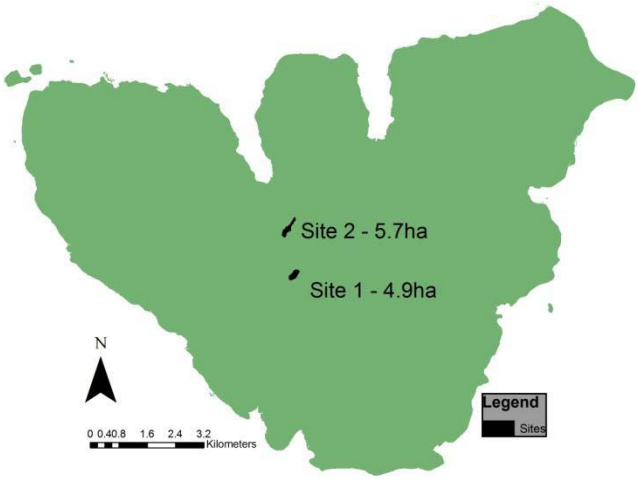
competes with native species in the remnant of natural forests (Friedman 1994; FAO 2003). The species' large roots can also alter soil erosion patterns and old or poorly rooted *P. falcataria* commonly fall, destroying native plants in the understory and leaving gaps where exotics can invade (Friedman 1994; Sylvio 2007). *P. falcataria* establishment is implicated in extinctions of native species because after it takes root, it allows other non-native species to take over native habitat (Sumida et al. 2005). The US Forest Service advises citizens in Hawaii with *P. falcataria* on their lands to not bulldoze the land because the species establishes most rapidly in areas where there has been disturbance (Sumida et al. 2005). In Moorea, this same phenomenon is observable, as *P. falcataria* is most often adjacent to disturbed vegetation along areas such as roads and pine plantations.

There are 253 ha of Caribbean pine on Moorea and the two species are tightly associated throughout the island (SDR 1981). *P. falcataria* has capitalized upon disturbance in and around plantations where it regenerates naturally (Gray 2007; Sylvio 2007). Certain characteristics, such as increased *P. falcataria* stem densities, along the edges between *P. falcataria* stands and *P. caribaea* plantation are interesting and display *P. falcataria's* invasive qualities.

Study site

Moorea, French Polynesia is a high oceanic island located in the Society Islands archipelago (17°52S, 149°56W), 20km southwest of Tahiti. It is 134 km^2, or 13,400 ha in area. The volcanic island is approximately 1.5-2.2 million years old and its tallest peak, Tohiea, extends above 1200m (ORSTOM 1993). Moorea experiences rainfall between 3000-4000mm per year (Pasturel 1993).

P. falcataria stands across the island were surveyed for the mapping portion of this study. Two sites in the Opunohu Valley were measured in detail for the second portion of this study. Both sites consisted of three forest types: *P. falcataria* (Pafa) type, edge type, and *P. caribaea* (pine) type. Site 1 was located at the base of Mt. Mouaroa and Site 2 was located uphill from the Opunohu Pasture (Map 1). In this study, *P. falcataria* forest type is defined as a stand where the species forms a dense, closed canopy in the overstory, edge type includes a mix of *P. falcataria* and *P. caribaea* stems at the edge of a plantation, and pine type is within a plantation and lacks a dominant *P. falcataria* overstory. Sites were chosen because they were both adjacent to pine plantations in the same watershed. However, the plantation in Site 1 was planted before the plantation in Site 2, and is not managed for timber extraction, as Site 2 is. Site 1 is one of the currently declassified and inaccessible plantations, while Site 2 is actively managed and accessible by motor vehicle (Sylvio 2007).



Map 1: Map of study sites 1 and 2 in the Opunohu Valley.

Mapping and stand measurement methods

Because *P. falcataria* is an emergent tree, it always achieves dominance in the overstory and can easily be identified in aerial photos. Using Google Earth Pro, polygons were drawn around *P. falcataria* stands and verified with data collected in the field. Stands were defined as an area with more than five *P. falcataria* trees forming a dense canopy in the overstory. Surveys were conducted between

September 20 and November 14, 2007, when nearly all main roads and accessible trails were traveled. Trails hiked on-foot included the Three Coconut's Pass trail, Mt. Rotui trail, Mt. Mouaputa trail, Paopao to Vaiare trail, Three Pines trail, and Cross-Island trail. A handheld Garmin GPSMAP 60CSX GPS unit was used to map trails and stands on foot. Tracks and waypoints marked served as ground-truthing data, and were used in conjunction with aerial photos. A species distribution map was created by converting polygons drawn in Google Earth Pro to shapefiles with Zonum's Kml2shp software. These data layers were then imported into ArcGIS's ArcMAP software. Polygon areas were calculated using Hawths Tools.

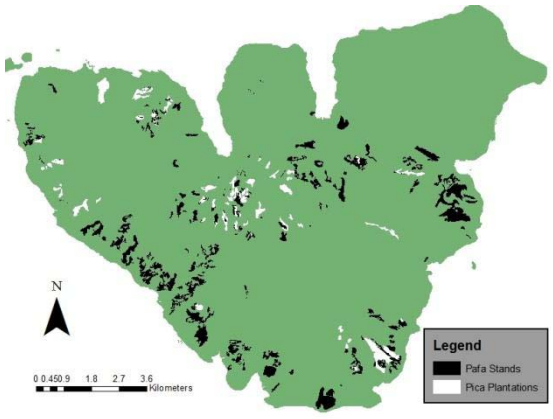
In order to both characterize individual *P. falcataria* stands and describe differences between *P. falcataria,* edge, and *P. caribaea,* fixed-size, nested survey plots were established at both sites. Three transects were run in each site, one through each stand type. Eight 100 m^2 (.01ha) square plots were located along each transect at variable random distances (48 plots total). Each large stem (above .3m) was measured in the entire plot, and each small stem (below .3m) was measured in a smaller 10m^2 nested plot. Each stem's species identity, diameter at breast height (dbh) (using a dbh tape), and canopy position was recorded. Plot canopy cover was estimated using a densitometer from plot center. I quantified the following at each site: small and large tree species composition, trees per hectare (tpha), average dbh by species, canopy position by species, and understory vegetation composition. Trees at different positions in the canopy were classified as either: emergent trees (those which emerge above the canopy level and receive the largest amount of sunlight), canopy trees (those which grow together to form the canopy), or intermediate trees (those small trees which occur under the canopy). Understory vegetation was sampled within each plot by randomly placing five 1m^2 quadrats to determine percent cover of fern, herbaceous material, litter, grass, soil and tree stems.

Various statistical tests run with JMP IN software version 5.1.2 were used to examine differences in stand characteristics between forest types. I used Shannon-Weiner diversity indices to describe small and large tree species diversity in all 48 plots, and ANOVA to compare indices by forest type. ANOVA was also used to look at variation in seedling number by forest type, with a Tukey-Kramer post hoc test. A Wilcoxon signed-rank test was used to test for differences in stems of each individual species by forest type, and a Chi-Square test was used to determine whether understory vegetation differences between forest types were greater than expected by chance. Multiple regression analysis was used to show positive correlations between certain vegetation types and seedling establishment.

RESULTS

Species distribution

202 *P. falcataria* stands were identified throughout the island with a total area of 577ha, or 4.3% of the island's total area. These stands are concentrated largely in the Opunohu Valley and along the coast in the lower half of the island (Map 2). *P. falcataria* stands are tightly associated with disturbed areas. 90.1% of *P. falcataria* stands are directly adjacent to visible habitat disturbance, while 9.9% were located in areas without visible fragmentation at the canopy level. Of the 90.1% in disturbed areas, 30% are adjacent to roads, 34% adjacent to pine/other plantations, and 59% adjacent to clearings, fields or pastures (Figure 1).



Map 2: Distribution of *P. falcataria* stands (in black) and *P. caribaea* plantations (in white) on Moorea.

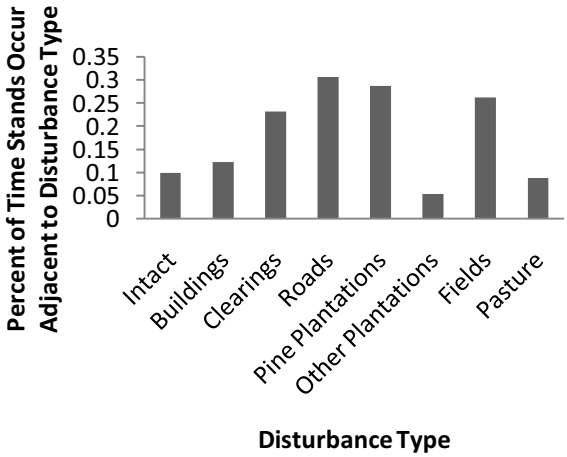


Figure 1: Stand disturbances adjacent to the 202 mapped *P. falcataria* stands on Moorea. 9.9% of stands are located in areas with intact vegetation, while 90.1% are located directly adjacent to disturbances to the vegetation. Some stands were adjacent to multiple disturbance types.

Of the 253ha of pine plantations documented by the government (SDR 1981), 218.3ha, or 86.3% were visible on Google Earth's aerial photos. 198.9 ha (91.1%) of all visible pine plantations had either adjacent stands of *P. falcataria,* or several visible trees of the species growing into the canopy within plantation.

P. falcataria Stand Descriptions

The two measured *P. falcataria* stands are dominated by large trees of the species which coexist with other species. *P. falcataria (Pafa)* co-occurred with *Neonauclea forsteri (Nefo), Hibiscus tiliaceus* ssp. *hastatus (Hiti), Mangifera indica (Main), Miconia calvescens (Mica), Pinus caribaea (Pica),* and *Spathodea campanulata (Spca)* in Site 1. Site 2 was similarly diverse, with all of the above species except *Pinus caribaea* present in *P. falcataria* stands (Figures 2 & 3). *P. falcataria* was the predominant large tree species in both sites, while *N. forsteri* and *S. campanulata* were the predominant small species in site 1 and *P. falcataria* and *S. campanulata* in site 2. There were 312.5 large *P. falcataria* per hectare at site 1 and 575 at site 2. *N. forsteri* and *S. campanulata* were the densest species at site 1, with 2000 and 1000 tpha respectively. *P. falcataria* and *S. campanulata* were the densest at site two at 2500 and 2375 tpha respectively (Figures 4&5).

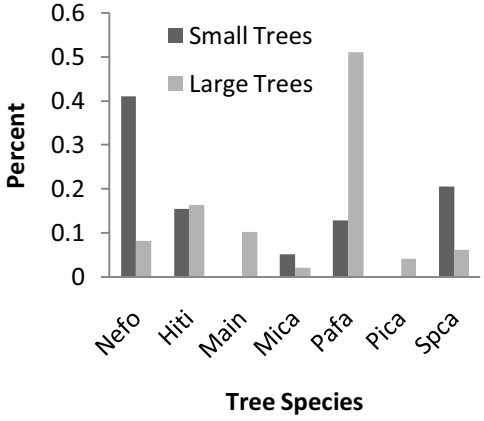


Figure 2: Site 1 *P. falcataria* stand large and small tree species composition percentages.

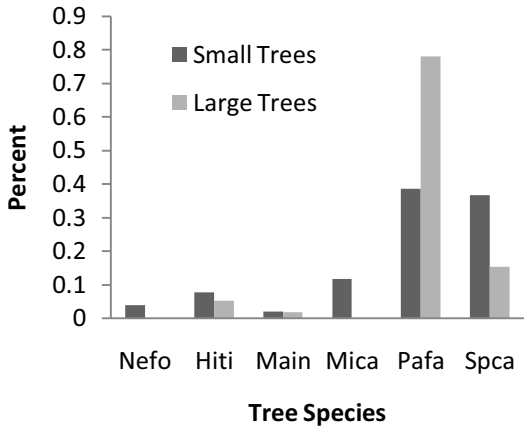


Figure 3: Site 2 *P. falcataria* stand large and small tree species composition percentages.

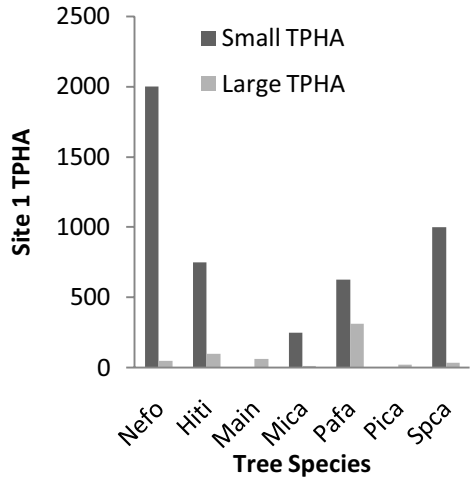


Figure 4: Site 1 *P. falcataria* stand trees per hectare (TPHA) by individual species.

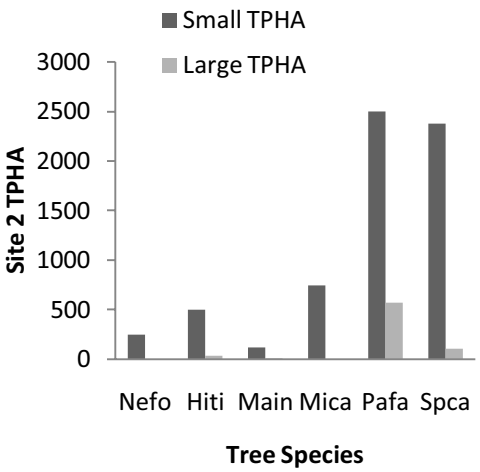


Figure 5: Site 2 *P. falcataria* stand trees per hectare (TPHA) by individual species.

The average large *P. falcataria* stem dbh at site 1 was 1.64m, double the .88m average at site 2. However, average small stem dbh at the two sites were very similar (.16 at site 1 and .13 at site 2). *P. falcataria* stems had the largest average dbh of any species at both sites, with *M. indica* and *S. campanulata* second largest at sites 1 and 2 (Figures 6 & 7). Along with largest average dbh, *P. falcataria* trees are the only emergent species in the canopy. No other species in the two stands measured emerge, and are either canopy trees or intermediate trees below the canopy (Figure 8). *S. campanulata* stems are most often in the lowest canopy levels, along with *N. forsteri* and *M. calvescens.*

Litter (i.e. leaves and sticks) predominated the understory vegetation in *P. falcataria* forest in both sites 1 and 2. Various fern species, including *Dicranopteris linearis* var. *linearis* and *Angiopteris evecta* and herbaceous plants such as the invasive raspberry *Rubus rosifolius* and *Wedelia trilobata*, and composed the next highest percentages of understory vegetation. Smaller amounts of grass and bare soil were found in quadrats within *P. falcataria* forest type (Figure 9).

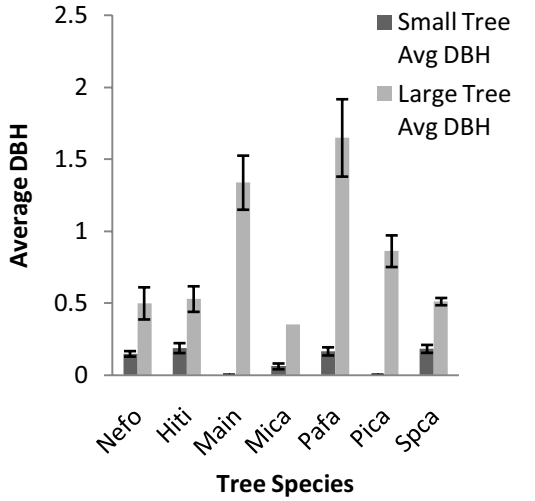


Figure 6: Site 1 *P. falcataria* stand average tree dbh by species with standard error bars.

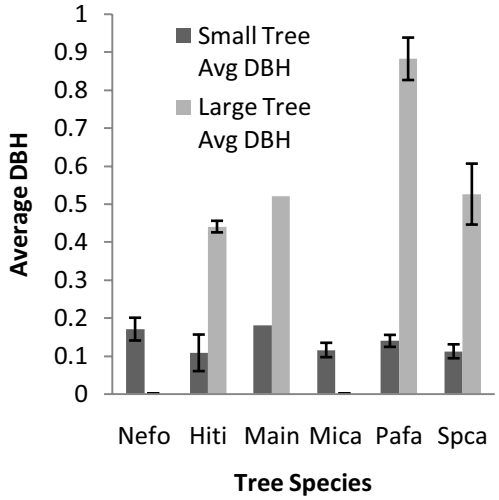


Figure 7: Site 2 *P. falcataria* stand average tree dbh by species with standard error bars.

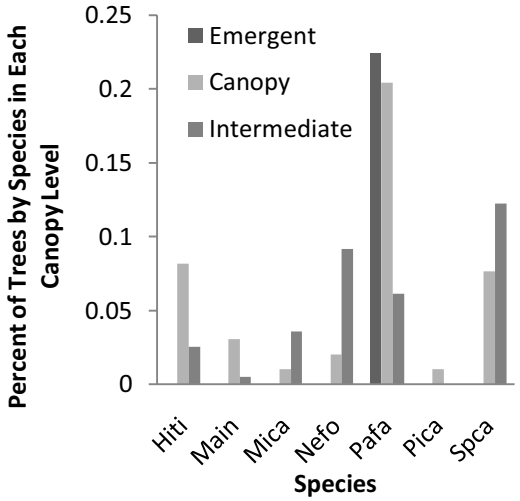


Figure 8: Percent of each tree species present in *P. falcataria* stands (sites 1 and 2) in each canopy layer (Emergent, Canopy, and Intermediate).

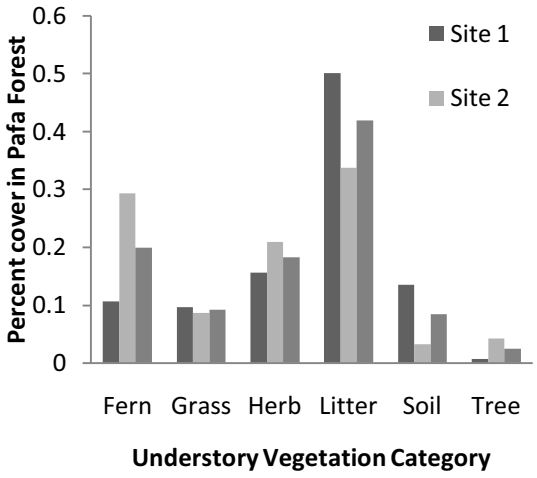


Figure 9: Percent of each understory vegetation type present in *P. falcataria* stands at sites 1 and 2.

Forest Comparison Study

Edge forest type had the greatest total number of stems, at 235 between sites 1 and 2, while *P. falcataria* type had 199 stems, and *P. caribaea* 127 stems. *P. falcataria* occurred most frequently in edge type, with 133 stems compared to 96 in *P. falcataria* and 41 in *P. caribaea* types (Figure 10). Overall diversities

calculated using the Shannon-Weiner diversity index were low, with diversity in pine type lower than edge, which was lower than *P. falcataria* type (Figure 11). *P. falcataria* seedling establishment was greatest on average in edge type at 4.4 seedlings per plot, but smaller in *P. falcataria* and *P. caribaea* (Figure 12). Small *P. falcataria* stems occurred most often in edge forest type as well, with fewer in *P. falcataria* and *P. caribaea* type (Figure 13). However, *P. falcataria* forest type is home to more large stems of the species than either edge or *P. caribaea* type (Figure 14). Edge forest type had the largest tpha at 14,637.5, compared to 12,725 in *P. falcataria* type and 3,837.5 in *P. caribaea* type (Figure 15). Small *P. falcataria* stems in edge forest type contribute most heavily to high tpha numbers for that forest type.

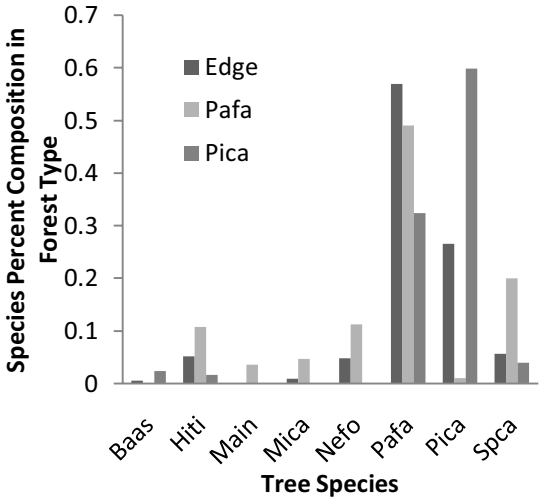


Figure 10: Percent tree species composition in each forest type.

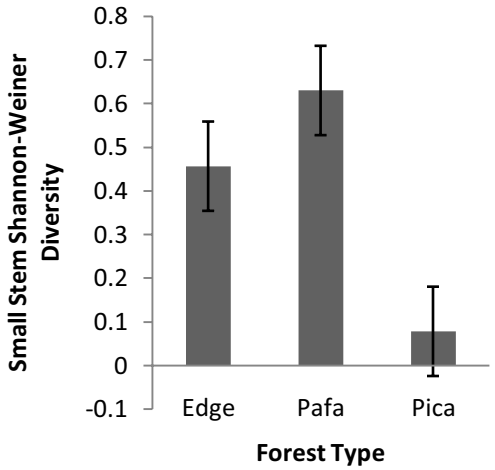


Figure 11: Mean Shannon-Weiner small stem diversities of all 48 plots by forest type. Pica type is significantly less diverse than either Edge or Pafa type with standard error bars. (ANOVA analysis. R^2=.252, p<.0014, DF=47.)

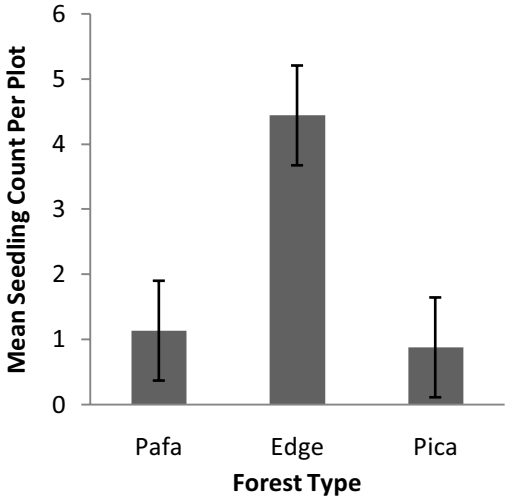


Figure 12: Mean seedling count for each plot by forest type with standard error bars. (ANOVA analysis. R^2=.222, p<.0035, DF=47.)

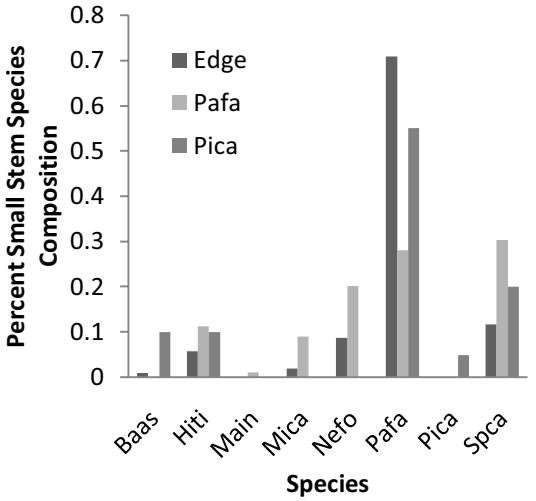


Figure 13: Small Stems of each tree species by forest type.

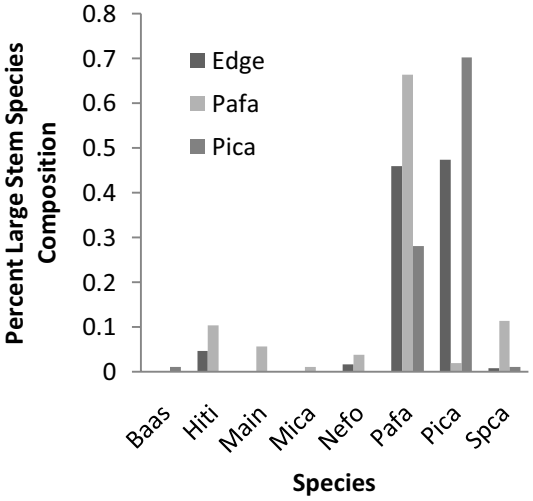


Figure 14: Large Stems of each tree species by forest type.

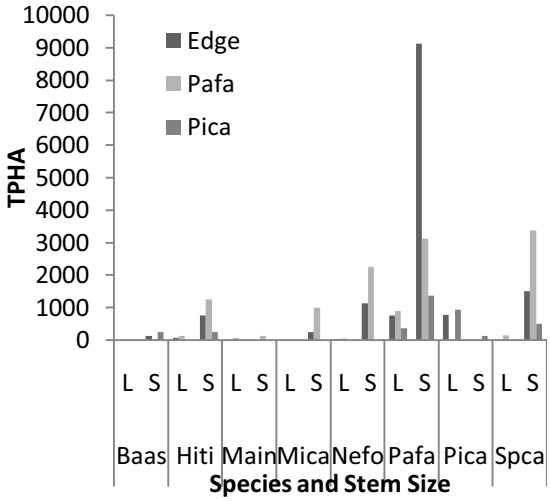


Figure 15: Trees per hectare (tpha) shown for large and small stems of each tree species by forest type.

Understory vegetation cover differs between forest type (Figure 16). There is significantly more fern in *P. caribaea* type than in either other types. Grasses are also at similar levels in edge and Pine type, but lower in *P. falcataria* stands. The most herbaceous cover was found on the edge, while the most litter was found in *P. falcataria* type. Little open soil was found. Trees were found in some of the plots and were separated out.

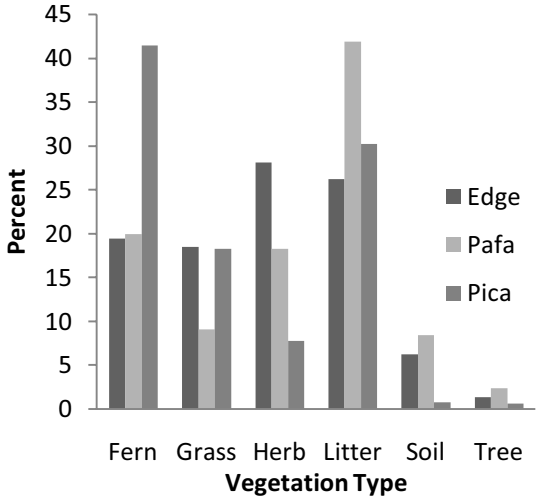


Figure 16: Understory Vegetation Percentages by Forest Type

DISCUSSION

Mapping Study

Data from the mapping study reveal a positive relationship between disturbance and the occurrence of *P. falcataria* stands. The characteristics of disturbance that enable *P. falcataria* seedling germination and subsequent stand establishment are likely more important than the particular category of disturbance (i.e. plantation vs. road vs. clearing). These characteristics include open soil in which seedlings may easily establish, breaks in the forest canopy that allow greater sunlight availability, and greater water availability. Seedlings observed in Moorea were most often found establishing in areas where there was open soil or some grass/herbaceous growth, fairly level ground, and parent trees in close proximity. Therefore, identifying disturbed areas could help managers wishing to control *P. falcataria's* advancement and predicting where species will spread. Different disturbance types could be studied and *P. falcataria* invasion could be further characterized in Moorea.

Monitoring the species' distribution over time would provide interesting information about rate and patterns of spread. Also, recording vegetation change and growth in *P. falcataria* stands would provide valuable information about the species' impact on the other species with which it coexists.

This mapping study could be improved with access to better aerial photography because although most of Moorea was visible, cloud cover on Google Earth's aerial photos prevented analysis of 1,114.5 ha, or 8.3% of the island's area. This area was calculated with the same techniques as stand area. Aerial photography without cloud cover and with an infrared layer would allow a more accurate description of *P. falcataria* stand distribution.

Pafa Stand Study

The differences between average dbh of large *P. falcataria* stems in sites 1 and 2 suggests the trees in these sites differ in age, as dbh is a reliable proxy for age. Because these stands are most likely different ages, species compositions, tpha, and average dbh were graphed separately for the two sites. However, it is useful to describe both because the island's *P. falcataria* stands vary in age.

Stand species composition was measured because is an important measure that tells about forest diversity, levels of endemism, and the presence of rare or endangered species. The species present in the two measured *P. falcataria* are largely introduced. *Pinus caribaea, M. indica, P. falcataria, M. calvescens, S. campanulata*. *P. caribaea and M. indica* have been classified as moderately invasive in some of the Society Islands, though this phenomenon has not been observed in Moorea (Sherley et al. 2000). *P. falcataria, M. calvescens, and S. campanulata* are all on the "most significant" invaders of French Polynesia (Sherley et al. 2000; Meyer 2004). *N. forsteri* and *H. tiliaceus* are the only two native species found in sites 1 and 2. *P. falcataria* has been implicated in enabling the establishment of other non-native species and it is possible that a similar phenomenon is occurring in Moorea, although this hypothesis would have to be tested through a long-term experiment monitoring a change in species composition over time. Regardless, the two *P. falcataria* stands measured are not high in species richness, endemism, and do not have many rare species present.

Trees per hectare is an interesting measure to quantify in a stand because it can describe the intensity of competition for resources such as water, light, and nutrients between individuals and tree species, as well as how much a stand is being used. Growth can slow down as forests get denser. Although *P. falcataria* stands are dominated by large trees of the species, small stems of other species are very dense. This disparity suggests that *P. falcataria* is an effective competitor as it is able to capture sunlight and grow larger than other

stems. Its presence may also facilitate the establishment of large numbers of other invasive species (i.e. *S. campanulata).* Similarly, it has the largest average dbh of all species present in its stands which reveals that it is able to put on more biomass than any other tree species in these areas. It is able to obtain enough energy to put on mass upward and outward faster than any other species in either site. An analysis of species by canopy levels quantifies the observation that *P. falcataria* competes well for sunlight across the island as large emergent stands are highly visible. It is part of *P. falcataria's* competition strategy to reach the canopy and emerge from it in order to receive the maximum amount of available sunlight for photosynthesis.

Percent cover by understory vegetation type is an important measure which could affect *P. falcataria* seedling establishment. Seedlings were observed commonly along trails throughout the island and in other areas where soil was disturbed. Seedlings also visibly predominated in areas where bare soil was covered with sparse litter and light herbaceous plants. Multiple regression analysis correlating seedling occurrence to understory vegetation type in all three forest types reveals a significant trend between increased grass and open soil cover and numbers of seedlings per plot. These correlations should be further studied in the future to examine factors leading to seedling establishment.

Forest Comparison Study

Paraserianthes falcataria stems are predominant in both *P. falcataria* type and edge type. Edge and pine types are least diverse, with *P. falcataria* co-occurring with very few species in both of these forest types. The graph of small stems shows many small stems in edge type, with *P. falcataria* unevenly distributed in the edge, while the species are more evenly represented in *P. falcataria* type. Nearly all small stems in pine type are either *P. falcataria* or *S. campanulata*. This is interesting because it shows the invasive potential of both species.

Although there are trends in the number and species of small tree species between the three forest types, results from a Wilcoxon test showed the data to be statistically insignificant. Further sampling and a larger sample size would have allowed for more conclusive results. ANOVA could have been used with a different sampling design because there were not enough of each small species per plot for this comparison.

A comparison using ANOVA between diversity indices for small stems calculated at each plot reveals significant differences between the mean diversity index in pine type compared to either edge or *P. falcataria* type (R^2=.252, p<.0014, DF=47). That Pine plantations are significantly less diverse than the other two forest types is hardly surprising – these plantations are meant to be monocultures. However, what is interesting here is that species composition graphs show *P. falcataria* stems in plantations more often than any other species (Pine excluded). *P. falcataria* stems are able to invade and grow in the midst of plantations where other trees are clearly unable to compete or capitalize on the disturbance caused by plantations. Managers wishing to halt *P. falcataria* spread should take into account the disturbance-adapted characteristics of the tree and take care when implementing projects that cause disturbance where parent trees are located, or where seeds could easily be dispersed.

Significant differences in mean diversity indices were not found between forest type for large stems using the same statistical tests (R^2=.074 and p<.1744, with DF=47). However, small stem diversities were more interesting in this analysis because in conjunction with species composition and density data, they show which species are regenerating in highest numbers and which species may be successful invaders if and when these small stems survive.

Seedling distribution by forest type was found to be significant using ANOVA.

Seedling numbers in edge plots were significantly higher than seedlings in either *P. falcataria* or *P. caribaea* types (R^2=.222 and p<.0035, with DF=47). It is possible that higher numbers of seedlings and small stems occur in edge type because the edge is the most disturbed habitat. Edges may be important in *P. falcataria* spread as the tree colonizes the disturbed area and is able to move further into more intact vegetation, or throughout plantations, if allowed. It is possible that movement into plantations may cause a detrimental economic effect, as timber harvesters and managers are forced to cut this economically undesirable species (see Appendix A for more information). Movement into more intact and especially native habitat is most certainly undesirable if species diversity maintenance is a management objective.

Differences in understory vegetation by forest type (analyzed using a Chi-Square test) as a whole are statistically significant at both sites 1 and 2, with p<.0001. The sum of vegetation between sites by each forest type was also significant (p<.000001) Levels of grass and litter differ most between forest types, and levels of fern are similar in edge and *P. falcataria* type, but higher in *P. caribaea* plantations. These differences are important because understory vegetation prevalence has an impact on seedling establishment. Seedlings were observed in greater numbers in areas with grass and open soil. *P. falcataria* seedling establishment was observed to be rare in the center of *P. caribaea* plantations where a thick pine needle litter/fern layer predominated.

Multiple regression analysis was run using seedling and understory vegetation data from all 48 plots. A significantly correlated, positive trend was found between increased seedling establishment and increasing amounts of two vegetation types: grass and soil. As amounts of grass found in each 100m^2 plot increased, so did the number of seedlings found in the plot (p<.0034). An even more significant relationship was found between increased amounts of open soil found in plots and increased number of seedlings (p<.0001). The entire model with both vegetation types had p<.0001 and an R^2=.475. Grass was most prevalent in the edge and pine understory. However, many less seedlings were seen in pine than in edge type, likely because grass co-occurs with thick *Dicranopteris linearis* fern cover and a thick pine needle duff layer in Pine plantations. Grass tended to grow in open soil in edge and *P. falcataria* type, and both of these types lacked thick fern and needle cover.

Seedling data were collected between 10/9 and 11/1, but seedling growth and germination was observed to have multiplied several fold at site 1 by 11/15. Although new seedling growth could not be quantified in this paper, *P. falcataria* and edge type were observed to have similar numbers of seedlings by 11/15, though there were significantly fewer in Pine type. Several 1m^2 areas on the trail at Site 1 had over 100 seedlings in one quadrat alone. It appears that several factors including the availability of open soil, plot slope, proximity to a parent tree, sunlight availability, and proper water drainage have effects on seedling growth and establishment. This phenomenon should be examined more closely.

Suggestions for Future Research

Seedling measurements were taken at each of the 48 measured plots. However, because much larger numbers of seedlings were observed in mid-November than at any other time, it appears there were certain factors at play which were not described by this study. A *P. falcataria* seedling study examining these various factors should be explored. A germination study could test whether soil types, soil moisture, canopy cover, or other variables affect germination rates.

Examining soil nutrient levels and its impacts on co-occurring vegetation would also make an interesting study because *P.*

falcataria fixes nitrogen and might greatly affect neighboring plants because of this property.

Finally, continued monitoring and a future mapping study could be done to look at *P. falcataria's* advancement over time. Records on *P. falcataria* planting in Moorea might be obtainable through the SDR, just as pine documents were available (although I was unable to obtain these records for this study). Better aerial photography might be available through the French Polynesian government and a similar analysis could be done with this species or another invasive species. It would also be interesting to note *P. falcataria* movement, especially into higher elevation, more intact forests on Moorea (One tree was observed at 850m up Mt. Rotui on a field expedition for this study).

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APPENDIX A

History of the species Paraserianthes falcataria and Pinus caribaea in Moorea.

P. falcataria was introduced to the Society Islands widely beginning in 1966 when a Water and Forests section was created within the Agricultural Service department (FAO 2003; Gray 2007). The department's main aim was to reforest land subject to erosion or previously destroyed by bush fires, to improve soil through nitrogen-fixing (FAO 2003). *P. falcataria* was the principal tree species used in this effort and 2375 ha (2469ha reported by Meyer and Tetuanui 2000) were planted across the islands (50% on the Windward Islands) (FAO2003; Gray 2007). There are 161 ha of *P. falcataria* plantations on the windward Society Islands, though data was not available on Moorea's individual distribution (Meyer and Tetuanui 2000).

Paraserianthes falcataria was not introduced for its wood on Moorea, and is used only for making palettes because it lacks the strength necessary in construction wood (Gray 2007; Sylvio 2007). Present-day species distribution on individual islands is unknown, though a 2003 vegetation study was completed in 2004 using aerial photos in the Opunohu Valley (Stoll and Capolsini 2004). A need for more detailed vegetation mapping of forestry and agroforestry species exists as few studies have created vegetation maps of forestry trees in French Polynesia, and to date no study has mapped the distribution of *P. falcataria* in French Polynesia (Meyer and Tetuanui 2000).

The first *Pinus caribaea* plantations on Moorea were planted in the Opunohu Valley beginning in 1967 (Sylvio 2007; SDR 1981). The species itself was introduced from the western Antilles and Central America after a new forestry policy was implemented 1977, beginning a pine plantation program with the intention of providing saw logs for local use (FAO 2003). Records from the Societe de Development Rural (SDR) show 69.27ha of government plantations on the island (26 sites), all planted between March, 1967 and June 1978. These records also show 183.686ha of pine planted on private properties between February 1971 and January 1988 over 28 sites (Sylvio 2007; SDR 1988). These plantations were established on degraded moors, covered largely with *Gleichenia, Melinis, or Miscanthus* ferns as not to compete with other uses (Gray 2007; Sylvio 2007; FAO 2003). Approximately 50% of these plantations are currently declassified because they were planted on inaccessible grounds with very steep slopes (FAO 2003; Gray 2007).

The species has been documented as a moderate invader of the Society Islands (Meyer 2000), though is neither considered invasive in Moorea, nor worldwide (Z score of -0.47) (Meyer 2002; Rejmanek and Richardson 1996).

THERMAL ECOLOGY AND HABITAT SELECTION OF TWO CRYPTIC SKINKS (SCINCIDAE: *EMIOA CYANURA, E. IMPAR*) ON MO'OREA, FRENCH POLYNESIA

MATT T. MCELROY

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. I studied the habitat selection and thermal biology of two cryptic South Pacific skinks (*Emoia cyanura* and *Emoia impar*) in order to determine whether or not differences in thermal preference affect habitat partitioning. I measured sun exposure and thermal characteristics of microhabitats selected by each skink, and then quantified preferred substrate temperatures and preferred body temperatures in a laboratory thermal gradient. Compared to *E. impar*, *E. cyanura* inhabited areas with open canopy cover, and selected significantly warmer substrates in the field and lab setting. *E. cyanura* also had a significantly higher preferred body temperature that *E. impar*. Furthermore, *E. cyanura* had significantly less variability in preferred body temperature than *E. impar*. These findings up hold Huey and Slatkin's (1976) theory on the costs and benefits of lizard thermoregulation, and support the hypothesis that differences in thermal preference provide *E. cyanura* and *E. impar* with a mechanism for habitat partitioning.

Key words: lizards, skinks, microclimate, microenvironment, resource partitioning, thermoregulation, thermal preference, thermal specialist, thermal generalist, substrate selection, Squamata

INTRODUCTION

Morphologically similar species often share ecological and physiological characteristics (Pianka 1973). Where such species occur in sympatry, limited resources will drive species to niche partition in order to reduce competition. Competing lizards partition resources along at least one of three axes: habitat, food, and time of activity (Pianka 1975). While lizard ecology has generally been considered in terms of niche partitioning and biotic interactions, few studies have been done on the relationship between thermoregulatory needs and habitat selection (Adolph 1990, Grover 1996)

As ectotherms, lizards must maintain a preferred body temperature in order for optimal physiological function (Bennet 1980, Huey 1982, Ji et al. 1996). Lizards are known to accomplish this by shuttling between sunny and shady substrates, changing their position in relation to the sun, and limiting their activity to times of day when the appropriate thermal environment is present (Grant 1988, Heath 1970). Furthermore, for small lizards with little thermal inertia, there is likely an increased importance to select substrates with temperatures approaching their preferred body temperature (Bartholomew 1982). Thus, lizards may finely partition habitat based on thermal microenvironments, reducing competition in sympatric assemblages of morphologically and ecologically similar species.

Recently, the Brown-Tailed Copper-Striped Skink (*Emoia cyanura*) was split into two cryptic species, *E. cyanura* and the Blue-Tailed Copper-Striped Skink (*Emoia impar*), based on morphological (Ineich and Zug 1991) and biochemical (Bruna et al. 1995, Guillaume et al. 1994) analysis. The two species occur in sympatry on many islands in the South Pacific, but quantitative data shows that *E. cyanura* occurs primarily in open canopy habitat (beach and disturbed) while *E. impar* prefers closed canopy habitat (coastal and interior forest) (Bruna et al. 1996, Schwaner and Ineich 1998). This distribution pattern could result from competitive exclusion interactions between the species, or from differences in thermal preferences (Bruna et al. 1996). Furthermore, if physiological requirements influence *Emoia* distributions, it is unclear whether sympatric assemblages of *E. cyanura* and *E. impar* result from physiological similarities in thermal requirements that force individuals to converge on one habitat type (Adolph 1990), or whether the two species are finely partitioning the microhabitat based on

differences in thermal preference (Roughgarden 1981, Hertz 1992,)

In this study, I explored the relationship between microhabitat selection and preferred body temperature of two closely related, morphologically similar skinks, *E. cyanura* and *E. impar*, on the island of Mo'orea, French Polynesia. First, I measured the thermal properties of microhabitats selected by each species in sympatric assemblages. Then, I quantified each species' selected substrate temperature and preferred body temperature (T_{pref}) in a thermal gradient in the laboratory. Using these data, I aim to (i) see if there are differences in thermal physiology between *E. cyanura* and *E. impar*, (ii) investigate the thermal properties of field substrates selected by each species, and (iii) determine whether or not such interspecific physiological differences provide a mechanism for habitat partitioning.

METHODS

Study site

Experiments were conducted on Mo'orea, French Polynesia (17° 30'S, 149° 50'W) from October 16 to November 14, 2007. Mo'orea, a volcanic island located in the Society Archipelago, encompasses an area of 134 km^2 and has many high peaks, including the highest, Mt. Tohivea (1207 m). The interior of the island is comprised of mountains and valleys covered in closed canopy forests with vegetation including Tahitian Chestnut (*Inocarpus fagifer*), Hibiscus (*Hibiscus tiliacious*), African Tulip Tree (*Spathodea campanulata*), Screw Pine (*Pandanus tectorius*), Tree Fern (*Angiopteris evecta*), and a variety of other ferns. Vegetation in open canopy and agricultural areas along the coast include Coconut (*Cocos nucifer*), Indian Almond (*Terminalia catappa*), Hibiscus, and a variety of ferns and grass.

Habitat characteristics and field substrate selection

Patches of skinks were observed along the Three Coconut Trail at the Belvedere, Mare Mare Kellum's property at PK 17.5, the Hati'tia center at PK 11.5, and in coastal coconut groves near Vaiare. Patches were selected based on lizard abundance and accessibility. At each patch I recorded i) landscape (interior forest, forest trail, coastal forest, agricultural area), ii) vegetation present, iii) percent substrate present (leaf litter, rocks, fallen branches), iv) sun conditions (overcast, direct sun, filtered sun), and v) percent canopy cover. Percent canopy cover was determined using a canopy densiometer.

During sunny days from 900-1500 sites were observed and digital photographs (200mm focal length, D40x, Nikon Inc.) were taken during a 10-minute scan for sun basking skinks within each patch. Following each scan, substrate temperatures of both shaded and sun exposed rocks, logs, and leaf litter were taken using a non-contact laser thermometer (MiniTemp6, Raytek, USA). Each photograph provided information for skink identification, substrate selection, sun exposure (sunny or shaded), and time of day. Substrate temperatures taken following scans were matched with photographs of skinks, and the photographs from each site were used to determine the species composition present there. Skinks in photographs were identified based on three visible characteristics: 1) absence or presence of an epiphyseal eye, 2) fused or unfused mid-dorsal scales, and 3) bluish or greenish tail color (Bruna, 1995). Because of individual variation, at least two of the three characteristics needed to be visible in order to identify a skink to species.

Thermal profiles of substrates used by skinks were created using a non-contact laser thermometer on rock, log, and forest floor leaf litter where skinks were sighted. Surface temperatures were recorded every 15 seconds at noon for at least five minutes to show variability in substrate surface temperature.

Preferred laboratory temperatures

During the field study, 40 skinks (*E. cyanura*: n = 20, svl = 48.4 ± .84 mm, weight = 2.29 ± .12 g; *E. impar*: n = 20, svl = 45.05 ± .64 mm, weight = 1.68 ± .06 g,) were captured both by hand and by strategically placed Victor rat glue traps. Upon capture, skinks were removed from traps using vegetable oil (Bauer 1992), and transported back the laboratory at the Richard B. Gump Station. Skinks were placed in a terrarium (80 cm x 43 cm x 52 cm) with gravel, leaf litter, and drinking water to imitate natural habitats. Skinks were kept overnight, and lab test were performed the following

morning. Two 100 W light bulbs were suspended 15 cm above a separate terrarium (57 cm x 41cm x 38 cm) with gravel, basking rocks, and leaf litter to create a thermal gradient of 25-60°C. The day following capture, individual skinks were placed in the thermal gradient, and observed during a 10-minute focal watch. Substrate temperatures in the cage were taken using a Rayetet Mini non-contact laser thermometer and were matched up with substrates each individual selected during the focal watch. Following the focal watch, body temperature was taken using a Schultheis quick-reading cloacal thermometer within 30 seconds of the initial re-capture attempt. If the body temperature could not be taken within the allotted 30 seconds, the skink was allowed five minutes in the cage to readjust to its preferred body temperature before a second attempt was made. Each specimen was then identified to species and photographed. Individuals were measured for SVL with calipers, weighed using a 10 g Pesola, and sexed via hemipene inversion.

Statistical analysis

All statistics were performed using JMP v5.1.2. The relationship between canopy cover and community ratio (*E. impar : E. cyanura)* was analyzed with regression. The Rank Sum Test was used to test for differences between species for all field substrate temperatures, and for preferred body temperatures. Five tests (O'Brien, Brown-Forsythe, Levene, Bartlet, and F Test 2-side) were used to test for differences between species in variance of preferred body temperature. The difference between species for selection of thermal substrates in the lab were compared with means.

RESULTS

Habitat selection, microenvironment, and substrate selection

Linear regression indicates that the ratio of *E. impar* : *E. cyanura* in assemblages of skinks responds to percent canopy cover. As canopy cover approached 100 percent, *E. impar*'s representation within the assemblage increased dramatically. The regression equation for *% E. impar* is y = 1.1463x - 20.414 (R^2 = .5226, P = .0079). Similarly, as canopy cover decreased, *E. cyanura*'s representation within the assemblage decreased in a reciprocal manner (Figure 1).

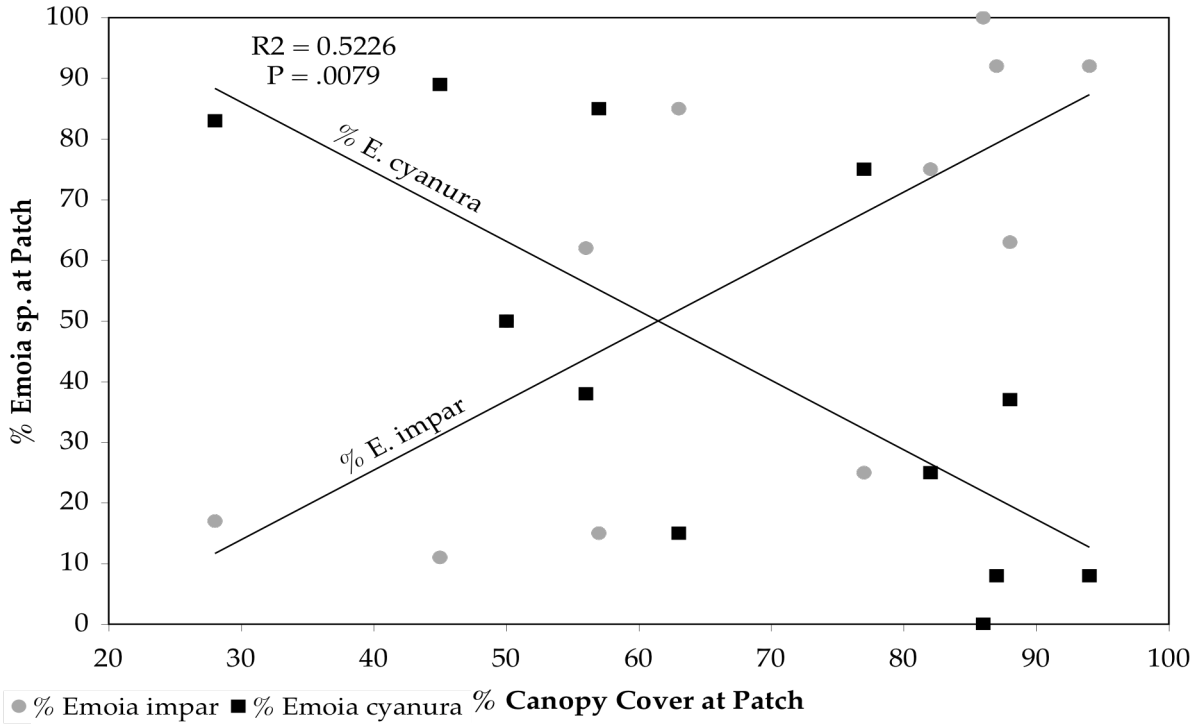

Figure 1. The ratio of *E. impar* : *E cyanura* at lizard patches in relation to the percent canopy cover.

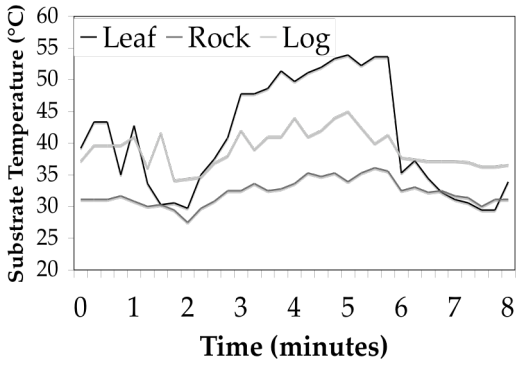

FIG. 2. Substrate temperature variability in response to sun exposure and shade. Upward temperature spikes result from brief sun exposure do to passing clouds. Between minutes two and six there was relatively constant sun exposure, and between minutes six and eight there was constant cloud cover.

A thermal profile of substrates selected by *Emoia* skinks, indicates that various substrates heat up and cool down differently when exposed to sun (Figure 2).

Substrate selection differed between species (Table 1). *E. impar* was more likely to select sunny leaf litter than shaded leaf litter, and more likely to select shaded logs and rocks, than sunny logs and rocks. *E. cyanura* had no preference between sunny or shaded leaf litter, and sunny or shaded logs.

Preferred temperatures in the field

A Rank Sum test indicates significant differences in temperatures of substrates selected by *E. cyanura* and *E. impar* in the sun (T_{sun}), shade (T_{shade}), and overall ($T_{substrate}$) (T_{sun}: Z = 1.9626, P = .0497; T_{shade}: Z = 2.6724, P = .0075; $T_{substrate}$: Z = 2.6251, P = .0087). Substrate temperatures selected by *E. cyanura* were significantly higher than those selected by *E. impar* for all three categories (Figure 3) (T_{sun}: E.c. = 46.67 ± 1.55 °C, *E.i.* = 44.05 ± 0.95 °C; T_{shade}: *E.c.* = 29.57 ± 0.64 °C, *E.i.* = 27.38 ± 0.43 °C; $T_{substrate}$: *E.c.* = 37.14 ± 1.4 °C, *E.i.* = 33.11 ± 1.09 °C).

Table 1. The frequency that sun exposed and shaded substrates were selected by *E. cyanura* and *E. impar*.

		Species	
Substrate	Exposure	E. c.	E. i.
Angiopteris	sun	1	0
	shade	0	5
Coconut	sun	6	1
	shade	1	0
Leaf Litter	sun	10	20
	shade	9	9
Log	sun	17	10
	shade	16	26
Rock	sun	0	2
	shade	3	6

Preferred temperatures in the laboratory

The temperature of substrates selected by *E. cyanura* were quite different than those

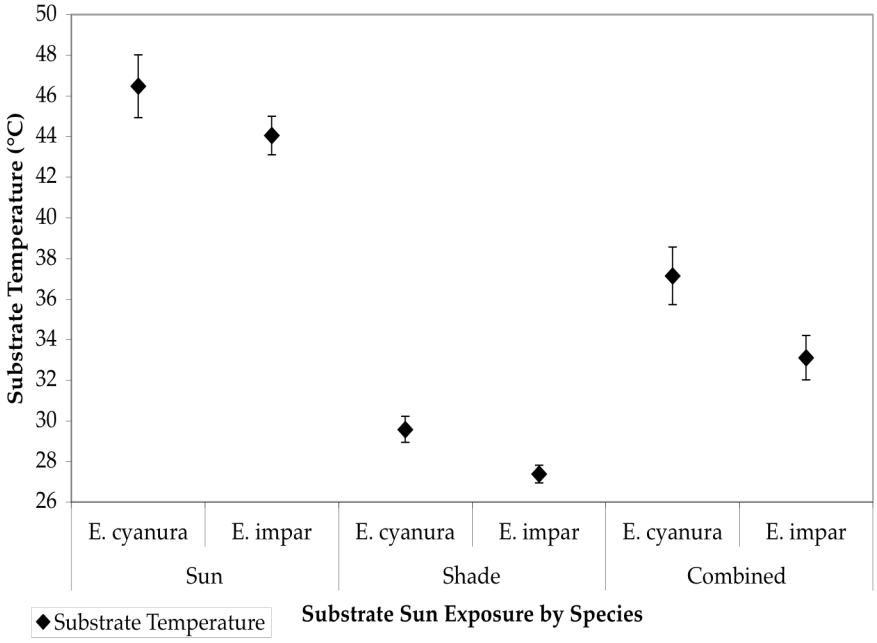

FIG. 3. The mean field substrate temperature selected by *E. cyanura* and *E. impar*. Selected temperatures are grouped by sunny substrates, shaded substrates, and both sunny and shaded substrates combined. Error bars represent ± 1 standard error.

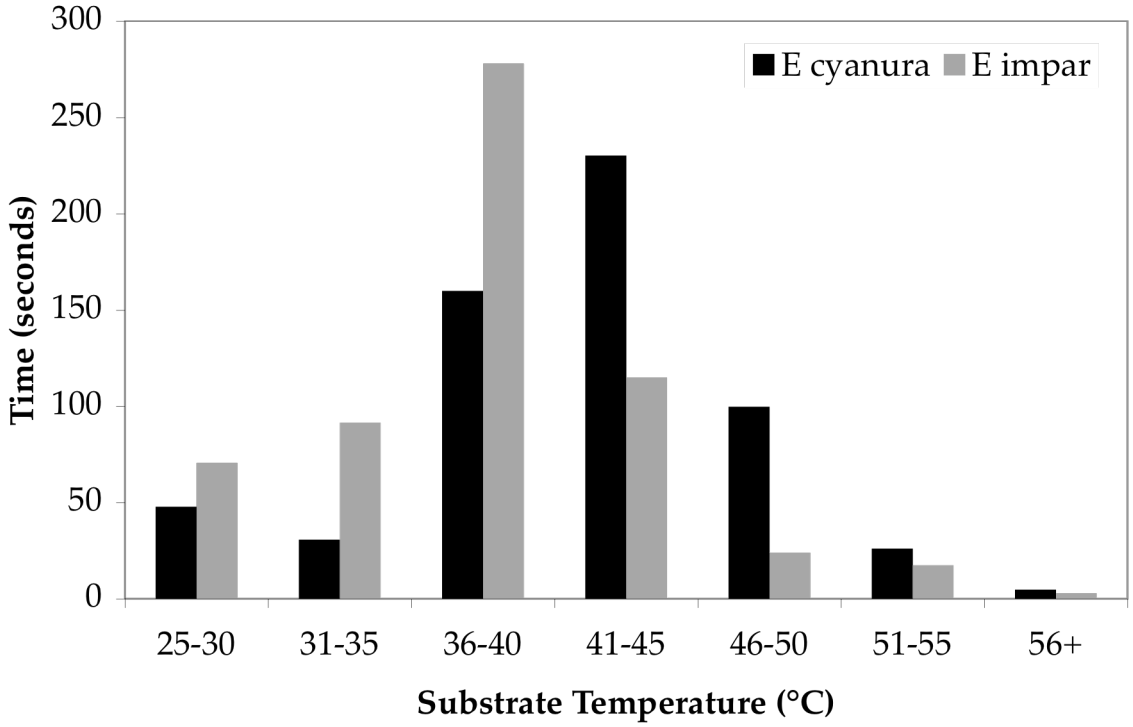

FIG. 4. This chart represents a mean 10-minute focal watch and shows the average time that each species spent on substrates of each temperature group within the gradient.

selected by *E. impar*. *E. cyanura* preferred substrates with temperatures ranging from 36-50 °C with substrate selection peaking between 41-45 °C while *E. impar* preferred substrates with temperatures between 31-45 °C with substrate selection peaking from 36-40 °C (Figure 3). The mean temperature selected by *E. cyanura* was 41.53 °C, and the mean for *E. impar* was 38.34 °C.

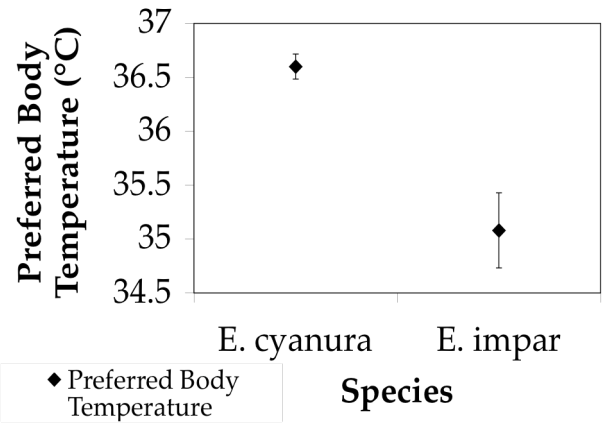

Fig. 5. Mean preferred body temperatures of *E. cyanura* and *E. impar*. The error bars represent one standard error.

A Kruskal-Wallis test indicated that preferred body temperatures (T_{pref}) differed between species (Z = 3.861, P = .0001). T_{pref} for *E. cyanura* was significantly higher than that of *E. impar* (*E. cyanura*: 36.6 ± 0.12 °C; *E. impar*: 35.08 ± 0.35 °C). Five tests confirmed that *E. cyanura* and *E. impar* had significant differences in variance of body temperature (Bartlett's: P = .0001; F-test 2 ways: P = .0001).

DISCUSSION

Emoia cyanura and *E. impar* are very similar in morphology and ecology and are syntopic on Mo'orea, French Polynesia. On Mo'orea, the species appear to partition the landscape based on canopy cover and sun exposure, such that *E. cyanura* prefers open canopy areas, and *E. impar* closed canopies. Similar *Emoia* distributions are known to occur on other islands in the South Pacific (Bruna et al 1996, Schwaner and Ineich 1998). However, the ratio of *E. cyanura* to *E. impar* within skink assemblages may be more responsive to percent canopy cover at a given location than the general landscape (Fig 1). Within the Belvedere, the species

ratio of lizard assemblages varied widely depending on the canopy cover, even though the general landscape was closed canopy interior forest. Both species could be found throughout the forest, but *E. cyanura* tended to congregate at piles of fallen branches along trails where the canopy was disturbed and sun exposure was direct. Assemblages predominated by *E. impar* could be found just 10 meters off the trail, where the canopy was generally >90% and sun light was heavily filtered.

Studies have shown that sympatric lizard assemblages may use microhabitat features differently to reduce competition (Grover 1996). Behaviors and substrate selection differed between *E. cyanura* and *E. impar* (Table 1). These differences likely result from habitat differences and sun exposure. In closed canopy areas, where the thermal environment is highly variable, *E. impar* behaved differently than *E. cyanura* did in more open areas. When passing clouds allowed for sun exposure, *E. impar* was observed rushing down from inconspicuous perches on *Angiopteris* and fallen logs to bask in small sun patches on forest floor leaf litter. After some time (usually less than 30 seconds), the skink would scamper off to presumably search for food, or even cool down. When clouds blocked out the sun, *E. impar* was usually found on rocks, fallen branches, and logs, but not leaf litter. Table 1 shows that *E. impar* is twice as likely to use sun exposed leaf litter than shaded leaf litter, and is twice as likely to use shaded logs than sun exposed logs for basking. Thermal data collected on substrates show that leaf litter is a very responsive heat pad, and will heat up/and cool down rapidly in response to sun exposure, while logs appear to be less responsive than leaf litter to sun exposure, but maintain heat during periods without direct sun exposure (Fig. 2). Therefore, *E. impar* appears to shuttle between shaded logs and sunny leaf litter when weather conditions allow for such behavior. The data shows that *E. cyanura* did not use sun exposed leaf litter more than shaded leaf litter. Furthermore, they did not use shaded logs more than sunny logs, indicating that *E. cyanura* does not perform such shuttling behavior. Since *E. cyanura* generally inhabits areas with more constant sun exposure, sun patches and substrate heat are not a fleeting and limited resource, so such behavior is not necessary.

Across landscape types and levels of sun exposure, *E. cyanura* appears to select hotter substrates than *E. impar* (Fig 3). Since both species are small lizards, temperatures of selected substrates likely correlate closely with their actual field body temperature due to their low thermal inertia (Bartholomew 1982). Such findings indicate that thermal characteristics of substrates may in fact provide a resource for microhabitat partitioning. However, no physiological studies have been done on *E. cyanura*, or *E. impar*, and biotic interactions, such as competitive exclusion between species, could also influence *Emoia* habitat selection in the field. One survey showed that on the fourth day of a removal experiment of *E. cyanura* from a transect, the number of *E. impar* increased from two of 18 skinks on the first day, to seven of 15 (Zug 1991).

In laboratory settings, where such competition and biotic interactions are removed, *E. cyanura* still appears to select warmer substrates than *E. impar*. During ten-minute focal watches of individually caged skinks, *E. cyanura* spent more time basking on the warmest substrates than did *E. impar* (Fig. 4). Furthermore, preferred body temperatures (T_{pref}) for *E. cyanura* were significantly high than those for *E. impar* (Fig. 5). These findings strongly suggest that physiological differences between *E. cyanura* and *E. impar* influence both habitat and substrate selection, and provide a mechanism for microhabitat partitioning.

The theory on costs and benefits associated with lizard thermoregulation helps describe *Emoia* distribution and habitat selection. From variability in T_{pref}, it appears that *E. cyanura* is a thermal specialist while *E. impar* is a thermal generalist (Fig 5). Theory states that a thermal specialist should benefit from a high energetic gain or increased physiological function when maintaining an optimal body temperature. A thermal generalist likely experiences less energetic gain from maintaining such an optimum body temperature, but is able to benefit nominally across a wider range of temperatures (Huey and Slatkin 1976). Furthermore, the energetic cost (locomotion) for a thermal specialist attempting to maintain a specific body temperature in highly variable thermal environments (i.e. closed canopy forest) might be too great, and therefore the costs associated with inhabiting such an environment would out weight the benefits.

A thermal specialist should seek environments with low thermal variability (open canopy areas) in order to maintain T_{pref}. In such an environment, a thermal specialist would not need to expend large amounts of energy performing excessive shuttling behavior, because thermal resources are not as scare and fleeting. A thermal generalist, however, should have little difficulty in environments with high thermal variability, since a wide range of temperatures are energetically beneficial. Based on the theory of the cost and benefits of lizard thermoregulation we could predict that *E. cyanura* (a thermal specialist) should inhabit open canopy areas, while *E. impar* (a thermal generalist) would inhabit closed canopy habitats. The theory provides insight into *Emoia* habitat selection and helps us to understand possible competitive interactions.

Zug's (1991) removal experiment took place in a relatively open canopy area. Since *E. cyanura* are slightly larger than *E. impar* and require open areas for proper thermoregulation, it is likely that to some extent they do competitively exclude *E. impar* from such habitats. Furthermore, since *E. impar* is a thermal generalist, it makes sense that they should be able to inhabit a variety of thermal environments, including relatively open areas, yet they tend not to. It would be unlikely, however, that a removal experiment of *E. impar* from a closed canopy habitat would result in an increase in *E. cyanura*. While *E. impar* may be limited to closed canopy areas due to biotic interactions with *E. cyanura*, *E. cyanura* is likely limited to open canopy areas because of abiotic and thermal constraints.

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LEAF LITTER PREFERENCE OF MICROGASTROPODS (MOLLUSCA) ON MOOREA, FRENCH POLYNESIA

KERRY MCNAUGHTON

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract: The first study of terrestrial microgastropod assemblages in different types of leaf litter was conducted on Moorea, French Polynesia. The field collection portion of this study showed that five out of seven species of microgastropods studied were found exclusively in the forest dominated by *Hibiscus tiliaceous* and not in the adjacent *Inocarpus fagifer* dominated forest. To determine if this discontinuous distribution was due to the presence of a barrier or due to a preference for *Hibiscus* litter as a microhabitat, a field experiment was designed. Both *Inocarpus* and *Hibiscus* litter were placed in *Hibiscus* dominated habitat in an area where I found the microgastropod population to be abundant. Preference was demonstrated by a significant difference in colonization of *Hibiscus* litter. Using the most abundant species of microgastropod collected, *Georissa striata* (Pease, 1871), I investigated whether the patterns observed in the field could be simulated in the laboratory, in particular, with choices between the two microhabitats (*Inocarpus* leaf litter and *Hibiscus* leaf litter). The aim of laboratory experiment was to quantify preference. Individuals of *G. striata* did show preference for *Hibiscus* litter significantly more often than *Inocarpus* litter.

Due to the important role calcium has in shell formation, calcium content was hypothesized to be the primary mechanism driving the preference for *Hibiscus* litter. Therefore, *Hibiscus* and *Inocarpus* leaves were analyzed using ICP spectrometry. Although thought to be higher in *Hibiscus* leaves, calcium content was highest in *Inocarpus* petioles. Other dissimilar physical features that I observed include: greater water retention in *Hibiscus* litter and a more rapid breakdown of *Hibiscus* leaves over *Inocarpus* leaves. Reduced drainage maybe associated with a higher abundance of snails because wet microclimates are more favorable for performance of a variety of behaviors. While *Inocarpus* petioles have greater calcium content, accelerated decomposition in *Hibiscus* leaves could allow calcium to be more readily available over a greater area. It is encouraging to note that in a relatively undisturbed, native forest the microgastropod fauna is composed predominately of native species, with the exception of one introduced species which was the least abundant of all species studied.

Key words: Gastropoda*; gastropod; microhabitat; snail;* Hibiscus*;* Inocarpus*; calcium content; decomposition*

INTRODUCTION

Many factors influence the distribution of organisms across habitats. Animals associated with a specific habitat or microhabitat are commonly assumed to "prefer" that environment over others likely because it offers certain factors necessary for survival or propagation of the animal (Bennett 1993; Cowie *et al* 1995). Molluscs are the second most diverse phyla of the kingdom Animalia and therefore occur in many different habitats (Menez *et al*. 2003*)*. There are may constraints affecting the distribution of gastropods, including: elevation (Cowie *et al* 1995), light intensity (Perea *et al*. 2006), inorganic compounds (Hermida *et al*. 1998), water availability (Cook 2001), and other factors. Due to the small size of microgastropods, defined as less than 5mm, the presence of

limiting factors is crucial in the microhabitats of which they are associated.

Little is known about habitat preference among terrestrial microgastropods (Perea *et al*. 2006). In French Polynesia, microgastropods are abundant in certain areas of the rainforest. I noticed significantly different assemblages of microgastropods between *Hibiscus tiliaceous* dominated forest and *Inocarpus fagifer* dominated forest. There are several physical characteristics that are different between forest habitats of *Inocarpus* and *Hibiscus* which could be attributed to the disjunct distribution of microgastropods. The species used in this study ranged in size from 1mm to 5mm. Despite its wide distribution and high diversity, knowledge of the most abundant snail found in this study, *Georissa striata* (Pease, 1871) is very limited (Haase et al 2006). No studies have investigated habitat preference of microgastropods in French Polynesia.

In this study, experiments were designed to test preference by allowing individuals to choice between two different types of microhabitats, that of *Hibiscus* or *Inocarpus* leaf litter. This experiments were preformed in both the laboratory and the field. Preference for a certain type of microhabitat was defined as microgastropods actively selecting one type of litter over the other. The microgastropods listed in TABLE 1 were used in this study to test the hypothesis that preference for *Hibiscus* litter existed.

TABLE 1. A list of the species surveyed in this study. Garrett's monograph was also used to determine which of the surveyed snails were native to Mo'orea.

Species	Native to Moorea
Georissa striata (Pease, 1871)	yes
Trochonanina sp. a	yes
Elasmias peasianum (Garrett, 1884)	yes
Ovachlamys fulgens (Guide, 1900)	no
Georissa parva (Pease, 1865)	yes
Coneuplecta calculosa (Gould, 1852)	yes
Helicarionidae *sp. a*	?

METHODS

Study site

This study was conducted in relatively undisturbed, native forest (-17.52935397, -149.84543421) in Moorea, French Polynesia. The site was chosen for the presence of an boundary between *Inocarpus* and *Hibiscus* forest. Snails were identified using morphological characteristics and the illustrations and descriptions in Garrett's series on the terrestrial molluscs inhabiting the Society Islands (1884).

Field Collection

All micro-gastropods were removed from leaf litter samples from 30 plots within this site. The plots were selected beginning at six random sites along a 100 meter transect running along the forest edge. A ten meter transect was placed from the edge at each of these six sites into strictly *Inocarpus* forest. From the edge, a thirty meter transect was also extended into mixed and *Hibiscus* forest. Each plot was measured in the middle by placing a ruler vertically on the ground and marking where the highest leaf hit the ruler. A standardized amount of leaf litter was collected by placing a $0.25m^2$ quadrat on the ground and collecting everything within the quadrat. Leaf litter was transported via plastic Zip-lock bags.

All leaf litter sorting was done at the U.C. Berkeley Gump Research station in Pao Pao, Moorea. One plot at a time, the leaves were removed from the plastic Zip-lock bag and placed on a white surface. Each leaf was thoroughly inspected for the presence of snails. Any snails that were found were picked up using a thin paintbrush and placed inside a container. After the entire plot of leaf litter had been examined, snails were counted and placed into morphological categories. The leaf litter of each plot was separated into three brown paper bags: *Inocarpus*, *Hibiscus*, and other litter (which was predominantly composed of the African tulip tree, *Spathodea campanulata*, and the tropical almond tree,

Terminalia catappa). Each brown bag was dried for 24 hours at 200ºF in a Q.L. Lab Oven, Model 40 GC. After 24 hours of drying, the litter was removed from the brown bag and placed in a pre-weighed plastic Zip-lock bag to be weighed on a 100g Pesola scale. Leaf litter was then thrown away with the exception of a few bags that were brought back to the U.S. to be analyzed for Calcium content.

Field Manipulation

Twenty 1/16 m^2 plots were raked in a strictly *Hibiscus* area of the forest. The plots were one meter apart from each other and were in two lines of ten. A standardized amount of *Inocarpus* and *Hibiscus* leaf litter was thoroughly inspected and cleaned. The *Inocarpus* litter was evenly distributed over ten of the twenty plots and was flanked by the ten *Hibiscus* litter plots. Each plot had 5 cm of leaf litter placed in order from most decomposed closer to the ground and least decomposed on top. After one week, the plots were individually placed in twenty Zip-lock bags and brought back to the laboratory to be sorted. Each leaf was examined for snails and snail totals were tallied for each plot. Individuals of *G. striata* were kept alive for use in the laboratory manipulation.

Laboratory Manipulation

One hundred individuals of *G. striata* collected from the field manipulation were used in a laboratory experiment. *Inocarpus* and *Hibiscus* leaf litter was cleaned before being placed on opposite sides of a 11" by 15" rectangular container with three centimeters of space between the leaves. The leaf litter was placed in order of most decomposed on the bottom of the container to least decomposed on top in a 5 cm pile. One ounce of water was shaken out of a cup with a lid containing holes in it over both piles of leaves. Snails were placed in a 5 cm line on the plastic within the 3 cm of space between the leaves. Another one ounce of water was shaken out over the leaves and snails. After one hour, the leaves were removed from the container and examined for snails. All ten snails were measured from the center of the line where they started to where they were found an hour later. The same procedure was replicated ten times.

Lab Analysis

Because calcium is required for shell formation, an analysis of the amount of calcium present in both *Hibiscus* and *Inocarpus,* was undertaken through ICP analysis. Inductively Coupled Plasma (ICP) spectrometry is a technique for elemental analysis which is applicable over a wide range of concentrations. Sections of *Hibiscus* leaves, *Hibiscus* petioles, *Inocarpus* leaves, and *Inocarpus* petioles were chopped into small pieces. One hundred milligrams of each sample were weighed and placed into digestion tubes. Each sample was digested in 2 mL of nitric acid along with NIST-1547, peach leaves, used as the standard for calcium. The samples sat for a few hours to ensure full digestion of compounds, then were heated in a heating block over night. The vials were filled with double-distilled water to a final volume of 12.5mL. The amount of calcium in each sample was then determined using ICP spectrometry.

Statistics

JMP software (version 5.1.2) was used evaluate the data collected. Two sample t-tests were used to analyze the data for the field manipulation portion of this study. For the lab manipulation data, a one sample t-test was used to analyze the data. A linear regression was used to analyze the data collected in the field.

RESULTS

Distribution

Altogether, seven species were collected in the leaf litter. Total snail abundance and species richness were graphed against *Hibiscus* content relative to *Inocarpus* and other. Species richness and snail abundance were both low in areas of lower relative *Hibiscus* content. Statistical analysis of the data collected from

the six transects showed the results were significant. Figure 1 shows that as the relative Hibiscus content increases, snail abundance increases significantly as well. A result not represented in figure 1, is that 5 of the 7 species studied were only found in *Hibiscus* dominated habitat. FIG. 2).

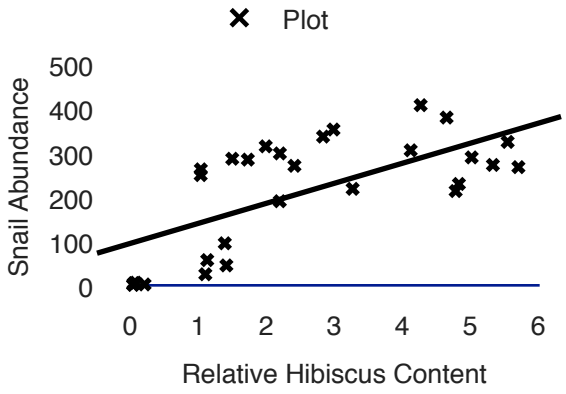

FIG. 1. Using a linear regression, I determined snail abundance is higher per plot when *Hibiscus* litter relative to other litter is greater than 1. (P= <.0001, RSquare= 0.5232, DF= 29)

Greater species richness is also significantly correlated with higher relative *Hibiscus* content.

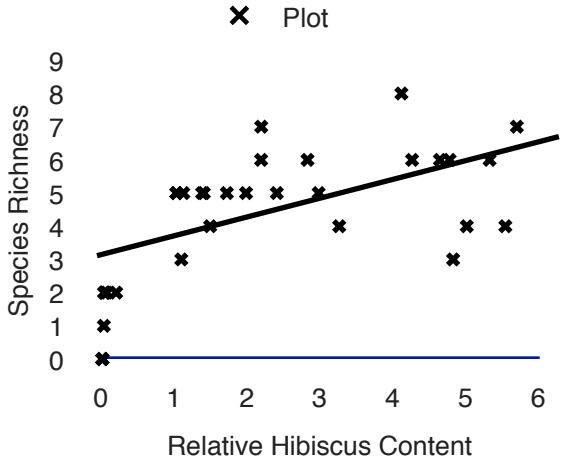

FIG. 2. Species richness is greater per plot when *Hibiscus* litter relative to other litter is greater than 1. A linear regression was used to analyze this data. (P=0.0005, RSquare= 0.3584, DF=29)

Field Manipulation

Species richness and snail abundance were also measured in the field manipulation. The snail abundance per plot is significantly higher in *Hibiscus* plots than *Inocarpus* plots. This study strongly shows microgastropod preference for *Hibiscus* leaf litter can be evident over the period of only one week. Snail abundance is on average 41 in *Hibiscus* litter and 17.9 in *Inocarpus* litter (FIG. 3).

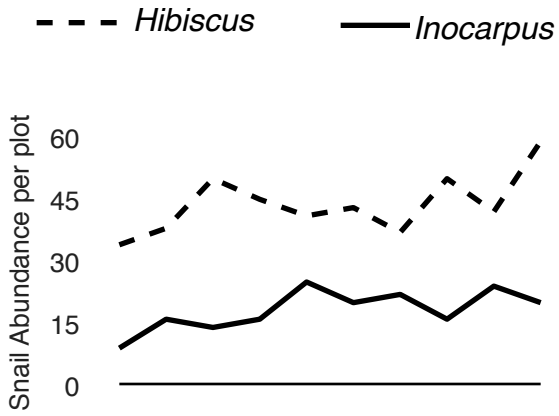

FIG. 3. Snail abundance is significantly higher in Hibiscus plots. Unequal variance test was performed to validate whether variances were similar between groups. The variances are similar. A two sample t-Test was used. (P= <. 0001, DF=19)

Species richness in *Hibiscus* litter on average was 4.5. While species richness in *Inocarpus* on average was 3.4 (FIG. 4).

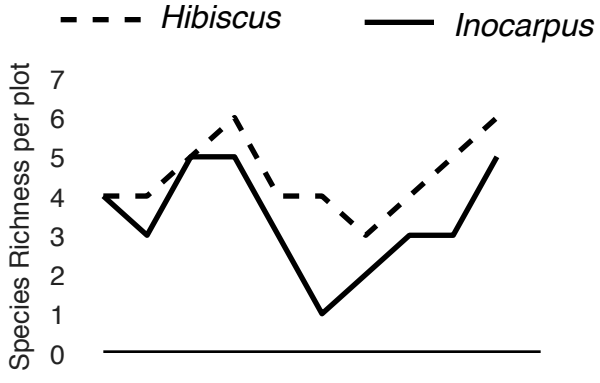

FIG. 4. Species richness is on average higher in *Hibiscus* litter per plot. Unequal variance

test was performed to validate whether variances were similar between groups. The variances are similar. A two sample t-Test was preformed. However, this data was not shown to be significant.

Lab Manipulation

If the choice between *Hibiscus* and *Inocarpus* was equal, I would expect on average number of five snails per trial to choose both types of litter. However, I found that on average 6.2 snails per trial chose *Hibiscus* litter over *Inocarpus* litter (FIG. 5).

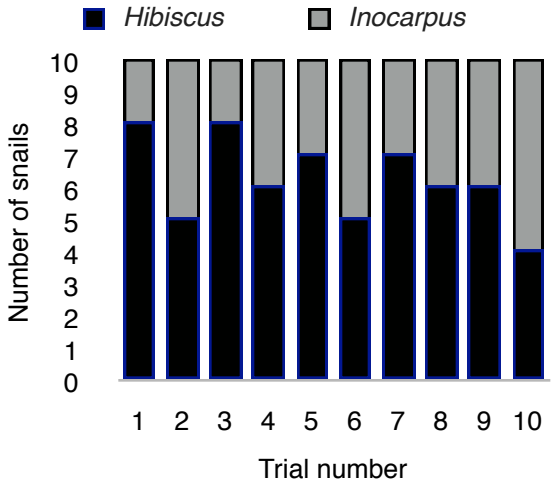

FIG. 5. Lab manipulation results. leafscore greater than 0.5 show preference for Hibiscus (DF= 9, Actual value= 0.62, SD= 0.1316)

Lab Analysis

The results for the lab analysis were reported in %calcium. Table 2 shows that *Inocarpus* petioles have a higher percent calcium.

TABLE 2. The results from the ICP analysis. Values are within an error of ±0.02.

		%Ca w/w	
QC	NIST 1547	1.57	NIST=1.56±0.02
Sample 1	*Inocarpus* leaves	1.92	
Sample 2	*Inocarpus* petioles	2.96	
Sample 3	*Hibiscus* petioles	2.31	
Sample 4	*Hibiscus* leaves	2.29	

Other Observations

While attempting to pick up an individual of *O. fulgens* in the field, it flipped out of my hand and landed about 6" from where I had tried to pick it up. I was able to repeat this behavior five times within a 20 minute period with an average recharge time of about 5-7 minutes. This behavior was repeated in three individuals.

In the field and in the lab I noticed that *Hibiscus* leaves stayed consistently more wet than *Inocarpus* leaves. This could be due to the more waxy cuticle of *Inocarpus*. I also noticed that *Hibiscus* leaves decompose more rapidly than *Inocarpus* leaves. These observations could be helpful in determining other mechanisms creating the discontinuous distribution.

DISCUSSION

The results overall indicate a preference for *Hibiscus* leaf litter over *Inocarpus* or other leaf litter. In all three studies, the snails significantly chose *Hibiscus* leaves over *Inocarpus* litter. This preference was thought to be driven by an exogenous demand for calcium by the snails for shell construction. However, as shown in Table 2, *Inocarpus* petioles have a higher %Ca then the values presented for *Hibiscus*. Despite *Inocarpus* petioles being higher in actual calcium content, the area presented by *Hibiscus* leaves

is much greater. This means that more calcium could be available in a forest floor covered by *Hibiscus* leaves than a forest floor covered by *Inocarpus*.

It is likely that other mechanisms are driving this preference because the calcium values are not that significantly different from each other and is probably not detectable by snails. Therefore, there most be something else driving this significantly divided distribution. There is the possibilty of the presence of a predator in the *Inocarpus* forest, but it is not likely that the predator would not also exist in the adjacent *Hibiscus* forest. I believe water availability may be the primary mechanism because it is essential for gastropod survival. If the *Hibiscus* forest has less drainage than the *Inocarpus* forest or the decomposing leaves of *Hibiscus* remain more wet, this could be significant for the survival of these microgastropods. Further studies are needed to ascertain what is driving the disjunct range.

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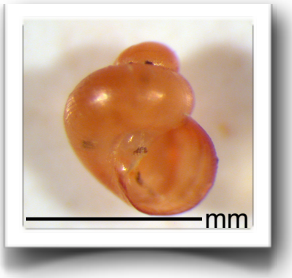
APPENDIX

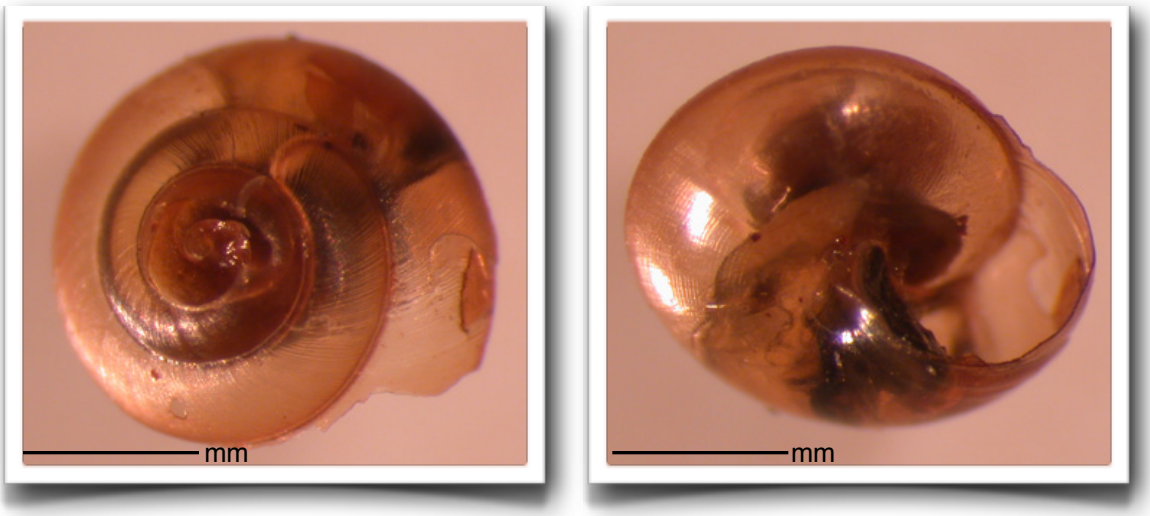
(sizes are approximate)



Georissa juvenile?

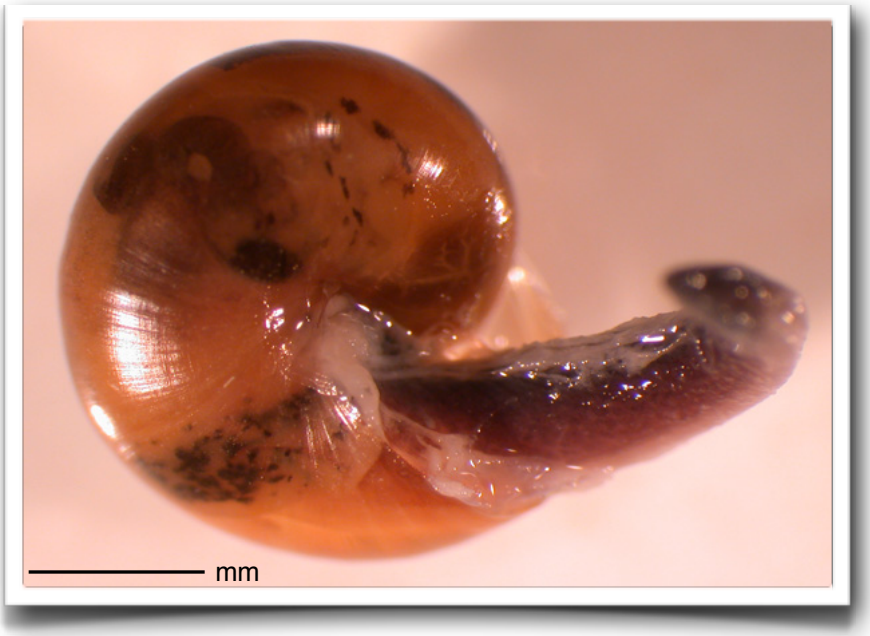
Georissa parva (Pease)

Georissa striata (Pease)



Trochonanina sp. a

Elasmias peasianum (Garrett)



Ovachlamys fulgens (Garrett)

Helicarionidae *sp. a*

Coneuplecta calculosa (Gould)

ENVIRONMENTAL FACTORS AFFECTING MICROBIAL MAT DISTRIBUTION IN MO'OREA, FRENCH POLYNESIA

ANGELA M. MINNAMEYER

Environmental Science Policy and Management, University of California, Berkeley, 94720
angelaminnameyer@berkeley.edu

Abstract Communities of photosynthetic prokaryotes are found around the world in a huge variety of locations, one of which is hypersaline mudflats. The estuary in Tamae, Mo'orea has been mostly filled in by a golf course and severely cut the population of microbial mats. Microbial mats in the Tamae mudflats in Mo'orea, French Polynesia were studied. Eight different morphologies were described and mapped. Additionally, their microhabitats described based on salinity, temperature, number of crab holes, and ground water depth and all but temperature saw certain significant differences. Transects were run from one end to another, and using the same environmental parameters, changes over the entire mudflat were observed. There were no trends with temperature. All of the other parameters exhibited trends and seem to have an influence over mat distribution; however there is not concrete evidence to support the claim that these are the factors that limit these microbial mat distributions. This ecosystem is very complex and it is probable that many more factors affect their distribution. If this habitat is to be conserved it will need to be studied more.

Key words: Microbial mats, hypersaline, French Polynesia, Lyngbya, Cyanobacteria

INTRODUCTION

Microbial mats are communities of oxygenic photosynthetic prokaryotes, typically composed of cyanobacteria. Cyanobacteria are thought to be the first living organisms, dating back to the Precambrian, which produced a large amount of oxygen, thereby changing the Earth's atmosphere (Stewart, 1983). Microbial mats have been extensively studied around the world because their lithified layers form stromatolite which paleontologists use to study the early history of the earth and astrobiologists use as indicators of life on other planet (Lau C., 2005). They are also studied because of their important role in nutrient cycling, their extreme living conditions, and PCR analysis of their communities. They can be found almost anywhere, especially in extreme environments where they do not get out competed by other organisms (58 Renaut, Robin W. 1993). They have been studied in French Polynesia because of their unique thick mats termed "Kopara" which are approximately 20-50 cm (Trichet, 1967, Mao, C.L, 2001). Inter-tidal regions with high salinity and fluctuating water depths are typical regions mats inhabit (Hoffman L., 1999), and are important to intertidal mudflat production and function (Zedler 1980, Cohen et al. 1984, Cohen & Rosenberg 1989). Other studies in Mo'orea have been conducted in the Tamae estuary by students who have examined which blue-green algal species made up the mats and environmental parameters in diel cycles across the mats. They have since been covered by a golf course leaving my site as one of the last populations on the island. Microbial mats are known to be influenced by environmental parameters. They have been shown to have differing levels in tolerance to salinity, temperature, and desiccation(Al-Thukair,A.A. 2007, Wrenn et al., 1997, Margesin and Schinner, 2001 and Yakimov et al., 2004,), and "extreme conditions… are known to be major factors in biodiversity distribution…"(Frontier, 1985 and Atlas and Bartha, 1997). This study aimed to *i.* describe the mats *ii* map their distributions *iii.* describe

each mat types' microhabitat *iv.* examine the environmental factors across the mudflat that could thereby influence mat distribution. I hypothesize that mats may exhibit different microhabitats and that certain parameters such as salinity and temperature may vary throughout the region and correspond to different mat type distributions.

METHODS

Study site

Mo'orea is a high volcanic island in the Society Island Archipelagos in the Pacific Ocean

The microbial mats studied are located on the northeast end of Mo'orea, French Polynesia at S 17◦ 28" and W 149◦46" on the Tamae mudflats. This site was chosen for its unique microbial mats and its accessibility. The majority of the original mudflats along the estuary in Tamae were completely covered by a new golf course adjacent to the site. The study site is separated from the golf course by a corridor of hibiscus and palm trees. The region with microbial mats is approximately 120meters by 230 meters. Due to time restraints and human disturbance only a portion of the mudflats were studied. The study area surveyed was approximately 100 square meters with a lagoon to the North East and hibiscus trees to the South West. The high tide covers some of the mats while others stay fairly dry throughout the entire day unless it is rainy or very windy.

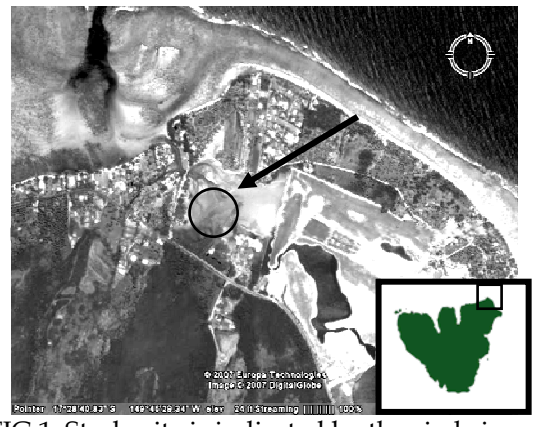


FIG.1. Study site is indicated by the circle in the large map, this is the magnified area displayed in the small box, Mo'orea, French Polynesia.

Study Organism

Microbial mats are oxygenic photosynthetic prokaryotes which are typically comprised of cyanobacteria. Some of the blue-green algae in the community are *Lyngbya* and *Microcoleus.* They lay on top of the mud, either attached or unattached, and help to stabilize the surface.

Mat Types

Eight mat types were defined by different morphologies. Color and texture were used to determine the different types. For each mat type an approximately 10cm by 15cm by 10cm square piece was obtained with a trowel. They were placed in tupperware for protection and taken back to the lab. Next, they were then sliced into layers in which color, texture, size (cm), and adherence to the layer below it were cataloged.

Mapping

Eleven transects were run at 75°N, roughly perpendicular to the shore. Every ten meters mat type was recorded. I also recorded points where mat type changed. These points were then transferred to graph paper to make a rough map. Many of the mats are very patchy, all of which are not displayed on the map.

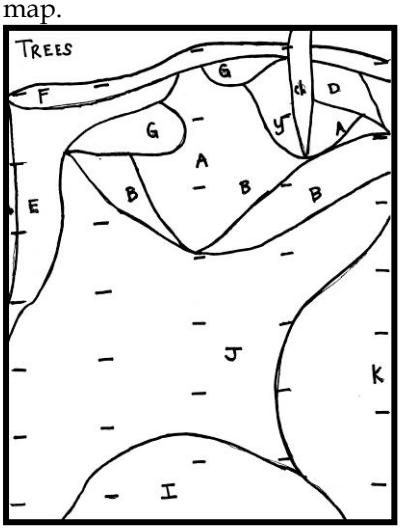


FIG. 2. Distribution Map, dashed lined indicates vertical transects.

Sampling

I laid five transects from the trees to the water approximately twenty meters apart at 75° North. Each transect was divided into six, fifteen meter sections resulting in 6 zones and 30 total points. Zone 1 was closest to the trees and zone 6 was generally closest to the water, although, the tide does not always flow over zone 6 first due to the direction of the water flow. Data was collected on 5 different days between October 31, 2007 and November 13, 2007. Each day 1 random point was sampled within each 15 meter section of each transect, 30 random points each day. This resulted in 25 points in each zone. First, mat type(s) present were recorded. Then, a Checkmate II was used to measure the surface temperature and subsurface temperature, approximately 5 centimeters beneath the surface of the mats. Additionally, temperature buttons were used to collect surface temperature every 10 minutes for 24 hours along each transect between November 6, 2007 and November 10, 2007. A hole was dug with a trowel to reach ground water and immediately the ground water depth was recorded. The holes were then left to fill with water until the water was significantly clear for salinity measurements. A refractometer was then used to measure salinity (ppt). The number of crab holes was counted in $1m^2$.

Statistics

JMP software was used to analyze the data. Oneway ANOVA's were used to analyze differences between zones for temperature, number of crab holes, salinity, and water depth. Means were compared using a Tukey-HSD analysis. The same was used to compare the mat types. Due to the unequal sample size of the mats sub-samples were taken randomly to obtain 9 points for each type, with the exception of types G and F, which had a lower sample size because of their restricted distributions. To analyze correspondence between ground water depth and; surface temperature, subsurface temperature, salinity, and crab holes a Bivariate test was run.

RESULTS

Mat Morphology

The different types of microbial mat were cataloged and recorded. After initial observations eight different morphologies were analyzed. *Lyngbya* was present in types A and G, and *Microcoleus* was present in G and F. Many of the mats exhibited a typical anoxic layer if the mats were well developed. Through observations I noticed a change in morphology after a long period with no rain or just after a storm. After a long period with no rain many of the mats had a white layer, presumably salt, and had cracks on their surfaces and had started to break apart. After rain algal blooms could be seen and then was not present a couple of days later. The mats were generally darker in color and softer after the rain. The mats were much more easily broken apart from footsteps in after the rain. For a detailed description of each mat type see Appendix A.

Table 1. General description and location of each mat type.

Mat	Color	Texture	Zones
F	Grey/Brown	Silty	1
G	Brown/Red	Smooth	1
Y	Green	Filmy	1
A	Green/Brown	Thick/Rubbery	1,2
Ch	Dark Brown	Grainy/Smooth	1,2,3
E	Grey/Brown/Blue	Grainy/ Smooth	1,2,3,4,5
J	Brown	Grainy/muddy	1,2,3,4,5,6
K	Grey/Brown	Sandy	3,4,5,6

Mapping

The rough distribution of mats was mapped. There is a wider range of mats found in the first and second zone, than in the others. (Species diversity decreases with every zone getting closer to the water with a chi^2 value of <0.001)?

Temperature

There was no significant difference found between the different mat types for temperature ($p<0.1754$). When comparing across the six different zones I found no

correlation with temperature (p< 0.7570). Using the data from the temperature buttons a high of 52°C and a low of 22°C was measured and an average change from day to night was measured at 24.5°C over the course of 4 sunny days. I found a significant correlation between surface and subsurface temperature to groundwater depth, both with a p-value less than 0.0001. As ground water depth increased so did temperatures.

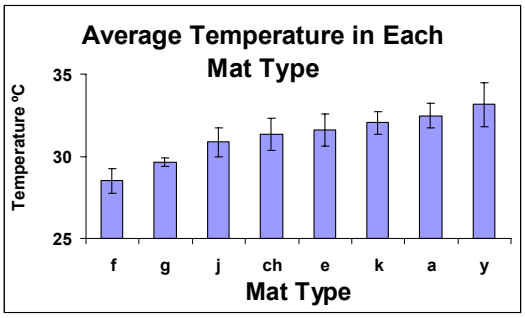


FIG. 3. Average temperature in each mat type (p-value =0.1754).

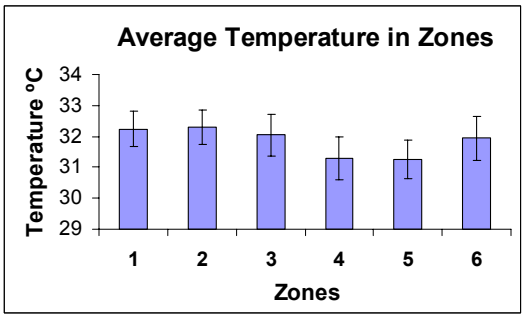


FIG. 4. Average surface temperature for each zone (p-value = 0.7570).

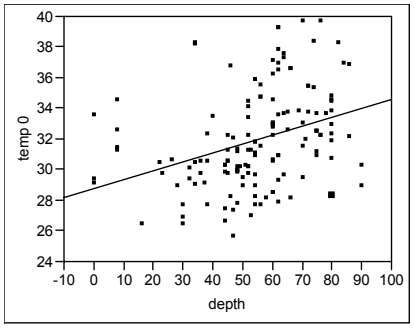


FIG. 5. Surface temperature compared to ground water depth (p-value=0.0001)

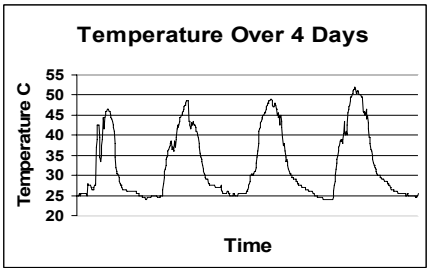


FIG. 6. Surface Temperature over the course of four days. Peaks occur between noon and 2p.m., lows occur between 2a.m. and 4a.m.

Salinity

Type "F" exhibits a significantly lower salinity (p-value=0.0025) than all of the other mats except for type G. Zone 1 showed a significantly lower salinity than zones 4 and 6 with a p-value of 0.007. There was no correlation between salinity and the other parameters and crab hole or temperature or the different days.

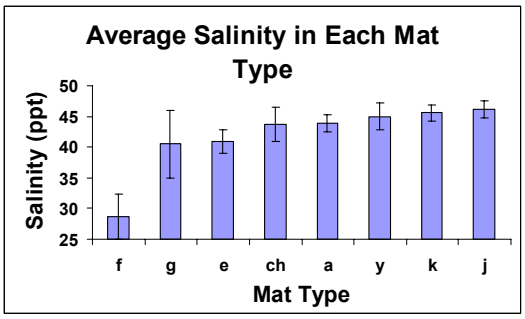


FIG. 7. Average salinity for each mat type (p-value=0.0025). F is different than all others, except for G. Additionally, K and J are different than E.

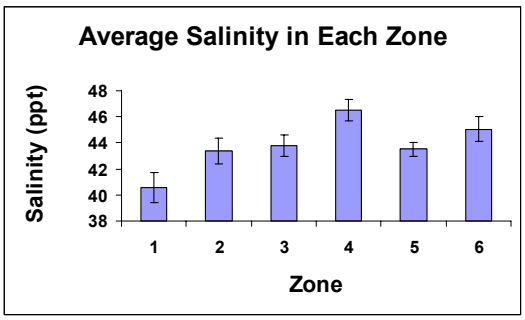


FIG.8. Average salinity in each zone (p-value= 0.007)

Crab Holes

The number of crab holes found in 1m² in the different mat types was significantly different with a p-value of 0.0001. Type "J" was found with the highest average number of crab holes and G, Y; A had the lowest numbers respectively. Although there are not clear trends, they are significantly different. Zones 1 and 2 had a significantly ($p<0.002$) lower number of crab holes than zone 5, which showed the highest average.

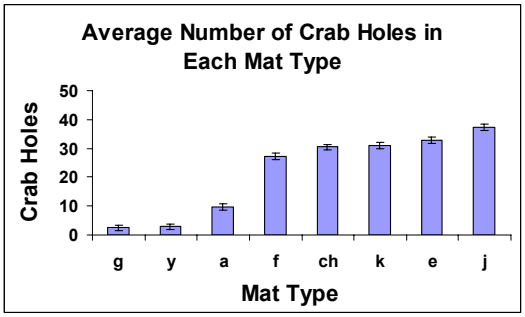


FIG.9. Average number of crab holes found in 1m² (p-value=0.0001).

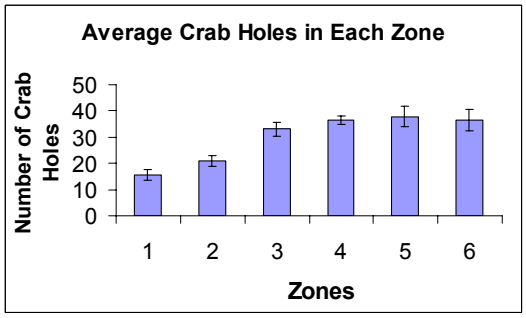


FIG.10. Average number of crab holes found in 1m² in association with each zone (p-value =0.002). Zone 5 is significantly higher than zones 1 and 2.

Ground Water Depth

Zone 6 had significantly lower ground water depths than zone 2 (<0.0194). I found no significant correlation between crab hole numbers and water depth (P<0.1584). There was also no correlation between salinity and ground water depth (P<0.1482).

Table 2. Average number of crab holes, ground water depth, surface temperature °C, subsurface temperature C°, and salinity for each mat type.

Mat Type	Crab Holes	Ground Water Depth(cm)	Surface Temperature °C	Sub-surface Temperature °C	Salinity(ppt)
A	10	28.5	32	29	43.8
Ch	30	29.8	31.3	29.5	43.8
E	33	30.2	31.6	29.1	40.9
F	27	26	28.5	27.7	28.7
G	3	29.5	29.7	29	40.5
J	37	24.6	30.9	28	46.1
K	31	37	32	29.8	45.6
Y	3	29.5	33.1	29.3	45

DISCUSSION

Mat Morphology

Mat types were distinguished by morphologies on the top and therefore it is possible that some of them are composed of similar communities, PCR analysis is needed to determine whether or not there are real differences between all of the mat types. The changes in mat morphology correlating to weather are typical responses to drying, "desiccation and dehydration are possibly the most cited causes of mat destruction or death" (Renaut W. 1993). The mats seemed to come back to life after rain and obtain similar morphologies to before the drying period, although some differences were noticed, such as a larger distribution of type Y. A typical

anoxic layer was seen in places where the mats were well developed (Villbrandt, M. 1991).

Mapping

Mapping was done by hand and is less accurate than using a GPS unit. The distribution of the mats probably changes over the different seasons. Long term aerial photographs and mapping could see a more detailed view of how the mats change.

Temperature

For the different mat types and zones we saw no difference between temperatures. Although the tide water does cover some of the mats for a period of time which could lower temperature, they are not significantly lower; the entire region exhibits very hot temperatures, which are similar to other findings in intertidal regions which displayed extremes of 55°C (Hoffman, 1996). They have very high heat tolerance and have a huge variation in temperature, for the four days the temperature buttons were out we saw an average difference of 24.5°C from day to night. Temperature increased with ground water depth most likely because water has a cooling effect. Because the temperature regime is so extreme it is likely that they are all adapted to very high and variable temperatures, therefore it would not affect their distributions. A common feature of microbial mat communities is their ability to rapidly acclimate to changing environmental conditions (Joye, B. 1993 ;). Therefore, the mat microhabitats, in reference to temperature, are not significantly different and there is no significant trend across the mats.
A desiccation experiment could show the limits of the mats. From these observations it is probable that the mats would display an extremely high tolerance to heat and possibly come back to more typical states after returning to "normal" conditions.

Salinity

When looking at salinity in each of the mat types "F'' is the only type that shows a significant difference from the rest (with the exception of type "G"), this is most likely due to the fact that it is uniformly the furthest from the tide water and closest to the influx of fresh water, and "G" is generally the close to "F". Except for "F" with an average of 28.7 ppt, their average salinities are in the low to mid 40's which is typical of intertidal mats (40 Al-Thukair,A.A. 2007;). Many of the mats are clustered in the same region and do have a lower average than type "J" which is found consistently closer to the water, however this is not a statistically significant difference. Even though some variation is seen, their microhabitats are not significantly different in regard to salinity, except for type "F". It is possible that some mats, like type "F", are restricted to their locations based on salinity, but experimental data would be needed to support these findings.

In the zones we did see a difference when comparing zone 1 to zone 1 and zone 1 zone 6. Salinity slowly increases when getting closer to the water, but only at the peaks is there a significant difference. The tide water does not come in over the site in a uniform pattern, this could account for zone 4 having higher average salinity than zone 5, however this difference is not significant. Although a trend is seen across the mudflat it is not conclusive evidence that salinity drives spatial differentiation.

Crab Holes

Although crab hole numbers are significantly different it is difficult to analyze the relationship between the mats and the crabs. The highest number is found in type J and the least in types G, Y and A, which are typically found in zones 1 and 2. These 2 zones have significantly lower crab holes compared to zone 5 which might be preferred by the crabs because it gets covered by tide water, but not as often or as long as zone 6. Crabs may not like to eat the mats in zones one and two as much (Walter et. al., 1973; De Deckker, 1987), but this does not seem to correlate with observations. It might also be harder for the crabs to dig their holes in zones one and two because some mats associated with that area have less porous soil under

them, like mat G, which also exhibits the lowest number of crab holes. It is also possible that because there are fewer crabs in zones 1 and 2 a wider variety of mats can establish themselves, possibly because they have lower tolerances for bioturbation. It is possible that they get too fragmented to stay established in the regions with higher crab densities (Fenchel T., 1998). Type "J", found with the highest amount of crabs is a lot patchier in its distribution; many times the bottom of the soil covers the mat because of the crab activity, although this does not necessarily prevent mat growth, which would allow type "J" to persist in a patchy distribution (McNamara, 1992). Therefore, although there are certain microhabitat differences it is unclear what drives the differences in crab hole numbers and if this influences the distribution of the mats. It seems like there would be a difference between crab hole number and depth, but no trend was observed. It is hard to conclude what influences crab hole distribution and thereby hard to say if it affects mat distribution. Although trends were seen it cannot be said if the crabs are necessarily preventing some of them from spreading to regions with higher bioturbation and/or herbivory.

Ground Water Depth

Zone 6 has a shallower water table because it is closer to the influx of tide water, while zone 2 was the furthest away from the tide water but not as close to the incoming fresh water as zone 1 and thus exhibits the deepest water table. Zones 6, 5, and 4 were typically covered by tide water for varying amounts of time. It seems like there would be a difference between crab hole number and water table depth, but no trend was observed. It is possible that trends would be seen if water was allowed to settle for a longer period of time.

Conclusion

Although trends were seen and certain factors are certainly correlated, the results do not indicate that these parameters dictate mat distributions. This ecosystem is much more complicated, there are clearly other unmeasured factors at play including nutrient availability, long term storm patterns, maximum and minimum microhabitat descriptions, desiccation patterns, and seasonal variability. This makes conservation of this area much more complicated than it appears. Although the parameters studied influence the mats, more experimental and long term data is needed to see the limits of the different types to test if these factors force their distributions.

ACKNOWLEDGMENTS

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Appendix A

Mat Type A

Layer	Color	Texture	Size	Adherence
1	Green/Brown	rubbery	0.05	pulls off
2	Green	fuzzy	0.05	scrape off
3	Brown/Black	fuzzy	0.05	scrape off
4	Brown	sticky	>1	scrape off
5	Brown	grainy	>1	scrape off
6	Red/brown	grainy	1	falls off

This Mat appears in patches typically on top of type J. It can be dark brown and wrinkly, but when it gets very dry it turns white and breaks apart. A portion of the blue-green algae is *Lyngbya.*

Mat Type Ch

Layer	Color	Texture	Size	Adherence
1	Dark brown, very few specks	Smooth/ Grainy	0.1	scrape off
2	Black	Smooth	1	scrape off
3	Grey, lots of white specks	Grainy	1	scrape off

This type was found in the channels and was always more wet than the surrounding areas unless it had just rained. When it got very dry this kind had still not cracked.

Mat Type E

Layer	Color	Texture	Size	Adherence
1	Grey /Brown/Blue,	Grainy	0.1	scrape off
2	Red	Sticky	Patchy	scrape off
3	Dark Grey	Grainy	2	falls off
4	Light Grey	grainy	>1	falls off

Mat type E had a blue tint, some patches showed a sandy surface and some were smooth.

Mat Type G

Layer	Color	Texture	Size	Adherence
1	Brown/Red	smooth	0.2	scrape off
2	Black	smooth	0.3	scrape off
3	Light Grey	grainy	0.4	falls off
4	Red/Grey	grainy	0.3	scrape off
5	Brown	sticky	0.2	scrape off
6	Light Grey	grainy	>1	falls off

This mat is very smooth and does not have any grains on the surface, unlike most of the other types. A portion of the blue-green algae is probably *Microcoleus* and *Lyngbya*.

Mat Type J

Layer	Color	Texture	Size	Adherence
1	Brown	Grainy	0.2	pulls off
2	Dark Brown, Green	Smooth/Rubbery	0.1	scrape off
3	Green	Fuzzy	0.1	Pulls off
3	Brown	Smooth	0.5	pulls off
4	Brown, specks	Grainy	>1	falls off

When dry J was cracked and broke apart. When wet it looses form and appears more like mud.

Mat Type F

Layer	Color	Texture	Size	Adherence
1	grey	grainy	0.1	scrape off
2	black	sticky	0.1	scrape off
3	dark grey	sticky	1.5	falls off
4	light grey	grainy	>2	falls off

This mat was found only under the trees. A portion of the blue-green algae is probably *Lyngbya* and *Microcoleus*

Mat Type K

Layer	Color	Texture	Size	Adherence
1	Grey/Light Brown , white specks	sandy	0.3	falls off
2	Dark grey/Black	smooth	<1	scrape off
3	grey/brown, white specs	sandy	>1	falls off

K is very grainy and sometimes shows a clear anoxic layer. It is much lighter in color than the others, even when wet. The second layer was not always present.

Mat Type Y

Layer	Color	Texture	Size	Adherence
1	Green	filmy	<0.1	scrape off
2	Brown/Light brown	smooth	<0.1	scrape off
3	Black	smooth	1	scrape off
4	Grey, white specks	grainy	2	falls off

This was very thin and its distribution got wider after rain fall.

INTRAGUILD PREDATION ON *LEUCAENA LEUCOCEPHALA* (LAM.) DE WIT: DISTRIBUTION OF *HETEROPSYLLA CUBANA* (HEMIPTERA: PSYLLIDAE) AND PREDATION AND COMPETITION BY *OLLA V-NIGRUM* (COLEOPTERA: COCCINELLIDAE)

LAUREN M. NOVOTNY

Department of Integrative Biology, University of California, Berkeley, CA 94720
laurnov@gmail.com

Abstract: Intraguild predation (IGP) is a widespread trophic system in which one species both consumes a second species and competes with it for a shared resource. This system is interesting not only because it is a complication in what were thought to be linear trophic systems, but current IGP theory does not accurately predict stability for systems which have been observed to be persisting and stable. Many studies attempt to account for variables like habitat structure, population structure, spatial and temporal refuge, cannibalism, and alternate resources to better understand IGP systems. This study focuses on population distributions, intraspecific competition and cannibalism, and prey preference in the IG predator, all patterns and behaviors that are necessary to understanding more complicated interactions, potentially lead to better systems modeling.

Key Words: Intraguild predation, populations distribution, Leucaena leucocephala, Olla v-nigrum, Heteropsylla cubana, *cannibalism, interference, French Polynesia, South Pacific*

INTRODUCTION

Leucaena leucocephala (Lam.) de Wit is an invasive tree originating in tropical America. It has been intentionally introduced widely as an agroforestry tree for fodder and is used as a shade tree in cacao plantations. In French Polynesia and other Pacific countries it is not under cultivation and is considered to be one of the most significant invasive plants affecting the South Pacific (Meyer 2000, Lubulwa 1998).

The psylla studied here, *Heterospylla cubana* Crawford is a sap-sucking pest specific to *L. leucocephala*, and is also preyed upon by a coccinellid beetle, *Olla v-nigrum* (Mulsant). *O. v-nigrum* also feeds on the nectar of *L. leucocephala* when prey resources are scarce (Coll 2002, JJ 2000, Pemberton 1993, L. Novotny, personal observation), however, observations and manipulations indicate that *H. cubana* is its preferred prey.

The trophic interactions described above are referred to as intraguild predation. *O. v-nigrum* and *H. cubana* both herbivorize *L. leucocephala* and thus are members of a guild of organisms consuming *L. leucocephala*. However, *O. v-nigrum* is an omnivore and is able to consume herbivores within its guild. Thus it both competes with and consumes *H. cubana*; intraguild predation (IGP).

Both the larval and adult stages of *O. v-nigrum* are predatory, but it is unclear whether or not the larval stage preys upon *L. leucocephala* (for trophic interactions in this system, see Fig. 1). There are two conditions necessary for co-existence of intraguild predator and prey populations, according to traditional IGP theory. The first is that *H. cubana* (the IG prey) be the superior competitor for *L.* leucocephala (the shared resource), second is that *O. v-nigrum* (the IG predator) gains significantly from attacking *H.cubana* (Polis 1898, Holt 1997). There are, however a number of factors that may expand conditions for coexistence, even in cases were the IG predator is the superior competitor (Amarasekare 2007, Borer 2007, Holt 2007, Janssen 2007, Rosenheim 2007, Rudolf 2007, Vance-Chalcraft 2007).

Cannibalism, especially amongst the IG predator, may significantly contribute to the coexistence of both species. Cannibalism allows the IG predator to persist at low IG prey densities (Rudolf 2007). The presence of alternative prey for both the IG predator and prey promotes co-existence. Even small populations of alternative prey may contribute to the stability and persistence of the IGP system (Holt 2007, Daugherty 2007).

IPG theory predictions are useful, even if imperfect. However, some of the assumptions it

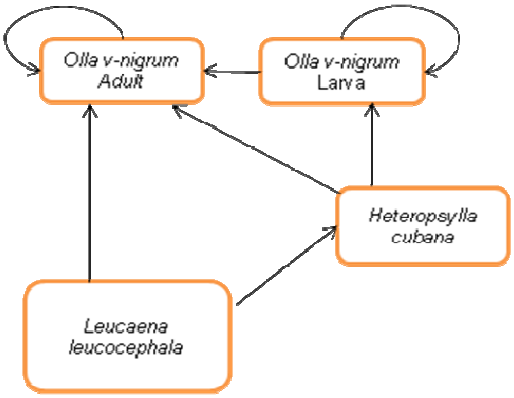

Fig. 1. Trophic interactions, arrows represent the flow of biomass. In this system, *L. leucocephala* is the shared resource. *H. cubana* feed on *L. leucocephala* and are preyed upon by both life stages of *O. v-nigrum*. *O. v-nigrum* adults feed on *L. leucocephala* and *H. cubana*, and are known to cannibalize conspecific larva and other adults. *O. v-nigrum* larva feed on *H. cubana* and are known to cannibalize other larva.

makes about the populations involved are not representative of real systems. One assumption is that populations are well mixed. Structural refuges, however, play an important roll in IG prey release (Janssen 2007). The leaf structure of the *L. leucocephala* leaf may impede predators in their search for prey. Individual leaves start with all of their leaflets folded tightly against each other and the pinnae are folded next to each other, creating a cage around any psylla eggs and nymphs on the adaxial surface of the leaf. As the leaf develops, the leaflets are still folded over each other, but their increasing surface area accommodating more nymphs and eggs that are laid there. Temporal refuges, potentially stemming from differing tolerances to disturbance, may also promote coexistence in a system that is predicted to be unstable. For example, in other IGP systems, if an inferior parasitoid competitor has a greater tolerance for cold than its IG predator, the colder months, when the IG predator is largely inactive, will give time for IG prey populations to recover (Amarasekare 2007). It is unknown if annual variance in temperatures plays a role in generational timing in this system, however, varying tolerance to rain and wind by both *H. cubana* and *O. v-nigrum* may play a role in stabilizing the system. Specific tolerances are currently unknown.

In order to better understand and model IGP systems there need to be long term studies investigating systems of differing players (i.e. parasitoids, herbivores, carnivores etc.) and in various habitats (i.e. arborial, benthic, pelagic etc.). However, investigators must first identify what factors are at play in the system (i.e. age-structured cannibalism, age-dependent diet and prey preference, etc.) before their influence can be understood and modeled. The focus of this study was centered on a few of these factors that may influence system dynamics, rather than examining the system as a whole. This study includes population distribution surveys and manipulations determining prey preference and examining intraspecific competition its effect on survivorship of the players involved.

Age-specific diet is a complex issue to understand and model. It is known that *L. leucocephala* has extrafloral nectaries (Lersten 1987), and observations in the field indicate that they are not generally tended by ants. It is unclear whether or not the larval stage of *O. v-nigrum* is omnivorous. This may lead to a difference in survivorship for both *O. v-nigrum* and *H. cubana* in experiments where resources are limited. The presence of an alternative prey should improve adult survivorship, however, improved adult survivorship may lead to better exploitation of *H. cubana* (the preferred prey) or it may lead to an increased reliance on the basal resource. Observations and field manipulations are necessary to better understand this system.

One important flaw in many models of predation is, as mentioned above, that the model assumes well mixed populations which are not seen in reality. Populations concentrate in areas where biotic and abiotic conditions are favorable to their persistence. One biotic factor was examined in this study, population distribution based on food quality. *L. leucocephala* is so widely used as a fodder crop because of its high nitrogen content. As *L. leucocephala* leaves develop, their nitrogen content decreases, and nutritive resources are used in leaf development. Thus, young, developing leaves are a higher quality food source and one would expect concentrations of *H. cubana* populations to correspond with this. Furthermore, developing leaves may provide a refuge from predators. *H. cubana* nymphs are small and mobile and may situate themselves in folded leaves, preventing attack leading to higher populations on younger leaves. Abiotic factors were difficult to quantify, and height was used as a proxy for these measurement based on the assumption that many of the abiotic factors would vary based on height. For

example, light exposure would have an inverse relationship with height as leaves intercept and block light from getting to leaves below. Also, mechanical disturbance might have a direct relationship with height. The majority of the trees used in this study were growing on the roadside. Passing cars would be a frequent source of mechanical disturbance. However, events such as storms with high levels of wind and rain would generate mechanical disturbance with an inverse relationship with height. With respect to height, one might expect mechanical disturbance to affect the larger predators more than *H. cubana* and further that more leaves would be developing in areas with increased light exposure. Both conditions would lead to increased populations with increasing height.

There is much research in the use of coccinellid beetles as biocontrol agents for *H. cubana*, however, this study first seeks to confirm that *H. cubana* is in fact the preferred pray for *O. v-nigrum* and then seeks to examine competition in *O. v-nigrum*. Because adults are capable of feeding at extrafloral nectaries known to be on *L. leucocephala* (Lersten 1987), one might expect *O. v-nigrum* larva to be the more efficient predator of *H. cubana* as adults have an alternative resource and are under less pressure to locate and consume mynphs.

METHODS

Site selection

All investigations were conducted on *L. leucocephala* on UC Berkeley's Richard B. Gump South Pacific Research Station property on Moorea, French Polynesia. At this site, *L. leucocephala* has colonized the disturbed habitat on either side of the main road. *L. leucocephala* grows in numerous stands with 2 main growth forms: (1) short and shrub-like, with numerous branches and (2) tall and straight, with thin and comparatively short branches. Different stands on the property are separated by the road, cleared areas, and other vegetation. All selected stands host the insect system of interest.

Population distribution by height

The first investigation into spatial structure of populations examined the influence of abiotic factors, with height being used as a general proxy for exposure. Fifteen trees were haphazardly selected from the study site. The total height of the tree and the height difference between the lowest branch with green leaves and the terminal shoot was determined. On each tree, leaves were collected at 4 heights distributed uniformly. A bag was placed over the leaf, the leaf was broken off and the bag promptly sealed to prevent the escape of insects. Bags were placed in a freezer for a minimum of 2 hours to insure all insects were dead before inspection. Numbers of leaflets on the leaf were counted and leaves were photographed for future reference. Leaves were examined under microscope at 40x magnification for the presence of sap-sucking insects and their predators. Insects were identified to the family level and their number and position on leaf (abaxial or adaxial surface of leaflet, pinna, or rachis) recorded.

Population distribution by leaf stage

Four stages of leaf development were identified, listed here in order of increasing age. (1) Pinnae folded, leaflets rolled. (2) Pinnae mostly flat, leaflets still rolled and light green. (3) Pinnae flat and fully extended, leaflets extended but still slightly wrinkled and light green. (4) Pinnae and leaflets flat and fully extended, leaflets dark green.

Fifteen trees were haphazardly selected from the study site. No trees used for the population survey by height were used in this survey. A single branch exhibiting all four identified leaf stages was selected and each leaf stage collected. Leaves were broken off and placed immediately into a bag and promptly sealed. Leaves were frozen for a minimum of 2 hours to ensure that all insects died before examination. Leaves for then examined under microscope at 40x magnification. Insects were identified to family and their number and position recorded.

Preferred prey experiments

O. v-nigrum larva and adults were collected and starved for at least 24 hours. The morning of the experiment, prey species was collected. Potential prey species were arranged in a circle in a large Petri dish. Potential prey included, *H. cubana* nymphs and adults, scale insects, stage 1 leaflets from *L. leucocephala*, stage 3 leaflets, and, as cannibalism was observed in original collections, dead *O. v-nigrum* larvae and adults, and *O. v-nigrum* eggs. The psylla adults were killed shortly before the experiment. Otherwise, their high mobility would have excluded their use. The coccinellid was released into the center of the Petri dish and observed until it attacked its first prey. There were 10 replicates for both the larval stage that the adult stage.

Enclosure experiments

O. v-nigrum larvae and adults were collected and starved for at least 24 hours. In the field, populations of 200 *H. cubana* nymphs were isolated in mesh bags with 4 replicates on each tree. Each population on each tree received 1 of 4 treatments.

1. 6 *O. v-nigrum* adults
2. 6 *O. v-nigrum* larvae
3. 3 adults and 3 larvae
4. no predators released (control)

After predators were released, bags were tied off to prevent escape and left for 48 hours. Immediately upon collection, predators were removed from all bags and survivorship assessed. Following removal of predators, survivorship of psylla nymphs was assessed.

Identification of Species

This system is widespread and widely studied (Elder 1998) and it is reasonable to assume that the organisms studied here are the same as those identified on other *L. leucocephala* systems. However, confirmation on species identity is still pending at the time of submission.

Statistical analyses

Correlation of insect populations and leaf height were determined by using linear regression of raw data and calculating Spearman's ρ. Population levels by leaf stage, and survivorship of psylla nymphs, coccinellid adults, and coccinellid larva by treatment in enclosure experiments were compared via Kruskal-Wallis oneway analysis of variance, then means were compared using Tukey's test when comparing more than two categories. Significance in the prey preference was determined using χ^2 test for independence with all expected values set as equal if selection were random. All analyses were performed using JMP 7 (SAS Institute 2007), with an $\alpha < 0.05$.

RESULTS

Population distribution by height

Two separate statistical analyses were performed correlating populations of *H. cubana* adults and nymphs with the height of the leaf collected. Populations of larva and adults of *O. v-nigrum* and other unidentified insects were excluded because of their rare occurrences.

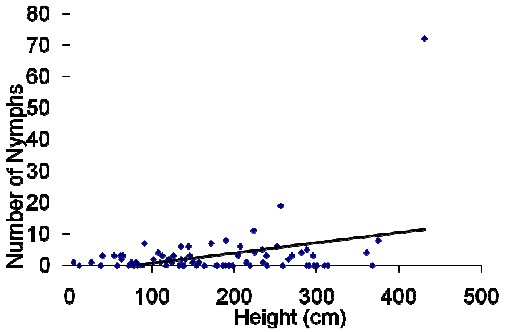

Fig. 2. Scatter plot of *H. cubana* nymphs versus height (in centimeters) of leaf collection. Number of Individuals = -2.559754 + 0.0326873 Height (cm), R^2=0.127719

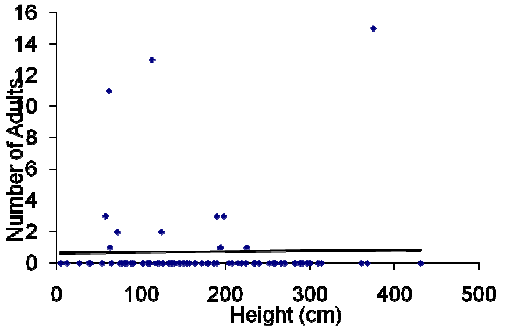

Fig. 3. Scatter plot of *H. cubana* adults versus height (in centimeters) of leaf collection. Number of Individuals = 0.6484251 + 0.000483 Height (cm), R^2=0.000301

Population of psylla nymphs correlated with height more strongly with height than did psylla adults. However, neither population showed much correlation with leaf height. For *H. cubana* nymphs, R^2 = 0.127719 (see Fig. 2 for linear regression). Spearman's ρ = 0.1041 with a non significant P value. For *H. cubana* adults, R^2 = 0.000301 (See Fig. 3 for linear regression). Spearman's ρ = -0.1206, also with a nonsignificant P value.

Population distribution by leaf stage

Numbers of both eggs and nymphs of *H. cubana* were found to vary significantly with leaf development stages. Means for all stages showed significant difference (P<.0001) excluding stages 1 and 4 which were not significantly different from

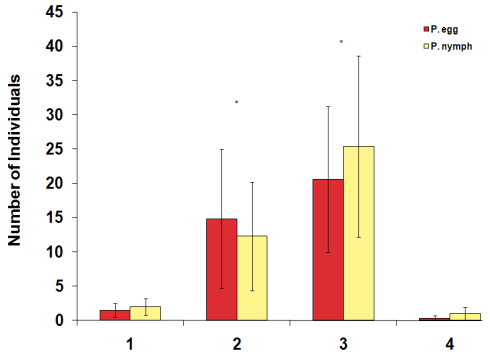

FIG. 4. Graph of mean population of *H. cubana* eggs by leaf development stage. Asterisks denote significant difference in averages (P<0.0001)

each other. See Fig. 4 for means comparison of *H. cubana* eggs and nymphs.

Prey preference

In eight of ten trials with different *O. v-nigrum* larvae the test subject stopped to feed upon psylla nymphs first when in an enclosure with eight different potential prey items. In identical testing with ten total *O. v-nigrum* adults, seven attacked psylla nymphs first. $\chi 2$ test for goodness of fit indicates that this result is not the result of random selection (P_{larva}<.0001, P_{adult}<.0001), and there is a clear preference for psylla nymphs.

Enclosure experiments

In enclosure experiments, mean survivorship of *H. cubana* nymphs were compared, however the only significant difference lay between the control treatment and the three predator treatments (P<.0001). Means for treatments L and A+L were strikingly similar however, one outlier in the A treatment prevented mean survivorship for this treatment from being significantly lower than the other predator treatments. The trend, however, is clear (see Fig. 5). Survivorship for *O. v-nigrum* adults did not vary significantly (P=0.5619) between the A and A+L treatments (see Fig 6). However, *O. v-nigrum* larval survivorship did decrease significantly (P=0.0055) in the A+L treatment from the L treatment (see Fig. 7).

DISCUSSION

Because of the nature of colonization by *L.*

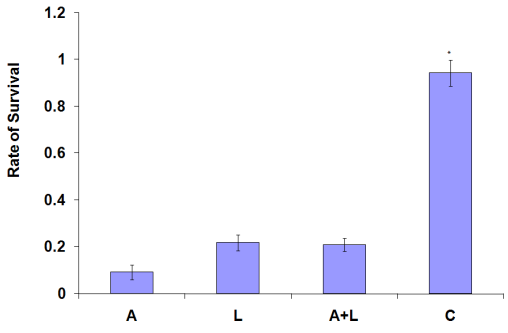

FIG. 5. Graph of mean survival rate of *H. cubana* nymphs by treatment, 6 *O. v-nigrum* adults (A), 6 *O. v-nigrum* larvae (L), 3 adults and 3 larvae (A+L) and no predators (C). Asterisk denotes a significantly different mean (χ^2=37.3870, d=3, P<0.0001).

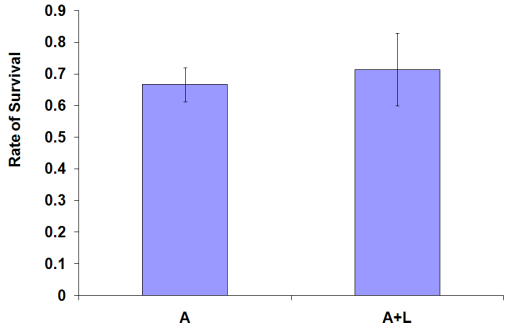

FIG. 6. Graph of mean survival rate of *O. v-nigrum* adults by treatment. (χ^2=0.3364, d=1, P=0.5619).

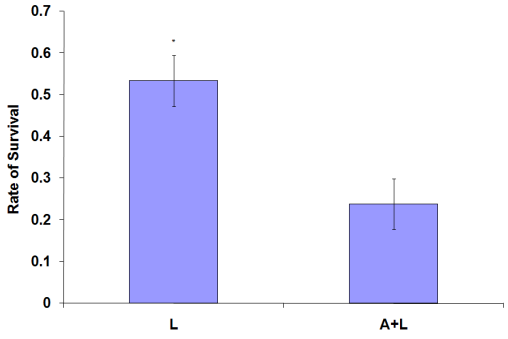

FIG. 7. Graph of mean survival rate of *O. v-nigrum* larvae by treatment. Asterisk denotes significant difference. (χ^2=7.7213, d=2, P=0.0055)

leucocephala, it is not surprising that population structure does not vary with height. *L. leucocephala* establishes in dry, lowland, exposed areas, and abiotic factors like light, wind exposure, rain exposure would be more uniform because the entire stand is exposed. However, there is a significant difference in populations based on the age of the leaf (here binned into four stages). The youngest leaves might have low populations of nymphs and eggs because of the fact they are so young. Not enough time had passed for adults to find the new leaf and lay their eggs. However, as time continues the leaf develops through stages 2 and 3 and more eggs are laid and hatch. These nymphs progress into adulthood and become far more mobile, leaving the leaf as it approaches its fully grown stage (Stage 4).

Enclosure experiments were run on leaf stages 1 through 3. Survivorship of both predator and prey was assessed. *O. v-nigrum* adults tended to be more effective in finding and consuming *H. cubana* nymphs than *O. v-nigrum* larvae and combinations of adults and larvae. Survivorship of *O. v-nigrum* adults was unaffected by the presence of conspecific larva, but as Fig. 6 indicates, *O. v-nigrum* larva survived better in the absence of conspecific adults. The reason for this decrease in survivorship, however is unclear. If conspecific adults are able to attack and consume Leucaena, then it is possible that the presence of alternative prey promoted survivorship. However, it may be more probable that adults were better able to cannibalize conspecific larva than the reverse relationship, accounting for the decreased survivorship in A+L treatments.

Finally, the prey preference experiment suggests that not only is *O. v-nigrum* the inferior competitor for the shared resource, but do significantly prefer psylla as their prey, suggesting that psylla are the superior food and consumption conveys a significant advantage over consuming *L. leucocephala*. It is important to note why extrafloral nectaries were excluded from the preferred prey manipulation. The problem lie in location and relative size of the extrafloral nectaries. It was unclear whether or not the would secrete nectar after being cut from the leaf and leaving it intact would make is considerably larger than all other prey items, possibly leading to confounding data.

H. cubana is a significant pest to an important crop species, even if it is considered an invasive pest in French Polynesia. There have been many studies on the influence of IGP on the efficacy of biocontrol measures (Rosheheim 1993, Rosenheim 1995). Further study is necessary to determine the efficacy of *O. v-nigrum* in this instance however it is known that other species of coccinella used in *L. leucocephala-H. cubana* system have had limited dispersal ability in comparison to the tree and the psylla (Follett 1996). To better understand IGP and biocontrol in this system, further study into life history and population structure of *H. cubana* and *O. v-nigrum*, attack rates, and dispersal are necessary.

CONCLUSION

Further research into this system should include a better understanding of life history information for both the psylla and the coccinellid, as well as investigations into attack rates, the effect of habitat structure on attack rates and possibly introduction experiments with ants since Leucaena's extrafloral nectaries are almost entirely untended.

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INTERSPECIFIC COMPETITION BETWEEN CONTAINER SHARING MOSQUITO LARVAE, *AEDES AEGYPTI* (L.), *AEDES POLYNESIENSIS* MARKS, AND *CULEX QUINQUEFASCIATUS* SAY, IN MOOREA, FRENCH POLYNESIA

KATHERINE R. POCOCK

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. The interspecific competition between three container sharing mosquitoes was investigated to further understand the reasoning for ovipositing partitioning previously analyzed. Past studies have demonstrated distinct difference in larval use of containers between *Aedes aegypti* and *Aedes polynesiensis*, preferring artificial and natural containers, respectively. Additionally, *Culex quinquefasciatus* is present in both types of containers. It was hypothesized that this partitioning was the result of interspecific competition between the species. To analyze this, two treatments were conducted to induce competition; food limiting (between *Ae. aegypti* and *Ae. polynesiensis*) and space limiting *(*between all three species), with the emergence rates being the calculated variable. ANOVA tests revealed that when food is present, *Ae. polynesiensis* competes better interspecifically than intraspecifically, suggesting that competitive displacement occurs in natural containers. It was also found that a space limiting environment does not provide a statistical significant difference between the emergence times of *Ae. aegypti, Ae. polynesiensis, and Cx. quinquefasciatus*, providing that larval density does not induce competition between these three species and therefore cannot be used to analyze theories for ovipositing partitioning.

Key words: Aedes polynesiensis, Aedes aegypti, Culex quinquefasciatus, *larval competition, interspecific competition, emergence rates, competitive exclusion, mosquito.*

INTRODUCTION

Mosquitoes in French Polynesia have been longstanding pests, particularly in their transmission of disease. *Aedes aegypti*, the yellow fever mosquito, a vector for Dengue fever, and *Aedes polynsiensis*, the Polynesian tiger mosquito, a vector of Wuchereria bancrofti(the parasite leading to lymphatic filariasis resulting in elephantiasis), are the two major vector-mosquitoes in Moorea, and well studied pests (Gubler, 1988; Rosen, 1955). The third species present in this study is the locally non-vector *Culex quinquefasciatus*; worldwide *Cx. quinquefasciatus* is a vector of West Nile virus; however this disease is not currently present in Moorea. *Cx. quinquefasciatus* is still equally important to study as it tends to share the same habitats as the *Aedes* genera mosquitoes (Becker, 1995; Russell, 2004; Hribar, 2007).

The impact of mosquito-borne illnesses is increasing as these vectors spread further into subtropical and tropical environments and species are becoming better adapted to a variety of conditions (Hammond *et al*., 2007.) Particular efforts have been established to combat the spread of lymphatic filariasis; with the goal of stopping the transmission of this disease in the 16 Pacific island countries and territories where it is present, the Pacific Program for the Elimination of Lymphatic Filariasis was established (Burkot & Ichimori, 2002; Burkot *et al.,* 2002). The program's current effort in the French Polynesian islands is to combine a program of mass drug administration and species eradication programs to completely rid the islands systems of *Ae. polynesiensis* and rid the human population of the respective parasite *Wucheraria bancrofti* (Cobbold).

An issue that arises with all species eradication programs is the biodiversity impacts, in particular the newly formed habitat resources present to other competing species. Tilman (1982) defines resource as "any substance or

factor which is consumed by an organism and which can lead to increased growth rates as its availability in the environment is increased". Resources are the fundamental factors that competitive exclusion principle. If two similar species are unable to coexist in the same niche, then it can be assumed that they are too similar in their resource consumption, i.e. one is outcompeting the other for resources, and competitive exclusion occurs (Hardin 1960).

For *Ae. polynesiensis*, one of the major resources that will be freed as a result of its eradication will be the larval habitats where mosquitoes oviposit. The aquatic larvae of *Ae. polynesiensis, Ae. aegypti,* and *Cx. quinquefasciatus* inhabit water-filled containers, receiving nutrients from microorganisms and other fine particulate food present in the water column (Braks *et al.*, 2004). However, *Ae. polynesiensis* and *Ae. aegypti* do not coexist in containers on Moorea. The breeding preferences of *Ae. polynesiensis* are those of natural containers (e.g. coconuts, crab holes, etc.) (Bonnet & Chapman, 1958), whereas *Ae. aegypti* prefers artificial containers (e.g. potting plants, empty cans and bottles, etc.), while *Culex quinquefasciatus* prefers both types of habitats (Russell & Richie, 2004; Burkot *et al*., 2007).

Juliano (1998) proposed that interspecific resource competition is the most viable rationale for the observed decline of *Ae. aegypti* presence in the United States, having been outcompeted by another species from its genera, *Ae. albopticus.* Both this experimental evidence and the theory of coexistence demonstrate that resources affect the outcome of competition. The goal of this project was to determine whether or not lack of coexistence in natural and artificial containers was the result of interspecific competition between the larvae of these species. Two major resources that provoke competition in all systems are nutrients and space. The mechanism of such an interaction is classified as exploitation competition, which occurs when the effects of one species on another are indirect, specifically through the reduction of the present pool of resources (Keddy, 1989). The first study analyzed limiting food while the second study limited space, specifically the volume of water per larva. Three parameters were examined to quantify the effects of competition; time of emergence of adults from the larval stage, number of adults emerging, species of adults emerging.

influence the organization of communities (Price, 1984). The existence of two closely related species in the same niche sharing the same resources is a theory associated with the

MATERIALS AND METHODS

Larvae collection

Larvae utilized in this study were collected from various field locations. *Ae. aegypti* larvae were collected from two outrigger canoes located at the Gump Station located on the Eastern end of the station; one was located next to the boat storage on the water, approximately 5 yards from the closest human inhabitation, while the other was located next to the cabana on the water approximately 15 yards from the closest human inhabitation. Larvae were collected on November 4th for both the food limiting experiment and space limiting experiment. Larvae collected from the outriggers were pippetted into 90 ml plastic cups for transportation to lab. *Ae. polynesiensis* larvae were collected from coconuts at two locations; Opunahu Coconut Grove located on the north side of the island between PK 14 and 15, and the Vaiare Coconut Grove located on the eastern side of the island between PK 5 and PK 6. Rat-chewed coconuts were examined for the presence of water, and if present was poured into an 11 inch by 12 inch metal tin to determine whether or not larvae were present (fresh water was used to dilute murky water for a clearer visual). If larvae were present, water and larvae were poured into 90 ml plastic cups organized by coconut for transport to the lab.

Larval age was estimated based on size of larvae, and only the smallest larvae were kept so that they would be starting at the earliest points of their larval stage.

Food limiting experiment

The experiment was conducted in the "wet lab" located at the Richard B. Gump Station in Cooks Bay, Moorea, French Polynesia. Mosquito larvae collected from the field were pipetted into white, plastic cups (8 cm in height, 3 cm base diameter) that were utilized as the larval containers. In each container there were a total of 20 larvae, and each cup contained 100 ml of fresh water. All cups were covered with a six inch by six inch square of fine green or gray

mesh situated with a rubber band to catch adults as they emerge as well as to prevent oviposition by wild mosquitoes. Cups were labeled (columns denoted with a number and mg of Tetramin (fish food) per larvae per day. Food was delivered in dry form and sprinkled over the top of the cup.

There were six treatments total. For *Ae. aegypti* intraspecific competition there were two treatments; *Ae. aegypti* with food and *Ae. aegypti* without food. For *Ae. polynesiensis* intraspecific competition there were also two treatments; *Ae. polynesiensis* with food and *Ae. polynesiensis* without food. For the interspecific competition between *Ae. aegypti* and *Ae. polynesiensis* the two treatments were both species together with food (ten *Ae. aegypti* and ten *Ae. polynesiensis*), and finally both species without food (ten *Ae. aegypti* and ten *Ae. polynesiensis)*. There were seven replicates for each treatment for a total of 42 containers and 840 larvae

Containers were examined on a daily basis for approximately 18 days, until November 21st. Intra- and interspecific larval competition was studied by monitoring the number of live larvae, pupae, and adults, as well as the number of deceased larvae, pupae, and adults present in each cup daily. When adults emerged they were identified, sexed, numbered, and day of emergence was recorded. At the end of the experiment the total number of individuals emerged was noted for each cup, as well as their species.

Two two-way ANOVAs were utilized to analyze the effects of intra- and inter-specific competition on each mosquito species; one two-way ANOVA for Ae. aegypti and one two-way ANOVA for Ae. polynesiensis. The emergence rate of each species from each cup was calculated. Next, the model effects were determined to be either the presence or absence of food and either intra- or inter-specific competition, with the y-variable being Ae. aegypti emergence rate for the first ANOVA, and the y-variable being Ae. polynesiensis emergence rate for the second ANOVA.

Space limiting experiment

The experiment was also conducted in the "wet lab" located at the Richard B. Gump Station in Cooks Bay, Moorea, French Polynesia. Mosquito larvae collected from the field were demonstrating treatment, and rows labeled with numbers and representing replicate). Cups were placed in a large table located in the open air wet lab. Treatments requiring food received 0.06 pipetted into white, plastic cups (8 cm in height, 3 cm base diameter) that were utilized as the larval containers. In each container there were a total of 20 larvae, 10 from a natural container (presumed to be *Ae. polynesiensis* with potentially *Cx quinquefasciatus*) and 10 from an artificial container (presumed to be *Ae. aegypti* with potentially *Cx. quinquefasciatus*). All cups were covered with a six inch by six inch square of fine green or gray mesh situated with a rubber band to catch emerging adults as well as to prevent oviposition by wild mosquitoes. Cups were labeled (columns denoted with a number and demonstrating treatment, and rows labeled with numbers and representing replicate). Cups were placed in a large table located in the open air wet lab. Food, 0.06 mg of Tetramin (fish food) per larvae was delivered on a daily basis. Food was delivered in dry form and sprinkled over the top of the cup.

The six treatments were; 2 ml of water/larvae, 3 ml of water/larvae, 4 ml of water/larvae, 5 ml of water/larvae, 6 ml of water/larvae, and 7 ml of water/larvae. There were six treatments with five replicates for each treatment, for a total of 30 containers and 600 larvae.

Each container was monitored daily for approximately 18 days, until November 21st; the number of live larvae, pupae, and adults were recorded, as well as deceased larvae, pupae, and adults. When adults emerged they were identified, sexed, and the number were recorded. At the end of the experiment the total number of individuals emerged was noted for each cup, as well as their species.

For analysis of the differences between the emergence times of the three mosquito species, three one-way ANOVA tests were conducted. The model effects for all three ANOVAS were treatment (volume of water) and emergence day, with the y-variable being one of the three species.

RESULTS

Food limiting experiment

Table 1. Two-way ANOVA results for emergence rates of *Ae. aegypti* and *Ae. polynesiensis*.

Source	Emergence Rates					
	Ae. aegypti			*Ae. polynesiensis*		
	df	F	P	df	F	P
Presence of Food	1	250.842	<.0001	1	456.188	<.001
Competition	1	0.442	0.5126	1	0.542	0.4686
Food _ Competition	1	0.006	0.9417	1	6.919	**0.0147**

The first two-way ANOVA conducted with *Ae. aegypti* yielded an r-square value of 0.910, demonstrating that the yield had minimal variation. The remaining variation had a standard error of 0.128. All effects had 1 degree of freedom. An F-value of 250.82 and a *p*-value of <0.001 were yielded for the presence of food. An F-value of 0.442 and *p*-value of 0.5126 were generated for the competition effect. The interactions between presence of food and competition produced an F-value of 0.006 and a *p*-value of 0.9417 (Table 1). Therefore, the data does not show a statistical difference between the performances of *Ae. aegypti* under intraspecific vs. interspecific competition.

The second two-way ANOVA performed on *Ae. polynesiensis* generated an r-square value of 0.951, explaining much of the variation in the yield. The remaining variation had a standard error of 0.089. All effects had 1 degree of freedom. The F-value was 456.188 and the *p*-value was <0.0001 for the presence of food, whereas the F-value was 0.542 and the *p*-value was 0.4686 for competition. However, a statistically significant *p*-value of 0.0147 (highlighted in Table 1) was also yielded (F-value was 6.919) for the interactions between competition and food, the variable most important in this study, showing evidence that the model adequately captured most factors present in this response (Table 1). This revealed that under a higher stress environment (food absent) Ae. polynesiensis performs better against itself (intraspecific comp.) rather than against Ae. aegypti (interspecific comp.). However, under a less stressful environment (food present) Ae. polynesiensis performs better against *Ae. aegypti* (interspecific comp.) rather than against itself (intraspecific comp.)

Space limiting experiment

The pattern of results from all three ANOVAs conducted did not find a significant relationship between species and emergence rates. *Ae. aegypti* yielded an r-square value of 0.232, with the remaining variance having a standard error of 0.591, demonstrating that there is a significant amount of variation in the yield. The significant lack-of-fit test, a *p*-value of 0.4661, with 5 degrees of freedom and an F-value of 1.689, shows evidence that there is something in the factors that is not being accounted for in the model, and the model is more complex than demonstrated. *Ae.* polynesiensis generated similar results with an r-square value of 0.055 and a root mean square error of 0.682. The results had 5 degrees of freedom, an F-value of 1.399, and a *p*-value of 0.7003. *Cx. quinquefascaitus* was also similar, producing an r-square value of 0.042, a root mean square error or 0.699. The results also had 5 degrees of freedom, an F-value of 2.269, and a *p*-value of 0.4654 (Table 2).

DISCUSSION

Food limiting experiment

My results show that when food was present, *Ae. polynesiensis* had a greater emergence rate when in a container with *Ae. aegypti* as opposed to a container with only *Ae. polynesiensis*. However when food was not present, *Ae. polynesiensis* had a greater emergence rate when in a container with only *Ae. polynesiensis* as opposed to a container with *Ae. aegypti.* That is, the results indicate that *Ae. polynesiensis* competes better against *Ae. aegypti* (interspecifically) when food is present, however when food is not present *Ae. polynesiensis* competes better against itself (intraspecifically) (Figure 1a and 1b). The analysis is similar for

Table 2. ANOVA results for emergence day for *Ae. aegypti, Cx. quinquefasciatus, and Ae. polynesiensis*.

Source	Emergence Day								
	Ae. aegypti			*Cx. quinquefasciatus*			*Ae. polynesiensis*		
	df	F	P	df	F	P	df	F	P
Model	5	1.689	0.9682	5	2.269	0.9290	5	1.399	0.5997
Error	16	5.583	0.4661	105	51.30	0.4654	52	24.208	0.7003

Ae. aegypti; given that artificial containers would not necessarily provide an abundance of nutrients, therefore providing a more stressful situation with the absence of food, *Ae. aegypti* would be less likely to be outcompeted by *Ae. polynesiensis* in these environments, and therefore would prefer to oviposit in such containers.*Space limiting experiment*

The lack of a significant relationship demonstrated between the emergence rates of the different species still provides implicative results. Given that there was not a significant difference in the emergence days of the three mosquito species based on the volume of water, it can be suspected that larval density is not a variable in the container environment that induces competition between the three species.

Nonetheless, these results might also be explained by examining the confounding variables that were present such as; location, larval stages, and larval abundances. The location of the experiment was conducted outdoors, therefore leaving the experiment exposed to such variables as wind, temperature, variating photoperiods, and uncontrolled evaporation. Additionally, when the different larvae were collected in the field, despite efforts to age them by size, there was still that variation present, which, given the relatively short periods for emergence, would highly influence the data.

My results are dissimilar to that of previous research which demonstrated that increasing larval density also increases mortality rates in the larval stages (Gama *et al.*, 2005). Some of the contradictory conclusions could have resulted from a series of differences. Though interpopulation differences in life history traits lending to competition are not generally observed, there have been cases of this occurring between varying geographic strains of the same species. Livdahl (1984) demonstrated differences in composite index of performance between different geographic strains of *Ochlerotatus triseriatus* (Say) in the United States. He suggested that the variability in prevalence of predation by *Toxorhynchites rutilus* (Coquillet) evolved differences in growth rate and competitive ability as a result of differences in effective predator avoidance mechanisms. The Gama *et al.* (2005) study that I compared my results to was conducted with a Brazilian strain of *Ae. aegypti* whereas my strain originated from Moorea.

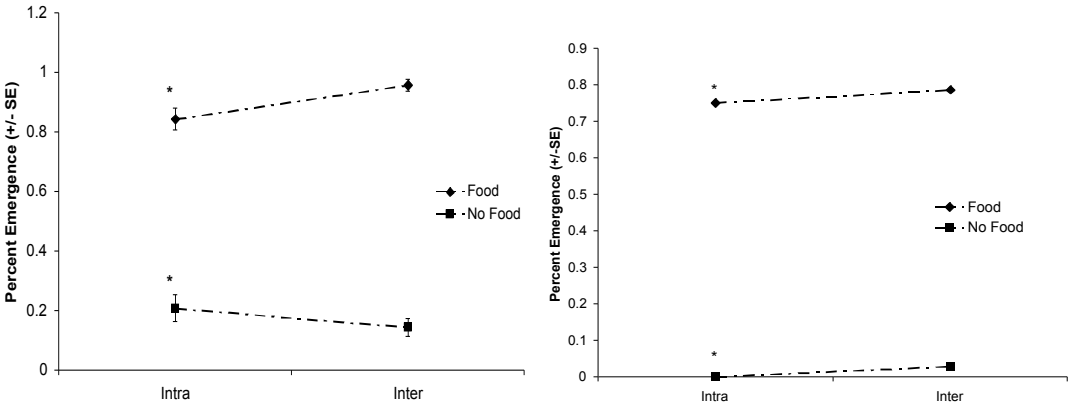
Additionally, my study was conducted at lower larval densities than previous studies. Despite the ratios of water to larva being similar, other studies were conducted with larvae counts in the upper 200s, however my study was done at a much smaller larval density, but similar ratios. An interesting explanation could also be the differences in the exposed surface area; larva require oxygen and can commonly be found floating on the top of the water source. Consequently, my containers may have provided an efficient amount of surface area for this resource to not by limited and therefore result in a smaller mortality rate.

As a result of the lack of conclusive data from the space limiting experiment, this resource will not be included in the following discussions.

Competitive advantage

Competitive advantage is achieved by the species demonstrating continuous or increased growth, whereas its competitor exhibits population decline (Pianka, 1988). The results of this study show evidence that when food is present, *Ae. polynesiensis* has the competitive advantage over *Ae. aegypti.* Applied to the

Figure 1. Effects of presence of food on the percent emergence between intra- and inter- specific competition of a) *Ae. polynesiensis* and b) *Ae. aegypti*



* In the analysis of this figure, it is not the slope of the two series but rather the difference in the location of the indicators between intra- and inter- specific competition.

Observed relationships in the field, this theory appears appropriate. Natural containers that *Ae. polynesiensis* is commonly found in (coconuts, palm fronds, and crab holes) biologically provide an abundance of nutrients; by nature species would prefer to reside in these habitats. However, based on the results of this experiment, it would be assumed that *Ae. polynesiensis* would outcompete *Ae. aegypti* for this niche, and this is exactly the pattern that is demonstrated in the field with *Ae. polynesiensis* present in the natural containers and *Ae. aegypti* present in artificial containers.

It is necessary to acknowledge that *Ae. polynesiensis* does not exclude *Ae. aegypti* completely from the system. That is, that *Ae. aegypti*, despite not being able to coexist in the larval habitats, is still able to coexist in the overall habitats. Hardin (1960) summarizes this as an 'ecological differentiation'. The two species may be too similar to allow coexistence in the larval stage, however they are able to find a level of coexistence in the adult stage and system. This theory is demonstrated in this study; the results provided evidence that *Ae. aegypti* is outcompeted only when food is present, so it has managed to inhabit a container that does not provide an abundance of nutrients and therefore would not induce competition that would inevitably exclude from this container as well.

Bedhomme *et al.* (2003) discusses the fitness consequences of differences in a particular life-history trait are not necessarily the same for the both species. While *Ae. polynesiensis* is native to the South Pacific, *Ae. aegypti* is a non-native species having originated in Africa (Kahmhampti & Rai, 1990; Mousson *et al.*, 2005) Consequently, *Ae. polynesiensis* would be genotypically and phenotypically more evolved to this environment, developing particular life-history traits that allow to adequately utilize resources and evolve to the abiotic and biotic conditions of the environment. This combination of population origin and adaptation to the local environment would allow *Ae. polynesiensis* to outcompete *Ae. aegypti* upon its arrival.

Species eradication implications

Furthering our understanding of the ovipositing and breeding sites of these mosquito species is imperative to develop efficient vector-control and species eradication programs that will not harm the system or, in this case, potentially influence the spread of another vector-mosquito, *Ae. aegypti.*

The implications of this study for the proposed eradication of *Ae. polynesiensis* potentially demonstrate that such an eradication program could provide more viable habitats for the spread of *Ae. aegypti*. Provided that, as the evidence supports, *Ae. polynesiensis* outcompetes *Ae. aegypti*, the removal of this species from the system could remove this competitive exclusion from *Ae. aegypti* and potentially encourage it to expand to areas with more abundant nutritional resources, natural containers. The potential influence that this has on the region is an increase in the rate of dengue fever across the region. This eradication program would therefore be replacing a high abundance of one disease with another.

This situation is delicate given that this eradication program is of a disease vector that is damaging the lives of many people in French Polynesia, as well as elsewhere around the world. The goal of the program is to eradicate a disease that hinders the lives of many. Once the elimination of the parasite from the human population is complete, it is expected that the unaffected species will be reintroduced, therefore returning the system to its initial state. With this in mind, the eradication program has the habitat and influence environment in mind with its program management.

Species eradication programs commonly target invasive species, not native species. As a result, there has been minimal research on the consequences of removing a native species from its habitat. Consequently, further research is required to determine the full affects of the removal of *Ae. polynesiensis* from the Moorean habitat.

Future research

Future research is required to further understand the interactions and relationships occurring within and between these species and containers. This experiment could be repeated under more controlled environments in a laboratory, and with a significantly larger sample size to account for more variance. Additionally, future research would benefit from utilizing a laboratory grown strain of larvae to account for exact age and species. Further research conducted should analyze other variables that induce competition, such as water temperature and light tolerance. To further research the implications of eradication *Ae.* polynesiensis, other species present in the system that can influence the resource exploitations should be analyzed to understand the balance of the system and how that would be affected.

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SUBSTRATA PREFERENCE IN FORAMINIFERA OF FOULING COMMUNITIES IN MOOREA, FRENCH POLYNESIA

MYFANWY E. ROWLANDS

Environmental Science Policy and Management, and Earth and Planetary Science, University of California, Berkeley, California 94720 USA

Abstract. Foraminifera are known to occur in fouling communities, but no extensive studies of foraminifera assemblages on these communities exist. We know little about the differences (if any) in the succession, diversity, distribution, and selective strategies of foraminifera found in fouling communities, and nothing at all has been documented about the foraminifera in fouling communities on Moorea, French Polynesia. This study examined foraminifera assemblages in fouling communities of three substrates on Moorea (cement, plastic, and metal). An experiment on the succession of foraminifera over the course of four weeks on submerged steel fouling tiles was also conducted. Hierarchical cluster analysis determined that forams in fouling communities do not show a preference for metal, plastic, or cement substrate, and that foram assemblages in fouling communities on the island are similar, regardless of their locality around Moorea. Succession followed a typical trend, but may have been accelerated by disturbance.

Keywords: Benthic foraminifera, fouling community, succession, artificial substrate, assemblage, French Polynesia.

INTRODUCTION

Marine fouling communities are dynamic systems, often developing integral roles in their surrounding environment. The epibiont biomass they represent provides habitat, as well as an important link in the local marine food web (Krohling 2006). Their man-made origin, combined with an influential role in the marine ecosystem, compels the need for an extensive scientific understanding of the fouling community system and the organisms found within. The more that is known about how a fouling community is established, composed, and affected, the better we can predict how a marine ecosystem changes in response to biotic and abiotic factors incurred by human populations.

The consistent pattern of succession in these communities culminates in a unique assemblage of organisms suited for the fouling habitat (Scheer 1945). The assemblages of common fouling organisms have been observed to correspond with substrate (Beatriz et al 2006, McGuinness & Underwood 1986, Scheer 1945), and fouling organisms are selective between artificial substrate types, favoring cement (Beatriz et al 2006). Pier pilings, docks, and the hulls of ships and boats are all very suitable environments for many varieties of organisms, such as of ascidians, bryozoans, mussels, tube building polychaetes, sea anemones, and foraminifera (Hewitt *et al.* 2002).

Foraminifera are useful bioindicators, and their presence in fouling communities may be valuable in future ecological studies of these systems. Given these applications, it is beneficial to describe the assemblages of fouling forams and what factors determine their distribution.

The composition of foraminifera in fouling communities has not been studied in depth, and we know next to nothing of the

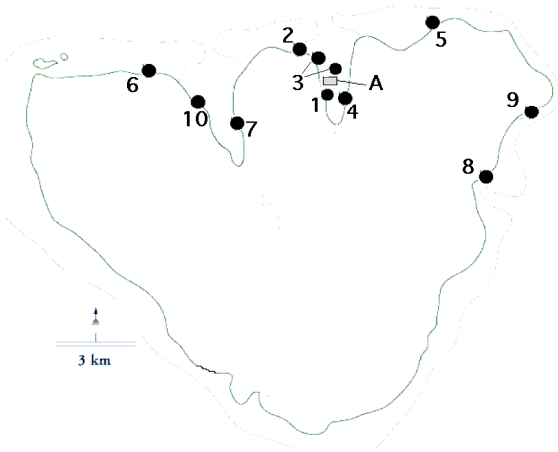

Figure 1. Sampling sites on Mo'orea, grouped into 10 localities.

foraminifera present in the fouling communities on Moorea Island, French Polynesia. Substrate is a determining factor in the distribution of benthic foraminifera (Murray 1991), but little is known about their succession. Their preference (if any) between artificial substrate is also unknown. The aim of this study is to provide data on the assemblages of foraminifera in fouling communities on Moorea, French Polynesia, and to demonstrate whether fouling forams select between three artificial substrates.

MATERIALS & METHODS

Sampling Fouling Community Sites

Twenty-nine different fouling community sites were sampled on Moorea, French Polynesia, comprising ten localities on the island (Fig. 1). A site was selected for substrate availability and stationary age (minimum one year). Examples of typical sampling sites include pier pilings, floating docks, and boat hulls. The samples were standardized for depth (6"-36"), and sampling took place on the leeward surface (the surface most protected from currents or disturbance) of the fouling site. Of the 29 samples, ten were from plastic substrate, ten from cement, and nine from metal.

The sampling method consisted of scraping the material present in a 25x25 cm quadrat into Ziploc bags, then filtering the material collected through a microsieve. Samples were treated with a solution of rose Bengal and 10% alcohol in order to to preserve and stain the protoplasm of any live foraminifera present, making differentiation between those forams that were alive or dead at the time of collection possible. Each sample was examined for thirty minutes under a dissection microscope, and all forams found during this period were identified and catalogued.

Succession experiment

A 5X4 grid of 15cm^2, hand-brushed galvanized steel tiles was constructed and placed in Cook's Bay, 0.4 km from shore (Site A, Fig 1). The tile grid rested on a 0.75x0.75x.01m^2 metal plate, oriented semi-vertically in the water column at a depth of 0.5-1.5 meters. Five randomly selected tiles were collected at the end of each week for four weeks. Immediately after collection, the material on each tile was scraped off and filtered through a microsieve, then examined in a Petri dish. The filtered material was examined in its entirety, and

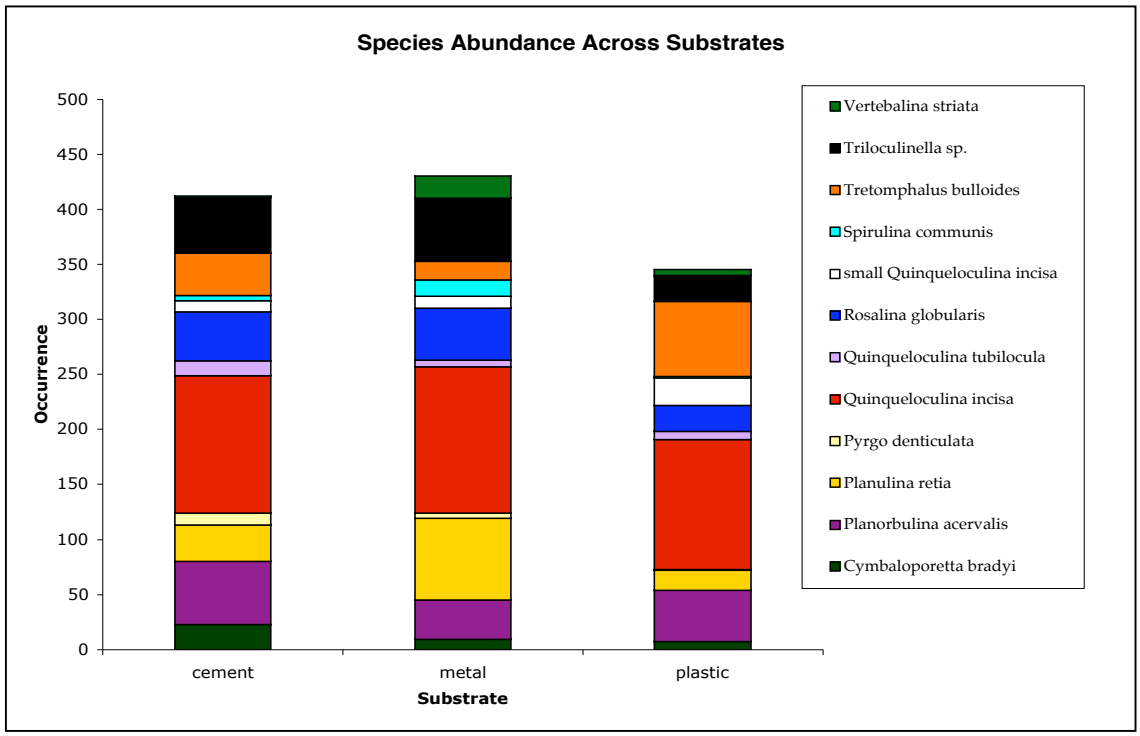

Figure 2. Distribution of the most abundant species by substrate.

all foraminifera present were identified and catalogued.

Statistics

A hierarchical cluster multivariate statistical test was performed for the group of 29 samples, generating separate clusters for substrate and locality. A one-way ANOVA test was conducted for the Shannon diversity indexes of the samples from each substrate, followed by a Tukey-Kramer test to determine the significance between the indexes. Chi-squared tests were performed on the distribution abundances of individual species across all three substrates.

For data collected from the succession experiment, a T-test was used to determine significant differences between the species richness and abundance values for each week.

RESULTS

Fouling community sites

A total of 1279 foraminifera were recorded, representing 29 different species (Appendix 1). Abundance across substrate type was similar (Fig 2), and differences between species diversity indexes across substrates were not significant ($p<.52$). Chi-squared tests performed on individual species distribution across substrates found that 11 of the 29 species were disproportionately distributed (Appendix 1). Examples of the distribution of two abundant species, *C. bradyi* and *T. bulloides*, are shown (Fig 3). Hierarchical clustering of foram assemblages at each sampling site did not show a clear pattern by either locality or substrate type (Fig. 4).

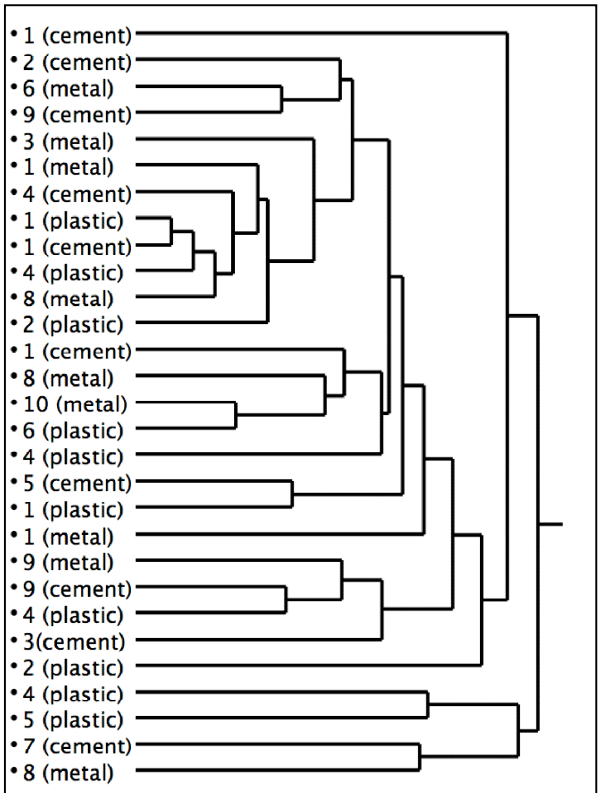

Figure 4. Hierarchical cluster by locality, substrate.

Succession experiment

When the tiles were grouped by week, the succession of species richness and abundance showed a slight trend (Fig. 5), with a significant increase in values between week one and week two. There was also a significant difference in species richness and abundance between weeks one and four.

DISCUSSION

Fouling community sites

Past studies of the role of substrate in fouling communities have found that cement is preferred by the largest number of fouling organisms (Krohling et al 2006, Flavia et al 2006, McGuinness & Underwood 1987). Since the distribution of foraminifera is controlled by substrate (Murray 1991), assemblages are somewhat determined by the group of species adapted to live on a particular surface type. The overall similarity of foram assemblages on all the fouling sites sampled suggests that there is a definable group of common fouling forams on Moorea. Furthermore, the consistent composition of this assembly regardless to substrate type or locality suggests that they are not selective for either.

The ecology of the individual species and not the characteristics of the fouling community sites themselves may provide an explanation for the similar assemblages of fouling forams. The majority of the species found are common epifaunal benthic foraminifera. Because these species are all able to exist as either free-living or clinging,

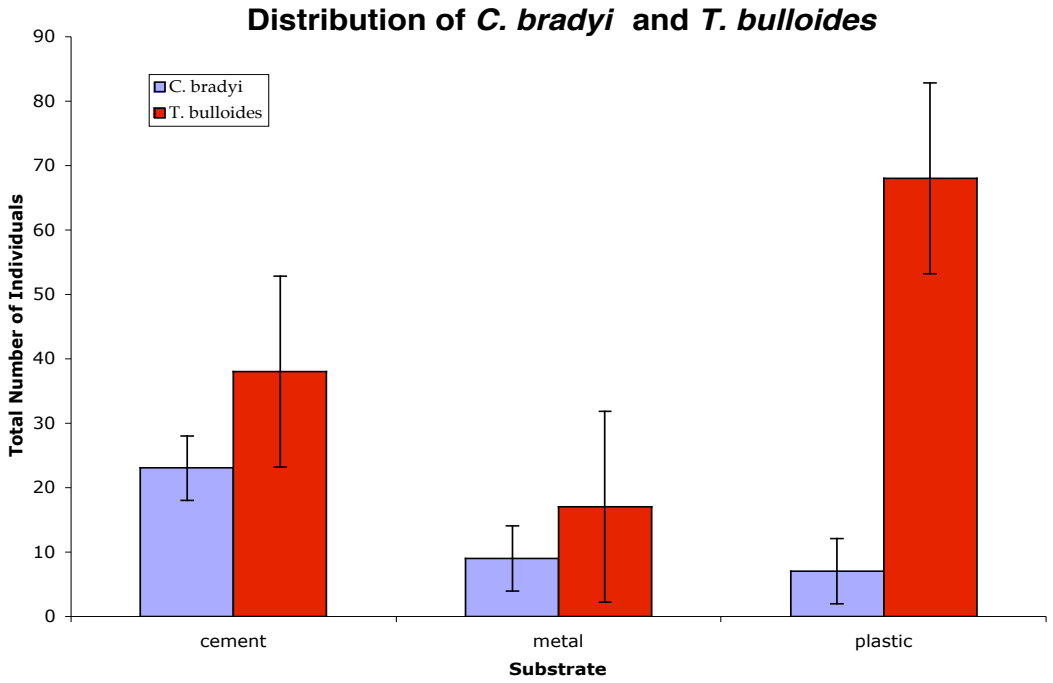

Figure 3.

they have the widest range of microhabitats available to them (Murray 1991). The distribution of benthic foraminifera is influenced by the hardness of a substrate (Murray1991), but it has not been demonstrated that epifaunal benthic foraminifera select between hard substrates. Considering this, it is possible that given a hard surface for attachment, artificial substrate type does not make a difference to the overall assemblage of fouling forams.

The mechanism of attachment differs between species of epifaunal foraminifera (Lee 1991), and it may also describe the preference of one substrate over others exhibited by *C. bradyi* and *T. bulloides*. The first stage of fouling community colonization is often characterized by a homogeneous covering of macroalgae (Scheer 1945), providing favorable attachment opportunities for benthic foraminifera in a free-living life cycle phase such as *T. bulloides*, which was overwhelmingly found on younger plastic fouling sites. Conversely, cement substrate, like a calcareous surface, provides a favorable surface for boring foraminifera (Venec-Peyre 1987), such as *C. bradyi*, which was observed to prefer cement fouling sites. The preference for one substrate type over another at different periods in a foram life cycle would be an interesting area of further research.

Succession Experiment

The foraminifera documented in the tile succession were all common, abundant species found in lagoons on Moorea, indicating that the unique substrate did not have an effect on colonization.

However, the relatively low abundance found in this study did not make it possible to run statistical tests on individual species, and it was not discernable whether those few species observed exemplify the first colonizing forams of Moorea. The trend exhibited in species richness and abundance, characterized by low initial values followed by a sharp increase shortly thereafter before leveling off, is consistent with patterns in succession in fouling communities first described by Bradley Scheer in his extensive study of the development of marine fouling communities (*Biological Bulletin*, Vol. 3 1945) and repeated in later studies (McGuinnness & Underwood 1986). However, the rapid rate of succession observed is not consistent with documented rates. In the two studies

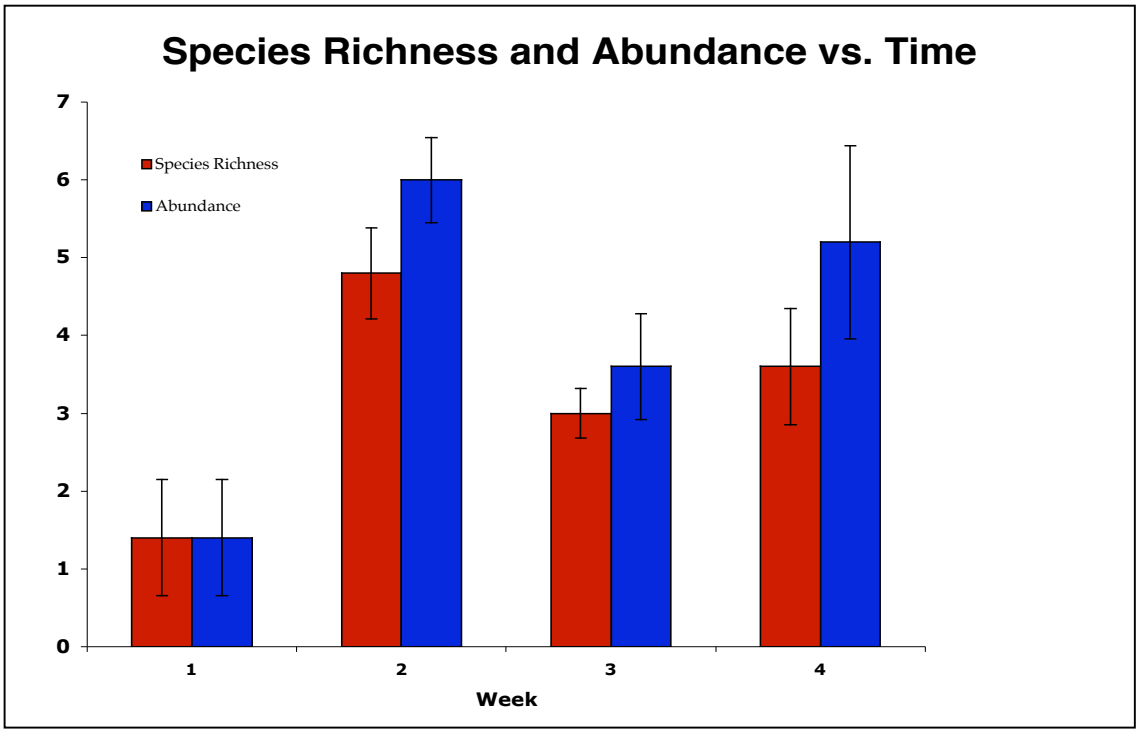

Figure 5. Succession of tile experiment.

mentioned above, the sharp increase in species abundance and diversity did not occur until after the eighth week of observation (McGuinness & Underwood 1986, Scheer 1945). Disturbance is one possible cause of the acceleration -- a large storm occurred in Cook's Bay less than 24 hours of the time the tile grid was placed. Field observations during tile placement note that there was so much material in the bay that visibility underwater became a problem. The abnormal amount of material in the water column may have settled on the tiles more readily than otherwise, accelerating succession. In light of this, a more long-term study with multiple trials would be required to define the rate of foraminiferal succession, as well as the relative abundances of initial colonizing forams.

CONCLUSION

The fouling forams on Moorea comprise a definable group, and the assembly of this group does not appear to depend upon artificial substrate type or locality around the island. Individual species of fouling forams show preference for substrate, but this does not affect the overall composition of assemblies. Succession in foraminifera can occur rapidly and may obey a normal fouling succession, but further studies of this aspect of foraminiferal ecology are needed to confirm the trend observed in this study.

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APPENDIX 1

Recorded Species Abundance and Substrate Preference

Species	Total number found	Substrate preference
Agglutinella arenata	10	
Ammodiscus sp.	15	
Amphisorus lessonii	4	
Amphistegina hemprichii	1	
Cheilochanus sp.	3	Cement
Cheilochanus minutus	3	
Cymbaloporetta bradyi	39	
Elphidium sp.	4	
Fischerinella diversa	3	
Laevidentalina sidebottomi	1	
Massilina timorensis	1	
Patellina corrugatta	2	
Peneroplis pertusus	8	
Planorbulina acervalis	140	
Planulina retia	125	Metal
Pyrgo denticulata	17	Cement
Quinquiloculina cuveriana	10	
Quinqueloculina incisa	376	
Quinqueloculina latidentella	7	
Quinqueloculina sp.	14	Plastic, cement
Quinqueloculina tubilocula	26	
Rosalina globularis	116	Metal, cement
Siphogenerina striata	4	Plastic
Juvenile Quinqueloculina incisa	46	Plastic
Juvenile Quinqueloculina tubilocula	2	
Spirilina communis	21	Metal
Tretomphalus bulloides	123	Plastic
Triloculina sp.	132	Metal
Vertebralina striata	26	Metal

FEEDING BEHAVIOR OF THE YELLOWTAIL CORIS (*Coris gaimard)* IN THE LAGOONS OF MOOREA, FRENCH POLYNESIA

MATTHEW W. STRAUSSER

Department of Integrative Biology, University of California, Berkeley, California, USA
Strausser@berkeley.edu

Abstract. Animals must be locally adapted to their habitat to optimize use of available resources. In highly variable environments, behavioral change allows animals to optimize resources quickly enough to keep pace with their environment (Luttbeg 1999). The factors that determine the animal's behavior are often difficult to uncover. *Coris gaimard* (Quoy and Gaimard 1824), a species of wrasse, exhibits different foraging frequencies across its range. This study attempts to determine what biotic factors may affect the foraging behavior. The study compares the behavior of two populations of *C. gaimard* in two similar lagoons around the island of Moorea, French Polynesia and a population in a previous study done in Japanese waters (Shibuno et al. 1994). Standardized timed observations from Moorea showed an increase in the amount of foraging behavior at the site with a smaller prey base. The behaviors, however, maintained the same relative frequency as the behaviors in the prey rich site. This frequency differed greatly from the relative frequency of behaviors seen in Japanese waters where the prey base was larger, but had a different species composition. These observations indicate that prey quantity determines the amount of foraging, but the type of available prey determines the foraging strategy. Additionally, *C. gaimard* engages in heterospecific feeding relationships, but the presence of other foraging species does not significantly affect its foraging behavior. These results indicate that prey populations are a major biotic factor in determine foraging strategies.

Key words: Coris gaimard*, Yellowtailed Coris; foraging; phenotypic plasticity; optimal foraging; feeding behavior; interspecific foraging*

INTRODUCTION

On a species level, animals are adapted to fill specific feeding niches in a habitat. However, these habitats can be highly variable across the animal's range. Animals must then be locally adapted to their habitat to optimize use of locally available food resources. Species that have phenotypically plastic behaviors can develop individual optimized strategies in response to resources in its specific environment (Houston 1992). In highly variable environments, these responses are usually behavioral changes that allow animals to optimize resources quickly enough to keep pace with their environment (Luttbeg 1999). The optimization of feeding behavior should follow optimal foraging theory to make best use of the local resources (MacArthur 1966). To determine the optimal forage strategy, the individual must respond to signals in the environment that affect feeding (Luttbeg 1999). The factors that determine the animal's feeding behavior are often difficult to uncover, but they are important to understanding behavioral choices.

This study examines the feeding behavior choices of a wrasse species, part of the family Labridae. The members of the

family Labridae, which also include parrotfish, are among the most diverse and abundant fishes in the coral reef ecosystem (Wainwright and Westneat 2004, Aronson 1987). Composed of more than 580 species, this family of fish appears in nearly all coral and rocky reefs worldwide (Wainwright and Westneat 2004). This great diversification is at least partially due to their exceptional range of trophic habits. Among the labrids are herbivores, planktivores, piscivores, ectoparasite feeders, durophagist, and carnivores (Wainwright and Westneat 2004). This great variety makes them attractive study subjects because they have unique feeding behaviors. Although the diet and feeding mechanics of many coral reef wrasses have been well studied, little is known about the feeding ecology and behavioral interactions of many of these fishes (De Pirrott 1999). Because most of this great variety of feeding habits is easily observable in tropical lagoons, labrid fish are ideal study subjects for observing a host of variations in foraging strategies and feeding behaviors.

One such wrasse, the Yellowtail Coris, *Coris gaimard* (Quoy and Gaimard), exhibits a rare foraging behavior of overturning coral rubble with its mouth to access the marine macroinvertebrate prey that hide underneath (Jennson 2005, Shibuno et al. 1994). The mechanics of this behavior are unique. However, other wrasses including *Coris aygula*, *Thalassoma pavo,* and *Novaculichthys taeniourus* also move pieces of coral substrate with their mouths in different ways for feeding or construction of sleeping mounds (Kabasakal 2001, Takayanagi 2003).

This rock flipping behavior varies in frequency across its range compared to the fish's other feeding behaviors. *C. gaimard* has an extensive range spanning from the Red Sea east to the Hawaiian archipelago (Shibuno et all. 1994). In waters off Kuchierabu-jima, Japan, *C. gaimard* has been observed scavenging for prey on the tops of coral rubble and feeding behind scarid fishes in addition to flipping rubble (Shibuno et al. 1994). *C. gaimard* populations off Moorea, French Polynesia, employ these scavenging methods with different frequencies. Additionally, the Moorea populations exhibit two feeding behaviors not observed in Japan. This study attempts to understand the biotic factors that account for the differences in foraging methods and their frequency.

Two hypotheses are proposed. The first hypothesis indicts interspecies interactions as a major factor in determining foraging strategies. *C. gaimard* engages in heterospecific feeding relationships with goatfish species and other wrasses. Goatfish (Mullidae) use sensitive barbels to troll through lose sand substrates in coral lagoons (McCormick 1994). This behavior attracts a variety of attendant species that attempt to eat prey that escapes the mullid's initial attack (McCormick 1994, Strand 1998, Silvano 2001). *C. gaimard* can act as an attendant species to a foraging goatfish. Similarly, several goatfish species were observed following behind *C. gaimard* as it flipped over coral rubble. The goatfish was observed sifting through the recently exposed sand that had been uncovered by the flipping of a piece of rubble. This feeding relationship may motivate *C. gaimard* to flip coral rubble more often in waters to attract mullid fishes from whom it can then feed behind. This hypothesis can only be true if there is a mutualistic relationship and, more over, it occurs frequently enough to significantly affect *C. gaimard's* feeding behavior.

A second hypothesis claims that a difference in prey quantity will result in a difference in feeding behavior. As prey availability increases, less energy expensive behavior (flipping rubble) will be preferred. *C. gaimard* is a dietary generalist preying on gastropods, polychaetes, foraminifera, crabs, amphipods, stomatopods, chitons, and a variety other marine macroinvertebrates (Shibuno et al. 1994, Hiatt and Strasburg 1960). Therefore, in any tropical reef, *C. gaimard* has a host of possible prey items. This host of prey, in combination with several foraging methods, gives *C. gaimard* multiple

available foraging strategies of which one must then be the most efficient. The determination of optimal foraging will depend on the caloric value of the prey and the ease of capturing it, according to optimal foraging theory (MacArthur 1966). Because prey varies with location, so then to must the foraging strategy.

The testing of these hypothesizes will attempt to determine the effect of biotic factors on fish behavior. This determination will lead to a better understanding of foraging theory choices and the mechanisms that control it.

METHODS

Feeding behavior

The study will attempt to account for variation in foraging behavior with a corresponding variation in biotic factors. To determine the variation in frequency of feeding behaviors, *C. gaimard* adults were observed in the field using snorkeling mask and fins. Individuals were observed no more than once a day and only between 0900 hours and 1600 hours, when the fish is known to be active and feeding. The total length (TL) of the fish was visually estimated to within 2.5 cm and identifying marks were noted to prevent sampling the same individual again that day. Identifying marks most often included tail injuries and the presence of a red outline on the end of the tail. During the ten minute observation time, the observer recorded the number of times the individual attempted the following behaviors: flipping over an object, biting prey off an object it had flipped, biting prey off a surface that it did not flip, digging in the sand for prey, and feeding in the wake of a goatfish trolling through the sand. Observations were performed in two coral rubble bottomed lagoons surround the island of Moorea, French Polynesia: Temae Public Beach (17° 29' 53.2" S, 149 °45 '21.7" W) and Motu Tiahura (17° 29' 19.0" S, 149° 54' 51.5" W) (Figure 1). Both lagoons had similar depths, similar substrates of coral rubble, and a nearly equal presence of live coral along the edges of large beds of rubble. The two populations of *C. gaimard* were sampled 20 times between 8 October 2007 and 14 November 2007. Additional observations were done offshore from Opunahu Public Beach (17° 29' 17.4" S, 149° 51' 10.7" W) during the same time period.

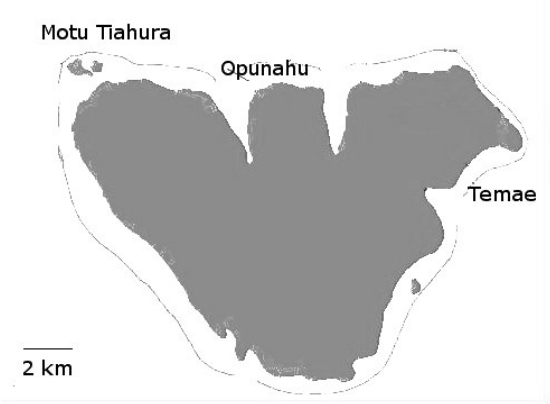


Fig 1: Map of Moorea, French Polynesia with the three study sites

Interspecies interactions

To measure the effects of interspecific feeding relationships, the frequency of feeding relationships between *C. gaimard* and other fishes were measured. All feeding relationships exhibited during the ten-minute observations were noted. Fish species feeding on rubble flipped or sand expose by *C. gaimard* were identified and recorded. These observations included all mullid fishes trolling through freshly exposed sand and other wrasses feeding off flipped rubble. Fish feeding off of flipped rubble more than 30 second after it was flipped were not included.

Rubble mass

The size of coral rubble is sometimes correlated with the amount of invertebrate prey that associates with it (Shibuno et al. 1994). Variation in the size of flipped coral rubble may correspond to a variation in prey or foraging strategy. To measure variation in the size of rubble *C. gaimard* flips, coral rubble

flipped during the ten-minute observations was collected. Coral rubble was only collected when it was possible to do so without risking losing sight of the fish and after the fish had moved over 1 m away from the rubble. The flipped rubble was brought back to the lab and weighed with a spring scale to the nearest 10 grams and then returned to the site where it was collected.

Pairing frequency

Although not hypothesized to affect feeding behavior, association with other *C. gaimard* individuals may attract more interspecific feeders. Pairing behavior was noted to discount the presence of interspecific feeders when the observed fish may not be the only factor attracting other foraging fish. To determine the frequency which *C. gaimard* pairs with other *C. gaimard* individuals, it was noted when an individual paired for 30 second or more during the ten-minute observation times. Pairing was classified as two *C. gaimard* individuals swimming within about .5 m of each other at the same speed and maneuvering around obstacles using the same path. Pairing individuals were not observed consecutively so as to not overestimate the frequency of the behavior.

Prey survey

To determine the relative abundance of prey items on the coral rubble, samples of flipped coral rubble were collected and the crustaceans living on the rubble were measured in a method outlined by an earlier study on *C. gaimard* behavior (Shibuno et al. 1994). Samples were gathered by covering a piece of rubble a *C. gaimard* individual had flipped with a 10 cm by 10 cm by 10 cm plastic box with an open bottom. The box covered the sample and was sunken 2 cm into the sand. A plastic slate was slid underneath the box. The sand and gravel was transferred to a plastic bag and brought back to the lab. At the lab, the sample was soaked in 90% ethanol. Using tweezers, a dissecting scope, and calipers, animals > 0.2 mm in the sample were removed, measured, and categorized. The mass and diameters of the rubble was measured to the nearest 1 gram and 1 millimeter using a spring scale and calipers. Sample collecting was haphazard. Rubble was chosen by either sampling the first piece of rubble flipped after the fish's ten-minute observation or by taking the first piece of rubble flipped one full minute after the fish was spotted. Individuals were sampled no more than once per day. Twenty crustacean samples were analyzed for each observation site.

Description of behaviors

To describe the behaviors cataloged in this study, all behaviors were recorded in the field using a digital camera with underwater housing set to video mode. The videos were then slowed down using Windows Movie Maker software and still shots of the behavior were taken separately, but with similar equipment.

RESULTS

Feeding behavior and Prey survey

In the ten-minute observation data set, all data were grouped by location. In comparing sites, a Students T-test revealed no significant difference in estimated total length of observed fish between the sites ($p = 0.222$). Additionally, except for two observations of males at the Motu site, all fish observed were female between 10 and 35 cm TL. At the Motu sites, 192 flipping events were recorded— a mere 41.5% of the 462 flipping events recorded at the Temae site (Figure 2). An unequal variance T-test showed significantly more flipping at the Temae site ($p = 0.005$). The fish were observed flipping not only dead coral rubble, but also occasionally turned over clam shells, live coral pieces, rocks, large snail shells, and live hermit crabs.

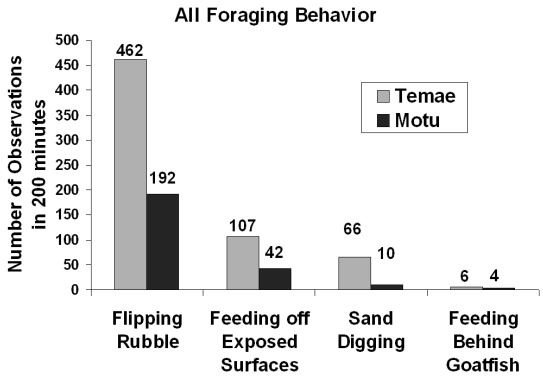


Fig 2: All foraging behaviors observed in standardize timed observations by site.

The number of bites taken on flipped rubble was also higher at Temae. At the Motu site, 139 bites on flipped rocks were observed resulting in a ratio of 0.556 bites per flip. That is less that the 0.724 bites per flip recorded on the Motu (derived from the 257 observed bites there) although this difference was not significant ($p = .260$). The number of bites at the Motu is 39.3% of the number of bites at Temae, a similar ratio to the number of flips between the two sites.

At the Temae site, the prey reward for flipping rubble was less consistent with flipping effort. The number of flips was poorly correlated ($R^2 = 0.108$) with the amount of bites taken on flipped rocks. At the Motu, however, increased flipping correlated much better with increased in bites on flipped rubble ($R^2 = 0.511$).

The more rare feeding behaviors of feeding behind goatfish and digging in the sand also were more common at the Temae site than at the Motu although significant difference could not be determined on such rare behaviors because of low sample sizes. Sand digging was observed 66 times at Temae and only 10 times at the Motu. Feeding behind a goatfish was observed a mere 6 times at Temae and 4 times at the Motu.

Regardless of the differences in number of foraging behaviors, proportionally there was little difference between foraging behavior at the Temae site and at the Motu site (Figure 3). Flipping accounted for 72.1% and 77.4% of the feeding behaviors at each site respectively. Biting prey off non-flipped surfaces accounted for 16.7% of the feeding behaviors at Temae and 16.9% at the Motu. Sand digging and feeding behind goatfish accounted for the remaining behaviors.

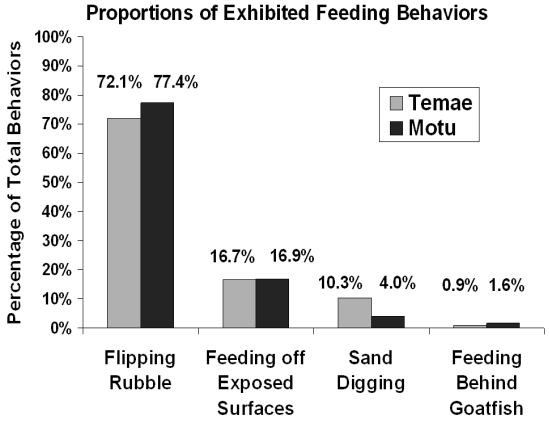


Fig 3. Relative proportions of each feeding behavior exhibited in 200 minutes of standardized observations.

Interspecies interactions

C. gaimard was observed feeding with 8 other fish species including most commonly other wrasses (Labridae), goatfish (Mullidae), and much more rarely trigger fish (Balistidae) and jacks (Caranx). No difference was observed in the frequency of these interactions between study sites. Other species of wrasse were the most commonly associated fish. They appeared in 61.9% of all observations (57.1% at Temae and 68.4% at the Motu). The most commonly associated wrasse was *Halichoeres trimaculatus* observed in 57.1% of all observations (57.1% at Temae and 57.9% at the Motu). Other wrasses observed feeding with *C. gaimard* including *Thallasoma hardwicki* and *Halichoeres hortulanus*. Both were recorded in less than 10% of the observations. All wrasses were observed feeding off the flipped coral rubble

after the *C. gaimard* individual had finished searching it for prey. However, outside of the standardized observation times, several wrasses were noticed capturing prey before the *C. gaimard* had finished searching the flipped rock.

Goatfish were the next most common associated species recorded in 47.8% of all observations (47.6% at Tamae and 55.0% at the Motu). Four species were identified and occurred in the observation time in various frequencies: *Parupeneus multifasciatus* (35.7%), *Mulloides flavoleatus* (11.9%), *Parupeneus barberinus* (7.1%), and *Parupeneus cyclostomus* (4.8% and only in juvenile stage). Combining interspecies data with foraging observations, one can deduce that in observations when *C. gaimard* was associated with a goatfish, *C. gaimard* flipping significantly more pieces of rubble (18.5 average) than when it was not associated (10.4 average) ($p = 0.024$).

Caranx sp. and *Rhinecanthus aculeatus* (Balistidae) were observed feeding with *C. gaimard* twice each. In contrast to the wrasses and goatfish, *Caranx* sp. and *Rhinecanthus aculeatus* only appeared when they were the only other associated fish.

Rubble mass

Three hundred pieces of coral rubble that were flipped by *C. gaimard* were retrieved and weighed totaling nearly 25 kg. They came from fish from 11 size classes estimated between 8 cm and 35 cm TL. Rubble ranged from less than 10 g to 590 g (Figure 4).

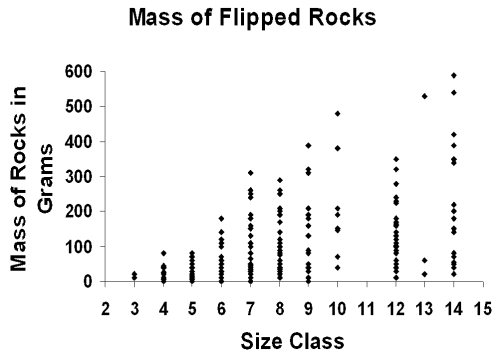


Fig 4. Mass of Flipped Rubble by Size Class

The maximum mass flipped correlated with the TL of the fish ($R^2 = 0.894$, $p < 0.001$) (Figure 5).

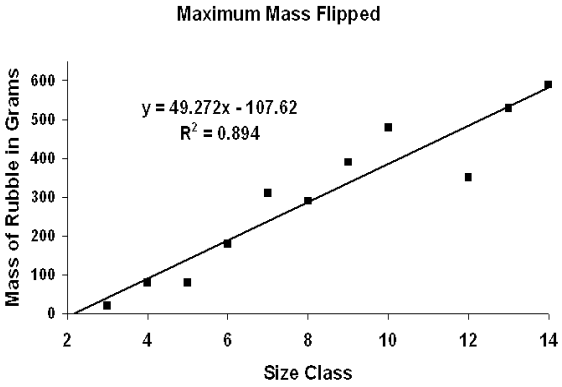


Fig 5. The maximum mass flipped by any member of the size category increase as the size category increases.

However, the minimum mass flipped by the fish remained around 10g regardless of size class. Between sites there was no significant difference in the size of rubble flipped when comparing fish in the same size classes.

Pairing frequency

Individuals often were seen accompanied by other *C. gaimard* as they foraged. In 52.0% of the observations, individuals swam together for at least 30 seconds at least once during the ten minutes. *C. gaimard* individuals were never observed feeding together or feeding behind another feeding *C. gaimard* individual. On several occasions a large male would charge smaller females, but the attack rarely lasted for more than a few seconds. Both individuals swam away following an initial charge. All observed pairs were composed of two females.

Prey survey

Twenty crustacean samples were performed at each site. The samples were collected haphazardly, and there was no significant

difference in the mass or diameters of the collected rubble pieces ($p = 0.351$, $p = 0.862$ respectively). Samples were grouped together by site. The Motu contained far more prey items than the Temae site. 463 prey items were discovered on the rubble pulled from the Motu compared to only 130 from Tamae. The Motu had more prey items in every category, especially in the category of crabs, whose biomass surpassed any other prey category (Figure 6).

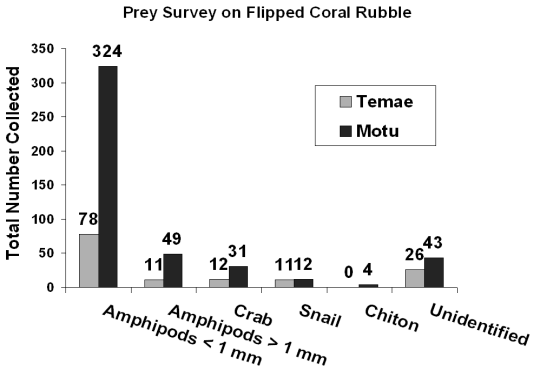
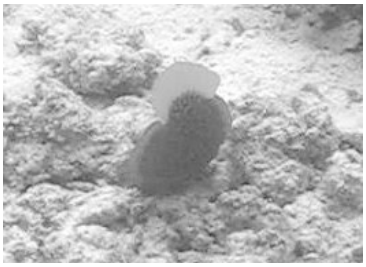


Fig. 6. The results of the prey survey of all the prey items on 20 flipped rocks at each site.

Description of behaviors

Only adult *C. gaimard* were observed flipping objects. Juveniles were observed only searching sandy surfaces and algae covered rubble for food. Several videos taken of the *C. gaimard* flipping were analyzed. Five distinct steps were present in all samples. First, the fish positions itself about 30 - 45 degrees from the substrate and straightens its body (Figure 7a). During this step, the individual positions its snout just under the piece of rubble as its tail sticks up in the water column pointing away from the rubble. Second, the individual folds itself into a U shape using the force of its bending body to lift the rubble on end (Figure 7b). The fish bends in such a way so that its tail it is now pointing towards the rubble. The fish is not making contact with the substrate and is only pushing the rubble with the teeth on its lower jaw, not its snout. Third, by swinging its tail around, the fish straightens its body, which provides the necessary force to overturn the rubble (Figure 7c). In this step it is most evident that only the jaw, not the fish's face or scales, is coming into contact with the often rough or sharp rubble pieces. Fourth, the fish will search the newly exposed substrate and the bottom of the flipped rubble for prey items (Figure 7d).

A.



B.

C.

D.

Fig. 7 Four steps *C. gaimard* performs to overturn coral rubble

Similar video analysis was done for *Novaculichthys taeniourus* and *Coris aygula*, two somewhat related species that perform similar foraging behaviors.

DISCUSSION

Feeding behavior

This study investigates what biotic factors may influence the foraging behavior of the wrasse *Coris gaimard*. A variation in foraging behavior of *C. gaimard* was observed between two lagoons around the island of Moorea, French Polynesia. There are two proposed explanations for this variation: a variation in prey presence or the effects of interspecies interactions. The *C. gaimard* individuals at the first site, the Motu site, performed 58.5% less foraging behaviors than a similar population at second, the Temae site. This difference can be simply explained by the large difference in prey items available between the sites. A prey survey of available prey items at the sites revealed that there is 71.9% less prey available at the Temae site. This means that the fish would need to exert more foraging effort to get its required amount of food to live and reproduce. This shows that the biotic factor of prey abundance affects the amount that *C. gaimard* forages. The mechanism driving this increased amount of foraging can be assumed to be caloric demands. It seems that a fish will continue to forage until it has a sufficient food resources.

Looking only at the behavior of flipping rocks over: when the number of bites off of flipped rubble was calculated, it was poorly correlated with the number of flipped rocks at the Temae site ($R^2 = 0.108$). The amount of bites off flipped rubble was more closely correlated with the amount of flipped rubble at the Motu ($R^2 = 0.511$). This indicates that the prey was not only less common, but also less evenly distributed. Fish flipping rubble at the Temae site then had to forage longer to find prey rich patches to feed in. This will also increase the amount of forage behaviors as the fish seeks out prey rich rocks.

Though the amount of foraging *C. gaimard* does increased, the strategies that both populations employed were strikingly similar. "Strategy" is defined here as the proportion of effort the fish spends on each foraging behavior. Both populations expended about 75% of their foraging behaviors flipping rocks. Both populations dug in the sand for 16% of their foraging behaviors. This ratio is not a species characteristic. *C. gaimard* populations elsewhere do not exhibit these behavior frequencies (Figure 8).

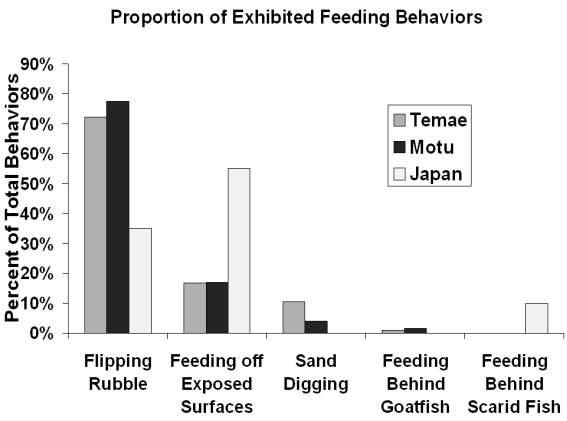


Fig. 8. Relative proportion of observe feeding behaviors in Moorea and those reported by in Japan by Shibuno et al. 1994. Note: The largest size class was used to estimate the frequencies from Japan.

In Japanese waters, a similar study of *C. gaimard* observed fish searching for exposed prey for greater that 50% of its observed foraging events (Shibuno et al. 1994). Additionally, the Japanese population was never observed feeding behind goatfish or sand digging, but instead it observed *C. gaimard* feeding behind scarid fish (Shibuno et al. 1994). The change in foraging strategies is due then, not to crustacean abundance, but instead of crustacean types. The Japanese population fed from a different crustacean food base, which many more mollusks and

crabs available to feed on (Shibuno et al. 1994). I hypothesize that the prey in those waters are more apt to be found on the surface of the substrate. *C. gaimard* then does not need to go through the energy expensive behavior of flipping rocks to uncover its required amount of prey. Different prey items demand different strategies to maximize caloric input. *C. gaimard* strategy for foraging then is not based on abundance of prey, but on composition. This variation in strategy also demonstrates that the fish has a phenotypic plasticity in its behavioral strategy. This plasticity makes it locally adapted to its habitat. This increases its fitness because it maximizes the use of variable habitats and expands its range of viable habitats. *C. gaimard* ranges throughout the tropical Pacific and Indian Oceans (Shibuno et al. 1994). This large variation can be partial explained by its ability to adapt its behavior in response to the variation in prey that is present across its range.

Interspecies interactions

An alternative hypothesis is that *C. gaimard*'s behavior was altered in Moorea by the presence of heterospecific feeding relationships. *C. gaimard* played an important role in heterospecific feeding by disturbing the substrate by turning over rubble. This exposes previously covered sand and exposes the underside of the flipped rubble. *C. gaimard* searches both the sand and the exposed rubble for prey. However, when *C. gaimard* finishes searching, goatfish would often sift the freshly exposed sand for hidden benthic invertebrate prey. Wrasses would often scavenge the newly exposed face on the rubble for prey that *C. gaimard* may have missed. These three roles: "substrate disturber", "sand sifter", and "scavenger" were filled by many different species (Figure 9).

This relationship is made more complex by three important observations. One, all three roles do not have to be filled for any of the species to forage. Occasions where only two of the roles were fill were often observed. All species were also seen feeding alone and do not seem to require the others presence. Scavenging wrasses often find food on exposed surfaces; goatfish often troll in open sand beds; and substrate-disturbing species often turn over rubble and sand unaccompanied. Two, goatfish forage after other foraging goatfish (McCormick 1994). A foraging goatfish provides enough of a substrate disturbance to attract other goatfish and scavengers. Three, *C. gaimard* can fill the role of both substrate-disturber and scavenger.

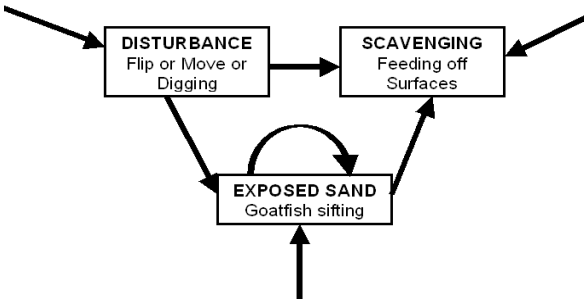


Fig 9. A conceptual diagram of roles in the heterospecific feeding relationships with *C. gaimard*

These heterospecific feeding relationships occur with notable frequency. *C. gaimard* individuals were accompanied by foraging goatfish in 47.8% of the observations and accompanied by scavenging wrasses in 61.9% of the observations. *C. gaimard* individuals accompanied by goatfish flipped significantly more rubble than those foraging alone. Goatfish are attracted to the disturbed substrate where previously covered sand is now exposed (McCormick 1994). Therefore, goatfish were more likely to find *C. gaimard* when it was flipping more often. The presence of a goatfish may provide *C. gaimard* with an additional motivation to flip over rocks. *C. gaimard* can feed after a trolling goatfish that is stirring up the sandy substrate and uncovering benthic invertebrate prey. *C. gaimard* scavenges the sand after the goatfish finish searching for prey. The proposed mutualistic relationship where *C. gaimard* over turns rocks to reveal fresh sand and a

goatfish sifts through that sand did not occur with any significant frequency. *C. gaimard* fed behind goatfish very rarely, about 1% of the time even though it was accompanied by goatfish in 47.8% of the observations. In heterospecific relationships, it is often hard to distinguish between mutualistic relationships and commensal relationships (Morse 1977). However, it does not seem that *C. gaimard* is rewarded by foraging with a goatfish for the presence of the goatfish to significantly affect its amount of prey captured. Although *C. gaimard* captured more prey when goatfish are around that is due to the fact that *C. gaimard* flipped more rocks when the goatfish was attending. The goatfish attending *C. gaimard* and *C. gaimard* attending a goatfish seem to be two separate commensal relationships that occur in different frequencies. Furthermore, this commensal relationship is not species specific to *C. gaimard,* nor is its specific to wrasses or even to fish; a diver kicking up sand easily attracts scavengers and goatfish.

Among the goatfish species that attend *C. gaimard,* there seems to be no species that associates more strongly. *Parupeneus multifasciatus* attended *C. gaimard* most often (35.7%). However, this may be a result of *P. multifasciatus* being a habitat generalist and being able to use area of reef that is covered by coral rubble and therefore preferred by *C. gaimard* (McCormick 1994). *Parupeneus barberinus* and *Mulloides flavolineatus* attended *C. gaimard* less frequently (7.1% and 11.9% respectively). These species more often select sandy habitats and are therefore less likely to encounter *C. gaimard*, which is almost always observed over coral rubble (McCormick 1994). *Parupeneus cyclostomus* juveniles attended *C. gaimard* only 4.8% of the time. Although *P. cyclostomus* is a habitat generalist like *P. multifasciatus*, it is very rare on the study sites (McCormick 1994). *P. cyclostomus* was only seen twice at the study sites and never as an adult. This lack of species specificity further indicates that there is no mutualistic relationship between the goatfish and *C. gaimard.* Therefore, there is no reason for *C. gaimard* to alter its foraging behavior in the presence of goatfish.

Scavenging wrasses like goatfish did not provided a significant benefit to *C. gaimard*. In some rare cases, wrasses were observed scavenging off flipped rocks before the *C. gaimard* individual had done so. This relationship is then at most a mildly parasitic one. However, there is no significant difference in the behavior of *C. gaimard* individuals that were accompanied by scavenging wrasses. Therefore, interspecies interactions did not play an important role in the foraging strategy of *C. gaimard.*

Rubble mass

The masses of the rubble that *C. gaimard* individuals flipped did not significantly vary between study sites. This is important for two reasons. First, this similarity shows that the foraging strategies between the Motu and Temae did not vary in this way. The fish were not selecting larger or smaller rocks depending on prey abundance. This may be because there is no benefit in selecting different sized rocks or because there is limited plasticity in the fish's behavior. Second, it demonstrated that the fish were expending on average a similar amount of effort per flip. This is important in evaluating the cost to benefit ratio of a foraging behavior, which in this case for rock flipping would be lower at the Motu sites where there was more prey items. This lower cost per benefit means that the behavior is more beneficial. This information could be applied to optimal foraging theory if more data was collected on prey consumption and search times.

Pairing frequency

Individuals swimming in pairs did not perform any foraging behavior. However, there was no significant difference between the amounts of pairing behavior between the sites. For this reason, the pairing behavior

does not account for any variation in feeding behavior. The motivation to swim in pairs is unknown. It was only observed with two females participating, which suggests it is not a mating display. However, because it is a protogynous species, it may be a method that females use to constantly measure their dominance against other females. There is currently no research on this species reproduction and interspecies interactions. This may be partial due to the fact that the species was previously reported as solitary (Shibuno et al. 1994).

Description of behaviors

The analysis of several video tapes of the behavior suggest that regardless of location, size, or sex, the general method of flipping rubble was consistent. This behavior is also similar to that of *Novaculichthys taeniourus*, a related wrasse that inhabits the same habitat as *C. gaimard*. Similar video analysis of *N. taeniourus* rock moving shows a similar behavior with several key differences. First, *N. taeniourus* begins the behavior in the water column above the rubble, not next to it, nearly perpendicular to the substrate. *N. taeniourus* then grabs the rubble in its jaws. Finally, it performs a similar body folding and straightening before opening its jaws and releasing the rubble a small distance away.

The sand digging behavior of *C. gaimard* is exactly mimic by *Coris aygula*. Both species shovel sand to the side with their snouts as they swim upright roughly 45 degrees from the bottom of the lagoon.

Feeding behind a goatfish like feeding off exposed surfaces is a behavior common to several wrasse species. All seem to position themselves a few centimeters above the substrate around the head of the goatfish catching whatever prey items might be thrown into the water.

The similarities in feeding behaviors with related species suggests that there may be overlapping feeding niches. This would suggest competition between *C. gaimard* and these fish. The abundance of fish that compete for a feeding niche may the affect the foraging behavior of *C. gaimard* because *C. aygula* or *N. taeniourus* may out compete *C. gaimard* for prey captured by moving rocks or digging in sand. Similarly, scavenging wrasse may clean all the prey items off the surface of rocks. Future research should attempt to quantify the influence of these fish in foraging strategies. Both substrate-disturbing species and scavenging species occurred at both sites on Moorea, but with unknown abundances.

Conclusion

Biotic factors were found to influence the behavioral choices of *C. gaimard*. However, some biotic factors such as presence of goatfish, scavenging wrasses, and other *C. gaimard* individuals were found to have no significant effect on foraging strategies. These results suggest that *C. gaimard* is a phenotypically plastic species that takes cues only from its foraging success to choose a foraging strategy. This adaptability may help the species have an extensive range and live in environments that are spatial and temporally variable. The limits to this plasticity are unknown. The similarities between the two studied populations may be due to strategic choices or plasticity limitation. Further research in the topic must test the limitations of the fish's ability to adapt. Alteration of habitat or replacement studies may reveal how quickly and how much an individual can adapt its behavior. Additionally, such a study would reveal what other factors, other than frequency and amount of behavior can be modified. Future research should also include a more complete analysis of the species optimal foraging strategy. Because the fish adapts to its locality, it should then exhibit the most efficient foraging strategy possible.

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FAIR IS FOUL AND FOUL IS FAIR: EFFECTS OF SUBSTRATE TYPE AND AGE ON THE COMPOSITION OF FOULING COMMUNITIES IN MO'OREA, FRENCH POYLYNESIA

KERRY WININGER

Integrative Biology, University of California, Berkeley, CA 94720

Abstract. Fouling communities are assemblages of marine organisms, including algae, mollusks & annelids, that colonize man-made submerged objects, most commonly boat hulls, docks and harbors. These communities have the potential to colonize ship hulls and increase drag through the water, thereby increasing fuel use. Hull fouling has also been identified as a mode of transport for nonindigenous marine organisms. Therefore, scientific interest in the structure and dynamics of fouling communities has been large. This study examines the response of fouling community richness to increasing substrate age, as well as to the microhabitat differences found on boats and docks in Mo'orea, French Polynesia. Additionally, a settling plate experiment was carried out to investigate short-term patterns of fouling community succession. A positive correlation was discovered between age of substrate and total taxonomic richness of the community, which was supported from the settling plate data. Richness was also found to be greater on docks than boats, and greater on the stern of one boat that was more closely studied than on its hull. These associations have potential implications in the shipping industry as well as in the study of ecological invasions.

Key words. fouling community, hull fouling, richness, succession, disturbance, nonindigenous species, Mo'orea, French Polynesia

INTRODUCTION

Fouling communities have been of great interest not only in the shipping industry for their affects on increasing water resistance on ship hulls, but also in the area of marine ecology due to their potential to introduce non-indigenous species (Floerl and Inglis 2005). The composition of fouling communities is influenced by a variety of factors in the surrounding environment. One factor of importance is the age of the substrate on which the community is found as successional studies have shown that temporal changes affect the community as the substrate becomes colonized (Scheer 1945). Another factor influencing composition is the habitat provided by the fouling community's substrate. (McGuinness & Underwood 1986). Artificial substrates vary remarkably in the microhabitats that they provide (Tyrrella & Byers 2006). For example, the communities found on boats and docks are affected by differences in mobility of location, rate of cleaning and surface material of substrate (i.e. presence of antifouling paint) and hydrodynamics. The hydrodynamics of a habitat have been found to affect the development of certain fouling species (Khalaman 2007).

Conclusions drawn from studies on the role of fouling communities in biological invasions have varied, ranging from suggestions that fouling communities play a minor role in algal introductions (Mineur et al 2006) to those that hull fouling is responsible for the majority of introduced tropical marine organisms (Hewitt 2002, Godwin 2003). This disagreement illustrates a lack of universal understanding of fouling community structure and function, indicating that additional work is needed to investigate the more basic components of community composition and what influencing factors may be. Previous research that combines the affects of age and substrate has shown significant results, such as the large influence of hull paint age on community composition (Floerl & Inglis 2005). Studies have also concluded that disturbance

increases community diversity (Sugden et al 2007).

Additionally, this study appears to be the first looking at factors affecting fouling communities on any of the islands of French Polynesia, with previous studies in these islands focusing on how fouling communities affect the surrounding mobile organisms (Nelson 2003). The variety of boats docked on Mo'orea, including the inter-island ferries between Papeete, Tahiti and Vaiare, Mo'orea in French Polynesia offer a novel system by which to study the composition of fouling communities of different ages both on docks and boats.

My objectives in this study were to investigate how fouling community composition varies by substrate, that is, between boats and docks, as well as how it is influenced by age of substrate. I hypothesized that richness of organisms would be higher on docks than boats and would also increase with age. I also predicted that community composition of organisms would vary with substrate type and age.

METHODS

Ferry colonization

The Aremiti 5, which docks in Vaiare, Mo'orea has its hull professionally cleaned by a team of SCUBA divers once every 14 days, creating an ideal system by which to observe successional colonization within the fouling community. During one complete cleaning cycle (Oct 22 – Nov 3, 2007) I characterized the fouling communities of the ferry and its three associated pilings immediately after cleaning (Day 1) and the day before the next cleaning (Day 13). I photographed three 25 cm^2 quadrats at a depth range of 0.5-2 m on both the ferry hull and stern, as well one quadrat per piling in a depth range of 1-2 m. I then destructively sampled each quadrat by scraping all visible organisms into sealing plastic bags. On Day 1 of sampling the ferry, I sampled an adjacent quadrat rather than that photographed. In the laboratory, I divided the collected organisms of each quadrat into categories based on visual and textual similarities. I then put each category into a separate container of salt-water and took photographs of each. Final classification of organisms into taxa was completed after return to UC Berkeley.

Colonization of other vessels

I sampled from a total of eight sites on Mo'orea, each site consisting of a boat paired with its associated dock. These sites included hotels (The Sofitel, The Intercontinental, and Pearl Hotel), the fish cooperative, Hiro Tours, Top Dive, the Gump Station and one private residence in Cook's Bay. After gaining permission to sample, the fouling communities on the boats and adjacent docks were photographed and collected using the same method as that used with the Aremiti 5 ferry. Samples were taken at depths as close as possible to 1 m, but were often less due to the shallow hulls of the vessels looked at. I also collected information on the length of time that the vessel had been docked at current location, the time since hull cleaning or dry-docking and age of current dock pilings. Organisms were placed into categories and photographed in the same way as those found at the ferry, and these photographs, as well as voucher specimens, were transported back to UC Berkeley where they were used for taxonomic classification.

Tile colonization

I attached 20 hand-brushed steel settling plates (15 cm^2) on a stationary submerged metal sheet (~1 m^2) covering a depth range of 0.5–1.5 m offshore in Cook's Bay, Mo'orea. To characterize succession in a fouling community, I collected five random plates each week for 4 weeks (Oct 15 - Nov 12, 2007) and categorized organisms found. I also categorized organisms in the surrounding water that appeared to be closely associated with the plates.

Statistical analyses

Statistical tests were run using JMP statistical analysis software. For all tests, a significance level was determined at a p-value of 0.05. For analysis of effects of substrate, overall richness of taxa, as well as richness of

functional groups, on boats was compared to that on docks using a t-test. A goodness of fit test to the normal curve and an unequal variance test for homogeneity of variance, which included O'Brian's, Brown-Forsythe, Levene's and Bartlett's tests, were run to verify that results of the t-test were applicable. For analysis of effects of substrate age, linear regression was used and age was log transformed. For analysis of effects of location on the ferry, that is hull versus stern, a one-way ANOVA was used and significance was found using a Tukey HSD test.

RESULTS

All organisms found in fouling communities, both on the tiles and in the field at the ferry and other 8 sites, were placed into 23 taxa (Table 1). These taxa were based primarily on taxonomic similarity, but also on frequency of occurrence of organisms within a group in the fouling communities studied. For example, whereas most taxa consist of 3-4 individual organisms, with no more than 2 taxa representing a major taxonomic group (i.e. there are 2 taxa that cover Annelids, with four types of worms total), 19 individual types of algae were seen and placed into 13 taxa, which is many more than any other group. Therefore, some analysis was done on total number of taxa, some on frequency of each taxon, and some on frequency of both an algae set and an invertebrate set. When the last of the above was analyzed, frequency was measured by a ratio of the number of taxa found in that site to total number of taxa in the set being analyzed (i.e. either algae or invertebrate). Substrate and age were found to be highly correlated with each other and were therefore analyzed independently.

Table1: Taxa used for community richness.

Organism Type	**Taxon #**
Algae	1-13
Annelids	14
Porifera	15
Gastropoda	16-17
Bivalvia	18-19
Other Mollusks	20
Crustaceans	21
Anthozoa	22
Fish	23

Effects of age

Linear regression results showed a significant, although not strong, positive correlation between richness of total taxa and age of substrate (r^2=0.3308, p=0.0125)(Figure 1). Richness of algae taxa and invertebrate taxa also correlated positively with age (r^2=0.2970, p=0.0193 and r^2=0.3790, p=0.0065 respectively), with invertebrates showing a slightly stronger correlation (Figures 2 & 3)

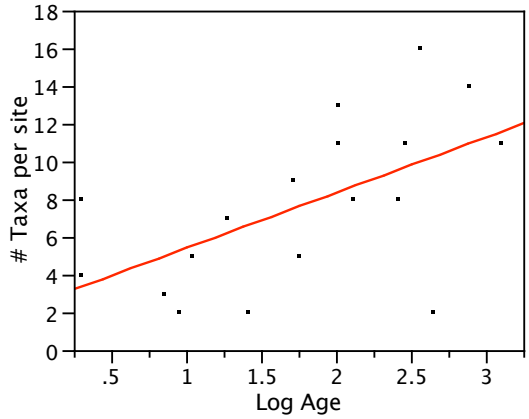

Figure 1: Affect of substrate age on richness; Increasing age was seen to significantly positively correlate to richness (r^2=0.3308, p=0.0125).

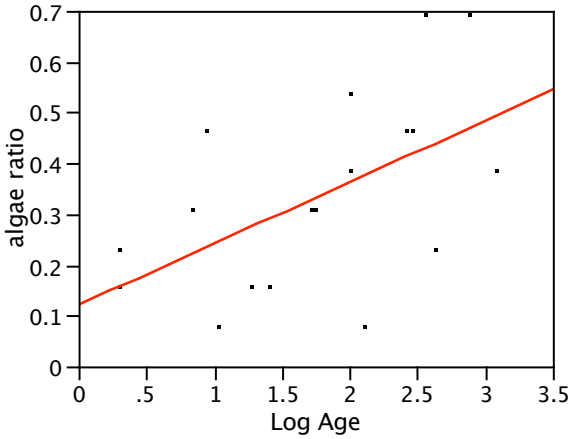

Figure 2: Affect of substrate age on algae richness; Increasing age was seen to significantly positively correlate to algae richness (r^2=0.2970, p=0.0193).

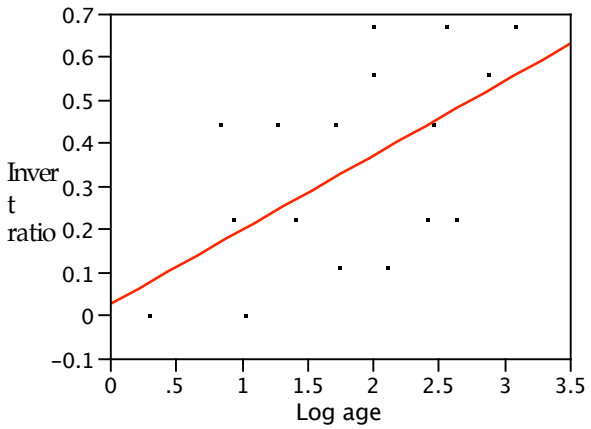

Figure 3: Affect of substrate age on invertebrate richness; Increasing age was seen to significantly positively correlate to invertebrate richness (r^2=0.3790, p=0.0065).

Effects of substrate

A t-test showed a highly significant difference between the richness of taxa found on boats versus docks (p-value=0.0002), with a higher number of taxa on docks (Figure 4). When testing richness of algae and richness of invertebrate taxa separately, both sets remained significantly higher on docks (p=.0029 and p=.0001 respectively), with invertebrates showing more significance (Figures 5 & 6).

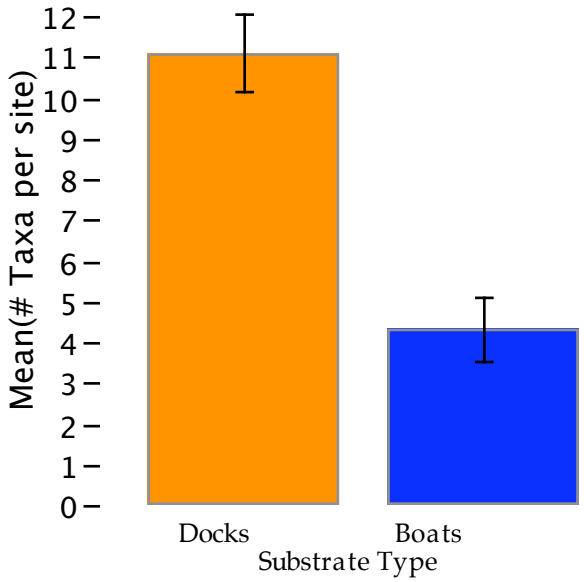

Figure 4: Effect of substrate type on species richness; a significantly higher number of taxa were found on docks than on their associated boats (p-value=0.0002).

Figure 5: Affect of substrate type on algae richness; a significantly higher number of algae taxa were found on docks than their associated boats (p=0.0029).

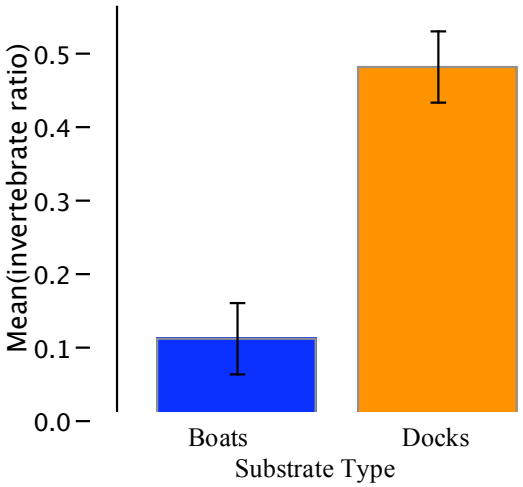

Figure 6: Affect of substrate type on invertebrate richness; a significantly higher number of invertebrate taxa were found on docks than their associated boats (p=0.0001).

Tile colonization

Each week that the tiles were allowed to sit increased the number of colonizing taxa by 3, with the tiles starting as blank plates containing zero taxa each and ending the fourth week with 12 taxa amongst the five collected at that time. This steady and consistent trend was not able to be statistically analyzed due to the small number of taxa found, and was instead represented graphically (Figure 7). Invertebrates did not appear until the second week's collection, with only different algae taxa appearing in week one.

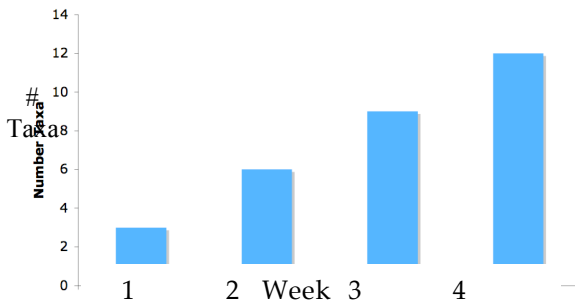

Figure 7: Number taxa found on collected tiles from each week; each week three more taxa were found than the week previous.

Ferry colonization

Tukey HSD analysis showed a highly significant difference between the richness of taxa found on the hull of the ferry versus the stern of the ferry (p=0.0006), with a higher number of taxa on the stern (Figure 8).

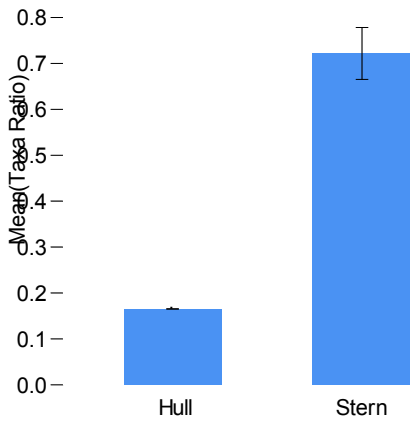

Figure 8: Effect of location on ferry on species richness; a significantly higher number of taxa were found on the stern than on the hull boats (p-value=0.0006).

DISCUSSION

In this study, I showed that the richness of taxa found in fouling communities increases with increasing age of substrate. This supports my hypothesis, and is to be expected on a shorter time scale. However, a saturation point where, without disturbance, no more taxa can colonize due to efficient and complete filling of substrate niches is to be expected at higher ages (Connell & Slatyer 1977). This was not seen in this study, which included boats that had not been cleaned or dry docked for 8.5 years and docks up to 24 years old. The key here could be that, although not purposefully disturbed by cleaning or removal from the marine environment, these systems are not actually free from disturbance. Disturbance in these systems may take the form of seasons, storms, or some other unknown factor. The Intermediate Disturbance Hypothesis proposes that diversity of a community is highest when disturbances are intermediate in intensity and frequency (Connell 1978). If these older sites were being periodically disturbed, succession may continue to occur on those places on the substrate where individuals were displaced or no longer alive, adding to the amount of richness over time, at the same time that those places undisturbed would maintain their composition. Thus, richness would increase in these communities while some later successional organisms would still be present, giving an overall higher richness than younger substrates. Another explanation is that these systems do in fact have a saturation point of richness but that the timescale needed to reach this is much larger than predicted. This may be due to the high complexity and intricate interactions that exist between organisms in coral reef environments when compared to other aquatic systems, providing a larger number of niches to fill. The seemingly continuous trend of increasing species richness on boats and docks tells us that there is no known point at which a fouling community in this habitat can be assumed to be stable. Therefore, the community is always at risk of invasion by nonindigenous species. If the community is on a mobile substrate such as a boat, there is the risk that this species may be transplanted to previously uncolonized habitats, emphasizing the need for conscientious cleaning schedules. This trend also encourages the cleaning of vessels because drag through the water, which creates a costly increase in fuel use, will keep increasing as growth continuously increases. It is also interesting to note that age is more strongly correlated to the richness of invertebrates than to the richness of algae. This could be because I found that algae are most often first among the colonizers, appearing before any invertebrates, but do not disappear with the arrival of invertebrates. This creates a period of time in which no invertebrates are present while no such period exists for algae. Therefore, growth in richness from zero invertebrate organisms appears more dramatic than growth in richness from some algae to more algae. This indicates that invertebrates colonize at a faster rate than algae.

I also found that richness is lower on boats than on their associated docks, supporting my hypothesis. This is to be expected, but, previous to this study, lacked any actual scientific verification. This pattern is

encouraging, demonstrating that the threat of nonindigenous species transfer is somewhat under control as not all the species found on foreign docks will be able to cross over onto visiting vessels to be transported to the home harbor. This is especially true for invertebrates, which showed a more significant correlation than algae. Two major qualities of mobile substrates that stationary substrates lack are variability of location and the potential to pick up and drop off fouling organisms, and increased turbulence due to movement through the water. If only these factors were at play, the results of my study would indicate that the tendency of turbulence to negatively impact richness overrides the tendency of location variability to positively affect richness. However, this result probably stems from the fact that boats are subject to more frequent episodes of purposeful disturbance than docks, such as through cleaning, dry-docking and painting. It follows that this relationship must be viewed as one consciously strived for and cannot be assumed to exist without the effort of humans.

Colonization of metal plates was also found to occur, even though they were all less than a month old, in a rapid and consistent manner. It can be predicted that this steady increase in taxa will level off at a certain age, but I was unable to see this saturation point in the amount of time I conducted this study. The appearance of invertebrates in week 2 suggests that algae are first colonizers in marine fouling communities on Mo'orea and animals are secondary. Other studies have found that algae are often the first successional organism to arrive in a fouling community (McGuinness & Underwood 1986, Scheer 1945, Fairfull & Harriott 1999). This trend supports my proposed explanation to the field data showing a stronger correlation of age with invertebrates than with algae. Tile data also backs up the field data collected showing increasing age, in general, leads to increasing richness in fouling communities, and gives us an idea of the successional timeline of fouling communities in this habitat.

Additionally, when examining data from the two locations of hull and stern on the ferry, I found a significantly higher richness of organisms on the stern than on the hull. These data suggest that not only habitat differences between boats and docks make an impact on community richness, but also the community's location on a single boat. This could be due to different water flow patterns and turbulence associated with these locations, but it could also be explained by differences in how thorough or often these two locations are cleaned. The stern also tends to be exposed to lower levels of light and is made up of a more complex surface structure, providing a higher number of crevices into which organisms can attach. More research on richness differences of communities found at different locations on the same boat are called for to further dissect this association and its possible causes.

It would also be interesting to look more closely at the order and exact time at which organisms appear in fouling communities on different substrates. This could have implications in the commercial shipping industry if it was found that there is a certain age at which organisms that greatly increase water-resistance start or stop colonizing, leading to a more or less rigorous hull cleaning schedule. Further study could also include a comparison on different substrate materials, such as PVC, cement, metal and wood. This could identify certain materials that might accumulate growth at a slower rate and could prove both more cost-effective when building docks so more time could pass between replacement of pilings, and also resist the growth of potentially invasive species from adjacent mobile vessels. Other future studies could investigate…

In conclusion, fouling community richness in Mo'orea is found to increase as a substrate ages and is expected to be higher on boats than on docks. Experimental tile data also supports the role of age on composition, and the location of a community on one vessel may have a large impact on the communities' richness

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THE EFFECTS OF PINEAPPLE FARM RUNOFF ON DIATOMS IN FRESHWATER STREAMS OF MOOREA, FRENCH POLYNESIA

EILEEN WONG

Environmental Science, Policy, and Management, University of California, Berkeley, 94720 USA
eileenw@berkeley.edu

Abstract. Pineapple farms dominate the agricultural landscape of Moorea, French Polynesia, with over 250 hectares of pineapple farmland.. Agricultural runoff has been well known to affect stream ecosystems, in particular, photosynthetic organisms such as diatoms. Few studies have looked specifically at environmental effects of pineapple farm runoff. This study looks at how 1) pineapple farms affect stream chemistry, 2) pineapple farms affect diatom assemblage, and 3) individual effects of herbicides (atrazine and diuron) and fertilizers on diatom populations. No significant differences in stream chemistry or diatom assemblages in farm affected and unaffected areas were observed. Herbicides and fertilizers did not have any significant effects on diatom species richness and abundance.

Key words: diatoms, pineapples, agriculture, freshwater streams, Moorea, French Polynesia

INTRODUCTION

The conversion of land into agricultural areas has had many negative effects on the environment, including soil nutrient loss, erosion, destruction of habitats, and accumulation of agricultural chemicals in water bodies. In particular, the effects of agricultural runoff, the leaching of surface water and chemicals from agricultural land, have long been studied. Previous studies have documented the presence of fertilizers and herbicides in streams near agricultural areas after application (Pfeuffer and Matson, 2001; Green et al., 1977). Fertilizers have been shown to increase nutrient load in water, causing quick and sometimes toxic eutrophication of surface waters (Silva et al., 2000; Csatho et al., 2007; Carpenter et al., 1998). Studies of herbicides in surface water have shown that they may negatively affect photosynthetic aquatic organisms, although the organisms may recover (Graymore et al., 2001; Gustavson 2003; Huber, 1993).

Diatoms, a fundamental component in many ecosystems, are sensitive to many biological, physical, and chemical changes in environment (Stoermer and Smol, 1999). In particular, studies have shown freshwater diatoms to be affected by agricultural runoff in continental streams (Winter and Duthie, 2000a; Lavoie et. al, 2004; Winter and Duthie, 2000b). Agricultural runoff is composed of many different types of fertilizers and herbicides. Added nutrients from agricultural fertilizers have been shown to increase diatom populations in some stream systems (Davies et al., 2006). However, the effect of herbicides on diatoms remains unclear (Legrand et al., 2006; Seguin, 2001; Leboulanger et al., 2001; Downing et al., 2004).

The island of Moorea in French Polynesia offers a unique setting in which to study the influence of pineapple farming on freshwater stream organisms. Although Moorea has several types of agriculture, including cattle pastures, pineapple farms, banana farms and papaya farms (personal observation), pineapple plantations are the most widespread and have the greatest potential biological impact, accounting for over 250 hectares of pineapple farms on the island (Coco Teraiharoa, personal communication). Although local government, farmers, and agricultural schools are currently working together to develop better and less invasive techniques for pineapple farming, Moorean pineapple farmers currently still use fertilizers, herbicides, and hormones to increase crop yield (Coco Teraiharoa, personal communication).

Although other studies have found agricultural runoff to affect freshwater stream ecosystems (Davies, 2006; Legrand et al., 2006; Winter and Duthie, 2000a), little information about pineapple farm runoff is currently available. This study explores the potential impact of herbicide and fertilizer use in pineapple agriculture on diatoms of nearby freshwater streams. I test the

following hypotheses: 1) agricultural runoff from pineapple farms affects stream chemistry; 2) herbicide and fertilizer runoff affects freshwater diatom assemblages; and 3) herbicides and fertilizers have respective negative and positive effects on diatom population sizes. These hypotheses were tested in the field and under controlled lab conditions. In the field component, water and diatom samples were collected from streams upstream, adjacent to, and downstream from pineapple farms. In the experimental component, diatoms were treated with herbicides or fertilizers commonly used in pineapple farms to determine individual effects of these chemicals.

MATERIALS AND METHODS

Study sites

The study took place in two freshwater streams on Moorea, French Polynesia (Fig. 1). Stream sites were selected based on whether they were year-round freshwater streams and if they ran within 50 meters of at least one pineapple plantation. For all streams, the study sites were chosen to have minimal impact from non-agricultural sources. Any additional influences were recorded. All stream collections were conducted in October and November, at the beginning of the wet season in Moorea.

The Pao Pao Valley site is a branch of the Pao Pao River that runs alongside a 2 hectares pineapple farm, with no observed upstream influences.

The Opunohu Valley Co-op is 20 hectares large, and is shared for pineapple farming by several different farmers. A year-round stream runs alongside the pineapple farms. There are few other agricultural plants in the area.

Sampling and sample preparation

Each stream site consisted of three sub-sites; one upstream, one in the middle, and one downstream of the pineapple farming area. Upstream sub-sites were at least 5 meters from the upper edge of the pineapple farms, as close to that measurement as was accessible. Middle sub-sites were judged to be as close to the middle of the pineapple

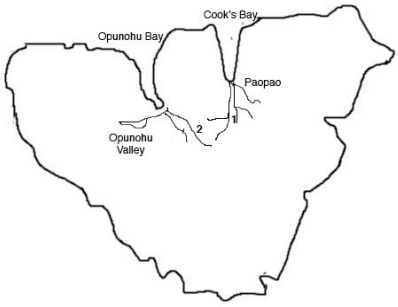


FIG 1. Locations of stream sampling sites on the island of Moorea, French Polynesia. Site 1 is in Pao Pao Valley and Site 2 is in Opunohu Valley. Both streams were adjacent to pineapple farms.

farm as possible. Downstream sub-sites were at least 5 meters from the downstream edge of the pineapple farms. At each sub-site, 4 samples were collected along a 15 meter transect, each collected at 3 meters, 6 meters, 12 meters, and 15 meters. Diatoms were collected by scraping a 2 centimeters by 2 centimeters square off the top of a rock retrieved from the middle of the stream into a vial of the stream water. All rocks sampled had a top surface area of at least 5 centimeters by 5 centimeters.

In addition, canopy cover, water temperature, stream width and depth, flow rate, and rock size were recorded at each sub-site. An additional cup of stream water was collected from where each rock was scraped and taken back to the laboratory for nitrogen, phosphorus, ammonia, and pH testing. Nitrogen levels were measured using the Lamotte Nitrogen-Nitrate testing kit (Chestertown, MD), while ammonia and phosphorus levels were measured using Sera aquarium testing kits (Heinsburg, Germany). The pH values were measured using a pH meter (YM Instrument Co. Ltd., Jiangyan, China). All water analyses were done within a week of collection date (Allen-Diaz et. al, 1998). Each diatom sample was mixed with a small amount of a 90% ethanol and Rose Bengal (Fisher Scientific, Waltham, MA) to preserve diatoms. After homogenizing, the samples were filtered through a 500 micrometer sieve, and 2 milliliters of hydrogen peroxide

was added to each sample. The samples were heated in a drying oven at 75 degrees Celsius until each sample had approximately 2 milliliters of liquid left. The samples were homogenized and mounted with Permount (Fisher Scientific, Waltham, MA) on cleaned glass slides. They were then inspected under a microscope at 1000x magnification to identify and count diatom populations. For each slide a line in the middle of each slide was inspected in order to estimate total populations.

Experimental component

Fifteen rocks were collected randomly from the upstream portion of the Opunohu Valley Co-op stream study site. The rocks had a surface area of at least 5 centimeter by 5 centimeter and approximately the same size. Each rock's initial diatom population was determined by scraping of a 1 centimeter by 1 centimeter square with a razor blade and smearing evenly on a glass slide. A line across the middle of the slide was inspected by microscope under 1000x magnification for diatom identification and numbers. Three of these sub-samples were done for each rock. The rocks were then placed in individual plastic containers with 2 liters of unfiltered stream water, and divided into 3 treatment groups, with 5 rocks in each treatment group. The first group was treated with herbicides, using atrazine and diuron. The herbicides were mixed in 2 liters of unfiltered stream water in a ratio of 1 μg/L atrazine and 0.25 μg/L of diuron before addition to each container. The next five containers were treated with a fertilizer that included nitrogen, potassium, and phosphate. The fertilizer was mixed in 2 liters of unfiltered stream water in a ratio of 3.5 milligrams fertilizer to 1 liter of water before addition to each container. The last five containers were untreated controls that were filled with 2 liters of unfiltered stream water.

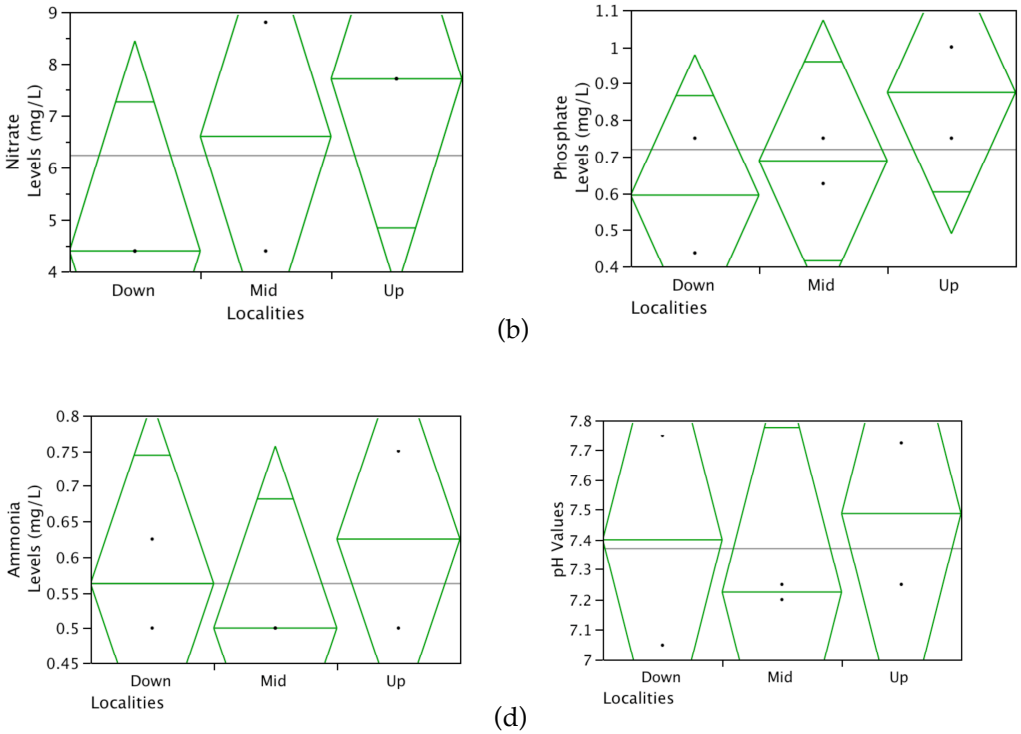


FIG. 2. Results of ANOVA tests of water analyses results by locality. (Up=upstream, Mid=midstream, D=downstream) (a) nitrate levels (mg/L), DF=2, F-ratio=1.75, p=0.3136; (b) phosphate levels (mg/L), DF=2, F-ratio=1.4, p-value=0.372; (c) ammonia levels (mg/L), DF=2, F-ratio=0.6, p-value=0.6037; (d) pH values, DF=2, F-ratio=0.2985, p=0.7617.

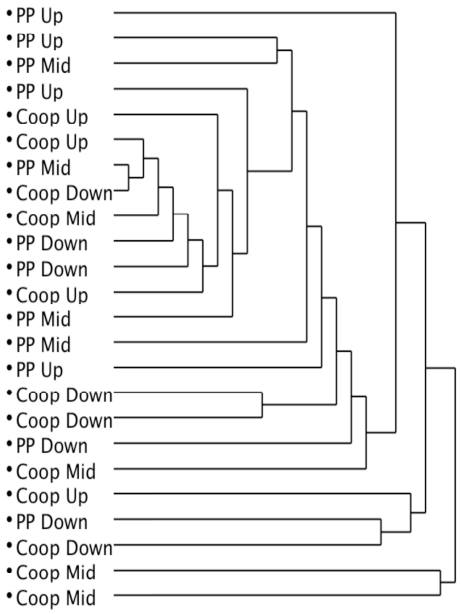


FIG. 3. Hierarchical cluster of diatom assemblages from upstream, midstream, and downstream of Pao Pao and Opunohu Valley streams. (PP=Pao Pao, Coop= Opunohu Valley)

The experiment was left to run for 27 hours. At the end of the experiment, two 1 centimeter by 1 centimeter squares were scraped off each rock with a razor blade and then smeared on a glass slide. A line across the middle of the slide was inspected by microscope under 1000x magnification for diatom identification and numbers.

Statistical methods

All statistics were conducted using JMP 7 Statistical Software. Differences in nitrate, phosphate, ammonia, and pH mean values between upstream, midstream, and downstream were examined by analysis of variance (ANOVA). Differences in diatom assemblages between the upstream, midstream, and downstream parts of the stream were analyzed with a hierarchical cluster. For the experimental component differences in mean before and after diatom abundance and species richness were examined by ANOVA and Tukey-Kramer tests.

RESULTS

Field results

Nitrate levels varied between 4.4 and 8.8 μg/L, with no statistical differences between the means of the upstream, midstream, and downstream samples (ANOVA, DF=2, F-ratio=1.75, p=0.3136) (Fig. 2a). Phosphate levels varied between 0.5 and 2 μg/L, also with no significant differences between the means of the different stages of the stream (ANOVA, DF=2, F-ratio=1.4, p=0.372) (Fig. 2b). Most samples had ammonia levels of 0.5 μg/L, with a range from 0 to 1 μg/L. Like the other nutrients, there were no significant differences in mean ammonia values (ANOVA, DF=2, F-ratio=0.6, p=0.6037) (Fig. 2c). The pH values from the upstream, midstream, and downstream were neutral, with a range from 6.8 to 7.9. The mean pH values of the three stages did not have any significant differences (ANOVA, DF=2, F-ratio=0.2985, p=0.7617) (Fig. 2d).

Diatom species composition and abundance widely varied across all the samples. No significant similarities were shown within upstream, midstream, or downstream samples, and no significant differences were shown between upstream, midstream, and downstream samples, as shown by the hierarchical cluster analysis (Fig. 3). Therefore, no particular area of the stream can be distinguished according to diatom assemblages. The small cluster in the middle of Figure 3 is most likely a result of particularly low numbers of diatoms in those samples.

Laboratory Results

A slight trend of decreasing diatom species richness after herbicide treatment as compared to the fertilizer or control treatment can be evident from a comparison of the species richness values from before and after treatment (Fig. 4). However, this trend has no statistical significance, as shown by ANOVA and Tukey-Kramer tests of changes in species richness (DF=2, F-ratio=1.9518, p=0.1846) (Fig. 5). Diatom abundance is variable, and the changes between the abundances before and after the experiment are not significantly different (DF=2, F-ratio=0.446, p=0.6504) (Fig. 5).

DISCUSSION

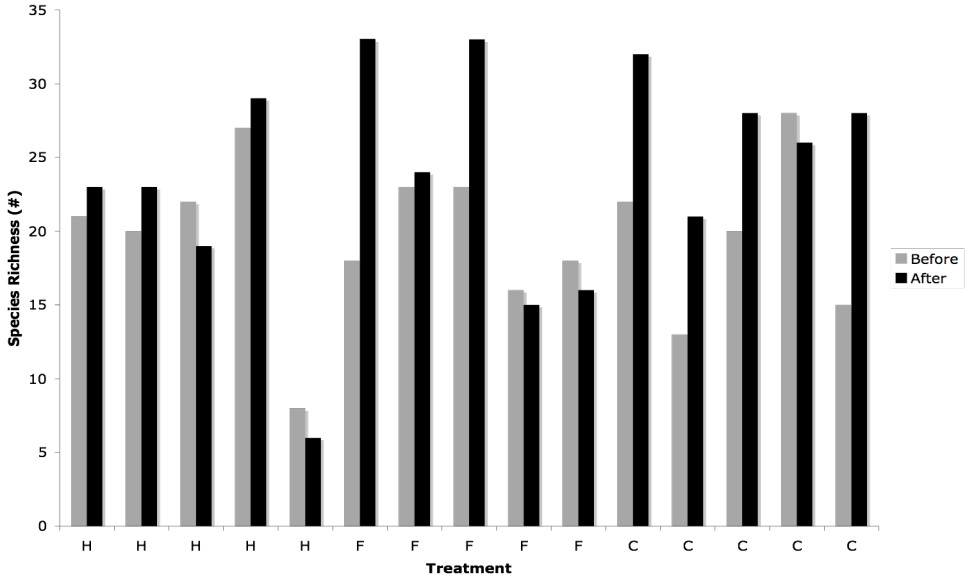


FIG. 4. Bar graph of delta species richness before and after treatment with herbicides, fertilizers, or control. (H=herbicides, F=fertilizers, C=control) Changes in species richness in herbicide treatment samples are noticeably less than changes in fertilizer or control treatments.

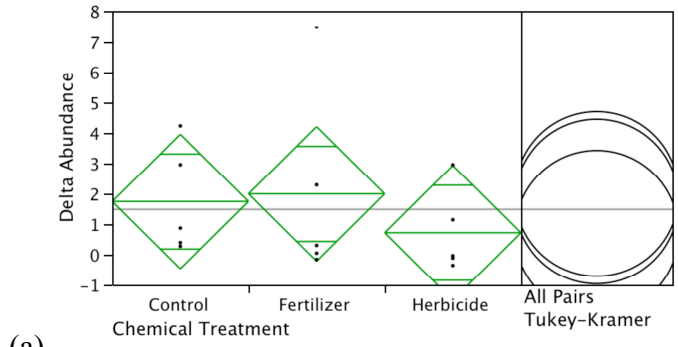
The results of this study show that pineapple farms of Moorea seem to have little effect on their neighboring streams. Any agricultural runoff appears to have no significant effect on the nutrient and pH levels in the stream. In addition, diatom assemblages do not seem to be noticeably affected by pineapple farms.

These results do not agree with the findings of previous studies of agricultural runoff on diatoms. Rott et al. (1998) found a clear correlation between diatom species composition and organic pollution from farmlands in the Grand River in Ontario. Lavoie et al. (2004) examined diatom communities as bioindicators and found a significant difference in diatom communities in agriculture sites compared to control sites. A study done by Winter and Duthie (2000a) was even able to find a calibration modeling for the relation of diatom populations and total phosphorus and nitrogen in the streams.

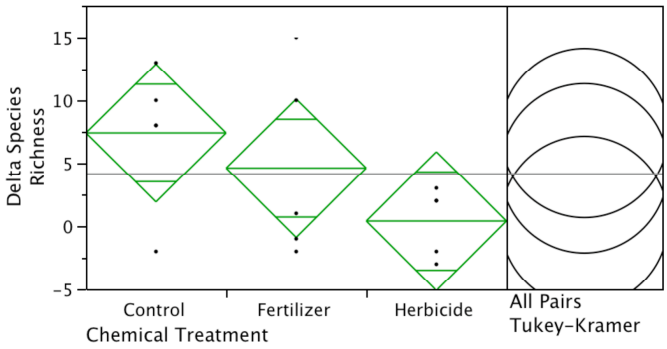
There are several reasons that could explain the contrasting results of this study. One explanation is that the pineapple farms of Moorea do not have any agricultural runoff. Perhaps this study took place in the wrong season, before the next set of chemical treatments, causing the streams to appear to be unaffected by pineapple farms. In a study by Winter and Duthie (2000b), there were no consistent differences in diatom species number until seasonal variation was taken into account. Although the exact dates of treatment are unknown, Moorean pineapple farmers typically apply fertilizer treatments two to three times a year, and herbicide treatments one to three times a year, both typically after the rainy season (Coco Teraiharoa, personal communication). This study began and ended at the beginning of the wet season in Moorea.

Also, there is a possibility that other factors in the stream that were not tested in this study had an overwhelming effect on the nutrients and diatom levels, so that any differences caused by runoff were overcome. Some past studies have shown mixed conclusions about factors, such as phosphate versus atrazine levels, canceling each other's effects (Guasch et al., 2007, Guasch et al., 1998). Finally, the way that the diatoms were sampled may have caused some error in counting of populations. I only tested and sampled two streams on the island, each from a different valley. The small sample size may not have accounted for unfactored variations in the streams.

The results from the experimental study of the direct effects of herbicides and fertilizers on diatom populations were inconclusive. Although a slight trend in herbicides having decreased species richness compared to fertilizer and control treatments is evident, no significant results could be concluded. However, since the herbicide treatment only shows a slight decrease in species richness, and not species abundance it may be that only some species



(a)



(b)

FIG. 5. Results of ANOVA and Tukey-Kramer of diatom experiment with herbicide, fertilizer, and control treatments. (a) Delta abundance of diatoms between the three treatments (DF=2, F-ratio=1.9518, p=0.1846); (b) Delta species richness of diatoms between the three treatments (DF=2, F-ratio=0.446, p=0.6504).

are affected by herbicide conditions. In the study by Leboulanger et al. in 2001, only a few species of diatoms were affected by herbicides.

Results from previous studies of herbicides on diatoms also show varied findings. Legrand (2006) found that increased amounts of atrazine and diuron herbicides caused decreased photosynthetic efficiency in diatoms. In contrast, a study by Downing et al. (2004) showed increases in diatom taxa and abundances after exposure to pesticides such as atrazine.

However, the lack of significant results in this experiment could be explained by the time limitations in the study. Although diatoms have a quick generation time, with doubling times possible from 0.3 to 5 days, the experiment may not have lasted long enough for the specific species of diatoms from Moorean freshwater streams (Cox, 1996). In addition, my sampling methods may have caused inaccuracies in species richness and abundance. Looking at only a small fraction of each slide may have caused some errors in counts of species richness, as some species may have been less common and thus not necessarily in the line of sampling.

To find more accurate, and perhaps more significant, results, larger sample sizes are needed. With more streams and better sampling techniques, more accurate counts of diatoms can be done, possibly leading to more significant data. Perhaps instead of looking at diatom abundances and species richness, measurements of chlorophyll a activity could be done, as in several other diatom studies. Future studies should also take into account seasonality and chemical application times, preferably looking at streams over an extended period. For future experiments, longer experiment times are necessary to ensure enough time for diatom population growth. Taking samples from experiment rocks more often would also

provide more complete data on the effects of herbicides and fertilizers on diatoms. Future studies could include a field experiment to simulate effects of runoff on the stream.

CONCLUSIONS

The results from this study show that agricultural runoff does not affect stream chemistry, nor does it significantly affect diatom assemblages in freshwater streams. Any effects of herbicides and fertilizers on diatom species richness and abundance were statistically insignificant. However, a slight trend toward herbicides decreasing species richness compared to fertilizer and control treatments show that further and longer experiments are necessary. Even though results from this study show little effect of pineapple farms on freshwater stream diatoms, more studies during different seasons are needed for more complete conclusions.

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SEED FATE OF THE TAMANU TREE *(CALOPHYLLUM INOPHYLLUM)*: VIABILITY, DISPERSAL, AND PREDATION AND ITS ECOLOGICAL IMPORTANCE IN MOOREA, FRENCH POLYNESIA

LAUREN ZERBIB

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. The growing concern for threatened or endangered species has made conservationists recognize the need to accurately assess the status of small populations. In order to do this, the survivorship and fecundity of each life stage must be established to determine the population's overall growth rate. A small population of the evergreen tree *Calophyllum inophyllum* can be found on the island of Moorea in French Polynesia. This tree is an excellent study organism because it has been internationally recognized as an endangered species and its large spherical seeds allow it to be easily traced. It grows along the coast, and the seeds float in water and continue to be viable for over three months. Determining the fate of the seed is one important step in developing useful models for conservation managers. The factors tested are survivorship, loss, and fecundity in the seed to seedling life stage. A seed-sowing experiment yielded 36.24% germination, which is much lower than past germination rates of this tree. The terrestrial crab, *C. carnifex,* was found to be the primary predator of the *C. inophyllum* seed, causing a 59% loss of seeds. This high predation loss could be impacting the population growth rate. The long-distance dispersal study provided evidence that seeds are capable of being moved past a reef by a current, which has important implications for studies of island colonization.

Key words: seed fate; Calophyllum inophyllum; *life history; seed predation, seed dispersal, French Polynesia; germination*

INTRODUCTION

Over the past thirty years there has been an increase in scientific research concerning the conservation and management of threatened or endangered species (Brigham 2003). There are several approaches for assessing the status of populations of at risk species, such as the use of simple surveys (Dennis et al. 1991), transition matrix population projections (Caswell 2001), life history attributes, and community-level models (Brigham 2003). The life history attributes can be used to build a demographic model, one of the first steps in forming population growth models. For plants, stage-structured models are useful because growth is indeterminate and growth rates are closely related to developmental stage (e.g. seed, seedling, juvenile, adult) (Beissenger 1998). A life history stage-structured model is a tool

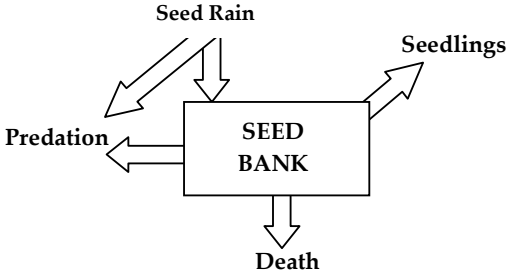

FIG. 1. Diagrammatic flow chart for the dynamics of the population of seeds in the soil. Based on Harper 1977.

used to determine the stage that has the largest influence on the population growth rate (Brigham 2003). This information is important because it allows conservationists to target their efforts toward the most vulnerable life history stage of an endangered plant (Caswell 1989). These models can also be used to predict how the outcome of changes due to management or the environment (e.g. habitat degradation, loss of pollinators, competition, disease, herbivory, and seed predation) may alter the overall growth rate (Brigham 2003).

In plant populations, past studies have shown the transition from seed to seedling to most frequently constitute the limiting factor (Harper 1977) [Figure 1]. One study tested the primary cause of endangerment of 98 threatened or endangered species and found that plant "development" constituted the most frequent threat (Schemske 1994). This study also found that the best approach to understanding the biological status of rare plants was to place emphasis on the ecology of the species (to determine the limiting factor) and the demography of the species (for monitoring populations) (Schemske 1994). There is a large range of potential limiting factors. For example, one study tested factors that limit germination and fecundity in a prairie forb and found that it was pollinator-limited, and reproductive rates sharply increased after a burning (Menges 1995). Another study argues that the importance of seed limitation has been underestimated in plants, and more research should be done looking at the fate of seeds from dispersal to germination (Eriksson et al. 1992). Seed dispersal is very important in influencing population persistence in endangered species because it determines where plant recruitment will ultimately occur (Chen et al. 2006).

In French Polynesia, the native tree *Calophyllum inophyllum* is a species with a restricted range and a small population that is in decline (Friday et al. 2006, Stevens 1998). This tropical evergreen tree appears to be naturally restricted to the coastal zone due to its specific nutrient and sunlight demands. In 1998 the International Union for the Conservation of Nature and Natural Resources (IUNC) placed *C. inophyllum* on the "Red List" for endangered species (Stevens 1998). Although considered "low risk" and of "least concern," the amount of time passed since the last study combined with the species' isolated location suggests a need to reassess its ecological position. It is alarming that a recent distributional study showed only approximately 400 trees left on the island of Moorea, one of French Polynesia's principal land masses (Howell 2006). Adding to this concern, *C. inophyllum* not only grows slowly, but its preferred habitat is white coral sand beaches in areas with plentiful sunlight; the habitat that is most at risk for development (Florence 2004).

Survivorship and fecundity of each life stage contribute to the recruitment of new individuals into a population. Although *C. inophyllum* populations are limited on Moorea, it produces many seeds. I hypothesized that if viable seeds are produced, the transition from seed to seedling is the stage in which the highest mortality occurs. Therefore, this study aimed to determine the mean survival rate of *C. inophyllum* seeds, and evaluate environmental factors that might hinder or aid germination (or seedling establishment) during the plant's reproductive life stage. I examined seed dispersal, seed viability, and seed predation to determine which factors might have a significant negative effect on seed survival rate and number of potential new seedlings for *C. inophyllum* on Moorea.

METHODS

Study site and species

This study was conducted from September 2007 to November 2007 at the Richard B. Gump South Pacific Research Station in Moorea, French Polynesia. Moorea is part of the Society Islands archipelago. This

tropical, volcanic island is located seventeen kilometers northwest of the Tahiti.

Voucher specimens were deposited in the University and Jepson Herbaria of the University of California at Berkeley. *Calophyllum inophyllum* seeds are commonly found along the coastline of Moorea. The tree's seeds are spherical, with diameters ranging from 2.5 to 3.5 cm (Florence 2004) [Figure 2]. It is native to East Africa, Southeast Asia, Taiwan, Australia, and southern and eastern Polynesia, but is currently distributed throughout the tropics (Friday et al. 2006). It is a coastal tree, growing primarily near the shoreline and prefers a warm and wet climate (Friday et al. 2006). The tamanu tree, using the Tahitian name, is a native tree of ethnobotanical importance to Tahitians. Traditionally the plant has been used as a mosquito repellent, a cicatrizing agent for wounds, and a remedy for eye ailments (Petard 1986). Tamanu has also been recently shown to have potential pharmaceutical benefits (Petard 1986). In addition, it has a valuable wood that Polynesians commonly use for boat building (Friday et al. 2006).

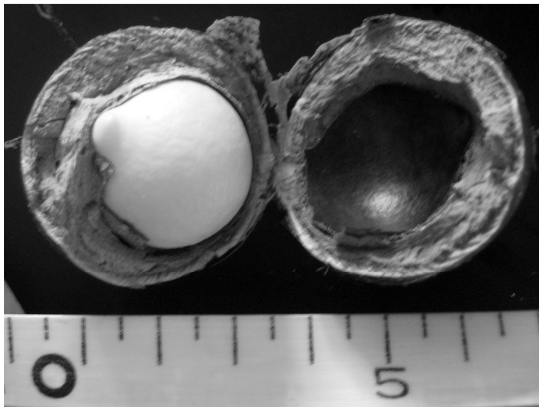

FIG. 2. *Calophyllum inophyllum* seed.

Demographic Survey

I performed six transects around the island to survey the demographics of *C. inophyllum* in the most populated areas of Moorea. The transect locations were determined using a recent distributional map of the species on Moorea (Howell 2006). I chose six areas of the island that had the highest known tamanu populations and performed 200 meter transects within these predetermined areas. The exact location was restricted by accessibility to sites, and private property. Each transect was four meters wide, and the center of the transect was five meters from the high tide line. All transects were parallel and equidistant to the ocean. [Figure 3] Within these 200 m x 4 m transects several different things were recorded: (1) Number of *C. inophyllum* trees and diameter at breast height, (2) number of seeds, (3) number of seedlings, (4) seedling height, (5) number leaves on seedling, and (6) herbivory of seedling.

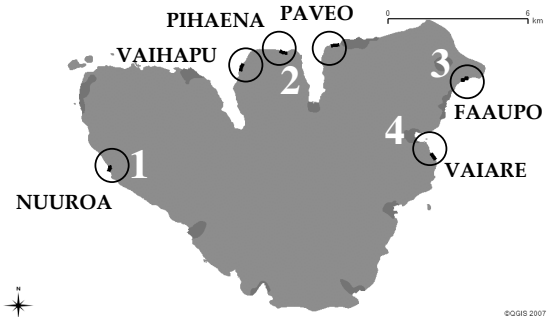

FIG. 3. The locations of six 200 meter transects in areas of high *C. inophyllum* density, where demographic information was collected. Seed collection sites 1 through 4 also shown.

Germination Trials

I established a caging experiment to determine the germination rate in the absence of seed predation by excluding land and aerial predators. A total of 150 seeds were collected from four sites across the island: Nuuroa, Pihaena, Temae and Vaiare [Figure 3]. Cages were built using 1.5 cm spaced caging wire to exclude rodents, terrestrial crabs and birds. Each cage had five sides forming a 30 cm x 30 cm plot with 15 cm height [Figure 4]. Twenty-five seeds were planted in each cage, with a total of six cages. The collection sites were

assigned numbers 1-4 and the seed's location in the grid was determined using random number generation. To minimize germination time the seeds were completely shelled before planting and their mass recorded. The seeds were planted in coral sand 2.5 cm below the surface. The plot was one meter from the shoreline on the property of UC Berkeley's Gump Station, which is three kilometers from southeast of Pihaena Pointe. The seeds were left to germinate for seven weeks. Each day it was noted how many seedlings emerged and their relative location in the grid. At the end of the seventh week, I dug each seed up and noted whether it rotted, successfully germinated, or was alive but did not germinate.

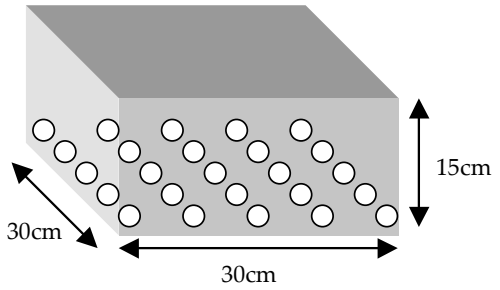

FIG. 4. Representation of seed layout in cages used in the germination experiment.

Dispersal Studies

I measured distances that fruit fell from a tree to determine seed rain and initial dispersal by land. Land dispersal was tested at Vaihapu Pointe on Opunohu Public Beach. I looked at a *C. inophyllum* tree that was dropping fruit. None of the branches from the tree hovered over the ocean. I recorded the distance fruit fell from the parent tree trunk every other day between 7:00am and 9:00am for two weeks. The seeds were removed before the following day, to prevent duplication.

To test marine dispersal, seeds were tracked using mark-recapture techniques. In the first trial, 150 seeds were painted pink and dropped approximately one meter from the low tide line at two separate sites to simulate falling from the tree. The first site was at Pihaena Pointe, which is located on the outer part of the island, and the second site was on the Gump Station, which is located in Cook's Bay. I tracked seed movement along the coast and recorded their locations at the following time intervals: 24 hours, 60 hours, and one week after being dropped. Seeds distances were recorded along the tide line 100 meters in each direction from the drop-site. The second trial followed the same method but the seeds were painted blue, and were dropped at high tide. To better document the seed's movement during the second trial, two people followed the seeds in the water for one hour after they were dropped and tracked their movement via GPS.

Predation Studies

I established experiments to determine, first, the predator of the tamanu seed, and second, the percent loss of the seed by predation. In a pilot study, shelled tamanu seeds were placed near the entrance of several crab holes to see whether the terrestrial crab, *Cardisoma carnifex* would eat them or crack the seeds open. A smokeplate was used to help determine the organism that was actively preying on the seed. Four shelled seeds and four cracked seeds were placed in a box, and the smokeplate was positioned at the entrance to the box.

To test for seed loss by predation, three types of caging treatments were established in an area rich in crabs and rodents: uncaged, caged no top, and fully caged. The uncaged treatment was a control. The second treatment, cage without a top, excluded crabs but not rodents. And the last treatment, fully caged with a top, excluded both rodents and terrestrial crabs. Each of the treatments was replicated three times. The cages were each 30 cm x 30 cm x 15cm. Sixteen unshelled seeds were placed in each plot on top of the soil. Each replicate consisted of the three different treatments, which were placed in a line to be

equidistant from the ocean. Their location in the line was randomly determined by drawing pieces of paper out of a hat.

Statistics

ANOVA was used to determine whether differences in loss under three predation regimes were larger than expected by chance. A logistical regression was used to determine whether seed mass had any correlation to seed germination. Both tests were performed in the statistics software program, JMP IN 5.1.2.

RESULTS

Demographic Survey

The results of the six transects are summarized in Figure 5. Seedling herbivory was evident in 65.8% of the seedlings found in the field. The means and standard error are represented in Figure 6.

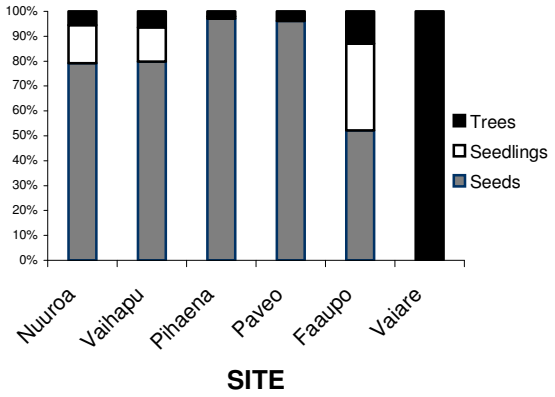

FIG. 5. Results from field survey at six different locations. Shows percentage of trees, seedlings, and seeds found at each location.

Germination Trials

In the germination experiment, the percent germination was found to be 36.24%. The average number of days for emergence was 37.6. The percent emergence was 26.85%. Using a logistic regression, the mass of the seed did not show any significant correlation to seed germination (chi-square= 3.56, intercept standard error=0.56; seed mass standard error=0.122). The results of the collection site in relation to seed germination are summarized in Table 1. It was also found that 74% of the seeds that did not germinate decayed. This left 26% in the dormant seed bank.

TABLE 1. Seed germination given by individual collection sites. Numbers (1-4) correspond to site locations given in Figure 3.

		Germinated		
Collection Site	N	YES	NO	Percent Germinated
1-Nuuroa	34	10	24	29.4%
2-Pihaena	47	16	31	34.0%
3-Tamae	41	12	29	29.2%
4-Vaiare	28	16	12	57.1%
Total	**150**	**54**	**96**	**36.24%**

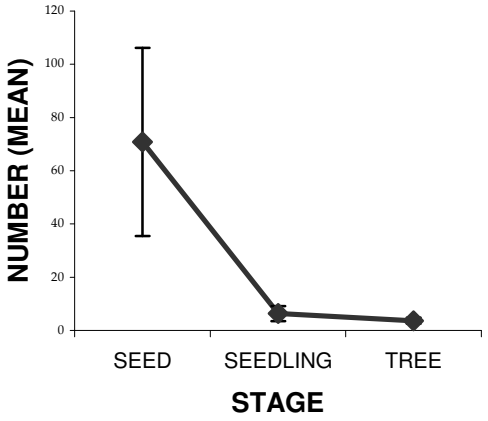

FIG. 6. Combined results for the demographic survey showing number of individuals found in each stage. Standard error included.

Dispersal Studies

The results of the land-dispersed seeds are shown in Figure 7. The results of the ocean dispersed seeds at Cook's Bay for high and low tide are shown in Figure 8 and 9, respectively. The dispersal experiment at Pihaena Pointe did not yield any results

during the first trial. When the seeds' movement was tracked during the second trial, they traveled with the currents away from the island at a rate of 0.2 kilometers per hour. Five hours after they were deposited, the group of seeds was sighted at the entrance to the reef pass at Cook's Bay approximately 1.3 km from where they were deposited.

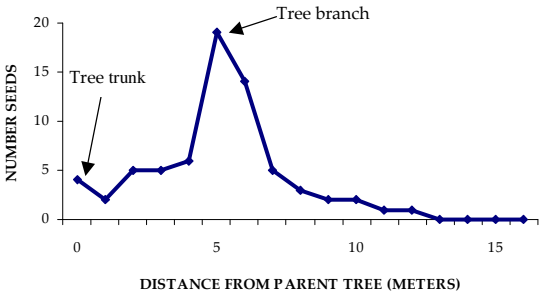

FIG. 7. *C. inophyllum* seed dispersal curve around a single parent tree.

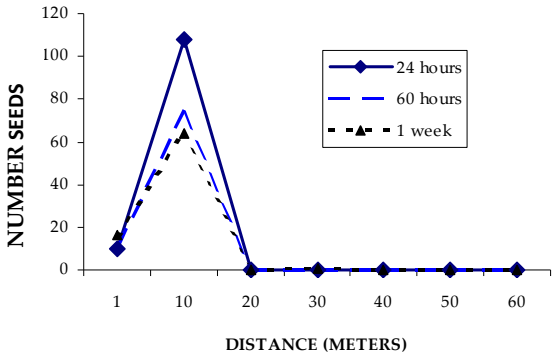

FIG. 8. *C. inophyllum* seed dispersal curve over time at high tide in Cook's Bay in Moorea, French Polynesia.

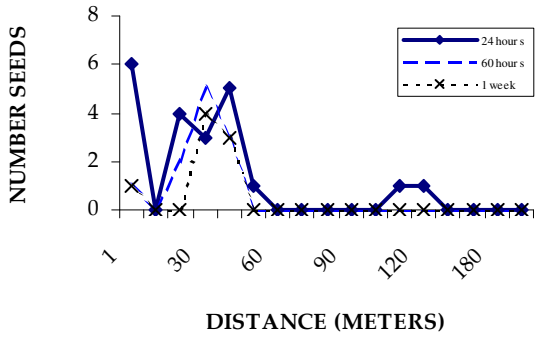

FIG. 9. *C. inophyllum* seed dispersal curve over time at low tide in a Cook's Bay in Moorea, French Polynesia.

Predation Studies

In the smokeplate experiment, 50% of the shelled seeds disappeared, and 25% of the cracked seeds disappeared. The smokeplate revealed scratch marks, which was evidence that crabs entered the cage and removed the seeds. No rodent footprints were found. The result for the caging experiment is shown in Figure 10. There was a significant difference in the uncaged treatment when compared to the caged no top and fully caged treatments (DF=8, P-value=0.0039, F ratio=16).

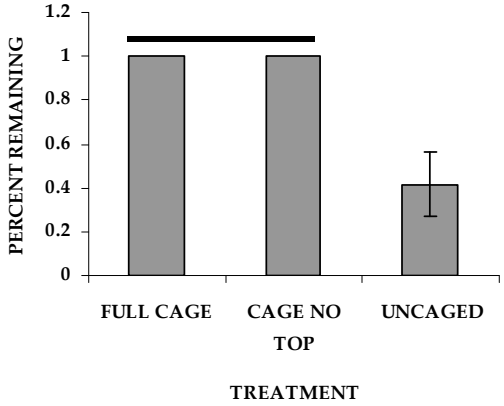

FIG. 10. Average percent *C. inophyllum* seed loss in caging treatments. Horizontal bar indicates no significant difference. Error bars represent ± 1 standard error.

DISCUSSION

Like other endangered species, *Calophyllum inophyllum* is limited during its developmental stage. A noticeable loss occurs from the seed to seedling stage and several contributing factors were discovered in this study. The field survey provided interesting insight into the population demographics of *C. inophyllum* on Moorea. The abundance of seeds, and low numbers of trees and seedlings on Moorea confirms population models that other plant biologists have found in the past (Harper 1977, Schemske 1994). There are several possible explanations for variations in

reproductive capacity. Individuals that colonize open environments face fewer interactions with competitors, and the chance of propagating depends on increased reproductive output (Harper 1977). As a marine-dispersing plant, *C. inophyllum* could be among the first colonizers on islands, and therefore employ this reproductive strategy.

The seed has many important roles in the function of plant persistence; these include dispersal, perennation (survival from season to season), food supply for the embryo, and the display of genetic variation (Harper 1977). The dispersal studies provide interesting data regarding the potential movement, and colonization by *C. inophyllum*. Long-distance dispersal is rarely studied despite its critical role in the dynamics of plant populations (Cain 2000). However, a recent surge in scientific literature regarding the so-called "tail" of the dispersal curve exemplifies the importance of long-distance dispersal (Cain 2000). Long-distance dispersal plays a key role in the colonization of islands, plant migrations, and plant invasions (Cain 2000). Although this study was limited in resources and tracking materials, it shows compelling evidence that long-distance dispersal is present in this species. Past studies have shown that the seed of *C. inophyllum* continues to be viable upward of three months (Green 1999). This study also provided evidence that these seeds are capable of being moved outside a reef pass, to potentially colonize new islands.

Returning to the theory of minimal competition in open environments, this may also explain the discrepancy between the number of seeds and seedlings. More specifically, it would explain why seed viability was so low when compared to those in the Agro-forestry industry (90% germination, 22 days for emergence) (Friday et al. 2006). Individuals that thrive in crowded communities have adaptations to cope with the need to partition resources. Early and fast seedling growth and higher foliage growth are examples of such adaptations (Harper 1977). *C. inophyllum*, on the other hand, is slow growing, and has no prospect of being an invasive species. In this study, the shell and husk were removed from the seed to allow faster germination, but this does not occur in nature, and past studies have shown that when the shell remains intact, the rate of emergence nearly doubles (Friday et al. 2006). On Moorea, *C. inophyllum* is faced with a habitat filled with introduced and invasive species, though it doesn't appear to have the reproductive strategy to compete. One problem with my methods was that the germination trial was conducted on a single plot site, and there were coconut trees and grass adjacent to the area filled with coral sand. If I had conducted this study at several different sites around the island, I would have been able to test for the effect of competition. These other plants in the seeds' vicinity may have lowered the germination rate. Coconut trees and grass, however, are very common along the shoreline of Moorea, and this rate could still be representative of the natural conditions in which *C. inophyllum* seeds germinate.

The seed is relied upon for dispersal, and species propagation, but the large fleshy seed of *C. inophyllum* is particularly vulnerable to predation. Other studies found that the fruit bat, *Cynopterus sphinx*, and the land crab, *Birgus latro* are predators of the seed, though neither are found on Moorea (Elangovan et al. 2001, Wilde et al. 2004). Another study found seedling herbivory of *C. inophyllum* by red crabs on Christmas Island, though they also are not found on Moorea (O'Dowd et al. 1990). Introduction of the terrestrial crab, *C. carnifex*, on Moorea added another barrier to the difficulty of seedling establishment. According to this study, the terrestrial crab is taking 59% of the fallen seeds, though it has never been identified as a predator in the past. This represents a huge loss in the seed stage, which, in turn, limits seedling establishment. In one study looking at seed fates in an Oregon forest, predation by birds and small mammals was particularly high and caused a

loss of 62% for the seeds of the *Pseudotsuga douglasii* tree (Gashwiler 1967). If *C. inophyllum* evolved in a predator-free environment, it would be particularly vulnerable to the effects of invasive predators. Another interesting hypothesis explains that long-distance dispersal might be an evolutionary mechanism for escaping predation near the parent tree (Janzen 1971). Furthermore, high seedling herbivory found in the field could also represent a potential threat to the seedling establishment and could be impacting the population growth rate of *C. inophyllum*. Focusing on the seedling stage would be the next area of importance in the development of the life history table for *C. inophyllum*.

CONCLUSIONS

C. inophyllum is a valuable species biologically, as well as culturally. As an endangered species, a need exists to further reassess its ecological standing. There is a huge loss occurring at the stage of the seed. This study pinpointed a few factors contributing to this loss, and predation appeared be impacting the fate of the seed the most. Although there was only 36% germination, a remaining 26% neither germinated nor died, so loss due to seed viability could be as high as 64% or as low as 38%. Loss due to predation was 59%, which is very high, though not far from the norm. The presence of long-distance dispersal also has important implications; primarily that it provides a mechanism for island colonization.

FUTURE RESEARCH

A complete life history should be compiled and tabulated for *C. inophyllum*. Such a resource would provide valuable information for targeting the specific conservation and management efforts that an endangered species such as this requires. Outside factors affecting this life history which should be studied include: human interference; habitat degradation; disease; and herbivory.

A comprehensive study of seed predation would also be useful for conservation purposes. A more precise measure of the impact of predation would require testing whether seeds continue to be viable after being partially eaten, as their primary predator, *C. carnifex*, does not appear to eat the entire seed. It is possible that the sea-dispersal mechanism of the plant evolved to evade predation, and a revealing study could be undertaken combining predation and dispersal data by testing whether the germination and survival rates of seeds varied with the distance from parent trees.

To improve the data found in this study, and to obtain more accurate results for the germination rate on Moorea, varying plot sites around the island would reveal the impact of variations in location, soil quality, water availability, and other environmental factors. Furthermore, three of four sites in this study had similar seed germination rates (approx. 30%) while the site at Vaiare saw a 57% germination rate. This would imply some trees are capable of producing seeds of greater viability than others. A study which could document the impact of different sites, or specific trees, on viability and survival would provide even more useful information for managing the future of the species.

MANAGEMENT RECOMMENDATIONS

While this study provides a good starting point for understanding the life history of *C. inophyllum*, further study would likely be necessary before any management recommendations could be implemented. However this study would appear to show that managing this endangered species into the future would have to focus on two factors, seed viability, and predation by *C. carnifex*.

The land crab *C. carnifex* is not only a threat to the long term viability of *C. inophyllum* but also a pest in French Polynesia. Control of this invasive species, while

difficult, could improve the biological stability of the islands. Methods to consider would include limiting the species food supply, eradication, or some method of biological control. However, it would have to be ensured that *C. carnifex* did impact the *C. inophyllum* population before any action was taken which would limit the crab population. Furthermore, such methods have shown varied success in the past, and their potential impact should be thoroughly studied before attempting what could be a costly and potentially fruitless endeavor.

An approach that has a potentially greater chance of success would be to take action to increase the viability of *C. inophyllum* seeds. The above-suggested study to determine differences in seed viability could allow for a selective planting program from trees of greater viability. If these trees were protected from predation during the germination phase, over time they could naturally increase the viability of the species on the island. Another, similar approach, could involve education and assistance in growing *C. inophyllum* as a domestic plant, thereby increasing its population and concentration in a more protected setting.

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